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LONG TERM STUDY

Predation risk drives long-term shifts in migratory behaviour and demography in a large herbivore population

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Abstract

1. Migration is an adaptive life-history strategy across taxa that helps individuals maximise fitness by obtaining forage and avoiding predation risk. The mechanisms driving migratory changes are poorly understood, and links between migratory behaviour, space use, and demographic consequences are rare.
2. Here, we use a nearly 20-year record of individual-based monitoring of a large herbivore, elk (*Cervus canadensis*) to test hypotheses for changing patterns of migration in and adjacent to a large protected area in Banff National Park (BNP), Canada.
3. We test whether bottom-up (forage quality) or top-down (predation risk) factors explained trends in (i) the proportion of individuals using 5 different migratory tactics, (ii) differences in survival rates of migratory tactics during migration and whilst on summer ranges, (iii) cause-specific mortality by wolves and grizzly bears, and (iv) population abundance.
4. We found dramatic shifts in migration consistent with behavioural plasticity in individual choice of annual migratory routes. Shifts were inconsistent with exposure to the bottom-up benefits of migration. Instead, exposure to landscape gradients in predation risk caused by exploitation outside the protected area drove migratory shifts. Carnivore exploitation outside the protected area led to higher survival rates for female elk remaining resident or migrating outside the protected area.
5. Cause-specific mortality aligned with exposure to predation risk along migratory routes and summer ranges. Wolf predation risk was higher on migratory routes than summer ranges of montane-migrant tactics, but wolf predation risk traded-off with heightened risk from grizzly bears on summer ranges. A novel eastern migrant tactic emerged following a large forest fire that enhanced forage in an area with lower predation risk outside of the protected area.
6. The changes in migratory behaviour translated to population abundance, where abundance of the montane-migratory tactics declined over time. The presence of

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diverse migratory life histories maintained a higher total population abundance than would have been the case with only one migratory tactic in the population.

7. Our study demonstrates the complex ways in which migratory populations change over time through behavioural plasticity and associated demographic consequences because of individuals balancing predation risk and forage trade-offs.

KEYWORDS
elk, migration route, partial migration, predation risk, survival, ungulate

1 | INTRODUCTION

Migration is a life-history strategy that helps individuals maximise access to resources, while minimising predation, in an attempt to maximise fitness (Dingle, 2014; Fryxell & Sinclair, 1988; Milner-Gulland et al., 2011). Migratory behaviour can thus increase abundance of migratory species than if they were resident year-round (Fryxell et al., 1988) with cascading ecosystem effects (Bauer & Hoye, 2014; Van Moorter et al., 2020). These ecosystem impacts include affecting landscape-scale processes such as vegetation productivity and fire frequency (Holdo et al., 2009; Sinclair et al., 2015), and by providing ecosystem services such as harvest and ecotourism (Bauer & Hoye, 2014; Gordon et al., 2004). Perhaps the most compelling example is the Serengeti wildebeest (*Connochaetus taurinius*) migration, but ecologists are recognising the important ecosystem roles of large herbivore migration globally (Kauffman et al., 2021). Despite their importance, migrations of large herbivores are globally threatened by overhunting, fencing, and habitat fragmentation (Berger, 2004; Harris et al., 2009; Xu et al., 2021). Migratory behaviour is also spatiotemporally dynamic, occurring over large spatial extents (Fryxell & Sinclair, 1988) and across political boundaries (Middleton et al., 2019), challenging traditional approaches to conservation (Reynolds et al., 2017; Tucker et al., 2017; Van Moorter et al., 2020). Large herbivores are also often long-lived, but few studies are sufficiently long-term to understand mechanisms driving changes in migration. Yet, understanding long-term drivers of migration is required to help guide dynamic conservation strategies (Berger, 2004; Bolger et al., 2008).

Most migratory species, including large herbivores, are partially migratory (Chapman et al., 2011). Partial migration occurs where some individuals migrate between seasonal ranges and others remain resident year-round on one range (Berg et al., 2019; Chapman et al., 2011). The first question in such partially migratory populations is often what determines whether an individual migrates or remains resident, that is, their choice of migratory tactic. Across taxa, some species' choice of tactic is genetically determined (e.g. Monarch butterflies, *Danaus plexippus*). In others it is maternally inherited or learned, such as European Shags (*Phalacrocorax aristotelis*, Acker et al., 2020). For some species, individuals are flexible in their choices of migratory tactic in accordance with either intrinsic or extrinsic factors. Berg et al. (2019) reviewed large herbivore studies and found that flexibility in choice of migratory tactic was perhaps the rule across large herbivores, with little basis for genetic determination. This then raises the second key question in partially migratory populations, namely what balances the ratio of migrant and resident individuals. Theory and empirical studies demonstrate that either density-dependence, frequency-dependence or environmental stochasticity (and their interaction) regulates the resident: migrant ratio in partially migratory populations either through population dynamics and/or individual switching between tactics (Kaitala et al., 1993). For example, environmental variation balanced the ratio of migratory versus resident European shags in a long-term study (Acker et al., 2020; Reid et al., 2020). But recent evidence in long-lived, large herbivores suggests density-dependence may be more important in driving choice of migratory tactics than environmental variation (Eggeman et al., 2016; Martin et al., 2021).

Understanding how ecological factors affect individuals' choice of migratory tactics over time is key to understanding regulation of partially migratory species. Individuals can change tactics over time, switching between different migratory tactics or residency (Eggeman et al., 2016; Berg et al., 2019). They can also change the migratory routes that they use or migrate to different seasonal ranges entirely (Bauer et al., 2016; Flack et al., 2016), perhaps in response to variation in the benefits and costs of migration (Bauer et al., 2016; Wheat et al., 2017). Few studies have been able to demonstrate demographic consequences of migration, however, to test whether changes in migratory tactics (i.e. change of tactic or route) translate to population dynamics (Gaillard, 2013; Gill et al., 2019). One study that was able to address potential fitness consequences showed that female mule deer's (*Odocoileus hemionus*) choice of migratory route to different summer ranges strongly affected their survival (Sawyer et al., 2019). Changes in migratory behaviour of different tactics likely changes over time in long-lived large herbivores in response to shifts in the costs and benefits of resources (Fryxell & Sinclair, 1988; Gill et al., 2019). Across the globe, migratory behaviours are now in flux due to carnivore recovery and shifting human land use (Hebblewhite, 2007; Middleton et al., 2013; Williams et al., 2021; Wilmers & Levi, 2013). Understanding demographic consequences of migratory behaviour is also a key question across other taxa such as migratory birds (Bauer et al., 2016; Flack et al., 2016; Gill et al., 2019).

Here, we use a nearly 20-year record of individual-based monitoring to test hypotheses for changing migratory behaviour in a large herbivore, elk (*Cervus canadensis*). Like many species, exposure to risk and forage resources in our system varies both by migration tactic (migrant vs. resident) but also between the different routes that migrants choose (e.g. Sawyer et al., 2019). Previous studies in this system established that migratory benefits are a result of predation risk-forage trade-offs such that individual elk seek to maximise exposure to forage quality while minimising predation risk (Hebblewhite & Merrill, 2007). Previous studies also demonstrated that individual elk switched migratory tactics an average of 15%/year, with evidence suggesting they are switching tactics to maximise lifetime fitness (Eggeman et al., 2016; Martin et al., 2021). And Martin et al. (2021) showed that population dynamics were being driven by individual choice of migratory tactics as individual females switched tactics towards the tactic with the highest relative fitness. Yet Martin et al. (2021) did not test for mechanisms driving such demographic shifts, which is our objective in the present paper. We use a hypothesis testing framework to examine whether such trends were consistent with differential exposure to bottom-up forage or top-down predation risk encountered by individual elk along migratory routes and seasonal ranges. We first assess trends in the proportion of the population that migrated in several migratory tactics. Second, we examined differences in a key demographic trait, adult female survival for consistency with bottom-up or top-down predictions. Previous studies demonstrated the key vital rate driving fitness differences in this system was adult female elk survival (Hebblewhite & Merrill, 2011; Martin et al., 2021), like many other long-lived large herbivore populations (Gaillard et al., 2000), though the amount a vital rate can vary also drives demography (e.g. Raithel et al., 2007). We next tested for differences in adult female survival between migratory routes and estimated cause-specific mortality from the two major predators, grey wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) during migration and on summer ranges. Finally, we related survival changes to population abundance of the different migratory tactics to test whether predation versus forage mechanisms were consistent with long-term population changes in migratory tactics.

2 | MATERIALS AND METHODS

2.1 | Study area

The partially migratory Ya Ha Tinda elk population dwells on the eastern slopes of the Canadian Rocky Mountains in Banff National Park (BNP) and Alberta provincial lands (Figure 1). The transboundary nature of the elk population, with seasonal migrations spanning the National Park protection gradient, leads to transboundary gradients in exposure of elk to large carnivore predation, forage and human activity (Hebblewhite, 2007). These gradients were driven by an east–west gradient of higher forage quality during summer-autumn on western mountain ranges in Banff National Park (Figure 1), but also by complete protection of large carnivores such as wolves and grizzly bears—the main predator of elk—inside BNP. This contrasts with high levels of large carnivore exploitation by hunting, trapping and conflict management outside in the province of Alberta (e.g. Hebblewhite & Whittington, 2020). Wolves also naturally recolonised the study area in the 1980s, restoring predation to a previously largely predator-free ecosystem (grizzly bears also recovered; see Hebblewhite et al., 2006). These gradients in forage and predation risk in space and time mirror those in other mountainous protected areas worldwide (e.g. in Yellowstone National Park; Middleton et al., 2013).

While sympatric on shared winter range, elk from all migratory tactics completely spatiotemporally overlap and usually live in one large group all winter long (Eggeman et al., 2016). Four main summer range areas span from the Continental Divide in the west in BNP to eastern areas of the upper Foothills ecoregion in Alberta (Figure 1). An important contextual feature of our study area is elk are exposed to very few agricultural subsidies (e.g. Wilmers & Levi, 2013). The population declined from a high of ∼1600 elk in 2001 to stabilise around ∼500 from 2010 to the present (Martin et al., 2021). The leading cause of the decline was predation by grey wolves on adult females (Hebblewhite et al., 2018; Hebblewhite & Merrill, 2011) combined with high predation by grizzly bears on neonate elk calves (Berg et al., 2022). While mountain lions (*Puma concolor*) are present, they were a trivial source of mortality for adult and neonate elk (Berg et al., 2022; Hebblewhite et al., 2018). Hunting by humans occurs on the winter and eastern summer ranges in two ways: licensed recreational hunting administered by Alberta, which was legal on male elk for the entire study, on females only until (2003/04) or through treaty First Nation harvest (Hebblewhite et al., 2018). Previous studies demonstrated no significant difference in exposure of different migratory elk tactics to harvest by humans, nor strong effects of environmental variation (winter severity, summer precipitation) on any elk demographic parameters, but strong gradients in exposure to predation by grey wolves and grizzly bears (highest inside BNP, Hebblewhite et al., 2018; Hebblewhite & Merrill, 2007).

2.2 | Elk monitoring

For the biological years of 2001–2019 (i.e. bioyear 2001 started June 1 2001–May 31, 2002), we captured adult (≥1.5 years age) female elk on the winter range using either corral trapping, ground darting or helicopter net gunning. Elk were captured under all necessary institutional and governmental permits; University of Alberta Animal Use Protocols (AUP) #353212, #611812, #000624; University of Montana Institutional Animal Care and Use Committee (IACUC) Permit #004–16; Parks Canada Research permits #16756, and Alberta Research and Collection permit #40549. We primarily used corral trapping and helicopter methods before 2012; since 2012, we used primarily ground darting. Previous studies revealed no capture-induced bias of different capture methods on migratory tactics (see supporting materials of Eggeman et al., 2016). We monitored individuals using Global Positioning System (GPS) collars (Lotek GPS 3300, 4400, 7000,

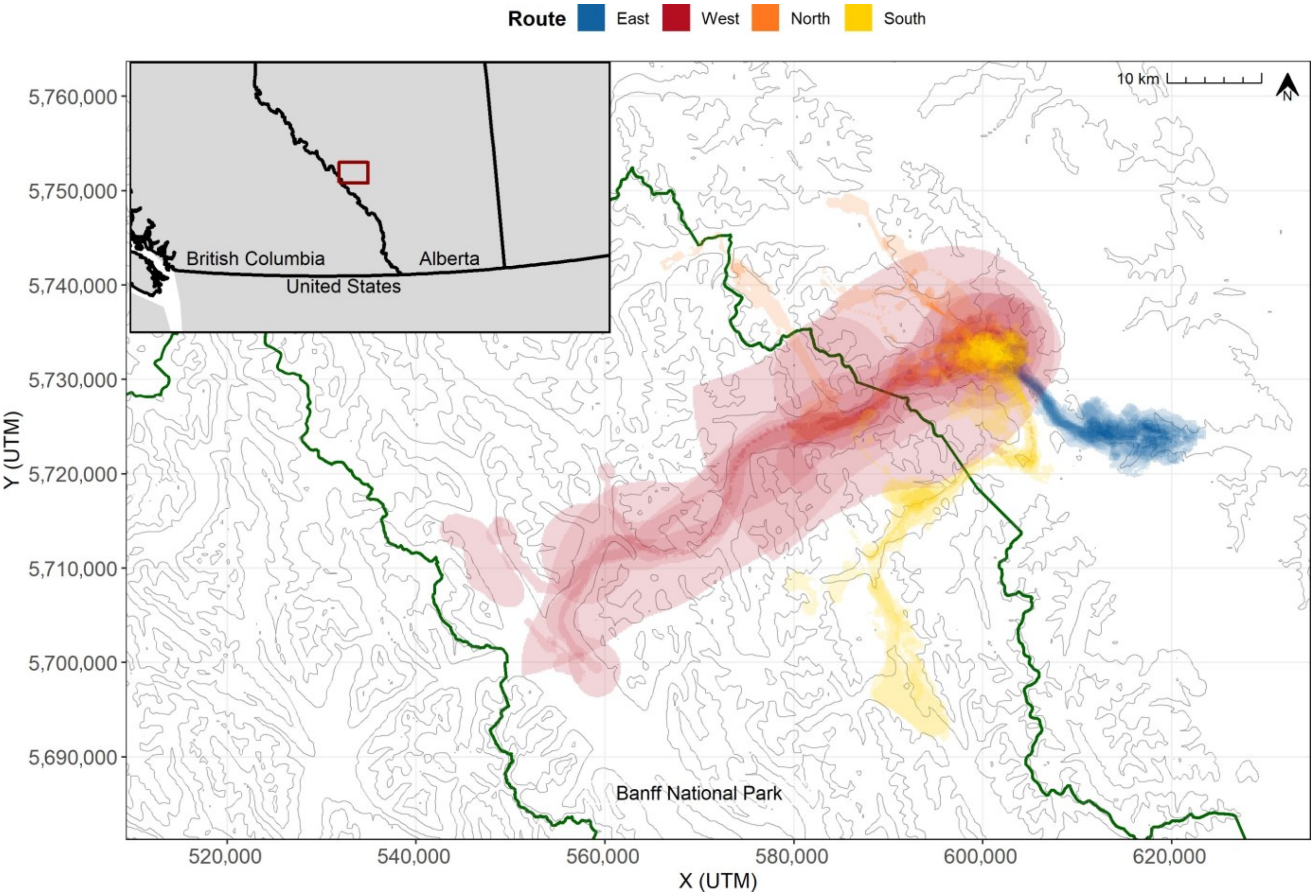

FIGURE 1 Migration route utilisation distributions generated by Brownian Bridge movement models for GPS collared elk (*Cervus canadensis*) classified as migrants during spring and fall migration periods in the Ya Ha Tinda population, Alberta, Canada, 2002–2019. Colour of polygon indicates classified migration route and transparency shows relative use (more transparent indicates fewer individual elk overlapping migration utilisation distributions).

Lifecycle; Vectronic GPS Survey) or Very High Frequency (VHF) collars (LMRT-4, LOTEK, Inc.). We obtained VHF locations on weekly flights or daily from ground-based observations. For individuals with GPS collars, we rarified GPS data to a 2-h relocation schedule. Location error was low for both collar types (34 and 218 m for GPS and VHF, respectively) and fix-rate bias was <10%.

Mortalities were detected from VHF-beacon mortality signals on both VHF and GPS collars, and electronic location alerts for GPS collars, and were investigated within mean 5.2 (SE = 7.98) days. We determined cause of death as one of predation by wolf, grizzly, mountain lion, human harvest, disease, or unknown cause (Hebblewhite et al., 2018). We tested for season and migration-tactic specific differences in cause-specific mortality due only to predation.

2.3 | Migration tactic and route classification

We classified each individual elk-year to a migrant or resident tactic using all locations based on the net squared displacement (NSD) method (Bunnefeld et al., 2010) in the R package `MigrateR` (Spitz et al., 2017). We used NSD combined with spatial rules and visual confirmation by plotting movements of individual animals (see Eggeman et al., 2016 for details). We assigned migrant animals to one of four migratory routes (Figure 1) based on visual classification in our highly mountainous system where individuals migrated through ~4 specific river valleys. We assessed trends in migration tactics and routes using the numbers of individuals classified to each migration tactic and route per year. We defined spring migration as from the first date to the last date of migratory movement away from winter range and to summer range. We used exact dates for migrants that had converged NSD models to estimate migration parameters. For other migrants that did not have NSD models, we used the migratory population-averaged 25th quartile date for the start and 75th quartile date for the end of each migration period across all years. We also used these dates to define similar seasons for non-migratory, resident individuals. These migration population-averages were calculated from all migration tactics combined. We defined the time period on the summer range (hereafter "summer range period") from ≥2 days after the end of spring migration to ≥2 days before the start of fall migration. We defined fall migration similarly to spring migration above.

2.4 | Space-use during seasonal periods

We estimated space-use during seasonal periods using Brownian bridge movement models (BBMMs; Horne et al., 2007). We constrained the analysis to only GPS collared individuals, subsetting locations for each elk-year into each seasonal period. We implemented models using the `BBMM` package (Nielson et al., 2013) in program R (R Core Team, 2019) for migrants and residents. We fit a BBMM for each individual elk-year-season, producing a utilisation distribution (UD) that estimated the use of each cell of a raster (300 × 300-m resolution) covering the study area by an elk during a particular migratory period (spring, fall) or summer. Following Sawyer et al. (2019), we then averaged each elk's seasonal UDs across years, generating a single UD and 99% contour per individual per season (spring/summer/fall). We classified individual UDs for each seasonal period as one of the five tactics that represented areas used by elk in summer: eastern, western, northern and southern migrants, or residents (Figure 1, Figure S1 for residents).

2.5 | Survival and mortality analyses

We tested for differences in adult female survival from the start of spring migration to the end of fall migration between migratory tactics and routes to test predation versus forage hypotheses for changes in migratory tactics. Previous studies in this system failed to identify a strong signal of environmental stochasticity (weather, i.e. summer precipitation, lagged effect of winter snow) on spring-fall survival (Hebblewhite et al., 2018; Hebblewhite & Merrill, 2011). We first tested for survival differences among three alternative categorisations of migratory tactics, two, three, four or five categories in a Cox-proportional hazards model using AIC to identify the most-supported number of migratory tactics. The best supported model included three categories, western (which combined west, north and south), eastern migrants and residents (see Figures S3 and S4; Table S3). We then derived Kaplan–Meier estimates of survival for each the three migratory tactics using the `survival` R package (Therneau & Grambsch, 2000). Next, we tested for differences in survival using these three categories of migratory tactics using Cox-proportional hazards survival models (Therneau & Grambsch, 2000), and used AIC to guide model selection (Burnham & Anderson, 1998). We tested the proportional-hazards assumption of the Cox-model using Schoenfeld residuals (Therneau & Grambsch, 2000).

To test the hypothesis that differential exposure to predators on migratory routes and on summer ranges drove differences in survival, we assessed the exposure of elk to multiple sources of mortality from known non-human predators (cougar, grizzly bears and wolves) using cumulative incidence functions (Heisey & Patterson, 2006). Because of the challenge of obtaining large enough samples of known-cause mortalities, we contrasted mortality causes simplified to two categories of (i) residents compared to (ii) all migrants (east, west, south, and north) in Table S4.

2.6 | Migratory route predation and forage covariates

To test drivers of migratory change, we evaluated differences in exposure of individual elk GPS locations to three covariates of forage biomass and wolf and grizzly predation risk using previously developed dynamic spatiotemporal models in our study area (Hebblewhite et al., 2008; Hebblewhite & Merrill, 2007). Under the forage hypothesis, we would predict elk exposed to the lowest forage biomass, and hence highest forage quality (see below) to experience higher survival rates. In contrast, if predation risk was driving migratory shifts, we predicted the largest declines in migratory elk would occur on those ranges experiencing the highest levels of wolf and/or grizzly bear predation. We measured forage and predation risk covariates at GPS locations for migratory routes and summer ranges, and for residents on the shared winter range during the same periods. We normalised estimates of forage and predation risk on a scale of 0 to 1 for comparison and visualisation. Because there were different numbers of GPS locations across individual elk seasons, we randomly sampled 2500 locations from each individual elk-year.

Herbaceous (graminoids and forbs) biomass (g/m^2) was predicted across the study area during the growing season (May–September) from a previously developed dynamic forage biomass model (see Hebblewhite et al., 2008 for full details). Briefly, this forage maturation model predicted herbaceous forage biomass during the growing season in 16 day intervals from a combination of ~1000 vegetation plots and spatial covariates of landcover type, time-varying MODIS NDVI (MOD13Q1, 250 m resolution, 16 day time periods), and topographic variables (Hebblewhite et al., 2008). Thus, our model combines in-situ and remotely-sensed variables to predict forage biomass, an improvement over models that simply assume some phenological parameter (e.g. instantaneous rate of green-up, IRG; Bischof et al., 2012) correlates with forage biomass or quality. Our previously developed annual biomass estimates were then combined with annualised landcover (including changes from fire and logging) to estimate availability of herbaceous forage biomass from 2002 to 2018 (see Hebblewhite et al., 2008).

Under the forage maturation hypotheses, as biomass increases over the growing season, forage quality declines for large herbivores (Fryxell et al., 1988). The inverse relationship between forage biomass and dry matter digestibility (DMD) was empirically confirmed in our study area by Hebblewhite et al. (2008). They used repeat sampling of 30 ground-based vegetation plots from 2002 to 2005 ($n = 254$ repeat sampling occasions) to establish empirical relationships between measured forage biomass of the top 25 plant species consumed by elk and their dry matter digestibility (%DMD), accounting for wild ruminant digestion. They showed a strong ($r = -0.60$, $p < 0.0005$) negative inverse correlation between forage biomass (g/m^2) and % DMD (forage quality). Here, we examined differences in migratory routes and summer ranges for herbaceous biomass only in early August during the height of the growing season for two reasons. First, an emerging consensus in the large herbivore literature is that summer-autumn nutrition is critical for temperate ungulate demography (e.g. Cook et al., 2013, 2016). And second, because forage biomass, and hence quality, was also strongly correlated in time in a summer range (Hebblewhite et al., 2008). Thus, we interpret higher "quality" summer ranges were those with lower biomass by late August. Previous studies in this system demonstrate that elk with higher forage quality also showed higher pregnancy rates, faecal nitrogen levels and calves that were 20 kg heavier at ~8 months of age, confirming our ability to relate demographic traits to forage quality (Hebblewhite et al., 2008). We extracted the covariate value for each elk GPS location from the appropriate year. We combined values from all locations that occurred during migration or during the summer range period according to their migratory tactic group.

We tested for differences within a season (migration, summer) in exposure to our normalised (between 0 and 1) forage and predation risk covariates using Generalised Linear Models in Program R (R Core Team, 2019) of the ecological covariate as a function of the different migratory tactics (i.e. wolf risk ~ migratory route). We averaged day and night wolf risk, and grizzly bear risk in both bear seasons for simplicity. We also considered including a random effect of individual ID to account for potential repeat measures of the same individual elk across years, but never found support for including such random effects.

We estimated wolf predation risk using a previously developed wolf predation risk models based on resource selection functions (RSF; Hebblewhite & Merrill, 2008). Wolf predation risk at elk GPS locations was extracted from day- and night-summer (April 15–October 15) wolf RSF models developed using GPS and VHF telemetry data. The RSFs were generated using GIS and spatial covariates from 2002 to 2005. Wolf avoidance of human development resulted in lower wolf predation risk outside BNP (Hebblewhite & Merrill, 2008). We then extended these RSF models to 2005–2019 by incorporating annual changes in landcover, for example, arising from fire or logging induced changes in wolf predation risk (Berg et al., 2022). We assumed the underlying relationships between wolves and their resource selection remained constant through our study (see our explanation of model validation below).

Grizzly bear predation risk was also estimated based on previously developed RSFs using data from GPS-collared bears from 1999 to 2006 (see Nielsen et al., 2006). Nielsen et al. (2006) developed RSF models for grizzly bears for two seasons, early hyperphagia (16 June–31 July) and late hyperphagia (1 August–15 October). Similar to wolves above, Berg et al. (2022) annually updated RSF maps to reflect fires and other vegetation change. Grizzly predation risk was finally weighted by estimates of grizzly bear abundance. Spatial density of grizzly bears inside BNP was ~2.6 times higher than outside the park (Boulanger et al., 2018), which we used to weight the RSF for our estimate of grizzly bear predation risk (Berg et al., 2021, 2022).

Because both wolf and grizzly bear predation risk models assumed carnivore resource selection remained static over this ~20-year period (though they incorporated annual changes in landcover arising from burns, etc.), we were concerned they would not predict predation risk accurately given annual variation in predator abundance, distribution, and so forth. Thus, we conducted an independent out-of-sample cross-validation of both sets of predation risk models following K-folds cross validation (Boyce et al., 2002). We collected spatiotemporal locations of wolf- or grizzly- bear killed adult and calf elk from 2001 to 2020. Most elk mortality locations were from radiocollared individuals, but we also included opportunistically located mortalities. We then conducted K-folds cross validation (sensu Hebblewhite & Merrill, 2007 for our original wolf predation risk model) for the wolf and grizzly-bear predation risk models during summer (which included the entire start through to the end of migratory period). If wolf and grizzly predation risk models were predictive of elk mortality risk, then we predicted a strong Spearman rank correlation between the ranked equal-area-bin of predation risk and the rank-order of the number of observed mortalities by each cause in each bin.

2.7 | Migratory-tactic population trends

To understand whether shifts in use of different migratory routes were reflected in population consequences, we derived annual, tactic-specific abundance estimates from a previously developed Integrated Population Model (IPM; Besbeas et al., 2002; Kery & Royle, 2015). Martin et al. (2021) developed an IPM for this population from a combination of demographic data (e.g. radiotelemetry-based survival; calf: cow recruitment surveys; pregnancy rates), aerial population counts (Hebblewhite et al., 2006) and migratory-tactic specific switching rates (Eggeman et al., 2016; Martin et al., 2021). This IPM also corrected for potential unlikely sampling biases in reporting the simple proportion of radiocollared individuals in each migratory tactic over time. Here, we derived annual population estimates from 2002 to 2019 for the best-supported migratory survival model (i.e. 2, 3 or 5 migratory tactics) from our adult female survival analysis.

3 | RESULTS

3.1 | Elk monitoring

We collected over 1.66 million VHF and GPS locations of 401 adult female elk from 2001 to 2019. We attempted to classify migratory behaviour of 1243 elk-years from 324 unique females. Migratory status (i.e. resident, disperser or migrant) could be classified for 1192 elk-years from 323 unique females (i.e. some individuals died before commencing migration, collars failed in some years, etc.). Of these, 416 elk-years were migrants and could be further classified to migration route (see Tables S1 and S2 for sample sizes for each analysis). There was an average of 65 elk-years/year to estimate annual migration, survival, and mortality rates. We located 296 mortalities of all adult female elk; a known date of mortality was not associated with 44 of these mortalities. Of the total 252 mortalities with a known date, 154 were radiocollared and 58 had known migratory status.

In total, 55 of the radiocollared and known migratory status female elk mortalities occurred during the spring migration, summer or fall migration. Elk that died prior to migration had collars that failed, or died mid-migration, explain the difference between 154 and 58.

3.2 | Elk migration trends

The proportion of individuals classified in each migration tactic varied over time (Figure 2). The ratio of migrants to residents was approximately even in 2002 then the proportion of migrants decreased until 2009, when the largest difference in migrants and residents occurred (only 9% migrants in 2009). However, the number of individuals using a migratory tactic then increased, reaching a high of 0.75 by 2012, and thereafter varied between 0.32 and 0.46 until 2019. These migratory proportions were driven in part by demographic differences between tactics where residents suffered lower calf survival but higher adult survival, opposite to migrant elk (see Martin et al., 2021). But these differences were also explained by individual-level tactic switching (see Figure S2).

The proportion of elk using each route also varied over time (Figure 2). In 2002, migrants were split between western, southern and northern routes; over half of migrants were classified using the western route and zero migrated east. By 2003, a small proportion of migrants adopted the eastern tactic, which increased largely by individual resident elk switching to the eastern tactic by 2008 (Figure S2). For example, ~25% of all individuals switched to the eastern tactic in the years of 2006 and 2008 (Figure S2), driving this population shift. Eastern migrants have since accounted for the largest proportion of all migrants (mean from 2009 to 2019 = 0.639). Since 2008 there were few elk using the northern route, and elk using the southern and western routes remained below 0.25 (Figure 2). We estimated space-use using 91 spring migrations and 83 fall migrations from 54 individuals to estimate BBMM migratory polygons (Figure 1).

3.3 | Survival and mortality analyses

Cox-model coefficients showed that eastern and western migrants had significantly lower survival than residents ($\beta_{\text{eastern}} = 0.94$, SE = 0.370, Hazard ratio = 2.56; $\beta_{\text{western}} = 1.04$, SE = 0.344, Hazard ratio = 2.84; see Table S3). Using the top Cox-model, we found survival from the start of migration to the end of fall migration differed amongst resident, eastern and pooled-western migrants (Figure 3, Table S1). For residents, survival was the highest; by Day 50, survival for residents was 0.98 (SD = 0.008), and by Day 175 (end of fall migration), survival was 0.95 (SD = 0.012). In contrast, eastern

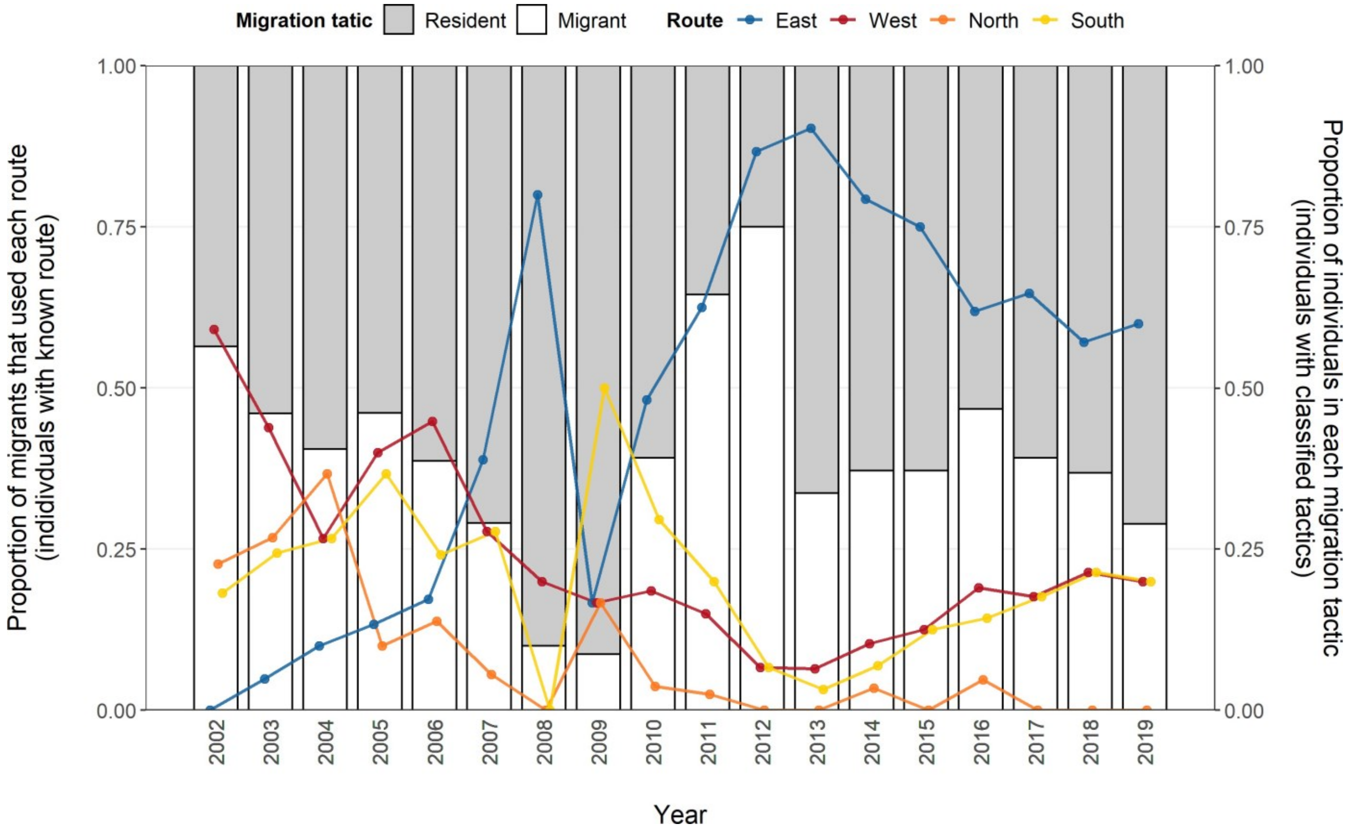

FIGURE 2 Trends in migration routes and tactics of 324 unique radiocollared adult female elk (*Cervus canadensis*) in the Ya Ha Tinda population, Alberta, Canada, from 2002 to 2019. We classified a total of 1243 elk-years, and an average of ~65 elk-years/year to characterise trends in migratory tactics.

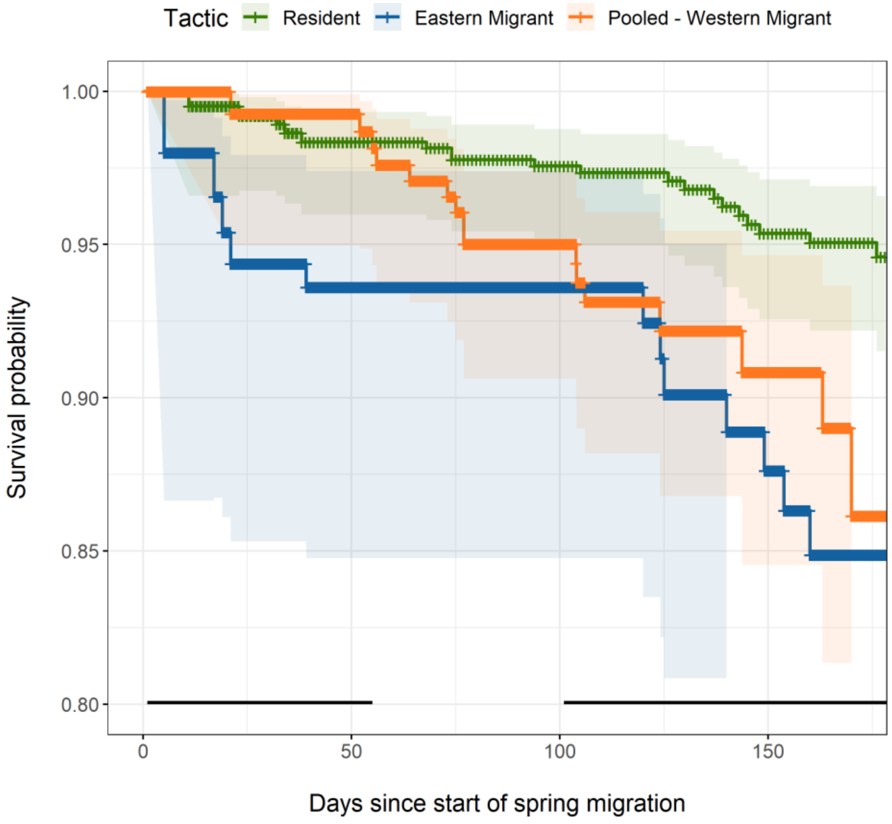

FIGURE 3 Kaplan–Meier survival plot for the probability of survival of adult female elk (*Cervus canadensis*) for three migratory tactics in the Ya Ha Tinda herd, Alberta, Canada from 2002 to 2019. Survival analysis covers the period from the start of spring migration to the end of fall migration annually with individual elk defined days since start of spring migration (see text). Model shows variation in survival probability between residents and migrants split into two migration routes (eastern and pooled-western, which includes northern, southern, and western routes).

elk showed the largest decrease in survival during the spring and fall migration periods. At Day 25 since the start of spring migration, survival of eastern migrants was 0.94 (SD = 0.281) and remained relatively unchanged until the start of fall migration around Day 100, when survival was still 0.94 (SD = 0.029). Survival declined, however, in the fall to 0.90 (SD = 0.024) and 0.849 (SD = 0.041) by Days 125 and 175, respectively. Pooled-western elk showed similar survival declines as eastern migrants but lower risk during spring migration, and declines occurred at a more constant rate once arrived on the summer range (Figure 3). Survival for pooled-western elk remained high until Day 50 following spring migration (survival = 0.99, SD = 0.007). Once on summer range, survival declined relatively consistently through the end of fall migration, when predicted survival was 0.861 (SD = 0.041).

We determined mortality cause for 28 mortality events for which the predator could be determined for radiocollared adult female elk. Wolf and grizzly bear predation each accounted for 12 mortalities and cougar accounted for four. Cause-specific mortality by predators varied by migration tactic and season (Figure 4; Table S1). Because of the relatively low number of total known cause predator-caused mortality events, we grouped spring and fall migratory periods together to estimate cause-specific mortality during migration. For residents, most mortality was due to wolves during spring and fall migration periods (Figure 4). For eastern migrants, mortality was caused by cougars during both migration and summer periods. And for pooled-western migrants, mortality was caused mostly by grizzly bears during the migration periods but by wolves during the summer period (Figure 4).

3.4 | Migratory route forage and predation risk covariates

Residents experienced the highest normalised herbaceous forage biomass availability across both seasons ($\beta_{\text{resident}} = 0.40$, $p < 2\text{e-}16$), which was equivalent to eastern elk biomass ($\beta_{\text{east}} = -0.03$, $p = 0.213$; Tukey test comparison between resident and east $p = 0.55$). In contrast, western ($\beta_{\text{west}} = -0.16$, $p < 0.0005$), north ($\beta_{\text{north}} = -0.18$, $p < 0.0005$) and southern ($\beta_{\text{south}} = -0.12$, $p < 0.0005$) migrants all had significantly (Tukey tests p-values all <0.005) lower overall forage biomass than residents and eastern elk, and thus, higher forage quality in both seasons (migration and summer; Figure 5). And while forage biomass was lower in the migratory season (i.e. earlier in plant growth), it was even lower for the western, northern and southern migrants in the summer (p-values all <0.05), confirming lower forage biomass and higher quality for ""western" (south, north and west) migrant elk (Figure 5).

We first report cross-validation of predation risk models. We found 51 elk (which included radiocollared females above, but also uncollared elk including all other age-sex classes) known to be killed by wolves during the summer migration period, and 22 elk (again, including both radiocollared and uncollared elk) killed by grizzly bears during the same time. The Spearman rank correlation (r_s) between the frequency of observed wolf-killed elk and ranked "bins" of wolf predation risk from our predation risk models was $r_s = 0.925$ ($p = 0.00012$), indicating that our predation risk model predicted elk exposure to wolf predation risk very well over the study. Similarly, the Spearman rank correlation (r_s) for our grizzly bear cross validation was $r_s = 0.899$ ($p = 0.00041$). Thus, we conclude that our

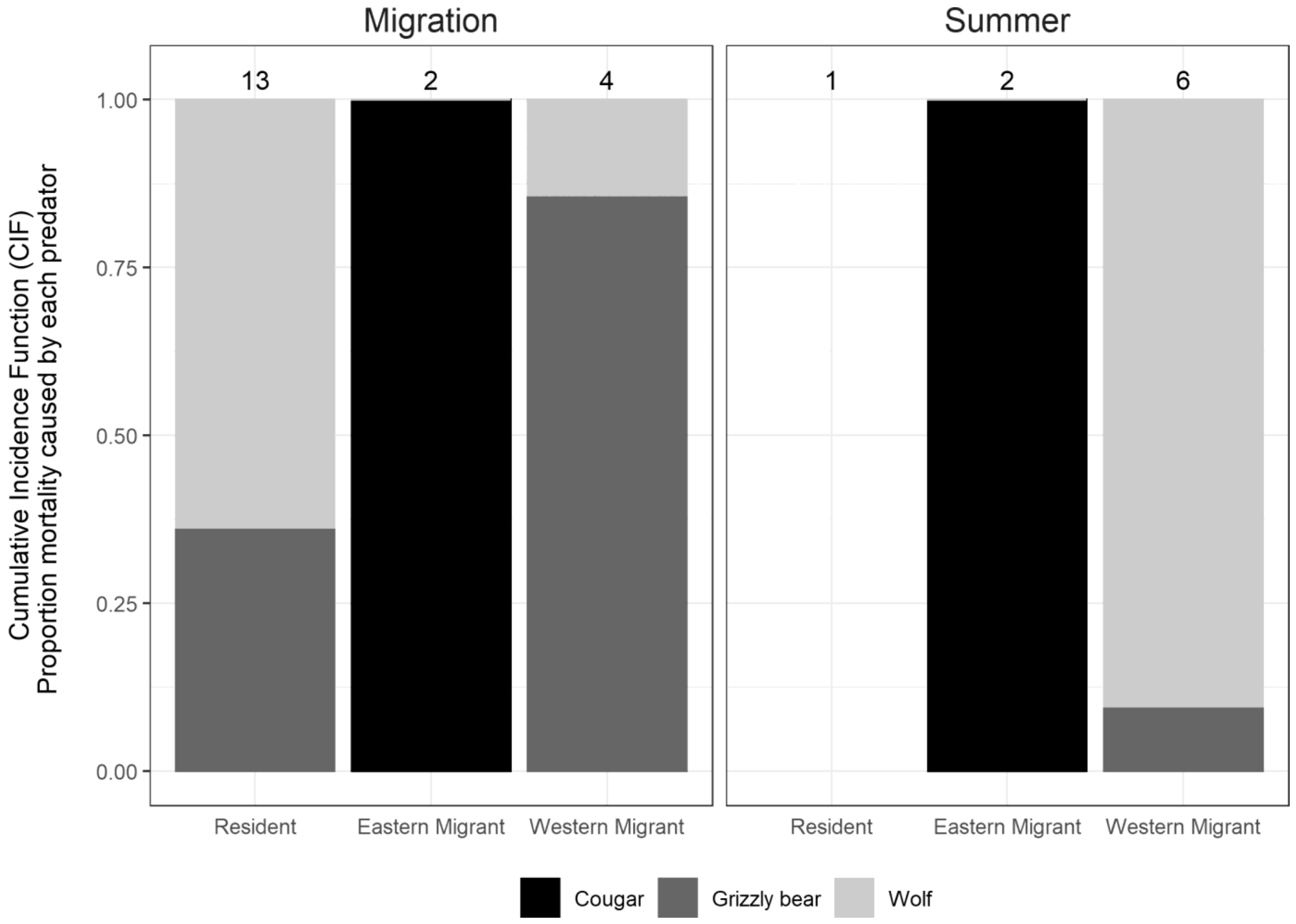

FIGURE 4 Proportional cause-specific mortality of migrant and resident adult females over the migration seasons (fall and spring) and summer season in the Ya Ha Tinda elk (*Cervus canadensis*) population, Alberta, Canada, 2002–2019. Integer above bar is number of nonhuman predator-caused mortalities during that annual period (migration or summer) per migration tactic classification.

predation risk models predicted elk spatial mortality quite well over our long-term study. Finally, the correlation between the wolf and grizzly risk models was very weak (e.g. $r = 0.04$, for averaged models), indicating that female elk could not simply avoid both predators and faced a real ecological trade-off between predators.

Residents experienced the highest level of wolf predation risk during both migration and summer periods ($\beta_{resident} = 0.42$, $p < 2e\text{-}16$; post-hoc Tukey tests confirmed all other pairwise comparisons between resident and other tactics were significantly different in both seasons; Figure 5). But there were no other significant differences in exposure to wolf predation risk between migratory routes within a season (i.e. west, south, east and north all had similar exposure to wolf predation risk; Tukey test p-values all >0.10; Figure 5). And there was no overall difference between seasons in exposure to wolf predation risk ($\beta_{season} = 0.004$, $p = 0.60$). But, for the migratory tactics, in general, they experienced lower exposure to wolf predation risk in the summer compared to the migratory period ($\beta_{summer*east} = -0.06$, $p = 0.015$; $\beta_{summer**west} = -0.13$, $p < 0.0005$; $\beta_{summer*north} = -0.11$, $p < 0.0005$; $\beta_{summer*south} = -0.11$, $p < 0.0005$).

Resident elk experienced intermediate grizzly bear predation risk ($\beta_{resident} = 0.42$, $p < 2e\text{-}16$), whereas southern migrants experienced the highest ($\beta_{south} = +0.08$, $p < 0.005$; Figure 5); the next highest were western migrants ($\beta_{south} = +0.03$, $p = 0.003$; Figure 5), followed by northern migrants ($\beta_{north} = +0.02$, $p < 0.18$; Figure 5), though northern and resident elk did not differ (Tukey post-hoc test $p > 0.2$). Eastern migrants experienced the lowestgrizzlybearpredation riskduring migration ($\beta_{east} = -0.13$, $p < 2e\text{-}16$; Figure 5). During summer (i.e. late hyperphagia), all migratory tactics experienced higher grizzly bear predation risk compared to during spring migration ($\beta_{summer} = +0.03$, $p < 2e\text{-}16$), but the effect interacted with migratory tactic where grizzly risk declined for eastern ($\beta_{summer*east} = -0.05$, $p < 0.0005$) and northern ($\beta_{summer*north} = -0.06$, $p = 0.009$) elk the most during summer, but not for southern ($\beta_{summer*south} = -0.01$, $p = 0.51$) and western elk ($\beta_{summer*west} = 0.01$, $p = 0.50$) that largely migrated into Banff National Park.

3.5 | Migratory-tactic population trends

Abundance of female elk of resident, eastern and western migrants estimated from our previously developed IPM (Figure 6) closely tracked the independent trends in the number of individual elk displaying different migratory tactics (Figure 2). In 2002, western

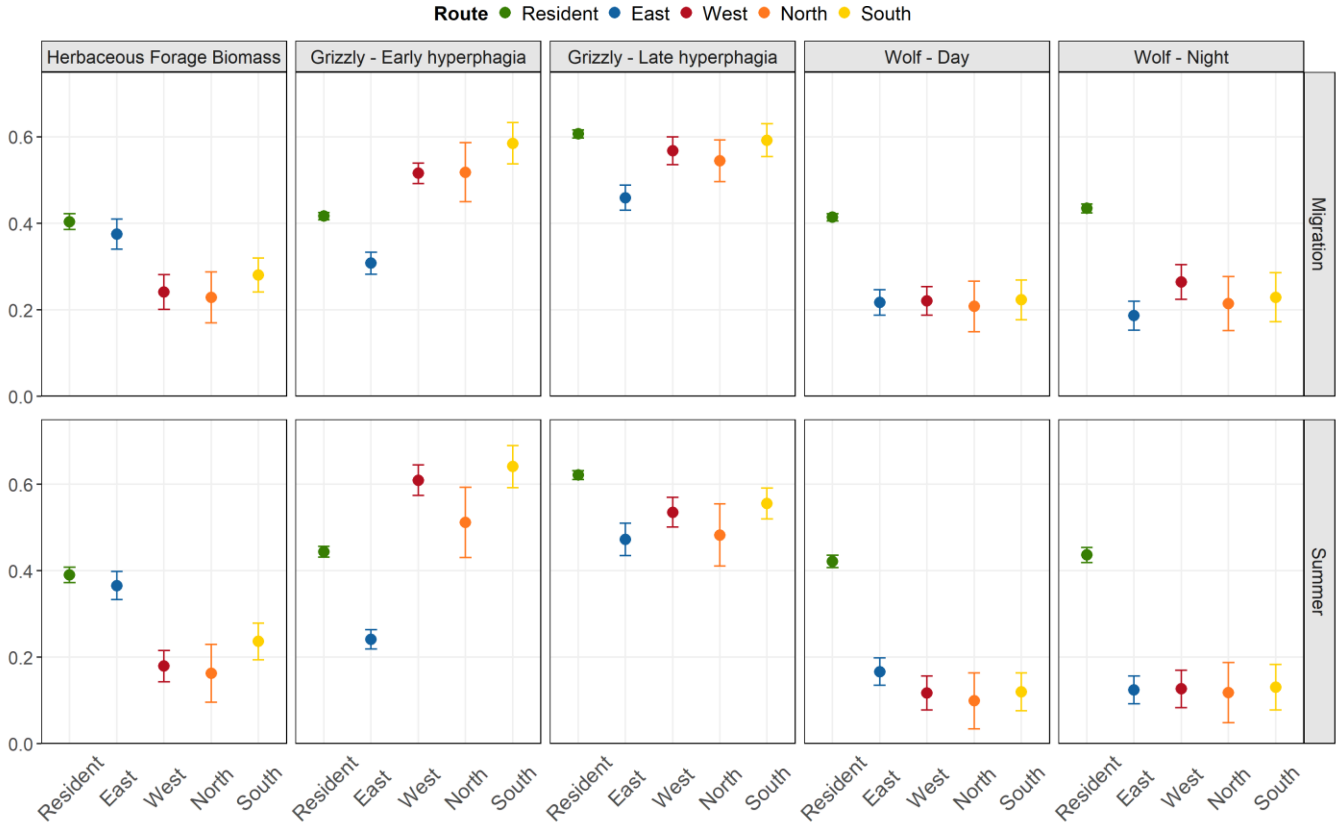

FIGURE 5 Plot of means showing mean and 95% confidence interval for scaled covariate values from individual GPS collared female elk (*Cervus canadensis*) during the migration and summer periods for each migratory and resident tactic in the Ya Ha Tinda population, Banff National Park, Alberta, Canada, 2001–2019. Top row is covariate values during migration (combined across spring and fall) and bottom row is during summer.

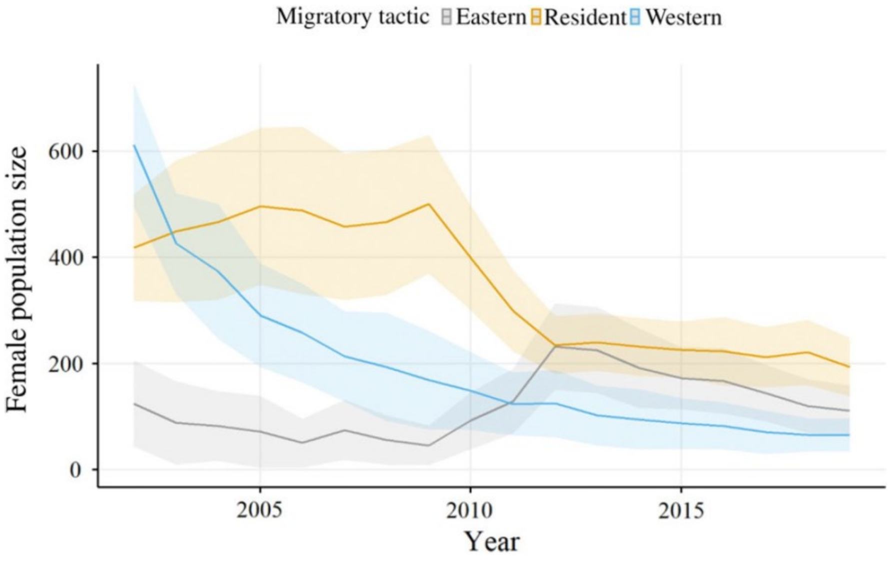

FIGURE 6 Estimated number of adult female elk and 95% credible intervals (shaded area) of the eastern, resident, and western migratory tactics of the Ya Ha Tinda elk (*Cervus canadensis*) population (2002–2019), Alberta, Canada, from Martin et al. (2021).

elk were the most abundant predicted tactic with ~600 females, compared with ~400 residents. There were a few (~100) eastern elk (Figure 6), though they were absent in our radiocollared sample (Figures 2 and 6). Western migrants rapidly declined until about 2012, while residents remained constant until 2009, and then declined to a stable abundance of ~200, and eastern migrants increased to 225 in 2012, and then gradually declined (Figure 6).

4 | DISCUSSION

The mechanisms driving migratory range shifts are complex, occur over large spatiotemporal scales, and yet, are fundamental to understanding migratory species (Bolger et al., 2008; Gill et al., 2019). Unfortunately, there are few long-term studies examining shifts in migratory behaviour and population consequences

(Gaillard, 2013). Models of red knot (*Calidris canutus*) migratory dynamics and long-term studies of Icelandic blacktailed godwit (*Limosa limosa islandica*) migratory route choice and survival show that the foraging benefits and predation risk costs of different routes drive migratory dynamics (Bauer et al., 2016; Gill et al., 2019). And in other species, environmental stochasticity drives migratory shifts (Acker et al., 2020; Reid et al., 2020). Sawyer et al. (2019) similarly showed different survival rates of migratory female mule deer choosing amongst different migratory routes and summer ranges, but not the causes of such differences. Few studies have been able to link long-term changes in migratory range dynamics to the costs and benefits of a migratory tactic to demography. Our two-decade study linked shifts in migration tactics with variation in risk and forage to changes in individual migratory behaviour and population consequences in a large herbivore, elk. Differential predation between different migratory routes and summer ranges by wolves and grizzly bears (Hebblewhite & Merrill, 2007), not bottom-up benefits of higher forage quality (Hebblewhite et al., 2008), explained long-term changes in migratory tactics over these two decades. Similar to recent work on shorebirds (Schmaljohann & Dierschke, 2005), our work suggests that top-down variation in predation risk drove shifting migratory behaviour for elk in our wildland study area.

Female elk showed changes in the proportion of individuals in different migratory tactics over time that corresponded with both differences in top-down driven survival and individual switching rates (Eggeman et al., 2016; Martin et al., 2021). Early in our study, most migratory individuals migrated west, seeking high-elevation summer ranges 20–60 km into Banff National Park, consistent with the classic expectation of elevational migration in montane systems driven by bottom-up forage benefits (Albon & Langvatn, 1992). Over nearly 2 decades, we saw an increase in individuals migrating eastwards, down an elevation gradient to areas that had earlier plant phenology, with perhaps some early spring foraging benefits but lower overall forage quality in summer (Hebblewhite et al., 2008). By the end of our two decades, most females chose to forego to migrate entirely, remaining resident year-round on the winter range. These changes corresponded to differences in long-term survival in these three tactics (Figure 3, Martin et al., 2021), whereby resident elk experienced the highest long-term survival, but the lowest cause-specific mortality from wolves and grizzly bears. In our system, this was driven by resident elk, despite being exposed to higher wolf predation risk (Figure 5), being able to exploit fine-scale human shields surrounding human development and higher harvest pressure on large carnivores (Hebblewhite & Merrill, 2007). These results were similar to Icelandic black-tailed godwits that showed long-term dramatic shifts to more northerly summer ranges that seemed to be consistent with predation over 3 decades. However, in Icelandic godwits, changes occurred over long-term generational shifts, and not by individual behavioural flexibility we note for elk (Eggeman et al., 2016), given the shorter generational times of shorebirds, and high fidelity to summer ranges (Gill et al., 2019). In contrast, shifts in elk were the result of differential spatial distribution of predators that had both direct effects on survival (our results) and behavioural influences on choice of migratory tactic (Eggeman et al., 2016).

Contrasting herbivores and shorebirds emphasises that in large mammals, flexibility in choice of migratory tactic can accelerate changes. In this sense, individuals selected amongst different migratory routes and hence summer ranges in a manner akin to second-order (home/seasonal range) resource selection. Across taxa as diverse as impala (*Aepyceros melampus*; Gaidet & Lecomte, 2013), moose (*Alces alces*; White et al., 2014), and Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*; Spitz et al., 2018), individuals switched migratory tactics from 10% to 33% per year. In our long-term study, Eggeman et al. (2016) showed ~15% of individual female elk changed tactics between years, and that both top-down (predation risk) and bottom-up (forage) drivers were potential drivers of year-to-year changes. Migratory plasticity has been broadly documented in dozens of elk populations in the Greater Yellowstone Ecosystem (Zuckerman et al., 2023). Martin et al. (2021) showed that such facultative switching was driven by female elk switching to the migratory tactic which demonstrated higher survival and reproduction in the previous year (similar to northern pike, *Esox lucius*, Haugen et al., 2006). We believe that the changes in migratory tactics by elk were driven by this behavioural flexibility and by spatial gradients in predation risk. In contrast, seasonal range use by shorebirds with high fidelity shifted much more slowly, over three decades, than the rapid shifts we report here. Thus, rapid shifts in migratory range use likely suggest individual plasticity as a driver in other taxa as well (e.g. in white storks, *Ciconia ciconia*; Flack et al., 2016).

The shifts in elk migration were consistent with top-down spatial gradients in predation risk across our transboundary landscape between a protected area (i.e. BNP) and managed, multiple-use lands. Our study area is no exception to the trends in recovering large carnivores across North America and western Europe. Yet such recovery is rarely complete because of the sensitivity of large carnivores to human persecution (Woodroffe & Ginsberg, 2001). Wolves and grizzly bears, the two leading non-human mortality causes, are protected in the National Park (Hebblewhite, 2007), but subjected to higher mortality outside park boundaries (Boulanger et al., 2018; Hebblewhite & Whittington, 2020; Nielsen et al., 2004), reducing predation risk for eastern migrants (Hebblewhite & Merrill, 2007). Unlike their eastern counterparts, western migratory elk could not easily avoid both predators because of the weak correlation between wolf and bear predation risk. In this regard, they were caught in a similar scenario to caribou in Quebec (Leblond et al., 2016) forced to trade-off between wolf and black bear (*U. americanus*) predation. In our system, such trade-offs between bear and wolves were evident in the changing exposure to their risk between migration and summer, and cause-specific mortality, where wolf predation was highest when migrating in valley bottoms, but bear predation risk was higher during summer for elk migrating into the protected area. We conclude that the strong transboundary gradient in human-caused mortality of large carnivores likely has contributed to the shift to eastern migration around 2009 (see also Martin et al., 2021). Similar changes are occurring in the Greater Yellowstone Ecosystem and more broadly across western North America (Middleton et al., 2013; Middleton et al., 2019) and the globe in response to landscape gradients in higher human-caused mortality of carnivores outside protected areas.

Differential exposure of the migratory tactics to spatial predation risk corresponded to cause-specific mortality (Figure 4). Migrants were more at risk to grizzly predation on migratory routes themselves (Figures 2 and 4; see also for wolves in Hebblewhite & Merrill, 2007). This was in contrast especially to residents, who enjoyed reduction in grizzly predation risk by exploiting human-shields surrounding infrastructure on their summer range (Hebblewhite & Merrill, 2009; Robinson & Merrill, 2013). Also, while we also only focused on adult survival here, reproduction is often the primary driver of migratory decisions across taxa (Bauer et al., 2016; Gill et al., 2019). Previous studies in our and other systems confirm that high predation risk by grizzly bears on juvenile elk calves (Berg et al., 2022) also reflected lower juvenile recruitment (Martin et al., 2021) and contributed to long-term summer range shifts, especially on western ranges inside BNP where grizzly densities were highest. In the migratory Atlantic puffin (*Fratercula arctica*), environmental stochasticity in marine primary productivity drove breeding performance. In our system, we do not yet have detailed information about reproductive benefits and costs of different migratory tactics, which could be driving the shifts reported here. Nevertheless, our results are similar to studies in other taxa that show that variation in adult and juvenile mortality between different migratory tactics helps explain migratory behaviour, range shifts, and demography (Flack et al., 2016; Schmaljohann & Dierschke, 2005; Sergio et al., 2014).

Despite the preponderance of top-down effects, bottom-up factors played a role here and could be more important in other species (e.g. Godwits; Gill et al., 2019). Western migrants experienced higher forage quality (i.e. lower forage biomass), had higher faecal Nitrogen, higher pregnancy rates and 8-month-old calf weights (Hebblewhite et al., 2008). Yet despite these benefits, western migrants experienced the most rapid decline (Figure 2), consistent with top-down predation risk. The western decline also occurred despite over 120 km^2 of prescribed wildfire encouraged by Parks Canada's fire restoration policies (Sachro et al., 2005). Bottom-up benefits of fire to ungulate forage were perhaps ameliorated because of increased grizzly and wolf predation risk in burns (Hamer, 1999; Hebblewhite & Merrill, 2008). Yet the eastern tactic shift may have been triggered by bottom-up factors in a lower predation risk setting. In 2001, a large wildfire burned 10,000 ha that improved forage quality (Hebblewhite et al., 2009) and was correlated with higher switching rates to eastern tactics in the 2000s (sensu Van Dyke & Darragh, 2007). Thus, a combination of reduced predation risk in the east because of human exploitation of large carnivores with a bottom-up pulse of enhanced forage due to fire may explain the novel shift to eastern migrants. Bottom-up agricultural subsidies such as irrigated alfalfa farming (Wilmers & Levi, 2013) are also a strong driver of shifting elk migratory patterns in western North America (Barker et al., 2019). Human subsidies (e.g. dumps) strongly affected white stork migration in Europe (Flack et al., 2016). Thus, reduction of predators due to human persecution and enhanced benefits from fire or agricultural subsidies may drive rapid shifts and losses of migratory behaviour across other taxa.

Regardless, changes in the foraging benefits and predation risk exposure of individuals to different migratory routes will determine the dynamics of migratory populations. Whether individuals are fixed in their choice of tactic, such as is the case in many birds, or show individual flexibility, such as in large herbivores (Berg et al., 2019; Eggeman et al., 2016), will drive the rate of changes that animals can make in the face of land use and climate change. Land use change has been demonstrably shown to benefit residency across taxa (e.g. Barker et al., 2019; Flack et al., 2016), and reduces movement rates in general (Tucker et al., 2017). Yet adaptation to shifts in climatically driven bottom-up benefits will require animals to either demographically (in high-fidelity species) or behaviorally (in plastic species) shift amongst different migratory routes and ranges to persist in the future.

AUTHOR CONTRIBUTIONS

S. Williams and M. Hebblewhite each contributed equally to the manuscript. E. H. Merrill and M. Hebblewhite conceived the ideas and directed the long-term data collection from 2001 to 2019; S. Williams, M. Hebblewhite, J. Kileen, K. MacAulay, P. Smolko, C. Meyer, J. Whittington, and H. Martin collected nad analysed the data; M. Hebblewhite and S. Williams led the manuscript writing. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Global Positioning System (GPS) from adult female elk are freely available on the Movebank Digital Data Repository https://doi.org/10.5441/001/1.5g4h5t6c (Hebblewhite et al., 2020). Associated data files and R code for trends in migratory classification, survival and cause-specific mortality are available from the Dryad Digital Data Repository https://doi.org/10.5061/dryad.83bk3j9zf (Williams et al., 2023).

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SUPPORTING INFORMATION

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

Table S1. Number of radiocollared (VHF, GPS) adult female elk used in this study, showing # of individuals outfitted with VHF or GPS radiocollars, the number of GPS or VHF locations obtained, and the number of mortalities of all radiocollared elk, and, the subset of radiocollared elk with known migratory status.

Table S2. Number of radiocollared (VHF, GPS) adult female elk classified into the 4 different migratory tactics (resident, migrant, disperser, unknown) by the Bunnefeld et al. (2011) Net-squared displacement method, and second, which migratory route (see Figure 1) each migratory elk was classified into (i.e. eastern, western, northern, southern or unknown).

Table S3. Candidate model set, AIC values and parameter estimates for Cox-Proportional Hazards survival models of adult female elk (*Cervus canadensis*) survival as a function of different migratory tactic categorization in the Ya Ha Tinda herd, Alberta, Canada from 2002 to 2019. Survival analysis covers the period from the start of spring migration to the end of fall migration. Italic covariate level indicates the reference category.

Table S4. Known-cause predator-caused mortalities for adult female elk (*Cervus canadensis*) separated by cause, 3-category migration tactic and season in the Ya Ha Tinda herd, Alberta, Canada from 2002 to 2019.

Figure S1. High-use boundaries and kernel density estimates of space-use of study area by individuals classified as residents during migration periods.

Figure S2. Adult female elk switching rates from the Integrated Population Model (IPM) of Martin et al. (2022) between tactics per year between the three migratory tactics in the Ya Ha Tinda elk population, 2001–2020. Show are the individual elk rates of switching per year to each tactic. For example, the blue line shows the rate of switching from the western tactic to other tactics.

Figure S3. Kaplan-Meier analysis plot for the model predicting probability of survival of adult female elk (*Cervus canadensis*) with classified migratory tactic in the Ya Ha Tinda herd, Alberta, Canada from 2002 to 2018. Survival analysis covers the period from the start of spring migration to the end of fall migration annually. Exact dates were used for migrant individuals that had converged NSD models and population-averaged quartile dates were used for migrant individuals that did not have NSD models and for residents (quartile spring and fall migration periods shown in black horizontal bars across bottom). Model shows variation in survival probability between residents and migrants.

Figure S4. Kaplan-Meier analysis plot from model predicting probability of survival of adult female elk (*Cervus canadensis*) with classified migratory tactic in the Ya Ha Tinda herd, Alberta, Canada from 2002 to 2018. Survival analysis covers the period from the start of spring migration to the end of fall migration annually Exact dates were used for migrant individuals that had converged NSD models and population-averaged quartile dates were used for migrant individuals that did not have NSD models and for residents (quartile spring and fall migration periods shown in black horizontal bars across bottom). Model shows variation in survival probability between residents and migrants split into four migration routes (eastern, western, southern and northern).

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