Long-term changes in migratory patterns of elk (*Cervus canadensis*) in the southern Rocky Mountain Trench of British Columbia, Canada

by

Kelly Leah Mulligan

A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in

Ecology

Department of Biological Sciences
University of Alberta

ABSTRACT

Migration can be described as a round-trip movement between distinct ranges and is thought to be a response to a spatiotemporal variation in resources. Large vertebrate herbivores such as ungulates often migrate to track seasonal variability in high quality forage and reduce predation risk. Recent evidence indicates ungulate migration is being lost globally, which has been attributed to human disturbances such as agriculture, barriers to movement including expanding human infrastructure, and recovering predator populations. In the southern Rocky Mountain Trench in British Columbia concerns over a reduction in the migratory portion of an elk (*Cervus canadensis*) population were concomitant with the recovery of wolves (*Canis lupus*), increasing grizzly bear (*Ursus arctos*) populations, increased wildlife exclusion fencing, and increasing forest encroachment. This work quantified Rocky Mountain Trench elk migratory decline by determining the ratio of migrant to resident elk (M:R) across three periods (1987–1993, 2007–2010, and 2014–2018). We then explored what might be driving this migratory decline by qualitatively assessing whether M:R trends were consistent with predictions from five non-mutually exclusive hypotheses—*competitive release, social fence, foraging areas, agriculture subsidy,* and *human shield*—postulated to influence elk migration over time. Finally, we compared trends in habitat suitability of high elevation (≥ 1,200 m) migrant and low-elevation (< 1,200 m) resident summer ranges using resource selection functions. Our results demonstrate that the proportion elk migrating in summer declined from 80% in 1987–1993, to 51% in 2007–2010, then to 39% in 2014–2018. Increasing elk residency was most consistent with the *human refuge hypothesis*, as elk residency on low elevation, human-dominated landscapes increased as both wolf and grizzly bear abundance increased. Both migrant and resident elk avoided areas with major roads and showed selection for natural herb-shrub areas and early seral vegetation found in areas of wildfire and timber harvest. Habitat suitability declined throughout the study for both migrant and resident elk, with a greater decline on migrant ranges. Results from this study will help managers address the challenges of restoring elk migrations amidst the challenges presented by predator recovery and on-going land use changes.

PREFACE

The following thesis is a combined effort between Kelly Leah Mulligan, and staff and contractors from British Columbia's Ministry of Forests, Lands, Natural Resource Operations and Rural Development. Field work and data collection were in accordance with the Live Animal Capture and Handling Guidelines for Wild Mammals, Birds, Amphibians & Reptiles, part of the Standards for Components of British Columbia's Biodiversity series. To date, no manuscripts have been submitted for publication, but authorship will represent project collaboration.

To my grandfather Gerald Alfred Mulligan—you inspire me to constantly learn

ACKNOWLEDGMENTS

First and foremost, I would like to thank Garth Mowat for introducing me to this project. I appreciate your infectious positive attitude and without you this project would not have been possible. To my advisor Evelyn Merrill, you are the hardest working individual I know. Thank you for helping me improve my writing skills and critical thinking. You have helped me become a better scientist. To Scott Nielsen, I appreciate the time taken to be on my committee and for providing feedback throughout my degree; your kind demeanor and clear explanations were invaluable to my analysis. To Mark Boyce, thank you for your helpful comments during lab meetings and sharing your perspectives on ecology. In addition, I would also like to thank Andrew Derocher and Mark Lewis for acting as my external examiner and chair, respectively.

To my U of A friends, I cannot adequately encapsulate your importance in such a small space, but I will try. Your support provided through friendship, humour, and analysis assistance has made my time at U of A particularly memorable. To Charlotte Brown, Allison Dunlop, Claire Edwards, and Grace Enns, thank you for the many whole-hearted conversations. To Kara MacAulay and Jacalyn Normandeau, thank you both for reminding me there is a light at the end of the tunnel. To Mitchell Flowers and Kelsey Gritter, I really appreciated having you both in the lab and hope to work together again. To Sean Konkolics, Yasmine Majchrzak, Michael Peers, Joe Silva, and Emily Studd, thank you for the random chats and lunch breaks; you helped keep the office days interesting. To Zachary Grant MacDonald, thank you for being so welcoming when I first visited U of A; you helped ease my transition into grad school. To Maria Dobbin, Jenny Foca, Natasha Hardy, Ally Menzies, and Karling Roberts, thank you for providing such great friendship at the end of my degree; you helped keep me motivated. I would like to

particularly thank Philip Walker, Meghan Beale, and Peter Thompson for their many hours of analysis support. My second chapter would not have been possible without your help.

To Alexandre Bevington, thank you for your assistance with my remote sensing layers; I appreciate your kind nature and willingness to help. To Txomin Hermosilla, thank you for your Landsat timeseries, these layers were invaluable to my second chapter. To Clayton Lamb, thank you for sharing your topographic GIS layers and knowledge on East Kootenay grizzly bears. Thank you to the many individuals associated with the Ministry of Forests, Lands, Natural Resource Operations and Rural Development: Emily Chow, Stuart Clow, Leanne Columbo, Merle Crombie, Randy Harris, Larry Ingham, Gerry Kuzyk, Deb MacKillop, Kathleen McGuinness, Kim Poole, Cassidy van Rensen, and Irene Teske, your insights and data sharing helped me gain knowledge of the study area and capture elk-related issues on the landscape. I would like the specifically thank Holger Bohm and TJ Gooliaf, both of whom were kind enough to provide me with lodging during my summers in the Kootenays. To Laura Smit, thank you for being a supportive cubicle buddy during my time in Nelson. To Tara Szkorupa, thank you for your time creating this project with Garth. I will never forget getting elk telemetry data off of that 5.25-inch floppy disk. To Patrick Stent, I really appreciate all the support you have provided.

To Maggie MacDonald, Drew Scott, and Madeline Trottier, thank you for being so kind during the first few months of the pandemic. Your friendship provided much needed support during a difficult time. To my roommate Camille Roberge, your constant choice of strange but excellent words used to describe life keep me going. To my best friend Lauren Welte, thank you for always being a phone call away. I will always appreciate your humour and insight. Lastly, I would like to thank my parents and sister: Don, Sharon, and Robyn Mulligan, your constant support through life’s many challenges is what keeps me going.

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INTRODUCTION

Migration can be described as a round-trip movement between distinct ranges and is thought to be a response to a spatiotemporal variation in resources (Fryxell et al. 1988, Berger 2004). Large vertebrate herbivores such as ungulates often migrate to track seasonal variability in high quality forage and reduce predation risk (Fryxell et al. 1988). Ungulate migrations have positive effects on ecological processes by altering plant composition, increasing grassland production, and increasing nitrogen mineralization (Frank 1998, Holdo et al. 2007). Recent evidence indicates these migratory behaviours and migratory populations are being lost globally (Berger 2004, Harris et al. 2009), which has been attributed to human disturbances such as agriculture (Barker et al. 2019*a*), barriers to movement including expanding human infrastructure (Haggerty et al. 2018), climate change (Middleton et al. 2013, Aikens et al. 2020), and recovering predator populations (Nelson et al. 2012). Because many migratory ungulate populations are in decline, understanding how environmental changes influence the trade-offs that individuals make in accessing food resources and avoiding predation risk is a conservation priority (Berger 2004, Harris et al. 2009, Berg et al. 2019).

Partial migration, where a portion of the population is migratory, is thought to result from density-dependent fitness related to outcomes of migratory tactics (Chapman et al. 2011). A growing body of literature has focused on partially migratory populations because comparing what features influence the success of different migratory tactics may provide insight into conserving these populations. A range of factors have been hypothesized to either increase (Fryxell and Sinclair 1988, Fryxell et al. 1988) or decrease (Hestbeck 1982) migratory populations. The *competitive release hypothesis* states that individuals who migrate to allopatric summer ranges can reduce intraspecific competition for forage on sympatric winter range in temperate zones. Some support for this hypothesis has been found in ungulates, where the probability of migration increased with increasing density (Fryxell and Sinclair 1988, Fryxell et al. 1988). At the same time, high conspecific density may decrease migration through the *social fence hypothesis,* due to increasing negative social interactions on summer ranges with neighbouring groups (Hestbeck 1982, Barker et al. 2019*a*). This hypothesis has been used to describe small mammal movement (Hestbeck 1982) but has only recently been explored in ungulates (Mysterud et al. 2011, Barker et al. 2019*a*).

Selection for high quality forage has been proposed as the primary driver of ungulate migration (Fryxell et al. 1988, Fryxell 1991, Middleton et al. 2013). According to the *forage maturation hypothesis*, ungulate movement is driven by access to large-scale phenological development of forage (Fryxell and Sinclair 1988). For example, Hebblewhite and Merrill (2009) found elk (*Cervus canadensis*) that migrated to high-elevation summer ranges in Banff National Park in Canada were exposed to higher forage quality because of delayed phenological development, whereas residents had lower forage quality. Further, spatial changes in forage may alter the large-scale distribution of migratory ungulates in a density-dependent habitat selection manner (Gaudry et al. 2015). Disturbances such as logging or burning create early seral habitat that can attract ungulates because of short-term increases in forage quality and longer-term (> 15 years) increases in forage biomass post-disturbance (Irwin and Peek 1983, Sittler et al. 2015, Proffitt et al. 2019). In this case, changes in migratory populations may relate to altered carrying capacity. Consistent with this hypothesis is the *agriculture subsidy hypothesis*, where high quality agricultural crops result in a higher proportion of time or a higher proportion of the population remaining on low-elevation ranges (Middleton et al. 2013, Lande et al. 2014, Barker et al. 2019*a*). For example, resident elk in Wyoming have been found to spend 47% to 52% of their time on irrigated fields in late summer (Middleton et al. 2013) and the presence of agriculture on elk winter range in western-Montana was found to decrease the likelihood of migration (Barker et al. 2019*a*).

Finally, predation risk may alter migratory patterns in ungulates. For example, declines in migratory elk in the Clarks Fork drainage in the Greater Yellowstone Ecosystem were associated with wolf (*Canis lupus*) recovery and a fourfold increase in grizzly bears (*Ursus arctos*) observed on migrant range in summer (Middleton et al. 2013). Consistent with the *predation reduction hypothesi*s, prey can alter their distribution by migrating outside predator home ranges (Fryxell et al. 1988, Middleton et al. 2013). For example, Hebblewhite and Merrill (2011) reported that elk on the eastern slopes of the Rocky Mountains that migrated onto summer ranges in Banff National Park were exposed to ~70% lower predation risk than that of resident elk. However, if resident elk used areas of high human infrastructure, migrant elk only had a ~15% lower predation risk than resident elk (Hebblewhite and Merrill 2011). As described by the *human shield hypothesis,* prey use areas of high human use to avoid predators (Berger 2007). Given human activity is often concentrated at low elevations and predators avoid human activity (Berger 2007), prey may reduce migratory behaviour and occupy low elevation winter range in summer. Determining how ungulate migration is affected by predator populations and human-use can offer direction to conservation actions aimed to mitigate ungulate migration loss (Bolger et al. 2008).

The elk population inhabiting the southern Rocky Mountain Trench (RMT) of British Columbia, Canada, is the largest population in British Columbia (Szkorupa and Mowat 2010). In the early 1990s most elk in this area exhibited an altitudinal migration to higher elevations but have more recently increased use of low elevations in summer resulting in increased crop depredation (Jalkotzy 1994, Phillips and Szkorupa 2011). In response, farmers have erected exclusion fencing eliminating elk from their fields and wildlife managers focused harvest on antlerless resident elk during the period 2004–2012 by restricting harvest to low elevations and closing the season before 15 October (Wilson and Morley 2005, Phillips and Szkorupa 2011). In addition to altered forage access and harvest pressure coinciding with decreased southern RMT elk migration, wolves in the area were nearly extirpated in the 1960s due to bounty hunting and organized predator control but have been recovering since the 1970s (Tompa 1983, Mowat 2007). Although, decreased elk migration in the southern RMT is similar to some of those observed elsewhere in the Rockies (Hebblewhite et al. 2006, Middleton et al. 2013, Muhly et al. 2013), the Elk Valley, an area ~100 km east of the southern RMT with five open coal pits, has an elk population with stable migratory trends at ~50% in both the 1980s and 2010s (Poole and Lamb 2020). This dichotomy of elk migratory trends across the Rockies highlights the complexity of elk migratory response to changing land-use and predator populations.

In this chapter, we take advantage of data from collared female elk across three periods (1987–1993, 2007–2010, and 2014–2018) to evaluate long-term migratory trends of a partially migratory elk population and to explore the possible causes of the observed declines in migratory elk. We start by classifying individual elk as migrant (M) or resident (R) and test whether the ratio of M:R changes over time. We then examine the evidence for whether changes in the M:R ratio were consistent with predictions from five non-mutually exclusive hypotheses—*competitive release, social fence, foraging areas, agriculture subsidy,* and *human shield*—postulated to influence the change in M:R over time (Table 1.1). If observed changes in M:R ratio were consistent with *competitive release,* we expected to see an increase in migrant elk as the elk population increased (Table 1.1: P1 [Prediction 1]) whereas if summer ranges were at capacity, migrant elk would decrease more than residents, consistent with the *social fence hypothesis* (Table 1.1: P2). If shifts in M:R were consistent with changes in the carrying capacities of summer ranges, we expected change in the M:R to be consistent with either changes in the extent of early seral stands at low or high-elevations associated with disturbances such as burning (Table 1.1: P3 and P4), or clear-cutting (Table 1.1: P5 and P6), that increase forage availability, or with *agriculture subsidy* where the relative change in resident elk would reflect changing access to agricultural fields (Table 1.1: P7). Finally, if predation has been a major driver of changes in M:R, we expected to see a decreasing trend in M:R consistent with the *human shield hypothesis* because of the increase of predators over time and their avoidance of humans at low elevations (Table 1.1: P8, P9). In contrast, if elk harvest was effective at reducing resident elk more than migrant elk, we expected to see an increasing M:R ratio as elk harvest increased over time. Our evaluation focuses on a qualitative discussion of the strength of evidence because of the nature of the available long-term data, and because outcomes for the hypothesized changes in the M:R are non-mutually exclusive.

METHODS

Study Area

Our study area is located in the southeastern corner of British Columbia, which we respectively acknowledge as being within amakʔis Ktunaxa, the territory of the Ktunaxa Nation (Figure 1.1). Within the region, the study area lies in the southern Rocky Mountain Trench (RMT), which includes a broad valley and the surrounding mountains. The valley width ranges from 6 to 20 km across and falls between the parallel northwesterly oriented Purcell Mountains and Rocky Mountains with the valley floor at ~1,000 m. Main communities within the southern Rocky Mountain Trench include Cranbrook (49°29’59”, 115°46’07”) and Kimberley (49°40’60”, 116°0’0”).

The southern RMT is arid with an annual mean precipitation of approximately 300 mm and mean snowfall of 120 cm recorded at the Cranbrook, B.C. airport (Environment Canada 2019). Low elevations are dominated by ponderosa pine (*Pinus ponderosa)*, Douglas-fir (*Pseudotsuga menziesii*), bluebunch wheatgrass (*Pseudoroegneria spicata*) dominated grasslands, and big sagebrush (*Artemisia tridentata*; MacKillop et al. 2018). Mid-elevations are dominated by white spruce (*Picea glauca*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), willows (*Salix* spp.), and sedges (*Carex* spp.; MacKillop et al. 2018). Engelmann spruce (*Picea engelmanni*) and subalpine fir dominant higher elevations, with fescue (*Festuca* spp.) grasslands covering the dryer avalanche slides (MacKillop et al. 2018). Agricultural lands within the southern RMT are used for hay production and cattle ranching, many of which are enclosed by wildlife exclusion fencing (Phillips and Szkorupa 2007).

Other ungulates inhabiting the area include moose (*Alces alces*), white tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), caribou (*Rangifer tarandus*), mountain goat (*Oreamnos americanus*) and bighorn sheep (*Ovis canadensis*). Large predators in the area include grizzly bears, black bears (*U. americanus*), cougars (*Puma concolor*), and wolves. Bobcats (*Lynx rufus*), lynx (*L. canadensis*), wolverines (*Gulo gulo*), and coyotes (*C. latrans*) are also present and may prey on elk calves but are thought to be minor predators to elk. Wolves were nearly extirpated in southeastern British Columbia in 1968, with rare sightings near the

British Columbia Montana border in the 1980s (Tompa 1983). In the 1980s, wolves immigrated to the southern RMT from Banff National Park in the north and Glacier National Park in the south (Boyd et al. 1995). By 2010 wolves were assumed to be recovered throughout the region (Garth Mowat, Ministry of FLNRORD, pers. comm).

Analysis Framework

We assessed the five non-exclusive hypotheses related to partial migration in three steps (Table 1.1). First, we estimated the migrant to resident elk ratio (M:R) based on collared elk for three periods (1987–1993, 2007–2010, 2014–2018). Second, we determined trends in elk population size, habitat conditions, and predator numbers over time. Population trends were assessed using regional government aerial surveys, so we present elk population estimates for six winters over the study. Habitat conditions were determined using the aerial extent of clear-cuts, wildfire, and agricultural areas, where we assessed trends based on either annual means or point estimates within the three periods. Predator trends were represented by three different sources of information. We assessed trends in grizzly bear abundance using grizzly bear population and density estimates, whereas we used annual estimates of wolf harvest to assess trends in wolves. Third, we qualitatively assessed our predictions (P1–P9) (Table 1.1) by comparing predicted changes in the M:R ratio for each factor to the observed M:R trends to determine support for the five non-mutually exclusive hypotheses.

Elk Capture, Monitoring, and Migration Classification

Adult female elk were captured by the British Columbia Fish and Wildlife Branch over seven winters (January–March) between 1987 and 2016, creating three monitoring periods: 1987–1993, 2007–2010, and 2014–2018. During the first period, elk were captured in the winters of 1987, 1991, and 1992 near Wardner and Skookumchuck, whereas in the winters of 2007–2010 and 2014 and 2016, elk were captured in the same two areas plus a third near Wycliffe (Figure 1.1). Capture methods included snares on the ground, corral traps, and net guns from helicopters. Field staff followed live animal capture guidelines approved during that period of work by a British Columbia government Animal Care Committee (RIC 1998). Elk in 1987–1993 were collared with very high frequency transmitters (VHF, Lotek Engineering, Aurora, Ont., Canada), whereas in the 2007–2010 and 2014–2018 periods elk were collared with global position system (GPS) collars. All collars were equipped with mortality sensors and were located as soon as practically possible when a mortality signal was detected. Lotek VHF collars were located to the nearest 100 m using a fix-wing aircraft weekly for low elevation elk and biweekly for high elevation elk. Advanced Telemetry Systems G2000 GPS (Advanced Telemetry Systems Inc., Isanti, MN, U.S.A.) collars were used in 2007–2010 with a 9-hour fix rate. Finally, VECTRONIC Lifecycle Pro GPS collars (VECTRONIC Aerospace GmbH, Berlin, Germany) were used in 2014–2018 with a 23-hour fix rate.

Migratory behaviour was assessed for individual elk-years if $>$ 10 locations were available between 1 March and 31 November. Migratory behaviour was classified using a combination of the Net Squared Displacement (NSD) method (Bunnefeld et al. 2011) and post hoc rule-based classification. The NSD method uses model selection based on Akaike's information criterion (AIC) to determine the most parsimonious model representing migrants, residents, mixed migrants, dispersers, and nomads for each individual elk in each year. Two models excluded from consideration included nomadism, which is commonly misclassified (Bunnefeld et al. 2011), and mixed migration (migrants who return to a different wintering area) as model complexity often inappropriately favoured their selection (Bunnefeld et al. 2011). NSD models were fit using the *migrateR* package (Spitz et al. 2017) in Program R version 3.5.2 (R

Core Team 2018). Additional spatial constraints were used to classify elk when movement data was inconsistent with models produced by the NSD method. Constraints included classifying elk as residents when their summer ranges were < 15 km from their winter range and they spent < 30 days between 1 March and 31 November on distinct summer ranges.

In order to determine trends in M:R we omitted elk that demonstrated dispersal and created a binary classification composed of migrant and resident elk. No individual was monitored across the three periods. Given switching between migrant and resident movement strategies within the same individual occurred, we treated each elk-year independently. We also determined M:R for each period treating “elk-years” non-independently and found no changes to M:R trends (Appendix 1.1). We calculated proportions of migrant and resident elk for each period with 95% binomial confidence intervals and compared differences in the ratio of migrant and resident elk among periods using a chi-square test followed by a pairwise Z-test with the Holm adjustment for family-wise error rates.

Elk Population Abundance

Elk surveys were conducted by the British Columbia Fish and Wildlife field staff or contractors and were based on a stratified random block design with the number and location of surveyed blocks varying over time (Szkorupa and Mowat 2010, Stent and Phillips 2013, Stent et al. 2018). Stratification flights were conducted to assign each block to a high, medium, or low strata. A proportion of blocks within each stratum were selected and surveyed based on a formula to minimize overall variance. The number of elk seen within each stratum were averaged and applied to blocks not surveyed. Counts within each block were considered minimum counts and were adjusted for sightability by using the Hiller 12-e sightability model (Unsworth et al. 1991, 1999). This model applied a correction factor to each observed elk group by multiplying the number of elk observed in each group by the inverse probability that the group would have been seen based on three covariates: group size, vegetation class, and snow cover (Unsworth et al. 1991, 1999, Stent et al. 2018). Strata estimates were then added together to produce final population estimates. We report the estimated population size of elk in the southern RMT for six years between 1991 and 2018 with 95% confidence intervals to approximate overall trends in elk population size. We used confidence intervals of estimates within each period to visually assess differences.

Migrant and Resident Ranges

To assess temporal changes in habitat conditions on migrant and resident ranges separately, we distinguished low-elevation resident range from high-elevation migrant range in three steps. First, we delineated the composite home range of all elk using a 100% minimum convex polygon (MCP) for all summer elk telemetry locations with a 5 km buffer. Summer was defined as 1 May to 15 November, when 50% of all migrant elk left and subsequently returned to winter range (Appendix 1.2). We used logistic regression to predict the probability that a 30 m × 30 m pixel was more likely to be used by a migrant than resident based on its elevation (m). We developed three candidate models, using elevation for each individual elk location, or as a median or mean per elk-year (Appendix 1.3). Model predictive accuracy was assessed using area under a receiver operating characteristic (ROC) curve (Hanley and McNeil, 1982) using package *pROC* (Robin et al. 2020) in Program R version 3.5.2 (R Core Team 2018). We selected the model with the highest area under the curve (AUC) value, which can range from 0.5 (no discrimination ability) to 1.0 (perfect discrimination ability) (Appendix 1.3: Pearce and Ferrier 2000). Once determined, all areas below this elevational threshold value were classified as resident range (R), whereas all areas above the values were defined as migrant (M) range.

Trends in Early Seral, Agriculture, and Predators

Early seral habitats. We estimated the annual area (km^2) of early seral habitats (1–15 years; Hebblewhite et al. 2009, Proffitt et al. 2019) created by clear-cutting and wildfire based on layers of provincial clear-cut boundaries of harvested areas on crown land and historical wildfire perimeters (Ministry of FLNRORD 2019*a*, *b*). To determine if mean area (km^2) significantly differed between periods for each disturbance type on each range, we used Kruskal-Wallis and Dunn-Bonferroni post-hoc tests.

Agricultural lands. We determined trends in agricultural lands by comparing amount of unfenced irrigated agriculture area (km^2) on resident range in three steps. Agricultural land was only located on low elevation (< 1,200 m) resident elk range and due to layer availability, only one-point estimate of agricultural extent in each period was available. We first created three irrigated land layers from five-year average spectral mosaics, 1989–1993, 2004–2008, and 2014–2018, representing 1987–1993, 2007–2010, and 2014–2018, respectively. Mosaics were made using Google Earth Engine (Gorelick et al. 2017) with images taken from Landsat 5 Thematic Mapper and Landsat 8b Onboard Land Imager. Images were 30 m × 30 m resolution and taken between 1 July and 15 September with ≤ 30% cloud cover. We then identified total area (km^2) of irrigated agriculture by selecting irrigated land that fell within agriculture GIS layers (Ministry of FLNRORD 2018*a*, *b*; Table 1.2). Finally, we masked out areas that fell within the boundary of regional wildlife exclusion fencing layers and compared unfenced areas that were accessible to elk (Table 1.2).

Predation risk. We compared changes in elk M:R only to wolves and grizzly bears. We did not include black bears or cougars in our analysis due to limited data on black bears and the unlikely applicability of the *human shield hypothesis* towards cougars given their extreme adaptability to human disturbance (Morrison et al. 2014, Nix et al. 2018).

Wolf population abundance was not directly monitored during the study, therefore we used provincial furbearer harvest data for the wildlife management units in our study area, literature review (Tompa 1983, Boyd et al. 1995, Mowat 2007), and expert opinion (Garth Mowat, Ministry of FLNRORD, pers. comm) to qualitatively estimate wolf abundance. Wolf abundance trends were determined using linear regression between 1987 and 2017 and a Kruskal-Wallis test with Dunn-Bonferroni post-hoc tests to compare between periods.

We assessed grizzly bear population trends using data from two sources: grizzly abundance estimates for the Temperate Mountains between 1985 and 2014 (Hatter et al. 2018), and more recent grizzly bear density estimates for the southern Rockies between 2006 and 2017 (Lamb et al. 2019). The Temperate Mountains data were for a 102,588 km^2 area in southeastern British Columbia of similar habitat and hunting regulations throughout, encompassing approximately 9,000 km^2 or 80% of our study area. Temperate Mountains population estimates were determined using statistical population reconstruction of age at death data and then fitting a polynomial regression to these estimates (Hatter et al. 2018). The southern Rockies was a 12,000 km^2 area, which encompassed approximately 4,800 km^2 or 40% of our study area (Lamb et al. 2019). The southern Rockies grizzly density estimates were determined using annual growth rates and spatially explicit capture-recapture methods (Lamb et al. 2019). To ensure the two estimates predicted similar trends, we tested for collinearity using Pearson's correlation coefficient between 2006 and 2014 data, when estimates were available for both sources. We found high correlation ($| r | = 0.83$) between the two data sources. We used a Wilcoxon rank sum test to determine differences between 1987–1993 and 2007–2010 using Temperate Mountains data, and between 2007–2010 and 2014–2018 using southern Rockies density estimates.

RESULTS

Elk Population

Elk population estimates were low in 1991/1992 with 7,697 individual elk (95% CI: 6,972–8,421), peaked in 2007/2008 with 11,968 individuals (95% CI: 10,600–13,335), and declined to 5,907 (95% CI: 4,858–6,955) individuals in 2017/2018 (Szkorupa and Mowat 2010, Stent and Phillips 2013, Stent et al. 2018; Figure 1.2).

Elk Capture, Migration Classification, and Range Modeling

Elk Capture. We used location data from 94 different collared cow elk, which generated 211 elk-years of data. Fifty elk were tracked during in 1987–1993, 30 in 2007–2010, and 14 in 2014–2018. Two out of 94 elk switched movement strategies among years with one in 1987–1993 switching from a migrant to resident and another in 2007–2010 switching from a resident to a migrant.

Migration Classification. We found the number of migratory elk differed among periods (chi-square, $\chi^2 = 26.07$, $df = 2$, $P < 0.001$). The proportion of migratory elk significantly decreased from 0.80 in 1987–1993 to 0.51 in 2007–2010 (Z-test, $Z = 14.31$, $P < 0.001$, Figure 1.3), whereas the decline from 0.51 to 0.39 was not significantly different between 2007–2010 and 2014–2018 (Z-test, $Z = 0.66$, $P = 0.418$, Figure 1.3). The decline in the proportion of migrants from 0.80 in 1987–1993 to 0.39 in 2014–2018 was significant (Z-test, $Z = 16.95$, $P < 0.001$; Figure 1.3).

Range Modelling. A better fit was found using mean elevation (*AUC* = 0.912, *n* = 211) than median elevation per elk-year (*AUC* = 0.867, *n* = 211) or elevation per elk-location (*AUC* = 0.774, *n* = 21,557, Appendix 1.3) in predicting probability of a location being used by a migrant rather than a resident. The best threshold from the mean elevation model was 1,196 m. We therefore used an elevation cut-off of 1,200 m, above or equal to which was considered migrant range and below as resident range (Appendix 1.3).

Trends in Early Seral, Agriculture, and Predators

Early seral habitats. Total early seral clear-cut area on migrant range significantly differed among the periods (Kruskal-Wallis, *H* = 11.42, *df* = 2, *P* = 0.003). The highest extent of clear-cuts occurred in 2014–2018, with the extent in that period being 29% greater than in 1987–1993 (Dunn-Bonferonni, *P* = 0.001), but only 6% greater than in 2007–2010 (Dunn-Bonferonni, *P* = 0.096, Figure 1.4). On resident range, total early seral clear-cuts did not significantly differ among periods (Kruskal-Wallis, *H* = 5.26, *df* = 2, *P* = 0.072, Figure 1.4).

Extent of early seral burned area on migrant range differed among periods (Kruskal-Wallis, *H* = 8.25, *df* = 2, *P* = 0.016). The greatest extent of burned area occurred in 2007–2010, which was 24% higher than the extent in 1987–1993 (Dunn-Bonferonni, *P* = 0.006), which was followed by a non-significant increase of 17% between 2007–2010 and 2014–2018 (Dunn-Bonferonni, *P* = 0.460, Figure 1.4). Extent of burned area did not differ between 2007–2010 and 2014–2018 (Dunn-Bonferonni, *P* = 0.140). Extent of early seral burned areas on resident range also differed among periods (Kruskal-Wallis, *H* = 9.86, *df* = 2, *P* = 0.007) with the extent of burned area in 2007–2010 being 52% lower than 1987–1993 (Dunn-Bonferonni, *P* = 0.006) and 2014–2018 being 51% lower than 1987–1993 (Dunn-Bonferonni, *P* = 0.031, Figure 1.4). Extent of burns in the latter two periods did not differ (Dunn-Bonferonni, *P* = 0.920).

Agricultural lands. Unfenced irrigated agriculture decreased by 30% from 1987–1993 (47 km^2) to 2007–2010 (33 km^2) and decreased slightly by 12% from 2007–2010 (33 km^2) to 2014–2018 (29 km^2, Table 1.2).

Predation risk. Number of wolves harvested per year increased between 1987 and 2017 ($r^2 = 0.57$, n = 32, $P < 0.001$) and differed among periods (Kruskal-Wallis, $H = 7.63$, $df = 2$, $P = 0.020$), increasing from a mean of one individual harvested per year in 1987–1993 to a mean of 43 individuals harvested per year in 2014–2016 (Dunn-Bonferonni, $P = 0.011$, Figure 1.5). Grizzly bear abundance increased significantly between 1987–1993 and 2007–2010 (Wilcoxon rank sum, $U = 0$, $P = 0.006$, Figure 1.6), but grizzly density remained constant between 2007–2010 and 2014–2018 (Wilcoxon rank sum, $U = 12$, $P = 0.240$, Figure 1.6).

Support for Hypotheses

We found little support for the *competitive release* and *agriculture subsidy* hypotheses (Table 1.1). We found mixed support for the *social fence hypothesis*, where the prediction of decreased migration at higher densities corresponded with a reduced M:R, however, M:R did not increase following a decrease in the elk density. Effects of changes in carrying capacity on resident and migrant summer range were unclear because of the opposing effects of wildfire and logging; however, the decrease in *foraging areas* due to wildfire on the migrant ranges in the late period corresponded with the decrease in the M:R. Instead, we argue that the greatest support was for the *human shield hypothesis*, where the increase in predator populations corresponded to decreases in M:R, with more resident elk using low-elevation human-dominated range.

DISCUSSION

Our results demonstrate that the proportion of elk migrating in summer in the southern Rocky Mountain Trench of British Columbia has declined by as much as 50% from 1987–1993 to 2007–2010 and has remained low through 2014–2018. Although these results could be biased by capture locations or sample size, capture locations in 2007–2010 (Phillips and Szkorupa 2011) were meant to replicate those in 1987–1993 (Jalkotzy 1994) and similar proportional shifts in M:R elk over approximately the same period have been reported in migratory herds elsewhere along the Rocky Mountains. For example, the M:R elk migrating westward into Banff National Park in Alberta Canada declined from 12:1 to 3:1 from 1977–1987 to 1988–2004 (Hebblewhite et al. 2006) and the migratory elk herd dropped from 81% of the population to 48% from 1979–1980 and 2005–2009 in the Yellowstone ecosystem (Middleton et al. 2013). Although migration remained similar in the Elk Valley between the 1980s and 2010s with ~50% of elk migrating in both periods, Elk Valley migratory elk had fewer and shorter movements into upper tributaries coupled with increased use of high elevation mine sites (Poole and Lamb 2020). The dissimilarity between the elk migratory trends in the southern RMT and the Elk Valley is likely associated with the five open coal pits covering the Elk Valley. These high-elevation areas alter forage availability, particularly at high elevations, due to seeding (Poole and Lamb 2020). These patterns are consistent with the Barker et al. (2019*b*) finding that elk were more likely to migrate if forage varied predictably on migrant range between years.

The increase in the southern RMT elk population and resident elk corresponded to the period when wildlife exclusion fencing increased, reducing access for elk to irrigated agricultural fields. Although we expected migration to increase as fewer agricultural crops were available, unfenced agricultural crops may still be subsidizing elk, particularly if forage quality or quantity decreases elsewhere on the landscape. For example, there was an increase in resident elk in Montana related to agricultural crops, which was dependent on the availability of natural vegetation (Barker et al. 2019*b*). We postulate that although a subsidy of high-quality forage from irrigated agriculture may have played a role initially in migration dynamics, it alone is not driving the current patterns of elk migration because most of these areas are now fenced. With the decline in access to irrigated agriculture we would have expected greater competition among residents that might have led to more elk migrating in the late period, which again we did not find. Instead, we suggest that as more areas were fenced over time, resident elk were moved to low-elevation natural vegetation (Barker et al. 2019*a*). The corresponding increase in crop damage in the early period with the increase in the elk population led managers to increase elk harvest, primarily focused on low elevation, agricultural areas, which targeted resident elk (Appendix 1.4). However, the differential harvest on residents likely did not contributed strongly to the change in M:R, as we would have expected an increase in the M:R ratio especially in the late period, which we did not find.

At the same time, we found little support for the *competitive release hypothesis* and mixed support for *social fence hypothesis* being consistent with changes in the southern RMT elk population and M:R. If the *competitive release hypothesis* were true, we would have expected that as the population increased, competition for high quality resources on shared winter ranges would promote migration (Gauthreaux 1982), which we did not see. Instead, the decrease in M:R between 1987–1993 and 2007–2010 was more consistent with the *social fence hypothesis*, which predicted a decrease in M:R ratio with increasing density. Although, if social fences were influencing elk migratory patterns, M:R would have increased following the decrease in elk density between 2007–2010 and 2014–2018. These hypotheses assume range conditions remain constant, and that it is the interactions among conspecifics that alters the fitness balancing between migratory tactics. Alternatively, changes in landscape composition, particularly extent of foraging areas across the landscape, may also influence shifts in elk distribution.

We found mixed support for migratory shifts being associated with changes in patterns of land use and disturbances between migrant and resident ranges. Early seral stands resulting from clear-cuts and wildfires provide higher forage biomass for ungulates than closed canopied forested areas. Trends in the extent of burned areas across migrant and resident range both declined significantly between 1987–1993 and 2007–2010, with migrant range decline being consistent with the observed M:R. This pattern is not surprising given the suppression of wildfires in this area since the 1940s (Iverson 2014). Fire suppression can lead to forest encroachment into grasslands and increased homogeneity in forest age structure (Tande 1979, Andison 1998) resulting in forage loss for early successional species, including ungulates (Holroyd and Van Tighem 1983). Extent of clear-cuts initially increased on both migrant and resident ranges but continued to increase only on migrant ranges. If these changes in summer range carrying capacity due to increases in forage influenced the shift in migrants and residents, we would have expected an increased M:R ratio because of the improved availability of forages due to continued logging on migrant ranges. However, this was not the case. Elk may not select burns or clear-cuts under high predation risk (Hebblewhite et al. 2009). For example, Smolko et al. (In Review) found elk selected less for burns and remained near edges when predation risk from wolves was high. The increase in wolves over the study coupled with an increase in grizzly bear abundance in the early 2000s could result in southern RMT elk avoiding open areas due to increased predation risk.

We suggest that as predators increased over the past decade, their distribution has played a role in maintaining the elk population on low-elevation areas, reflected in the continued low M:R ratio consistent with the *human shield hypothesis* (Berger 2007). We argue resident elk use of low-elevation human-dominated range is a result of them seeking refuge from recovering predators. Migration originally was assumed to reduce predation risk by moving away from predator territories or den sites (Fryxell 1991); however, Berger et al. (2020) in their review highlighted that ungulate use of human-created predator refuges is wide-spread. Ungulate migratory decline during periods of increase in wolf and grizzly populations has been documented in both moose (Berger 2007) and elk (Hebblewhite et al. 2006, Middleton et al. 2013) in other montane areas in the Rocky Mountains. Low elevation areas within the southern RMT are heavily settled, creating a human refuge for elk from predators that elk appeared to exploit during predator recovery.

Our study provides an additional example of the decline in ungulate migration coupled with large predator recovery (Hebblewhite and Merrill 2007, Middleton et al. 2013). In the southern RMT, we suggest that over time the decline in elk migratory behavior resulted from a combination of the attraction of agricultural subsidy that was re-enforced by increasing predators. Decreased wildfire on migrant range may have also contributed to migratory decline, but an increased understanding of elk selection of early-seral habitat, particularly within human dominated landscapes and in the face of increased predation risk, would help further elucidate drivers of elk migratory decline.

Table 1-1 Five non-mutually exclusive hypotheses, associated factors, and predictions explaining changes in the ratio of migrant to resident elk (M:R) in the southern Rocky Mountain Trench, British Columbia, Canada, during three periods (1987–1993, 2007–2010, and 2014–2018). Predictions in bold are best supported by the data summarized in this analysis.

Hypothesis		**Factor**	**Prediction**	**Data Reference**
Competitive Release	Migration to other ranges in summer reduces intraspecific competition for resources on winter range (Gauthreaux 1982)	Conspecific Density	P1: If conspecific density increases, elk migration will increase	Fig. 1.2
Social Fence	High conspecific density increases social interactions that decrease migration to summer ranges (Hestbeck 1982, Mysterud et al. 2011)	Conspecific Density	**P2: If conspecific density increases, migration will decrease**	Fig. 1.2
Foraging Areas	Ungulate migration is influenced by increased availability of foraging areas (Fryxell 1991)	Clear-cuts (Migrant Range)	P3: If early seral habitat created by clear-cutting on migrant range decreases, elk migration will decrease	Fig. 1.4
		Clear-cuts (Resident Range)	P4: If early seral habitat created by clear-cutting on resident range decreases, elk migration will increase	Fig. 1.4
		Wildfire (Migrant Range)	**P5: If early seral habitat created by wildfire on migrant range decreases, elk migration will decrease**	Fig. 1.4
		Wildfire (Resident Range)	P6: If early seral habitat created by wildfire on resident range decreases, elk migration will increase	Fig. 1.4
Agriculture Subsidy	Ungulate migration is influenced by access to high quality agricultural forage (Middleton et al. 2013, Barker et al. 2019*a*)	Agriculture Access	P7: If elk access to agricultural lands on resident range increases, elk migration will decrease	Table 1.2
Human Shield	High human activity repels predators, allowing prey a spatial refuge (Berger 2007, Hebblewhite et al. 2009)	Wolf Density	**P8: If wolf density increases, elk will utilize low elevation human refuges and decrease migration**	Fig. 1.5
		Grizzly Density	**P9: If grizzly bear density increases, elk will utilize low elevation human refuges and decrease migration**	Fig. 1.6

Table 1-2 Area (km^2) of unfenced irrigated agriculture accessible to elk in the southern Rocky Mountain Trench, British Columbia, Canada for three periods (1987–1993, 2007–2010, and 2014–2018) determined by masking irrigated agricultural layers acquired from three 5-year spectral mosaics (1989–1993, 2004–2008, and 2014–2018) developed from Landsat 7 Enhanced Thematic Mapper (ETM+) and Landsat 8 Onboard Land Imager (OLI) imagery with provincial wildlife exclusion fence layers.

Period	**Spectral Mosaic**	**Area (km^2) of Irrigated Agriculture**	
		Total	**Unfenced**
1987–1993	1989–1993	47	47
2007–2010	2004–2008	50	33
2014 –2018	2014–2018	50	29

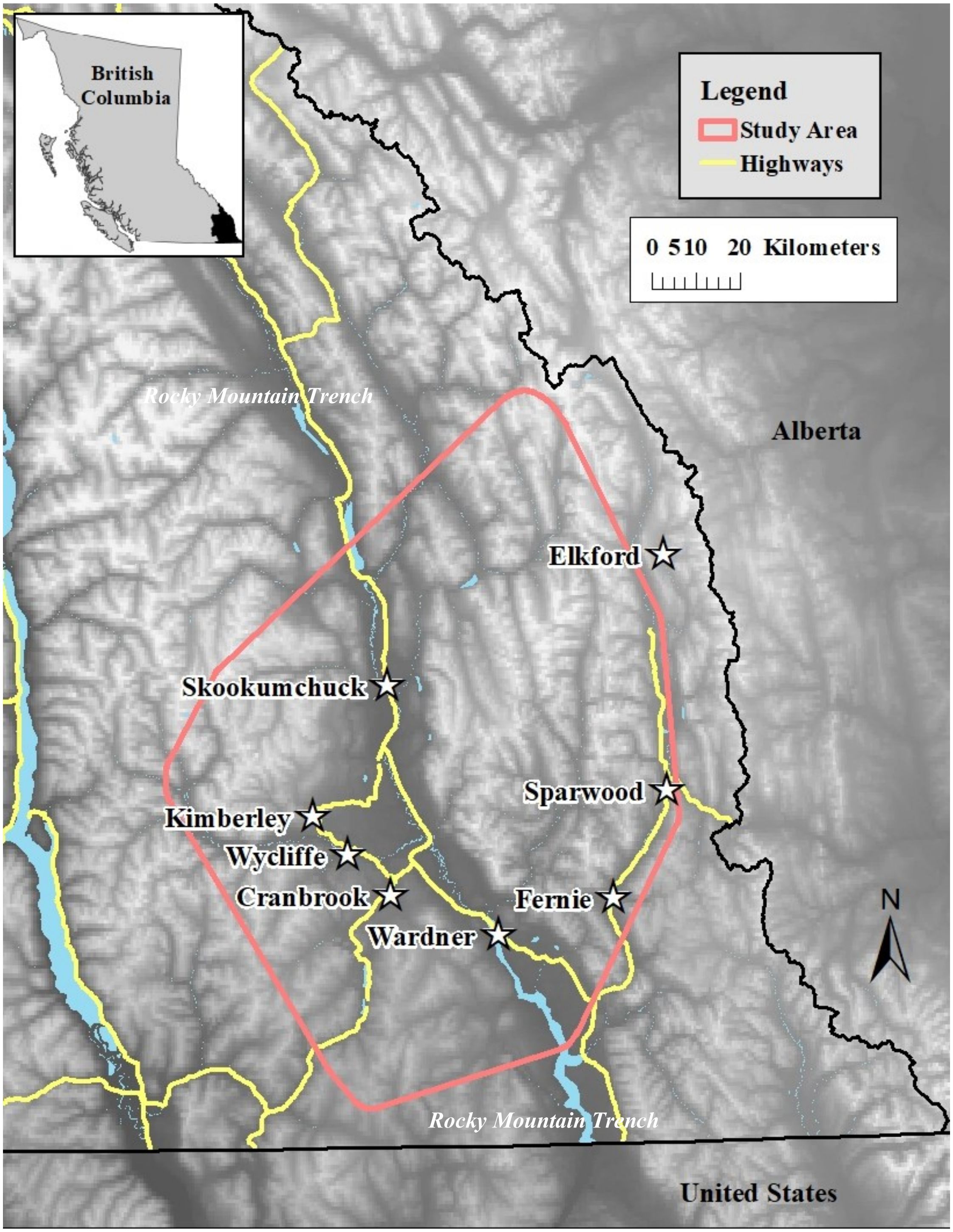

Figure 1-1 The southern Rocky Mountain Trench (RMT) in southeastern British Columbia, Canada. The coral colour indicates the study area, a 100% minimum convex polygon with five-km buffer derived from summer (1 May to 15 November) cow elk telemetry locations between 1987 and 2018.

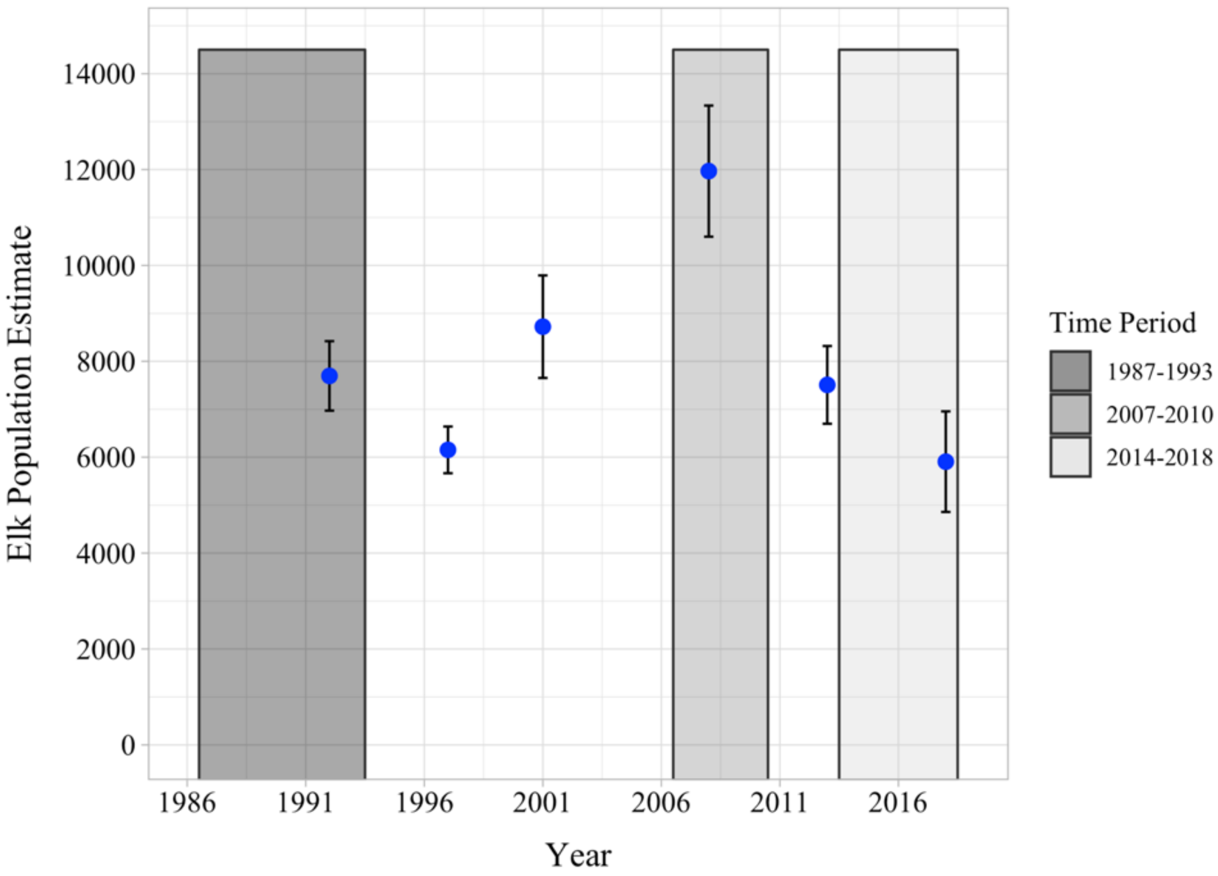

Figure 1-2 Winter elk population estimates with 95% confidence determined through stratified random block aerial surveys in the southern Rocky Mountain Trench, British Columbia, Canada. Shaded areas indicate the three periods (1987–1993, 2007–2010, 2014–2018) with elk telemetry data.

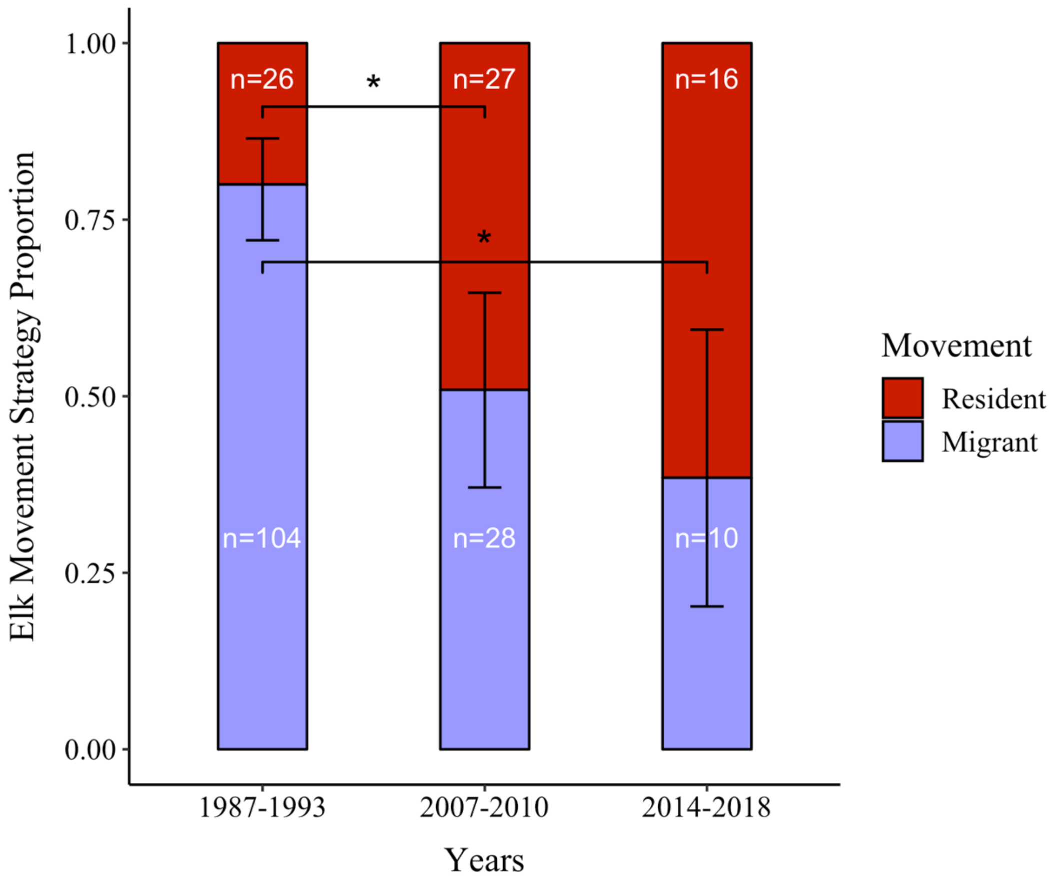

Figure 1-3 The proportion and sample sizes of collared migrant and resident elk in the southern Rocky Mountain Trench, British Columbia, Canada, during three periods (1987–1993, 2007–2010, and 2014–2018) with 95% binomial confidence intervals indicated. A chi-square test followed by pairwise Z-tests with Holm adjustments were used to determine differences between the number of migrant elk between each period (chi-square, $\chi^2 = 26.07$, df = 2, $P < 0.001$) with "*" indicating significant pairings ($P_{\text{87-93 to 07-10}} < 0.001$, $P_{\text{07-10 to 14-18}} = 0.660$, $P_{\text{87-93 to 14-18}} <$ 0.001).

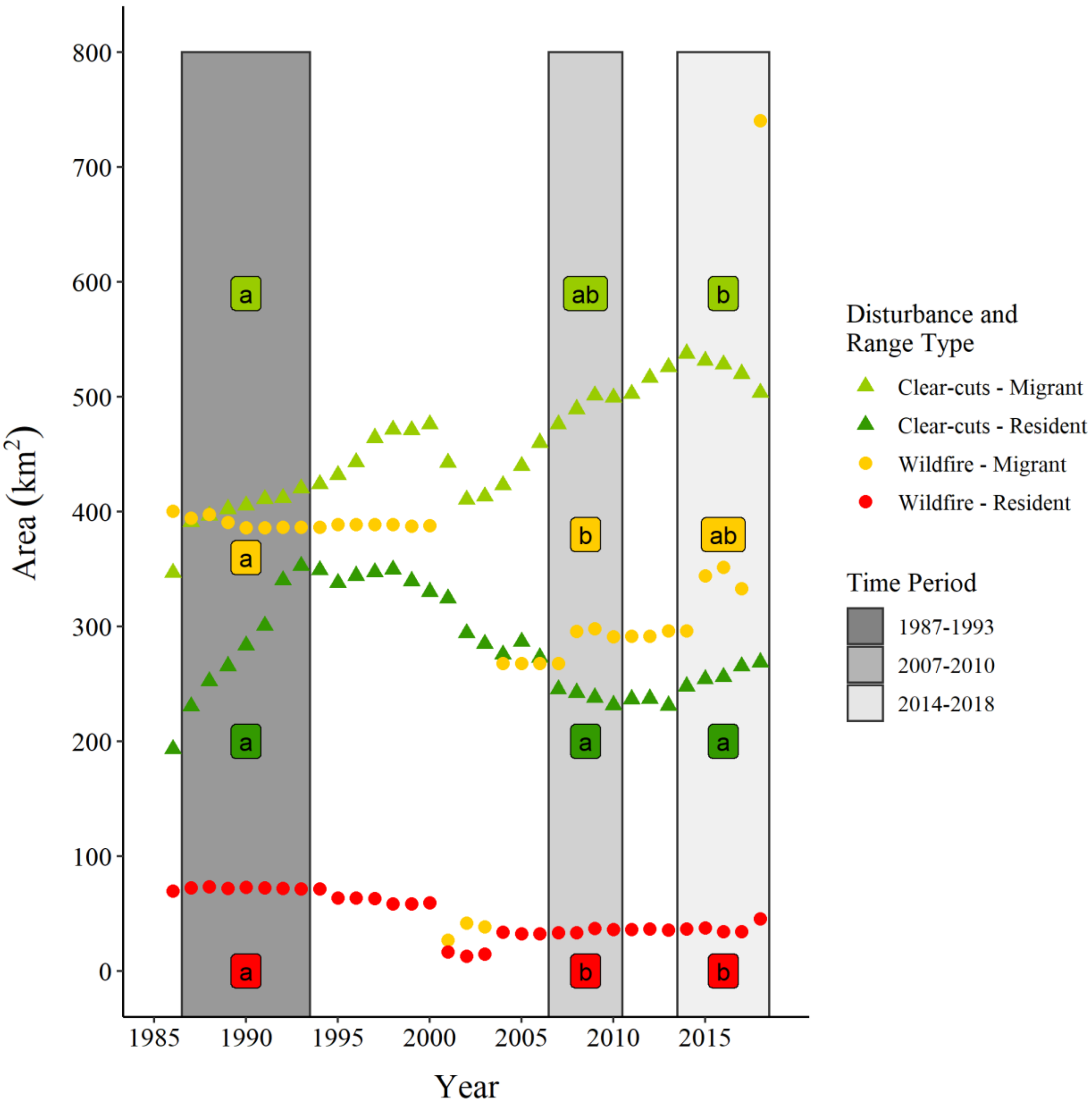

Figure 1-4 Annual total area (km^2) of early seral (1–15 year old) clear-cuts and wildfire between 1986 and 2018 within the 100% minimum convex polygon of elk summer ranges in the southern Rocky Mountain Trench, British Columbia, Canada. The area of disturbance was classified as occurring on migrant versus resident range based on a 1,200 m elevation threshold. Kruskal-Wallis and Dunn-Bonferroni post-hoc tests were conducted for each disturbance and range combination with compact letter indicating significance between groups. Shaded areas indicate three periods (1987–1993, 2007–2010, and 2014–2018) with elk telemetry data.

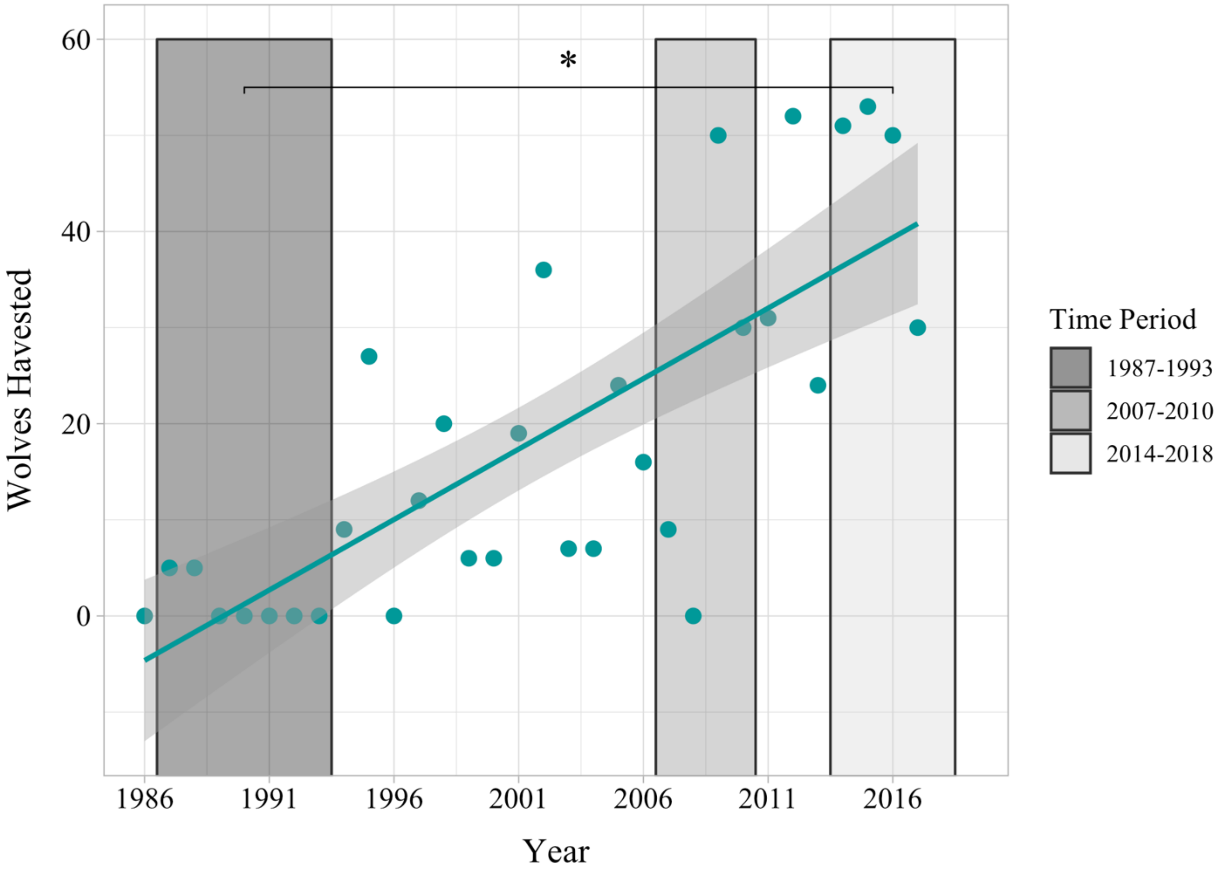

Figure 1-5 Total number of male and female wolves harvested by resident and non-resident hunters in wildlife management units 4-02, 4-03, 4-04, 4-05, 4-20, 4-21, 4-22, and 4-24 within the southern Rocky Mountain Trench, British Columbia, Canada. Number of wolves harvested per year increased between 1987 and 2017 ($r^2 = 0.57$, n = 32, $P < 0.001$) and differed between periods (Kruskal-Wallis, H = 7.63, df = 2, $P = 0.020$), significantly increasing, denoted by "*", between 1987–1993 and 2014–2016 (Dunn-Bonferroni, $P = 0.011$). Shaded areas indicate three periods (1987–1993, 2007–2010, and 2014–2018) with elk telemetry data.

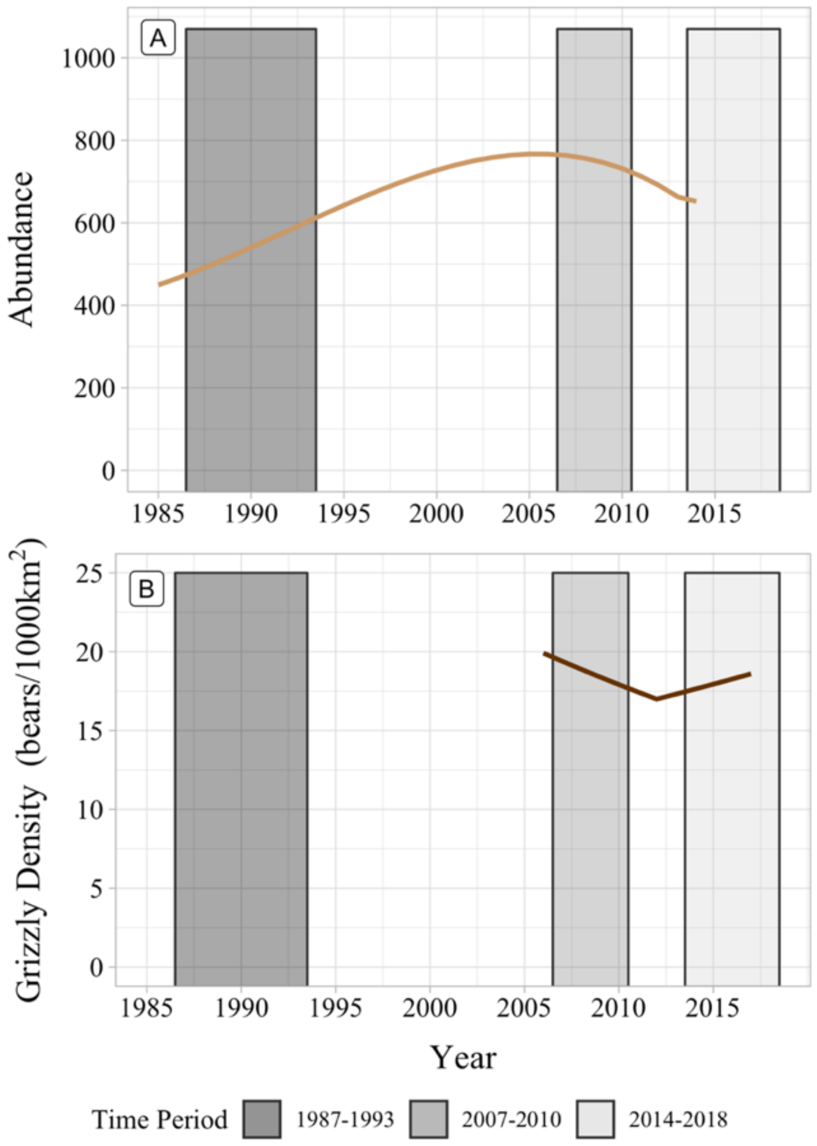

Figure 1-6 Grizzly bear A) population estimates between 1985 and 2014 fitted with a third order polynomial regression of male grizzlies ≥ 3 years of age in British Columbia's Temperate Mountains (Hatter et al. 2018) and B) density/1,000 km^2 estimates between 2006 and 2017 in the southern Rocky Mountains (Lamb et al. 2019). Grizzly bear abundance increased significantly between 1987–1993 to 2007–2010 (Wilcoxon rank sum, U = 0, *P* = 0.006), but grizzly bear density remained consistent between 2007–2010 and 2014–2018 (Wilcoxon rank sum, U = 12, *P* = 0.340). Shaded areas indicate three periods (1987–1993, 2007–2010, and 2014–2018) with elk telemetry data.

Chapter 2 - Migrant and resident elk (*Cervus canadensis*) habitat selection and long-term changes in habitat in the southern Rocky Mountain Trench, British Columbia

INTRODUCTION

Partial migration, where a portion of a population migrates, is thought to be maintained by density-dependent fitness balancing where individual vital rates are influenced by trade-offs associated with variable migratory tactics (Kaitala et al. 1993, Berg et al. 2019). For example, the associated benefits of increased access to forage may be offset with elevated predation risk (Chapman et al. 2011, Hebblewhite and Merrill 2011). Understanding migratory trade-offs has become increasingly important in recent years as there has been a global decline in ungulate migratory behavior (Harris et al. 2009, Berg et al. 2019).

Ungulate migratory decline has occurred in many species across western North America, coinciding with wolf (*Canis lupus*) recovery and dynamic disturbances on the landscape altering forage availability (Bunnefeld et al. 2011, Middleton et al. 2013, Sawyer et al. 2016). Two major influences on landscape conditions in the Rocky Mountains that may have altered the portion of migrant individuals in a population include habitat disturbances and recovery of large carnivores (Mao et al. 2005, Hebblewhite et al. 2006, Proffitt et al. 2016). Although disturbances such as wildfire and clear-cuts increase forage availability for species such as elk (*Cervus canadensis*) (Holroyd and Van Tighem 1983, Canon et al. 1987, Raynor et al. 2016), the impact of disturbances on elk selection is unclear as these disturbances can bring individuals closer to human activity and increase predation risk (Lyon and Jensen 1980, Hebblewhite et al. 2009, Mathisen 2018, Wisdom et al. 2018). Elk may select for clear-cut or burned areas to access better foraging opportunities but may also avoid these areas due to increased predation risk by wolves and close proximity to active logging (Lyon and Jensen 1980, Hebblewhite et al. 2009). In addition, although elk may avoid human activity directly, they may also use humans as a refuge from predators, also known as the human shield effect (Theuerkauf et al. 2003, Berger 2007). Although it is difficult to elucidate the effects of disturbance, human use, and predation risk on ungulate migratory patterns, further understanding of how disturbances affect selection of migrant and resident elk can help identify causes of ungulate migratory decline.

An area where there has been growing concern for the loss of elk migratory behavior is in the southern Rocky Mountain Trench (RMT) in British Columbia, Canada (Phillips and Szkorupa 2011). Elk within this region historically exhibited an altitudinal migration following the summer green-up to higher elevations, but more recently the proportion of elk migrating has decreased, resulting in increasing elk use of human dominated areas at low elevations (Phillips and Szkorupa 2011, Poole 2017). In the same period, large predators returned to the landscape, major changes to the extent of natural and human-caused disturbances occurred, and a targeted resident harvest was implemented, all of which have likely influenced elk migratory patterns (Chapter 1). Southern RMT elk populations have fluctuated over time increasing by 55% between 1991/1992 and 2007/2008 followed by a 51% decrease between 2007/2008 and 2017/2018 with the proportion of migrant elk decreasing during this period (Chapter 1). Wolves in this region were nearly extirpated in the 1960s due to bounty hunting and organized predator control, but have been recovering since the mid-1990s (Mowat 2007). Irrigated agricultural areas were widely available at low elevations in the 1990s, but large-scale fencing has reduced elk access to these areas by ~30% since 2006 (Chapter 1). Although irrigated crops provide high quality forage, elk migratory behavior is also influenced by the availability of other forage such as early seral habitat created by wildfires and clear-cuts (Barker et al. 2019*a*). Wildfire suppression has increased in the area since the 1920s, resulting in denser forests and reduced quantities of elk forage (Ross and Wikeem 2002, Forest Practices Board 2016). In contrast, clear-cutting has increased, creating open habitat with increased forage biomass (Chapter 1). Determining how migrant and resident elk select these disturbances, as well as the effects these disturbances have on southern RMT elk habitat suitability is unknown.

Here we use data from collared cow elk across three time periods (1987–1993, 2007–2010, 2014–2018) to determine how migrant and resident elk select for disturbances such as clear-cuts, wildfire, and paved roads, a metric for human activity. We also compare strength of selection of each disturbance relative to one another within each migration strategy. Finally, we determine trends in habitat suitability on migrant and resident ranges from 1987 to 2018 by calculating annual mean selection values and comparing these trends to the ratio of migrant to resident elk over time.

First, we hypothesize the effect of disturbances such as wildfire and clear-cuts on migrant and resident elk selection. Migrant and resident elk might select foraging areas of high-biomass, because nutrition in summer is vital for elk to recoup body fat losses from winter and lactation (Cook et al. 2004, Shallow et al. 2015). Under this hypothesis we predict both migrant and resident elk would select for herb-shrub landcover and for recent open-canopy disturbances, such as clear-cutting and wildfire, to access increased plant diversity and palatable plant biomass (Van Dyke and Darragh 2007, Long et al. 2008, Lord and Kielland 2015, Proffitt et al. 2019). We also predicted migrant elk would select for areas of lower solar radiation because plant productivity in this relatively arid environment is related to soil moisture (MacKillop et al. 2018); in particular, we expected the effect would be greater for migrants than residents because of the diversity of topographic conditions at high elevation. Alternatively, migrant and resident elk may avoid burns and clear-cuts due to increased predation risk or avoidance of human-activity. Under this hypothesis we predict elk would avoid open habitats such as clear-cuts and burns.

Second, we hypothesize the effect of roads on migrant and resident elk selection. Migrant and resident elk may avoid roads due to increased mortality risk associated with human-use (Creel et al. 2005, Mao et al. 2005, Frair et al. 2008). Alternatively, elk may select for areas near roads due to the human shield effect (Berger 2007, Chapter 1), in particular for resident elk as paved roads were found only at low elevation resident range.

Finally, we hypothesized that migrant and resident habitat suitability trends would reflect changing migration trends. Given southern RMT elk migration has declined (Phillips and Szkorupa 2011), we predict migrant elk habitat suitability will decline, whereas resident habitat suitability will increase, particularly between 1987-1993 and 2007-2010 when both the population and number of resident elk increased. If we find no evidence of changes in migratory tactics associated with landscape changes, this suggests that other factors are at play such as predation.

METHODS

Study Area

We conducted our elk selection analysis in a 11,941 km^2 area located in the southeastern corner of British Columbia, Canada, which we respectively acknowledge as being within amakʔis Ktunaxa, the territory of the Ktunaxa Nation (Chapter 1: Figure 1.1). The area includes the southern Rocky Mountain Trench, a large valley running northwesterly from Montana, U.S.A. bounded by the Purcell Mountains and Rocky Mountains located to the west and east, respectively. The southern RMT ranges from 6 km to 20 km in width with elevation varying from 750 m to 3,000 m. Human settlement is concentrated at the valley bottom and includes the cities of Cranbrook (49°29’59”, 115°46’07”) and Kimberley (49°40’60”, 116°0’0”).

The study area is dry, with mean precipitation of 300 mm of rainfall and 120 cm of snowfall between 1987 and 2018, recorded at the Cranbrook Airport (Environment Canada 2019). Low elevations are dominated by ponderosa pine, Douglas-fir, bluebunch wheatgrass (*Pseudoroegneria spicata*), and big sagebrush (*Artemisia tridentata*) (MacKillop et al. 2018). Mid-elevations are dominated by white spruce (*Picea glauca*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), willows (*Salix* spp.), and sedges (*Carex* spp.) (MacKillop et al. 2018). In mid-elevations Douglas-fir, Idaho fescue (*Festuca idahoensis)*, rough fescue (*F. campestris*), spreading needlegrass (*Stipa richardsonii*), and Rocky Mountain fescue (*F. saximontana*) are dominant (MacKillop et al. 2018). High elevations are dominated by Engelmann spruce (*Picea engelmanni*) and subalpine fir with fescues covering avalanche slides (MacKillop et al. 2018).

Agriculture is present at lower elevations with some irrigated and fertilized fields increasing the abundance and quality of elk forage. To mitigate elk crop depredation, wildlife exclusion fencing has been increasing in the area since the early 2000s (Chapter 1). Cattle ranching is common in the area with elk and cattle often competing for the same open range. To decrease grazing pressure, an early fall antlerless hunt (closing before October 15th) in low elevation areas (< 1,100 m) was introduced in 2004, before being closed in 2012 (Wilson and Morley 2005; Phillips and Szkorupa 2011).

Disturbances on the landscape include clear-cut logging, wildfire, and roads. Clear-cutting is common in the southern RMT at both high and low elevations, increasing at high elevations over the past three decades (Chapter 1). Wildfires were common in ponderosa pine and Douglas-fir dominated forests in the 1800s and early 1900s, which maintained a mixture of grassland, open forest, and closed forest. Wildfire suppression has increased since the 1920s, resulting in denser forests and reduced quantity of elk and cattle forage on open range (Ross and Wikeem 2002, Forest Practices Board 2016). To restore grasslands and open forests, the Ecosystem Restoration Program of the Ministry of Forests, Lands, and Natural Resource Operations was introduced (Bond et al. 2013). This program is a multi-million-dollar collaboration of over 30 partners, highlighting the importance of range management in the region (Bond et al. 2013).

Predators in the area include grizzly bears (*Ursus arctos*), black bears (*U. americanus*), cougars (*Puma concolor*), wolves (*Canis lupus*), and coyotes (*C. latrans*). Ungulates other than elk include white tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), caribou (*Rangifer tarandus*), and mountain goat (*Oreamnos americanus*).

Elk Capture, Monitoring, and Migration Classification

Elk were captured in 1987–1993 near Wardner and Skookumchuck, and in the later years near Wycliffe (Chapter 1: Figure 1.1). Elk were captured using snares on the ground, corral traps, and net guns from helicopters. Capture protocols followed live animal capture guidelines approved during each period of work by a British Columbia Government Animal Care Committee (RIC 1998). Elk in 1987–1993 were collared with Lotek VHF collars (Lotek Engineering, Aurora, Ont., Canada) with mortality signal with locations recorded to the nearest 100 m resolution using fixed wing aircraft, weekly for low elevation elk and biweekly for high elevation elk. Elk were collared with Advanced Telemetry Systems G2000 GPS (Advanced Telemetry Systems Inc., Isanti, MN, U.S.A.) collars in 2007–2010 with a 9-hour fix rate, whereas elk in 2014–2018 were collared with VECTRONIC Lifecycle Pro GPS collars (VECTRONIC Aerospace GmbH, Berlin, Germany) with a 23-hour fix rate.

We assessed migratory behaviour for individual elk-years if $>$ 10 locations were available between 1 March and 31 November. We classified elk as migrants or residents using a combination of the Net Squared Displacement (NSD) method (Bunnefeld et al. 2011), post hoc rule-based classification, and visual confirmation. NSD models were fit using the *migrateR* package (Spitz et al. 2017), in Program R version 3.5.2 (R Core Team 2018). Elk were classified as residents if their summer range was $<$ 15 km from their winter range and they spent $<$ 30 days between 1 March and 30 November on distinct summer ranges.

We quantified elk resource selection values for each year elk telemetry data were available using three steps. First, we developed resource selection functions (RSFs) for migrant and resident elk independently at the scale of the individual home range by pooling elk locations across all collared elk within a migration class and using elk-year as a random effect. Top models for each migratory tactic were determined using the Akaike information criterion (AIC) (Burnham and Anderson 2004). Second, we applied the migrant and resident RSFs to predict habitat suitability to their respective summering areas. We distinguished migrant and resident elk summering areas using logistic regression based on mean elevation per elk-year, as described in Chapter 1 (Appendix 1.3). We used the resulting 1,200 m threshold to identify areas corresponding to migrant and resident ranges and eliminated non-habitat including high elevations ($>$ 2,400 m) and non-vegetated landcover. Third, we determined trends in habitat suitability by predicting selection values for migrant and resident summer ranges range based on existing conditions during each year elk were collared. We assessed the patterns in mean RSF values for migrant and resident range across time.

Resource Selection Functions

We developed two resource selection functions (Manly et al. 2002, Johnson et al. 2006) reflecting relative summer elk habitat selection for migrant and resident elk. We used a random effect for elk-year to account for variation in sample sizes and combined data from collared individuals within each migratory tactic across periods using a third order (home range) selection scale (Johnson 1980). Using data across periods, we assumed selection remained constant at the home-range scale and landscape predictions reflected changing availabilities over time. Summer was defined as 1 May to 15 November, when 50% of all migrant elk left and subsequently returned to their winter range as described in Chapter 1 (Appendix 1.2). We employed a use vs. available design, where used locations came from individual VHF or GPS-collared animals and available points were generated at a density of 10 points per km^2 (Hebblewhite et al. 2008, Denny et al. 2018) within each individual's summer home range. We chose the most parsimonious model for each separate migratory tactic determined using the Akaike information criterion (AIC); models within ΔAIC ≤ 2 were considered competitive (Burnham and Anderson 2004).

Migrant and Resident Ranges

We consider very high elevations (> 2,400 m) and non-vegetated landcover as non-habitat and unavailable to elk. High elevation non-habitat was determined based on the drop in the distribution of elevations used by elk. We visually selected a threshold (2,400 m), above which the number of elk use locations across all years dropped below 50 based on 50 equal-sized distribution bins. Because non-vegetated landcover (*i.e.* water, snow/ice, rock/rubble, and exposed/barren land) changed annually, we created annual masks of non-habitat for each year elk were collared. We used the same elevational boundary as Chapter 1 (1,200 m) to separate migrant and resident elk range.

Long-Term Habitat Trends

We quantitatively assessed the change in habitat suitability of allopatric summer range of migrant and resident elk using the mean RSF values predicted from the respective top models of resource selection over time. We predicted RSF values of 30 m × 30 m pixels across the migrant and resident ranges and calculated the annual mean RSF value with 95% confidence intervals for all years elk were collared between 1987 and 2018. We created habitat maps for each year of predicted habitat values. To compare the same extent of migrant and resident range over time, any area classified as non-habitat over the study was removed before the mean annual RSF values were calculated. Temporal trends in mean RSF values for each tactic-specific range were plotted over time. The trends were then characterized using the β coefficient of a linear regression between the mean RSF value and year.

Environmental Covariates

Environmental factors were represented by open-canopied and treed landcover types, disturbances, solar radiation, and distance to roads. Landcover covariates were derived from a time series of annual gap-free Landsat image (TM, EMT+, and OLI sensors) composites 30 m × 30 m resolution between 1984 and 2018 created for the forested areas of Canada (Hermosilla et al. 2018). Composites were created using the best pixels available based on data quality with gaps filled using temporarily smoothed proxy values (Hermosilla et al. 2018). To create disturbance informed landcover maps, information such as *a priori* knowledge of ecological succession, landcover transition likelihoods, and year on year class membership likelihoods were incorporated using a Hidden Markov Model (Hermosilla et al. 2018). A total of 12 landcover classes were identified, which Hermosilla et al. (2018) collapsed into non-vegetated (water, snow/ice, rock/rubble, and exposed/barren land), vegetated non-treed (bryoids, herbs, wetland, and shrubs), and treed vegetation (wetland-treed, coniferous, broadleaf, and mixedwood). We renamed the “vegetated non-treed” category to “herb/shrub” for the remainder of the analysis. Within the time series, validation was conducted for the 2005 landcover map using high spatial resolution satellite images and an interpreter, resulting in an accuracy of 83% (± 2%) using the collapsed classes (Hermosilla et al. 2018).

For inputs into candidate RSFs, we used landcover types collapsed into non-vegetated, herb-shrub, and treed, as done in Hermosilla et al. (2018). In particular, irrigated agriculture was not included directly in our land cover evaluation as the availability was limited for both collared migrant and resident elk; instead, irrigated agriculture fell within the herb-shrub land cover type. Proportion of the three landcover types were derived within a 90 m × 90 m buffer around each use and available location. Other land cover types included clear-cuts and wildfires 1–15 years of age, which were both derived from provincial GIS layers (Ministry of FLNRORD, 2019*a,b*), and integrated into the annual landcover layers. Clear-cuts were integrated first, followed by wildfire.

A solar radiation index was created using slope, aspect, and latitude (Dicus n.d., Keating et al. 2007). Solar radiation index values range from -1 to 1, with higher values indicating increased solar radiation and drier sites. Elevation was also included as a covariate, which was derived from the NASA Shuttle Radar Topography Mission. Finally, human activity was represented by paved roads that included major highways and secondary roads, but not gravel or unmaintained roads. The road layers were available from the regional government for 2005 and 2017, representing 2007–2010 and 2014–2018, respectively. To represent 1987–1993, a 1991 road layer was created using a combination of Landsat imagery and manual removal of paved roads from the 2005 layer in ArcGIS (ArcGIS Desktop version 10.7.1). In this process we assumed little deactivation of the paved roads in 2005. We did not include forestry roads due to insufficient Landsat imagery resolution. To incorporate a decay effect with increasing distance, distance to nearest road was calculated for each layer (1991, 2005, and 2017) and transformed with a natural logarithm of the distance +1, hereafter called *RoadDec* (Prokopenko et al. 2017).

Covariates were tested for collinearity using Pearson’s correlation coefficient and were not included in the same model if $| r | > 0.65$. We applied a 90 m × 90 m buffer to account for location error to all covariates except *RoadDec*, which was already transformed. All continuous covariates other than proportions of the landcover within a buffer were standardized by subtracting each value by the mean of all values across years then dividing by the standard deviation of all values across years.

RESULTS

Elk Capture and Migration Classification

Resource selection functions were derived using 170 elk-years of data from 91 collared adult cow elk. Forty-eight elk were used during 1987–1993 (76% migrants and 24% residents), 30 during 2007–2010 (53% migrants and 47% residents), and 13 during 2014–2018 (40% migrants and 60% residents). Although we used a subset of elk-years available due to limited telemetry locations, we found the same migratory trends as Chapter 1 (Appendix 1.1, Appendix 2.1). This subset of elk-years resulted in no individuals in 1993, therefore we did not predict selection for 1993. To be consistent “1987–1993” was used to describe the first period.

Resource Selection Functions

Because the proportion of herb-shrub and treed landcover in the 30 m × 30 m buffers around locations of both migrant and resident data were negatively correlated (Pearson's correlation, $r_{\text{mig}} = -0.77$, $r_{\text{res}} = -0.81$), we included only herb-shrub in candidate models; no other variables were correlated (Pearson's correlation, $|r| > 0.65$). Models with environmental variables were better supported than the null model for both migratory tactics (Appendix 2.2 and 2.3). The top two models for both migratory tactics included the same covariates (Table 2.1), where ΔAIC was ≤ 2. We chose the most parsimonious model for each tactic, which excluded solar radiation (Table 2.1).

Migrant elk selected for intermediate elevations within their range based on the positive coefficient for elevation and the negative coefficient for elevation squared, whereas resident elk selected for low-elevation areas within their ranges based on the negative sign of both elevation and elevation squared (Figure 2.1). Both migrant and resident elk selected for all three types of foraging areas. Resident elk selected more strongly for wildfires than either clear-cuts or herb-shrub land cover and migrant elk selected more strongly for clear-cuts and herb-shrub cover. However, selection was more variable among individuals for wildfires than the clear-cut and herb-shrub land cover types (Figure 2.1). Both migrant and resident elk selected for areas farther from roads (Figure 2.1).

Migrant and Resident Ranges

Given we used high elevation (> 2,400 m) and annual non-vegetation masks, area available on migrant and resident range varied annually. However, using the combined mask developed to compare predicted RSF values over time, we found resident range comprised 2,693 km^2 and migrant ranges comprised 6,151 km^2.

Environmental Change on Elk Ranges

Total area of herb-shrub significantly differed among our three periods on migrant range (Kruskal-Wallis, $H = 10.68$, $df = 2$, $P = 0.005$) and on resident range (Kruskal-Wallis, $H = 10.68$, $df = 2$, $P = 0.005$). Less area of herb-shrub was available to migrant elk in 2014–2018 ($\tilde{x} = 1{,}087$ km^2, $IQR = 27$) compared to 1987–1993 ($\tilde{x} = 1{,}396$ km^2, $IQR = 72$) (Dunn-Bonferonni, $P = 0.002$, Figure 2.2), whereas more area of herb-shrub was available to resident elk only in 2007–2010 ($\tilde{x} = 1{,}317$ km^2, $IQR = 20$) compared to 1987–1993 ($\tilde{x} = 1{,}231$ km^2, $IQR = 42$) (Dunn-Bonferonni, $P = 0.002$, Figure 2.2).

Total clear-cut area also significantly differed among our three periods on migrant range (Kruskal-Wallis, $H = 9.10$, $df = 2$, $P = 0.011$) and on resident range (Kruskal-Wallis, $H = 8.16$, $df = 2$, $P = 0.002$). More clear-cut area was available to migrants in 2007–2010 ($\tilde{x} = 351$ km^2, $IQR = 1$) compared to 1987–1993 ($\tilde{x} = 228$ km^2, $IQR = 14$) (Dunn-Bonferroni, $P = 0.006$, Figure 2.2). In contrast, residents had less areas of clear-cut available in 2014–2018 ($\tilde{x} = 189$ km^2, $IQR = 2$) compared to 1987–1993 ($\tilde{x} = 223$ km^2, $IQR = 38$) (Dunn-Bonferroni, $P = 0.007$, Figure 2.2).

Total area of wildfire also significantly differed among our three periods on migrant range (Kruskal-Wallis, $H = 9.76$, $df = 2$, $P = 0.008$ and on resident range (Kruskal-Wallis, $H = 9.10$, $df = 2$, $P = 0.011$). Migrants had more area of wildfire accessible in 2014–2018 ($\tilde{x} = 145$km^2, $IQR = 90$, Figure 2.2) compared to 1987–1993 ($\tilde{x} = 111$ km^2, $IQR = 9$) (Dunn-Bonferroni, $P = 0.003$), whereas residents had less wildfire area in 2007–2010 ($\tilde{x} = 19$ km^2, $IQR = 3$) compared to 1987–1993 ($\tilde{x} = 51$ km^2, $IQR = 1$) (Dunn-Bonferroni, $P = 0.006$).

Long-Term Habitat Trends

Mean annual RSF values declined over time for both migrant ($r^2 = 0.60$, $n = 13$, $P = 0.002$, Figure 2.3) and resident ($r^2 = 0.77$, $n = 13$, $P < 0.001$, Figure 2.3) ranges, with the overall rate of decline being greater for migrant (β = -1.30e^{-4}, *SE* = 3.22e^{-6}, Figure 2.3) than resident (β = -1.01e^{-4}, *SE* = 1.67e^{-5}, Figure 2.3) elk. The most rapid declines in RSF values on migrant ranges occurred within 1987–1993 and 2014–2016. RSF values for resident range initially increased within 1987–1993, but declined within 2007–2010, while remaining relatively consistent within 2014–2018. Predicted maps of habitat for each year allowed for visualization of declining habitat suitability on both ranges (Appendix 2.4), particularly when comparing 1987 habitat suitability to 2018 (Figure 2.4).

DISCUSSION

We used changes in selection value based on key factors such as clear-cuts, wildfire, herb-shrub landcover, and paved roads to indicate changes in range suitability of migrant and resident elk in the southern RMT between 1987 and 2018. We did not find that habitat suitability trends reflected migration trends because the proportion of resident elk increased with decreasing habitat suitability. Although these results highlight that additional factors such as predation are missing from our analysis, the more rapid decline in habitat suitability on migrant range than resident range is consistent with the shifting proportion of migrant to resident elk.

Declines in habitat suitability for both migrant and resident ranges were primarily related to changes in foraging areas. Both migrant and resident elk selected for areas of high forage such as clear-cuts, wildfires, and herb-shrub landcover. Although southern RMT elk selection of disturbances, such as clear-cutting and wildfire, was consistent with other elk selection studies (Lyon and Jensen 1980, Collins and Urness 1983, Heinen and Currey 2000, Hebblewhite et al. 2006, Proffitt et al. 2019, Smolko et al. In Review), the strength of selection between disturbances was not expected. Migrant elk selected clear-cuts more than areas with recent wildfire, contrary to findings from Davis (1977) where elk residing at high elevations were recorded to use burns more than clear-cuts. It is likely that the extent of these areas in the landscape and quantity of standing timber are affecting selection by both migrant and resident elk (Pearson et al. 1995, Franklin et al. 2019, Smolko et al. In Review). Weak selection for wildfire by migrants may be due to greater availability on migrant range in contrast to that of residents (Figure 2.2). Selection may not be as strong with increased availability (Smolko et al. In Review). Quantity of standing timber is particularly important for ungulate species to reduce predation risk, with increased quantity of standing timber enhancing the probability of occupation by ungulate species (Davis 1977, Fisher and Wilkinson 2005). Determining how elk select disturbances in response to altered availabilities and configurations could provide further insight into trade-offs associated with migrant and resident movement strategies.

Consistent with selection for foraging areas created by forest disturbances, both migrant and resident elk selected herb-shrub landcover. On migrant range, the area of herb-shrub habitat declined over time, consistent with declining elk habitat suitability trends. The decline in herb-shrub habitat on migrant range was likely due to forest succession (Ross and Wikeem 2002, Forest Practices Board 2016). In contrast, increases in the area of herb-shrub habitat on resident range was inconsistent with declines in resident habitat suitability, suggesting other variables, such as declining wildfire, may be driving trends in resident habitat suitability. Given the strong positive selection for wildfire by resident elk, we expected stronger selection for herb-shrub habitat given it included disturbances that should be selected for by elk such as fenced and unfenced agricultural lands and ecosystem restoration. Ecosystem restoration is conducted to improve range condition and explicitly takes into consideration forage response as well as amount of cover (Bond et al. 2013). Within the current study, we could not isolate selection for agricultural and ecosystem restoration areas because only 85% of the resident elk had access to agriculture on their summer home ranges and ecosystem restoration was not present in the earliest period, therefore these categories were combined with open herb-shrub habitat. It is possible the herb-shrub landcover type on resident range was not selected as strongly as expected due to inclusion of inaccessible fenced agriculture, which increased from 0 km^2 to 21 km^2 between 1987–1993 and 2014–2018 (Chapter 1). On the other hand, ecosystem restoration increased across the study as the program was introduced in 2006, and likely increased resident herb-shrub positive selection, buffering the impact of inclusion of fenced agriculture. The positive effect of ecosystem restoration on elk habitat is reflected in the increased area of herb-shrub habitat on the resident range across the study.

In addition to forage biomass, we found evidence that human use across the landscape may influence elk selection of migratory tactics by elk directly avoiding areas near major roads (Wisdom et al. 2018, Prokopenko et al. 2017). Although these results do not support the human shield effect, we do not rule this hypothesis out as elk may avoid human activities associated with roads at a local scale but use areas of high human activity at a larger scale to avoid wolf predation (Rogala et al. 2011).

These results suggest habitat conditions may be contributing to shifting migratory patterns, but other additional non-habitat factors may also contribute. We have argued that predation and human harvest have had an effect on the elk population in the southern RMT during the study period (Chapter 1). Here we argue elk residency between 1987–1993 and 2007–2010 is not explained by the decreasing resident habitat suitability, but rather follows a pattern consistent with the human refuge effect where elk residency decreases predation risk by use of low elevation human dominated areas which exclude predators. This effect continues into 2014–

2018 as the proportion of residents remains high in this period, with the low number of resident elk in 2014–2018 likely the result of high harvest of resident elk between 2004 to 2012 (Appendix 2.5). Although decreased elk migration has caused crop depredation (Phillips and Szkorupa 2011), low population estimates are also cause for concern. The positive selection of clear-cuts, wildfire, and herb-shrub landcover highlights the importance of open habitat for both migrant and resident elk, suggesting a potential mechanism to increase elk abundance. As for altered migration patterns across the landscape, these results highlight the complexity of managing predator-prey dynamics in the face of human activity on the landscape (Creel et al. 2005). Increased knowledge of predator use across migrant and resident range, particularly the role of human refuges on elk survival, would help further elucidate the causes of southern RMT elk migratory decline. These results suggest habitat conditions may be contributing to shifts in migratory patterns, but other non-habitat factors such as predation may also contribute.

MANAGEMENT IMPLICATIONS

Our study provides habitat selection maps to wildlife managers for land-use planning, providing a better understanding of how landscape features such as wildfire, clear-cuts, and roads influence elk selection and how elk habitat quality has changed between 1987 and 2018. We found both migrant and resident elk selected for herb/shrub areas and early seral (1–15 years) clear-cuts and wildfire, which highlights the importance of open habitat for elk. In order to increase the proportion of migrant elk, we recommend that managers open forest canopies on migrant elk range. Although canopy-opening disturbances on migrant range such as clear-cuts and wildfire might increase the proportion of migrants, we suggest assessment of resident elk selection of ecosystem restored areas, which are targeted specifically to increase ungulate habitat condition.

Although direct hunter harvest of resident elk between 2004 and 2014 did not increase the proportion of migratory elk between 2007–2010 and 2014–2018, resident elk may have increased use of human dominated areas post wolf-recovery, masking the effects of the resident elk harvest on the migrant to resident ratio. In order to further elucidate the effectiveness of the resident elk harvest we suggest additional assessment of the human shield hypothesis, such as resident elk habitat selection of roads interacted with distance. Resident elk may avoid roads directly but use intermediate distances from roads to reduce predation risk. If resident elk do use human-populated areas or man-made features as a human shield, it is possible that targeted resident harvest may have buffered elk migratory decline. Further understanding of elk selection of open-canopy habitats, response to wolf recovery, and the use of a human shield is key to understanding and managing elk populations.

Table 2-1 Summary of model selection results for migrant elk (n = 62) and resident elk (n = 108) in the southern Rocky Mountain Trench, British Columbia, Canada, indicated number of parameters (k), Akaike information criterion (AIC), change in AIC (ΔAIC), model weight (w_i) and log likelihood (LL). Models included a random effect for each elk-year (1| elk-year). Annual metrics considered for landcover include herb-shrub (HrbShr), clear-cuts (Clear-cut), wildfire (Wildfire), and tree (Tree) as the reference. Topographic metrics include solar radiation (SolRad) and elevation (Elev). Paved roads distance decay (RoadDec) represents an urban metric.

Model	**Model variables**	**k**	**AIC**	**ΔAIC**	w_i	**LL**
Migrant elk						
23	HrbShr + Clear-cut + Wildfire + Elev – Elev^2 + RoadDec	8	86708.91	0.00	0.73	-43346.45
2	HrbShr + Clear-cut + Wildfire + Elev – Elev^2 + RoadDec - SolRad	9	86710.91	2.00	0.27	-43346.45
20	HrbShr + Clear-cut + Elev - Elev^2 + RoadDec	7	86723.87	14.96	0.00	-43354.93
12	HrbShr + Clear-cut + Wildfire + Elev - Elev^2	7	86738.06	29.16	0.00	-43362.03
24	HrbShr + Clear-cut + Wildfire + Elev + RoadDec	7	86789.05	80.14	0.00	-43387.52
16	HrbShr + Clear-cut + Wildfire + RoadDec	6	86868.74	159.84	0.00	-43428.37
21	HrbShr + Wildfire + Elev - Elev^2 + RoadDec	7	88646.86	1937.95	0.00	-44316.43
22	Clear-cut + Wildfire + Elev + Elev^2 + RoadDec	7	89224.92	2516.02	0.00	-44605.46
1	Null	2	90319.89	3610.99	0.00	-45157.95
Resident elk						
23	HrbShr + Clear-cut + Wildfire - Elev - Elev^2 + RoadDec	8	40354.66	0.00	0.67	-20169.33
2	HrbShr + Clear-cut + Wildfire - Elev - Elev^2 + RoadDec + SolRad	9	40356.08	1.42	0.33	-20169.04
24	HrbShr + Clear-cut + Wildfire - Elev + RoadDec	7	40383.25	28.59	0.00	-20184.63
16	HrbShr + Clear-cut + Wildfire + RoadDec	6	40396.64	41.98	0.00	-20192.32
20	HrbShr + Clear-cut - Elev - Elev^2 + RoadDec	7	40406.23	51.57	0.00	-20196.11
12	HrbShr + Clear-cut + Wildfire - Elev - Elev^2	7	40506.04	151.38	0.00	-20246.02
21	HrbShr + Wildfire - Elev - Elev^2 + RoadDec	7	40722.05	367.39	0.00	-20354.02
22	Clear-cut + Wildfire - Elev - Elev^2 + RoadDec	7	40879.44	524.78	0.00	-20432.72
1	Null	2	41260.76	906.09	0.00	-20628.38

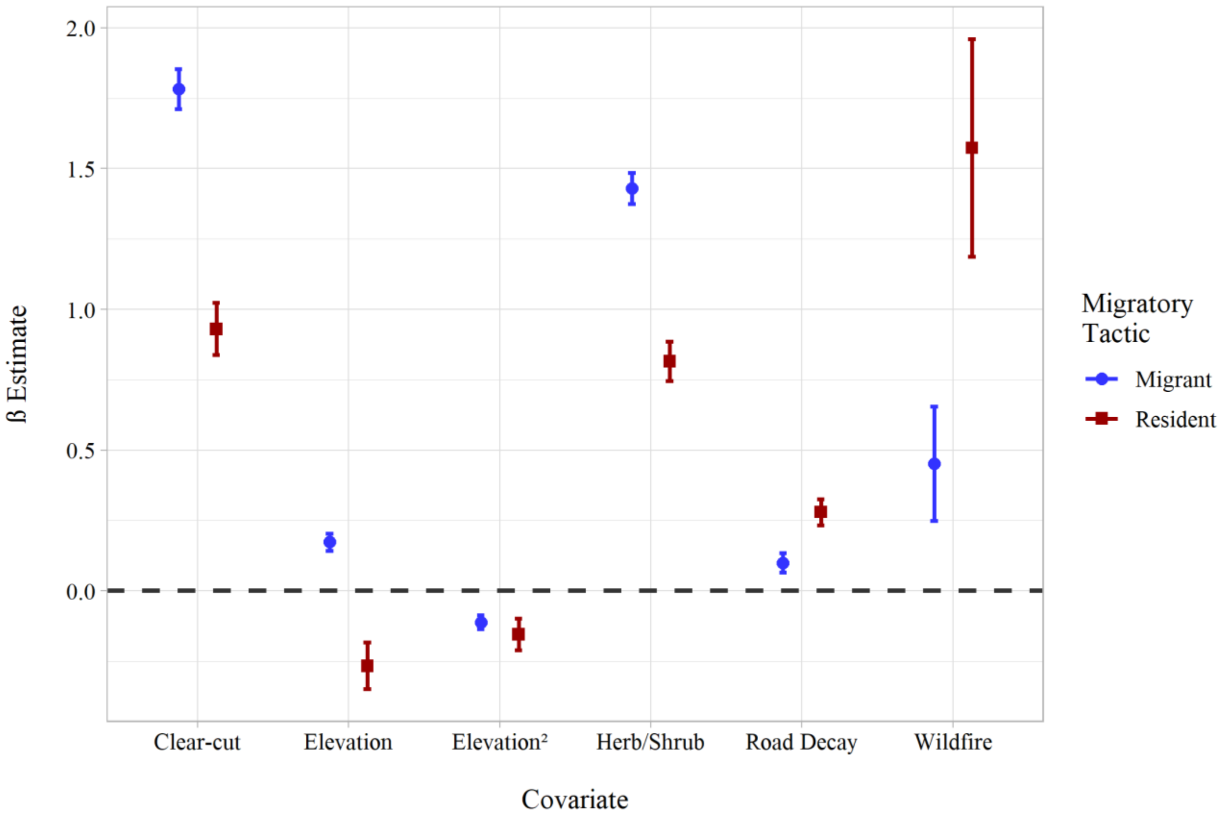

Figure 2-1 Magnitude of the standardized beta coefficient of the most supported exponential resource selection function model for migrant (blue circle) and resident (red square) elk selection relating to environmental variables in the southern Rocky Mountain Trench, British Columbia, Canada. Both models included a random effect for elk-year (1| elk-year). Paved roads distance decay (RoadDec) represents an urban metric.

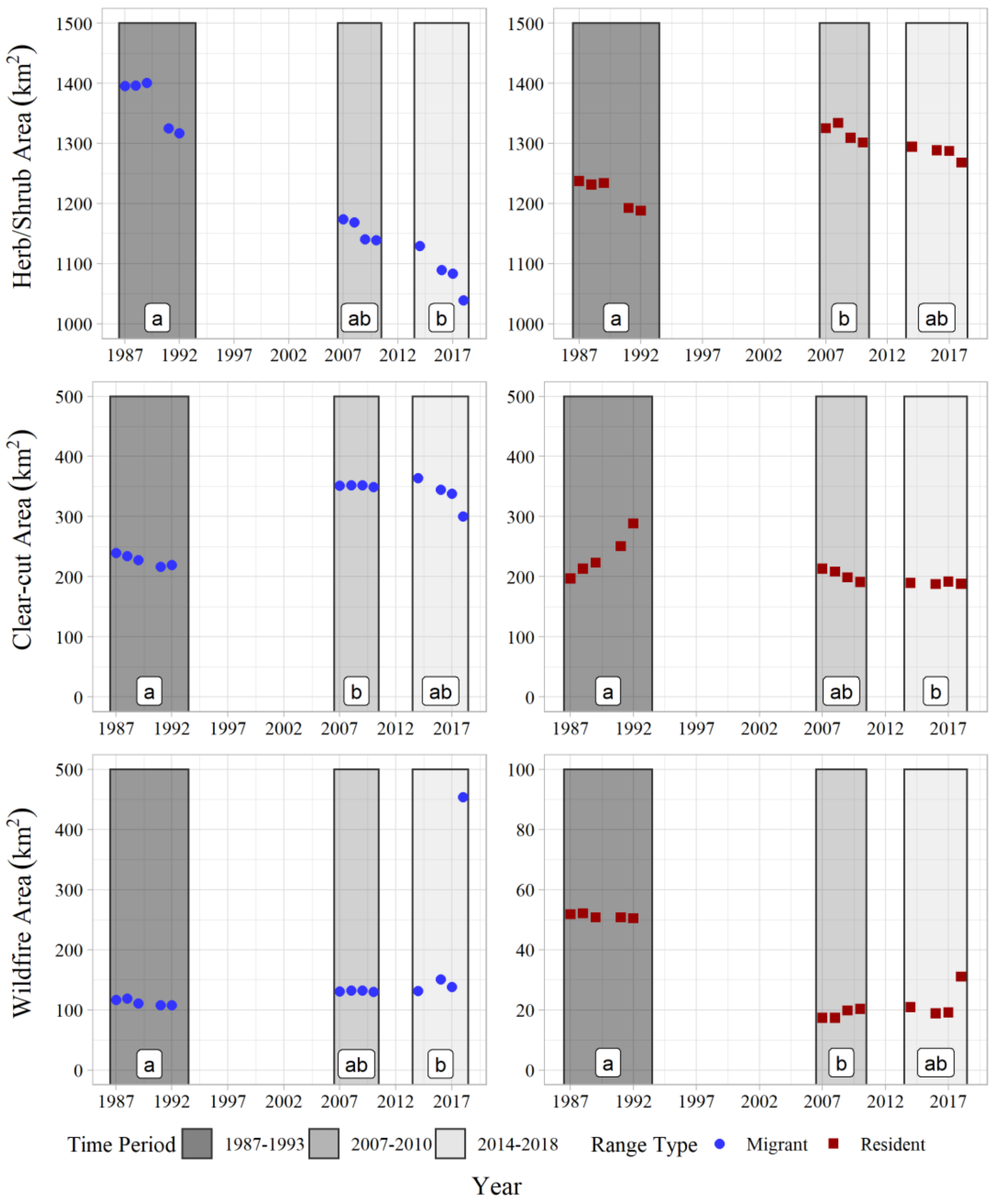

Figure 2-2 Annual total area (km^2) of herb-shrub, and early seral (1–15 year old) clear-cuts and wildfire between 1987 and 2018 on migrant (blue circle) and resident (red square) ranges in the southern Rocky Mountain Trench, British Columbia, Canada. All area above 2,400 m was considered non-habitat and removed from this analysis. Shaded areas indicate three periods (1987–1993, 2007–2010, and 2014–2018) for which there were elk telemetry data.

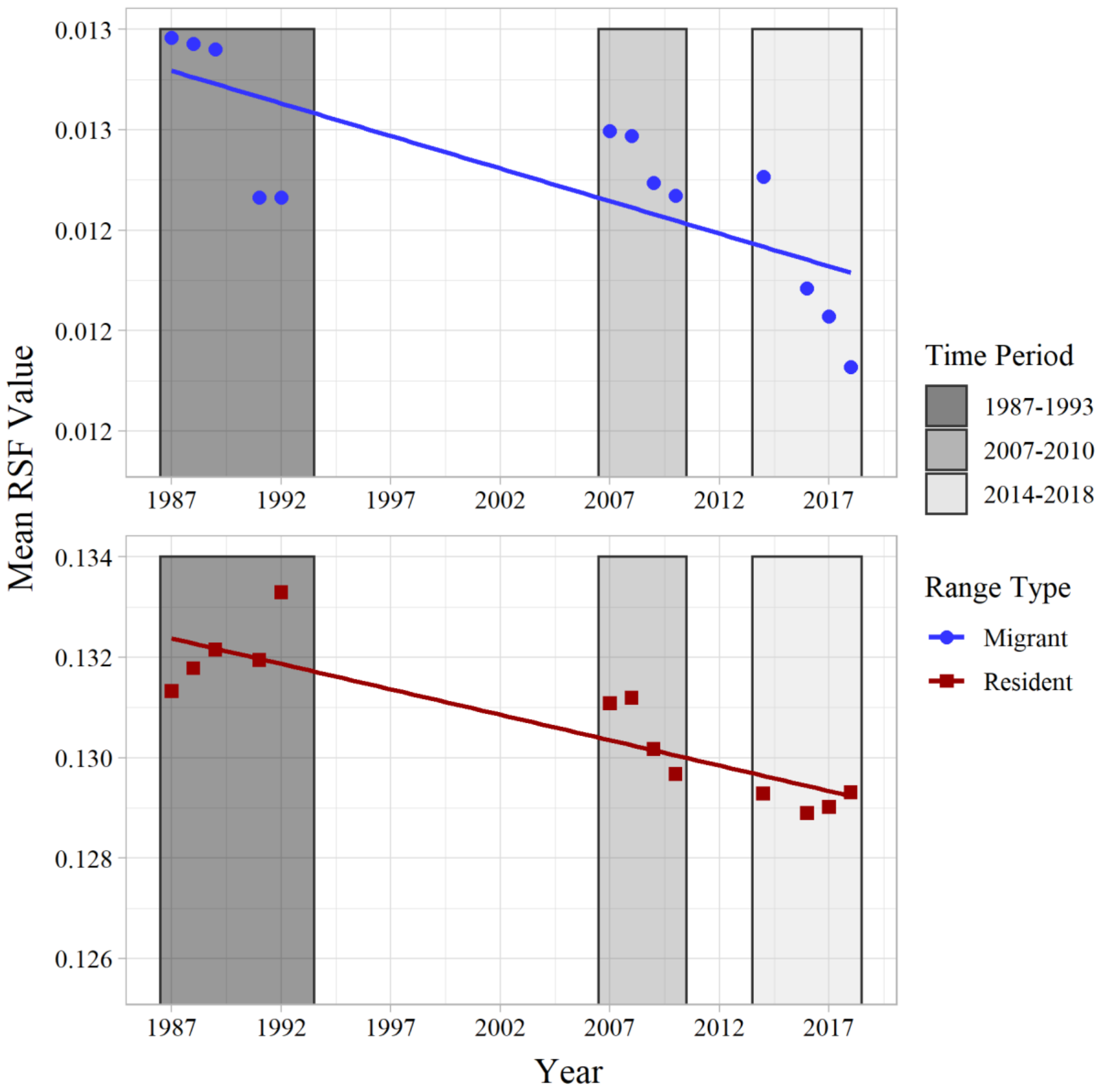

Figure 2-3 Trends over time in the mean resource selection function values on migrant (blue circle) and resident (red square) ranges in the southern Rocky Mountain Trench, British Columbia, Canada. Shaded areas indicate three periods (1987–1993, 2007–2010, and 2014–2018) for which there were elk telemetry data.

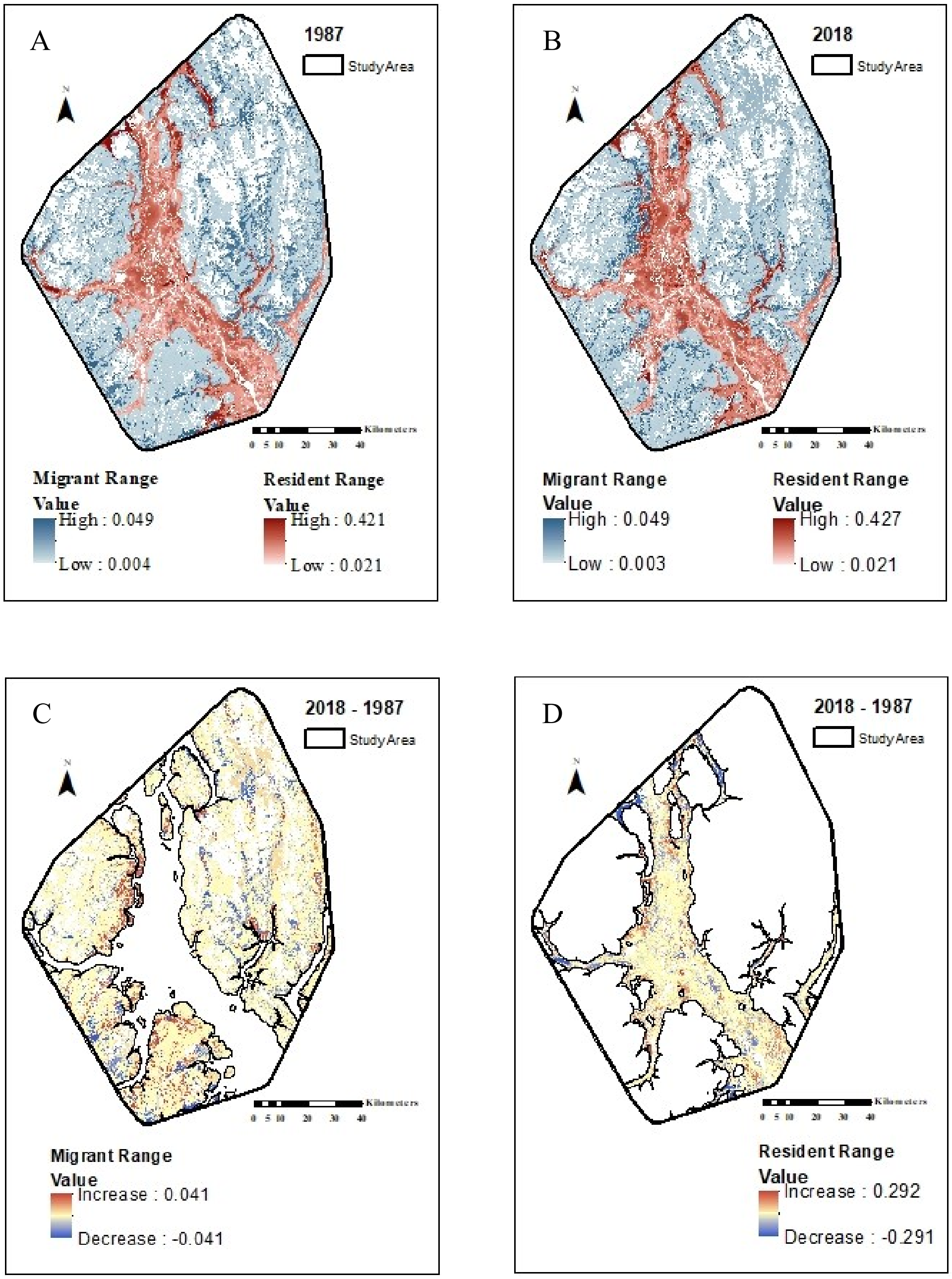

Figure 2-4 Maps of the southern Rocky Mountain Trench, British Columbia, Canada, migrant and resident elk range showing predicted values for summer elk migrant and resident resource selection functions (RSFs) for 1987 (A) and 2018 (B). RSF values from 1987 were subtracted from 2018, with areas of greatest increase and decrease in values on migrant (C) and resident (D) elk range depicted.

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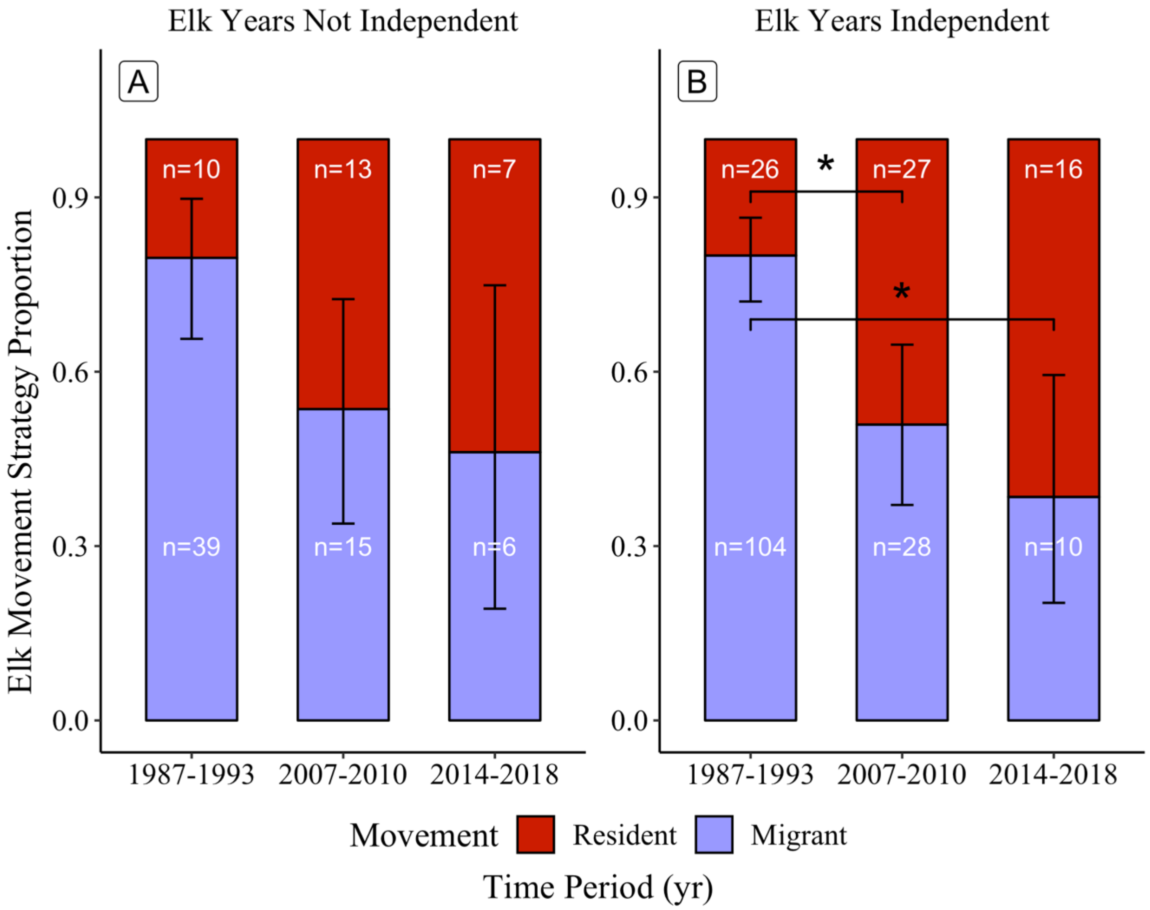
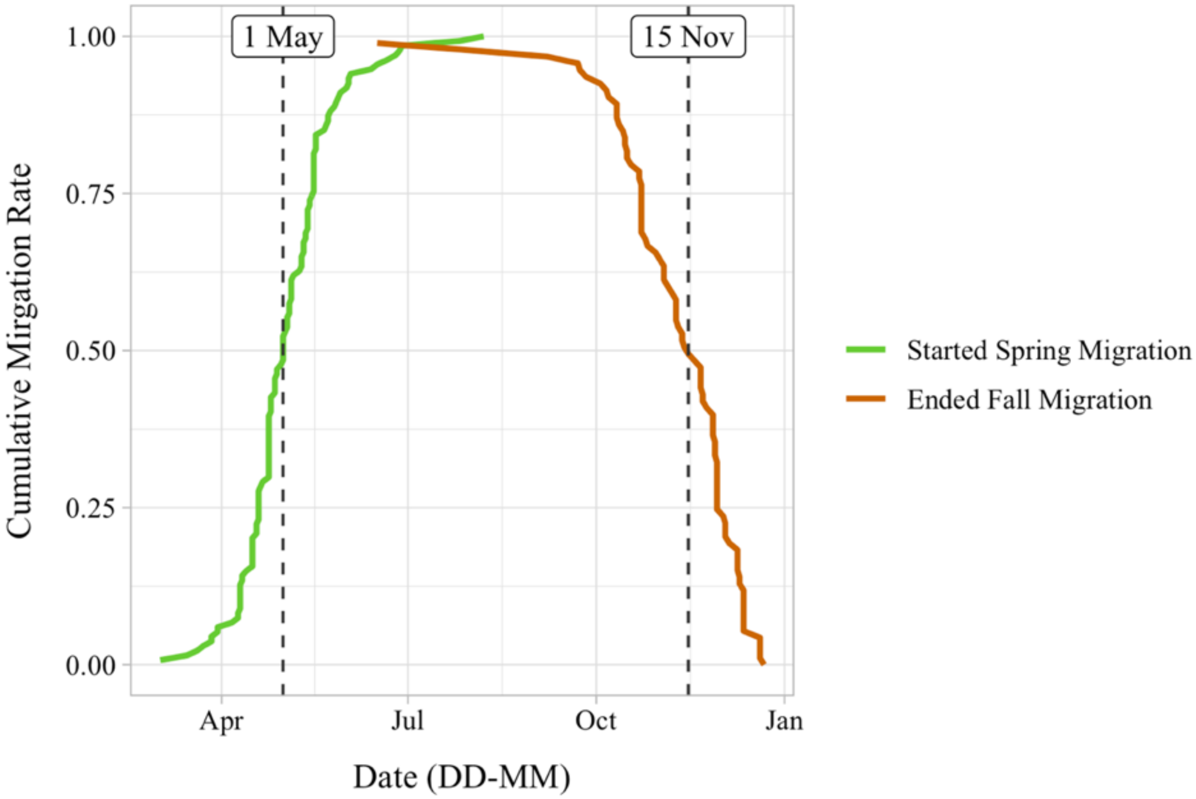
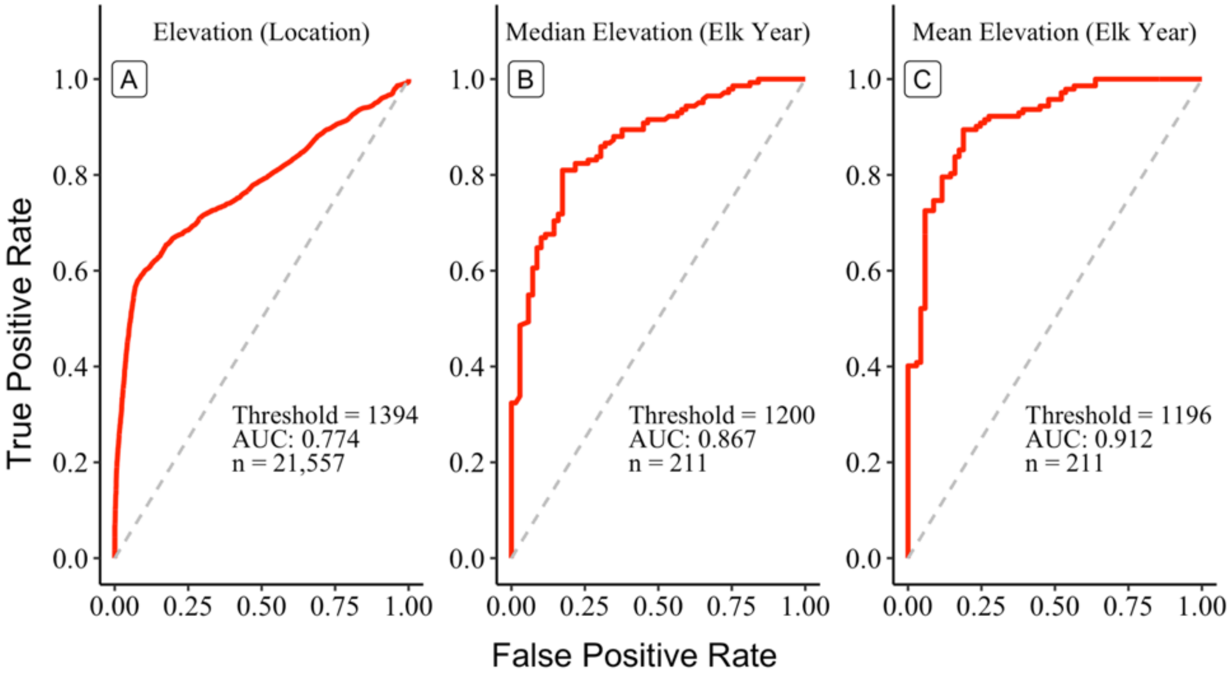
SUPPLEMENTARY MATERIAL



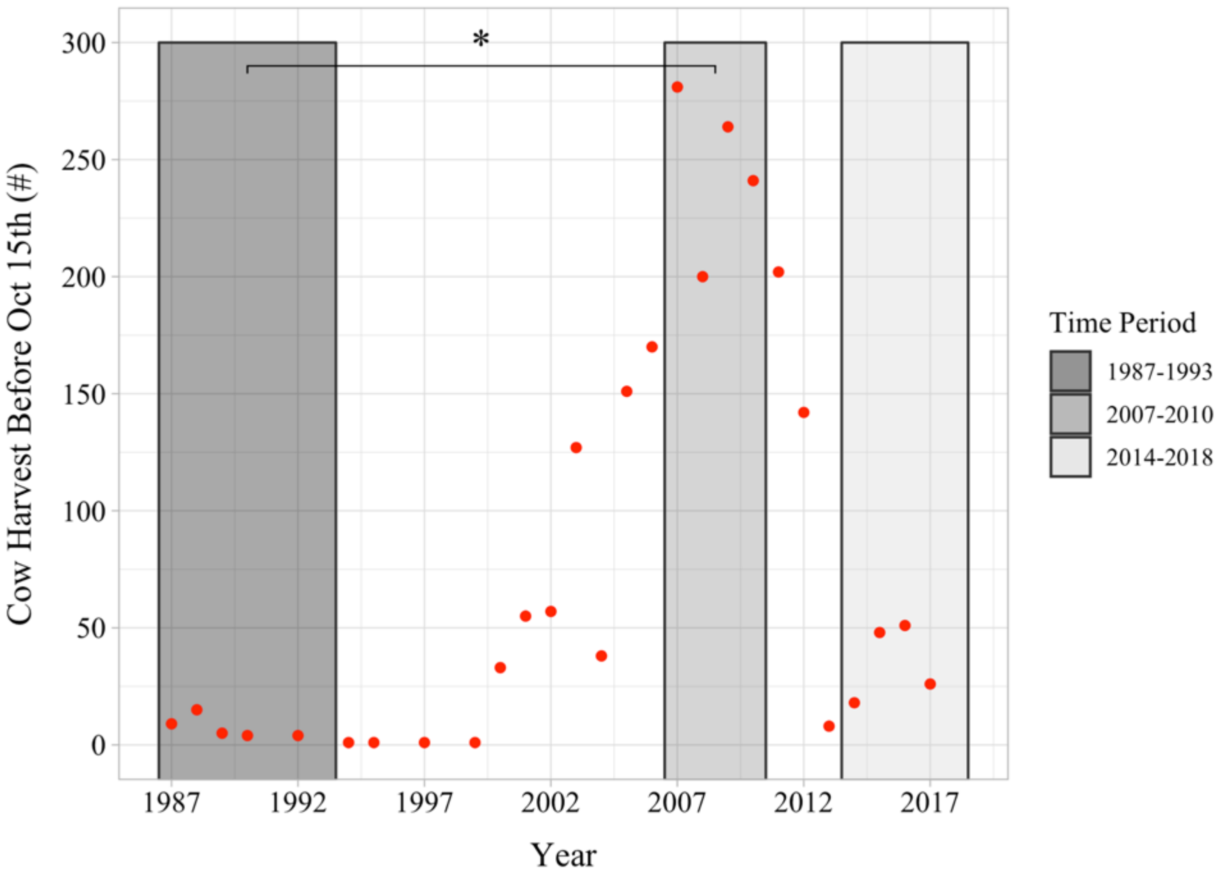
Appendix 1.1. The proportion and sample sizes of collared migrant and resident elk in the southern Rocky Mountain Trench, B.C, Canada, during three periods (1987–1993, 2007–2010, and 2014–2018) with 95% binomial confidence intervals indicated. A) Elk-years were treated non-independently when comparing numbers of migrant elk between each period using a chi-square test (chi-square, $\chi^2 = 8.30$, $df = 2$, $P = 0.015$) followed by pairwise Z-tests with Holm adjustments ($P_{87\text{-}93 \text{ to } 07\text{-}10} = 0.097$, $P_{07\text{-}10 \text{ to } 14\text{-}18} = 0.920$, $P_{87\text{-}93 \text{ to } 14\text{-}18} = 0.097$). B) Elk-years were treated independently when comparing numbers of migrant elk between each period using a chi-square calculation (chi-square, $\chi^2 = 26.07$, $df = 2$, $P < 0.001$) followed by pairwise Z-tests with Holm adjustments with "*" indicating significant pairings ($P_{87\text{-}93 \text{ to } 07\text{-}10} < 0.001$, $P_{07\text{-}10 \text{ to } 14\text{-}18} = 0.66$, $P_{87\text{-}93 \text{ to } 14\text{-}18} < 0.001$).



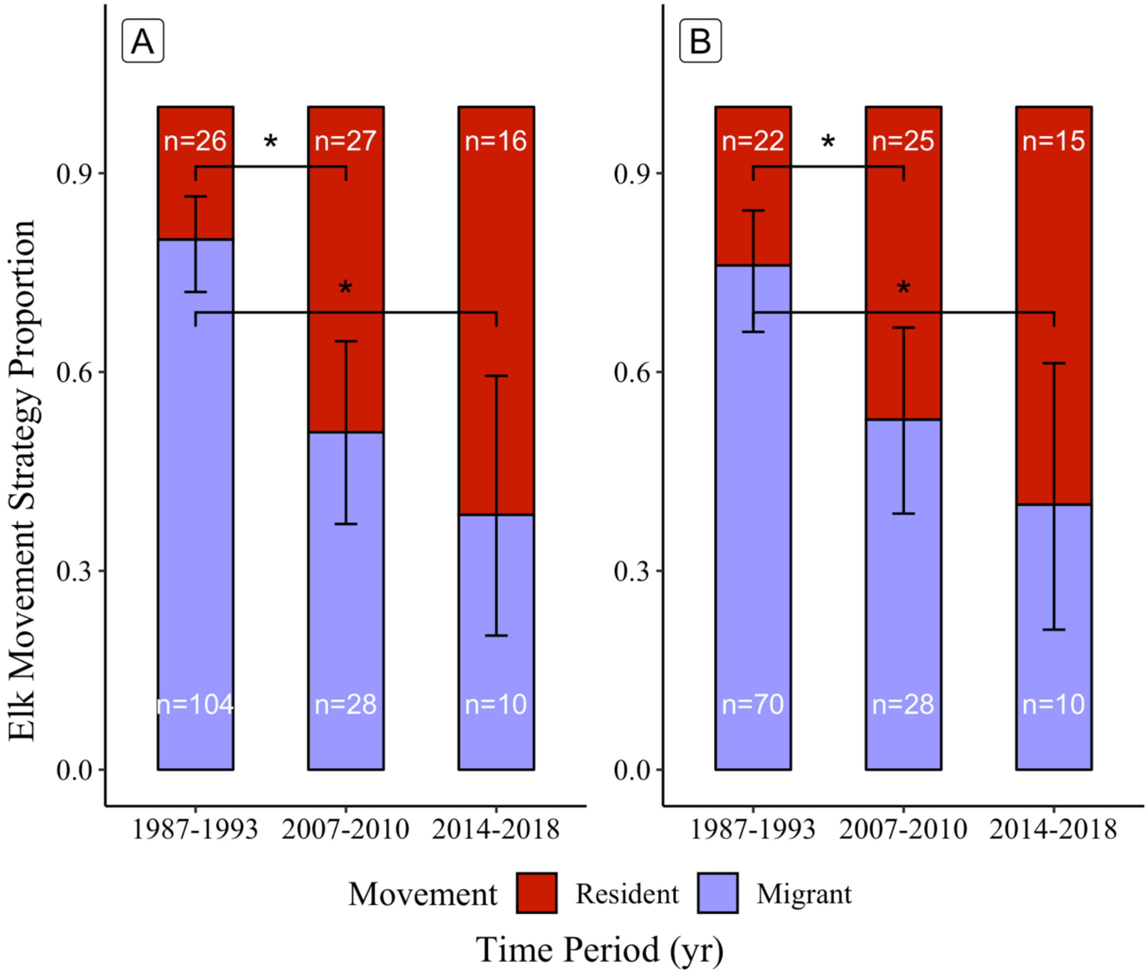
Appendix 1.2. Cumulative migration rate of 134 migrant elk-years starting spring migration (day-month) and ending fall (day-month) in the southern Rocky Mountain Trench, British Columbia, Canada. Only migrant elk-years with both spring and fall migration dates were included in this analysis. We determined our summer season, 1 May to 15 November, using dates where 50% of individuals had started spring migration and when 50% of individuals ended fall migration.



Appendix 1.3. A comparison of receiver operating characteristic (ROC) curves for elevation per elk location (A), median elevation per elk-year (B), and mean elk elevation per elk-year (C) in evaluating migration strategy (migrant or resident) of elk-locations between 1 May and 15 November in the southern Rocky Mountain Trench, British Columbia, Canada. The true positive rate (sensitivity) is plotted in function of the false positive rate (100-specificity). The area under the curve (AUC) corresponds to overall accuracy in predicting migration strategy. Mean elk elevation using 1 May to 15 November locations (F) maximized sensitivity (AUC = 0.912, *n* = 211). A threshold elevation that best distinguishes the two migration strategies was indicated (best threshold = 1,196 m).



Appendix 1.4. Number of cow elk harvested before 15 October below 1100 m in southern Rocky Mountain Trench, British Columbia, Canada (Wildlife management units: 4-02, 4-03, 4-04, 4-05, 4- 20, 4-21, 4-22 and 4-24). Harvest date and elevation cut-off were used by the regional government to target resident elk. Number of cow elk harvested differed among periods (Kruskal-Wallis, $H = 8.91$, $df = 2$, $P = 0.010$), significantly increasing, denoted by “*”, between 1987–1993 and 2014–2016 (Dunn-Bonferonni, $P = 0.004$). Shaded areas indicate three periods (1987–1993, 2007–2010, and 2014–2018) for which there were elk telemetry data.



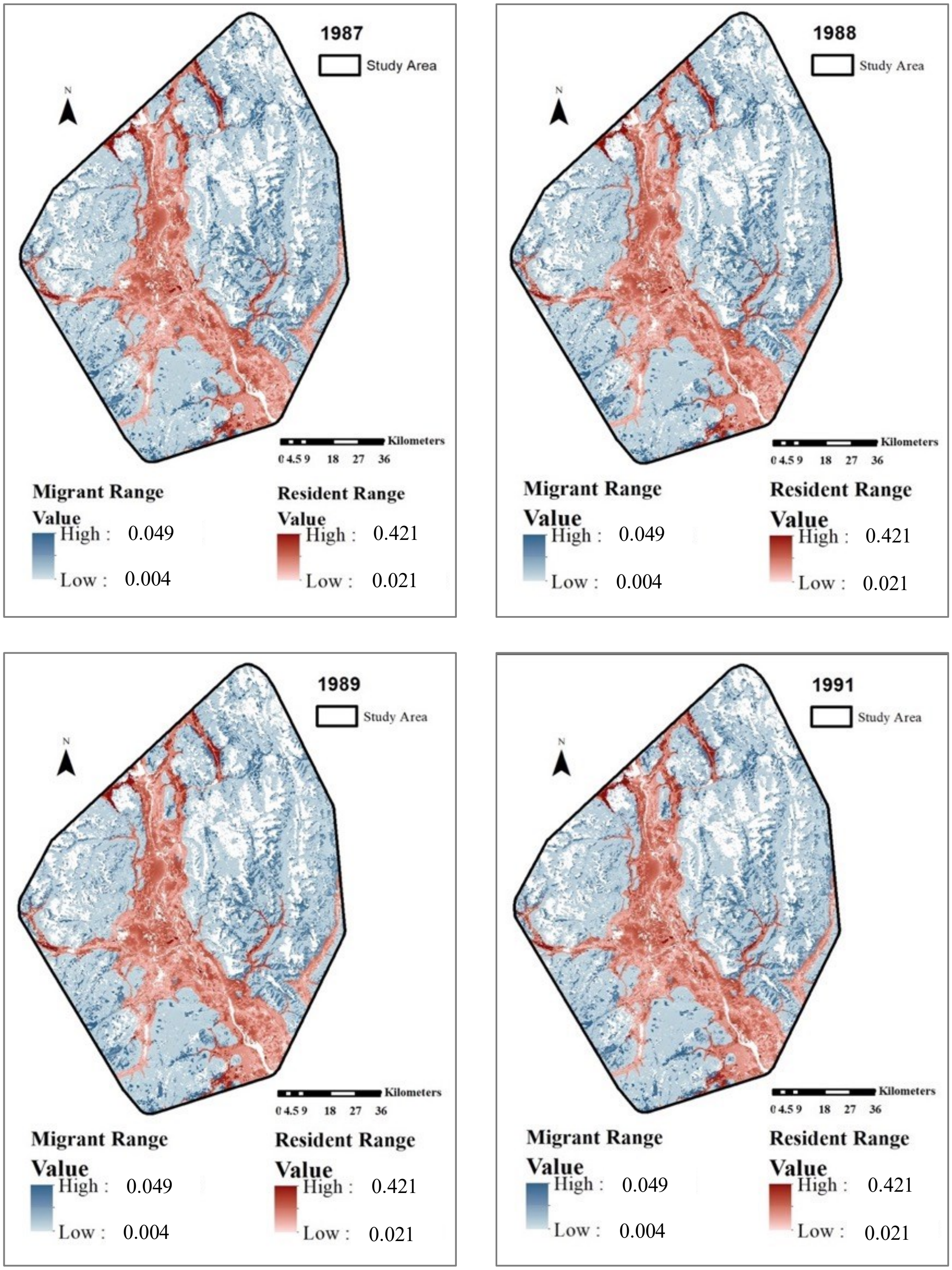
Appendix 2.1. The proportion and sample sizes of collared migrant and resident elk in the southern Rocky Mountain Trench, British Columbia, Canada, during three periods—1987–1993, 2007–2010, and 2014–2018— and with 95% binomial confidence intervals indicated. A) 211 elk-years were used when comparing numbers of migrant elk between each period using a chi-square calculation (chi-square, $\chi^2 = 26.07$, $df = 2$, $P < 0.001$) followed by pairwise Z-tests with Holm adjustments with “*” indicating significant pairings ($P_{87\text{-}93\text{ to }07\text{-}10} < 0.001$, $P_{07\text{-}10\text{ to }14\text{-}18} = 0.660$, $P_{87\text{-}93\text{ to }14\text{-}18} < 0.001$) B) 170 elk-years were used when comparing numbers of migrant elk between each period using a chi-square calculation (chi-square, $\chi^2 = 14.85$, $df = 2$, $P < 0.001$) followed by pairwise Z-tests with Holm adjustments with “*” indicating significant pairings ($P_{87\text{-}93\text{ to }07\text{-}10} < 0.014$, $P_{07\text{-}10\text{ to }14\text{-}18} = 0.41$, $P_{87\text{-}93\text{ to }14\text{-}18} = 0.0041$).

Appendix 2.2. Model results for migrant elk (n = 62) selection in summer (1 May to 15 November) from 1987 to 2018 in the southern Rocky Mountain Trench, British Columbia, Canada. Models included a random effect for each elk-year (1| elk-year). Annual metrics considered for landcover include herb-shrub (HrbShr), clear-cuts (Clear-cut), wildfire (Wildfire), and tree (Tree) as the reference. Topographic metrics include solar radiation (SolRad) and elevation (Elev). Paved roads distance decay (RoadDec) represents an urban metric.

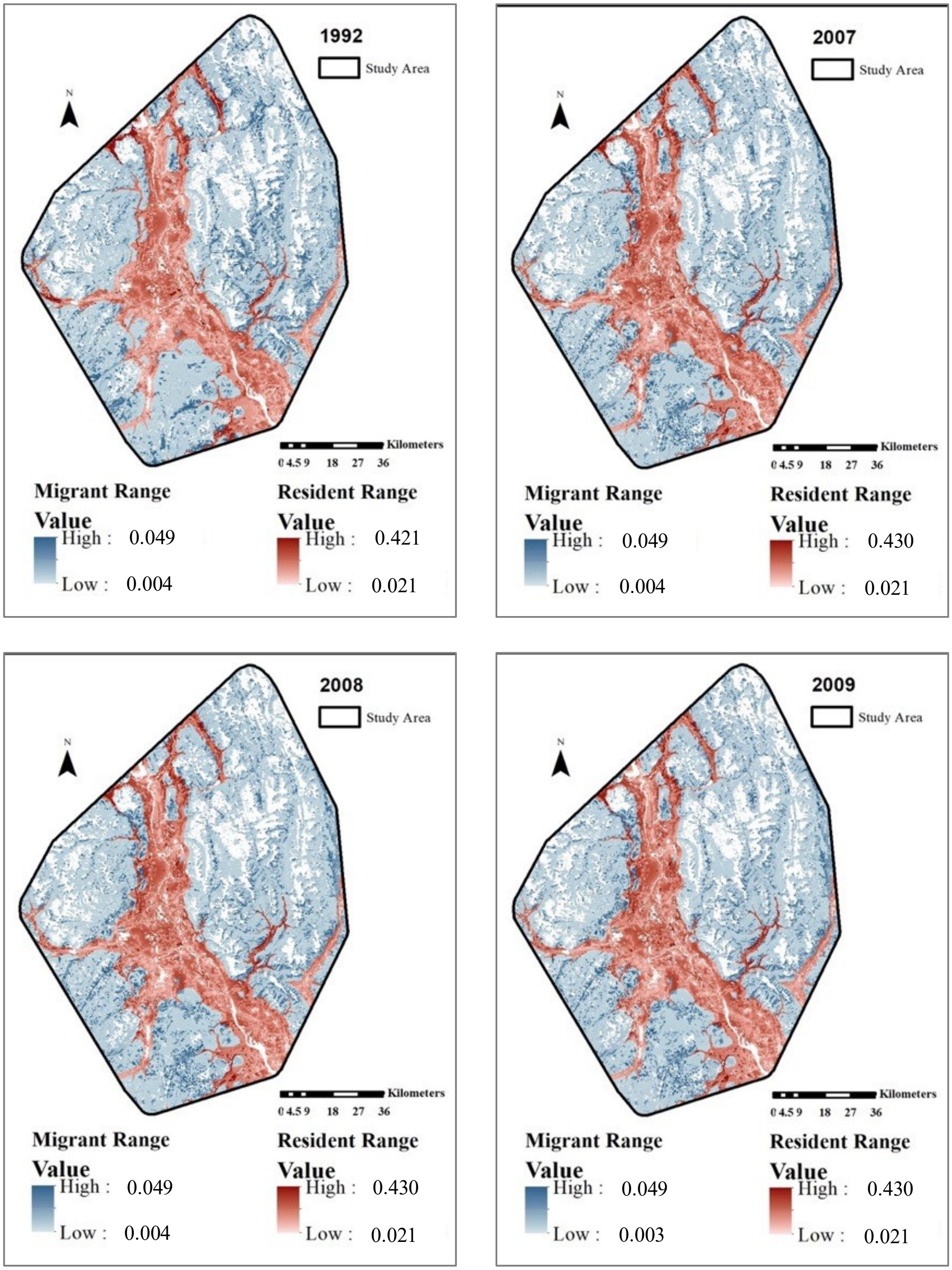
Model #	**Model**	**k**	**AIC**	**ΔAIC**	**Wt**	**LL**
23	HrbShr + Clear-cut + Wildfire + Elev – Elev^2 + RoadDec	8	86708.91	0.00	0.73	-43346.45
2	HrbShr + Clear-cut + Wildfire + Elev – Elev^2 + RoadDec - SolRad	9	86710.91	2.00	0.27	-43346.45
20	HrbShr + Clear-cut + Elev - Elev^2 + RoadDec	7	86723.87	14.96	0.00	-43354.93
12	HrbShr + Clear-cut + Wildfire + Elev - Elev^2	7	86738.06	29.16	0.00	-43362.03
9	HrbShr + Clear-cut + Elev - Elev^2	6	86754.29	45.38	0.00	-43371.14
24	HrbShr + Clear-cut + Wildfire + Elev + RoadDec	7	86789.05	80.14	0.00	-43387.52
16	HrbShr + Clear-cut + Wildfire + RoadDec	6	86868.74	159.84	0.00	-43428.37
13	HrbShr + Clear-cut + RoadDec	5	86882.16	173.25	0.00	-43436.08
8	HrbShr + Clear-cut + Wildfire + Elev	6	86909.87	200.96	0.00	-43448.93
7	HrbShr + Clear-cut + Wildfire + SolRad	6	87361.51	652.60	0.00	-43674.75
6	HrbShr + Clear-cut + Wildfire	5	87367.77	658.87	0.00	-43678.89
3	HrbShr + Clear-cut	4	87384.49	675.58	0.00	-43688.24
17	HrbShr + Elev - Elev^2 + RoadDec	6	88646.73	1937.82	0.00	-44317.36
21	HrbShr + Wildfire + Elev - Elev^2 + RoadDec	7	88646.86	1937.95	0.00	-44316.43
10	HrbShr + Wildfire + Elev - Elev^2	6	88675.04	1966.13	0.00	-44331.52
14	HrbShr + Wildfire + RoadDec	5	88778.28	2069.37	0.00	-44384.14
4	HrbShr + Wildfire	4	89136.50	2427.59	0.00	-44564.25
18	Clear-cut + Elev + Elev^2 + RoadDec	6	89222.92	2514.02	0.00	-44605.46
22	Clear-cut + Wildfire + Elev + Elev^2 + RoadDec	7	89224.92	2516.02	0.00	-44605.46
15	Clear-cut - Wildfire + RoadDec	5	89228.47	2519.56	0.00	-44609.23
11	Clear-cut + Wildfire + Elev - Elev^2	6	89231.15	2522.24	0.00	-44609.57
5	Clear-cut + Wildfire	4	89262.92	2554.01	0.00	-44627.46
19	- Wildfire - Elev - Elev^2 + RoadDec	6	90289.19	3580.29	0.00	-45138.60
1	Null	2	90319.89	3610.99	0.00	-45157.95

Appendix 2.3. Model results for resident elk (n = 108) selection in summer (1 May to 15 November) from 1987 to 2018 in the southern Rocky Mountain Trench, British Columbia, Canada. Models included a random effect for each elk-year (1| elk-year). Annual metrics considered for landcover include herb-shrub (HrbShr), clear-cuts (Clear-cut), wildfire (Wildfire), and tree (Tree) as the reference. Topographic metrics include solar radiation (SolRad) and elevation (Elev). Paved roads distance decay (RoadDec) represents an urban metric.

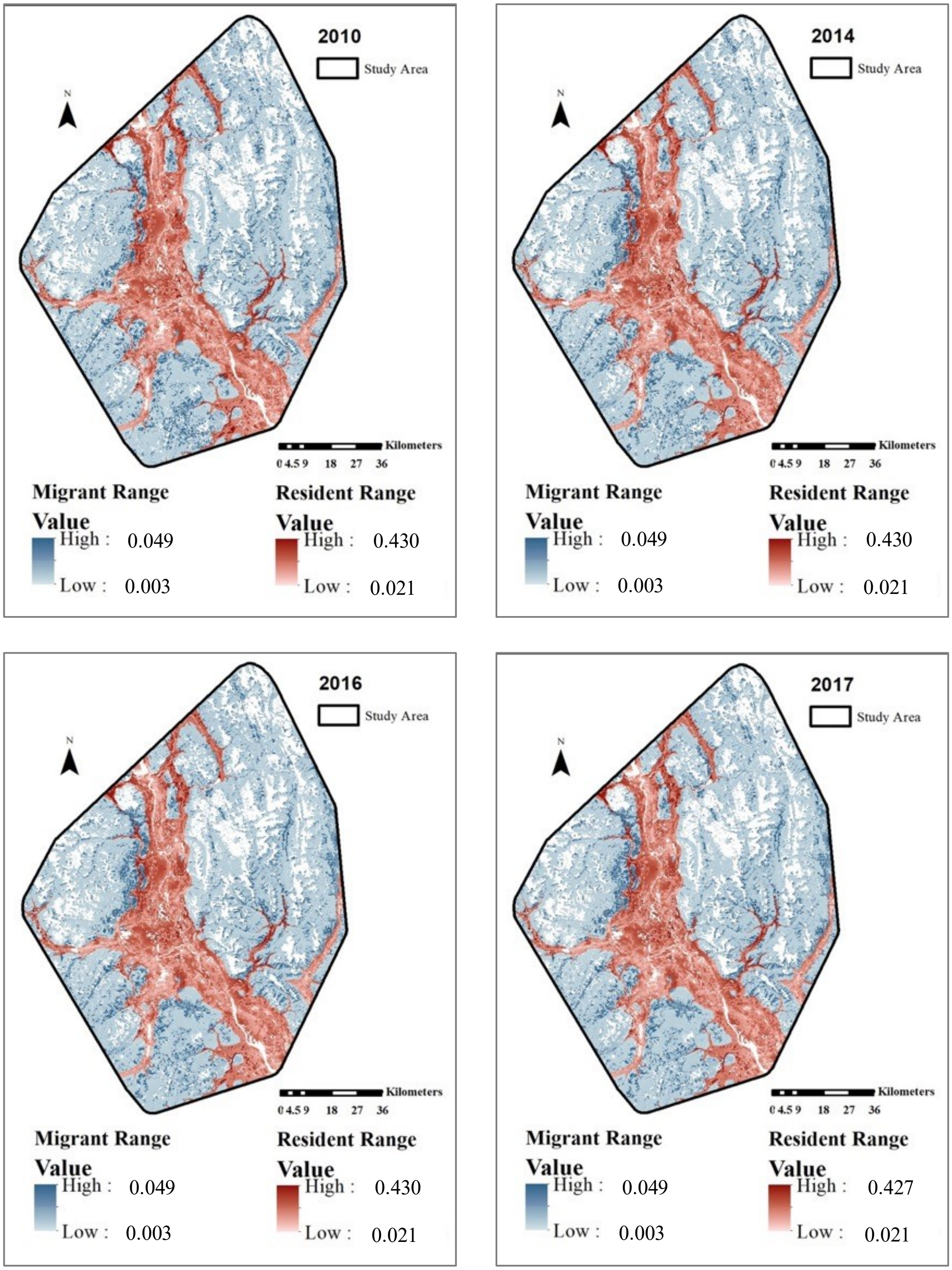
Model #	**Model**	**k**	**AIC**	**ΔAIC**	**Wt**	**LL**
23	HrbShr + Clear-cut + Wildfire - Elev - Elev^{2} + RoadDec	8	40354.66	0.00	0.67	-20169.33
2	HrbShr + Clear-cut + Wildfire - Elev - Elev^{2} + RoadDec + SolRad	9	40356.08	1.42	0.33	-20169.04
24	HrbShr + Clear-cut + Wildfire - Elev + RoadDec	7	40383.25	28.59	0.00	-20184.63
16	HrbShr + Clear-cut + Wildfire + RoadDec	6	40396.64	41.98	0.00	-20192.32
20	HrbShr + Clear-cut - Elev - Elev^{2} + RoadDec	7	40406.23	51.57	0.00	-20196.11
13	HrbShr + Clear-cut + RoadDec	5	40450.73	96.07	0.00	-20220.36
12	HrbShr + Clear-cut + Wildfire - Elev - Elev^{2}	7	40506.04	151.38	0.00	-20246.02
9	HrbShr + Clear-cut - Elev - Elev^{2}	6	40549.16	194.50	0.00	-20268.58
8	HrbShr + Clear-cut + Wildfire + Elev	6	40583.62	228.96	0.00	-20285.81
7	HrbShr + Clear-cut + Wildfire + SolRad	6	40587.78	233.12	0.00	-20287.89
6	HrbShr + Clear-cut + Wildfire	5	40589.44	234.78	0.00	-20289.72
3	HrbShr + Clear-cut	4	40631.13	276.46	0.00	-20311.56
21	HrbShr + Wildfire - Elev - Elev^{2} + RoadDec	7	40722.05	367.39	0.00	-20354.02
17	HrbShr - Elev - Elev^{2} + RoadDec	6	40758.66	404.00	0.00	-20373.33
14	HrbShr + Wildfire + RoadDec	5	40806.40	451.73	0.00	-20398.20
22	Clear-cut + Wildfire - Elev - Elev^{2} + RoadDec	7	40879.44	524.78	0.00	-20432.72
10	HrbShr + Wildfire - Elev - Elev^{2}	6	40892.64	537.98	0.00	-20440.32
18	Clear-cut - Elev - Elev^{2} + RoadDec	6	40905.98	551.31	0.00	-20446.99
11	Clear-cut + Wildfire - Elev - Elev^{2}	6	40993.14	638.48	0.00	-20490.57
4	HrbShr + Wildfire	4	41014.28	659.61	0.00	-20503.14
15	Clear-cut + Wildfire + RoadDec	5	41014.90	660.24	0.00	-20502.45
19	Wildfire - Elev - Elev^{2} + RoadDec	6	41026.89	672.23	0.00	-20507.44
5	Clear-cut + Wildfire	4	41058.13	703.47	0.00	-20525.07
1	Null	2	41260.76	906.09	0.00	-20628.38



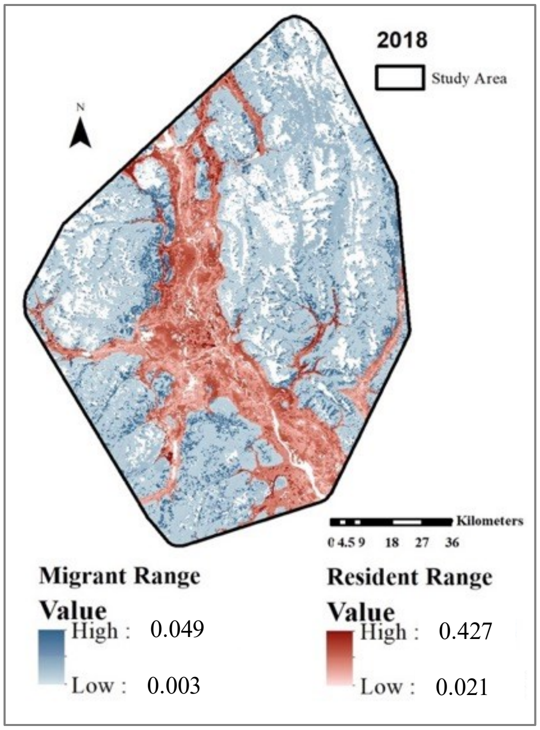
Appendix 2.4. Maps of southern Rocky Mountain Trench, British Columbia, Canada, migrant and resident elk range showing predicted values for summer elk migrant and resident resource selection functions (RSFs) for each yeah habitat variables were available (1987, 1988, 1989, 1991, 1992, 2007, 2008, 2009, 2010, 2014, 2016, 2017, and 2018).



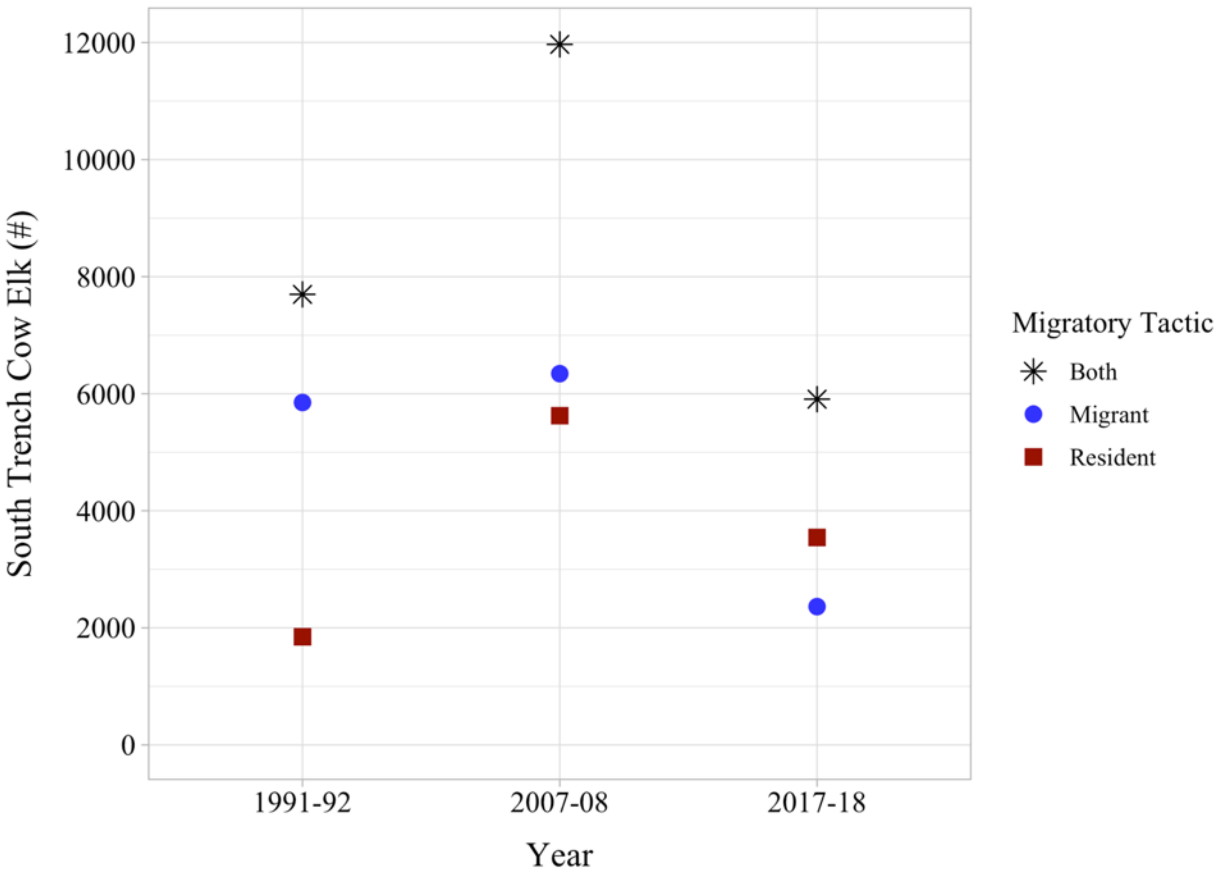
Appendix 2.4 continued.



Appendix 2.4 continued.



Appendix 2.4 continued.



Appendix 2.5. Winter elk population estimates in 1991/1992, 2007/2008, and 2017-2018 determined through stratified random block aerial surveys in the southern Rocky Mountain Trench, British Columbia, Canada, for migrant elk (blue circles), resident elk (red squares), or both tactics combined (black asterisk). Migrant and resident estimates were determined by multiplying the combined estimate by the M:R ratios for period the estimate fell within including the 1987–1993 period (76% migrants and 24% residents), 2007–2010 period (53% migrants and 47% residents), and 2014–2018 period (40% migrants and 60% residents).