Shifts in strategy: Calving and calf survival in a partially migratory elk population

by

Jodi Elizabeth Berg

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

Doctor of Philosophy

in

Ecology

Department of Biological Sciences

University of Alberta

ABSTRACT

Partial migration, a phenomenon wherein only one fraction of a population migrates, is taxonomically widespread. While well-studied in birds and fish, partial migration in large herbivores only recently has come into the spotlight due to migratory ungulates' global loss. In this dissertation, I summarized both individual- and population-level mechanisms for partial migration in ungulates, showing how density-dependent and -independent factors, alone or together, can combine with genetic variation and individual differences to maintain both migrants and residents within a population. Evidence suggested that partially migratory behavior is a state-dependent response of individuals, but data that empirically demonstrate which factors determine the relative costs and benefits to using migratory versus resident tactics are wanting. I sought to fill this void by monitoring elk (*Cervus canadensis*) that used 3 migratory tactics (resident, western high-elevation migrant, eastern low-elevation migrant) in the eastern slopes of the Rocky Mountains, Alberta.

The Ya Ha Tinda elk population declined by almost 70% over the last several decades, and the migratory patterns shifted towards residency and a relatively new, low-elevation migration. During two time periods (2002 – 2006, 2013 – 2016), I assessed whether differences in selection for forage and avoidance of predation risk during calving might contribute to shifts in the number of individuals following each of the migratory tactics across time. I employed a machine-learning algorithm to predict dates of parturition based on GPS movements of elk equipped with vaginal implants ($n = 60$) and found predictions were within 1.43 ± 0.85 days of the known date. I applied the model to an additional 58 GPS-collared elk without vaginal implants and found parturition occurred 8 May – 11 July with median parturition dates differing among migratory tactics in 2013 – 2016 and residents shifting towards an earlier date. Using the

26 days that elk remained relatively localized in their post-parturition movements, I compared habitat characteristics of calf-rearing areas to 10 similar-sized areas centered on random locations from summer for the same individual in a latent selection framework. All elk, regardless of migratory tactic, consistently selected for forage resources during calving more than during summer, with limited evidence for trading off forage due to predation risk. Selection for forage exposed western migrants to high risk of bear (*Ursus* spp.) predation, residents to high risk of wolf (*Canis lupus*) predation, and eastern migrants to low bear and wolf predation because they avoided risk by using areas of high human activity. Patterns of spatial use during calving were consistent with the recent decline in western migrants and increase in eastern migrants, implying that conditions on calving areas contributed to these changes.

I next estimated timing and causes of neonatal juvenile mortality, and the spatiotemporal scales for which biological and environmental factors were related to risk of mortality for elk calves. During 2013 – 2016, I captured 94 neonates, monitored risk of mortality to neonatal elk to 90 days of age, and assigned cause of death based on field evidence. The overall mortality rate for calves from all causes to 90 days of life was 0.61 (95% CI: 0.52, 0.70). Mortality hazard peaked at ~3 – 7 days of life and remained high in the first 20 – 30 days of life when 90% of deaths occurred. The overall mortality rate for calves of resident females to 90 days of life (0.69, 95% CI: 0.13, 0.99) was over 80% higher than for calves of eastern migrants (0.37, CI: 0.03, 0.97). Of 57 mortalities, I attributed 29 deaths to bears (51.7%), 7 to cougars (*Puma concolor,* 11.7%), 4 to wolves (6.7%), 8 to unknown predators (15.0%), and 9 to other causes (15.0%). Daily risk of mortality was most influenced by available forage biomass and low predation risk associated with human infrastructure on the summer range. Differential exposure to environmental factors on summer ranges resulted in variable predator-specific mortality and higher calf survival of eastern migrants, consistent with the shift in the number of elk migrating onto industrial forest lands. This study is one of the few that documents factors contributing to emerging migratory behavior in maintaining a partially migratory population.

PREFACE

The following dissertation draws from the combined efforts of past and present students, researchers, and faculty at both of the Universities of Alberta and Montana, as well as staff and managers from Parks Canada and Alberta Environment and Parks. To date, no manuscripts have been submitted for publication, but authorship will reflect the collaborative nature of this research. For this reason and for consistency, I use the collective "we" throughout the remainder of the dissertation after the acknowledgements. All field work and data collection were in accordance with the Canadian Council on Animal Care Guidelines and approved by the University of Alberta Animal Care and Use Committee (Protocols # 611/11/13 (2012 – 2013), AUP00000624 (2013 – 2017), Parks Canada [Permits # YHTR-2009-2875 (2009 – 2014), BAN-2014-16756 (2014 – 2017)], and Alberta Environment and Parks [Research Permits # 52119 (2012 – 2013), 52120 (2013 – 2014), 40535 (2014 – 2015), 55565 (2015 – 2016), 56371 (2016 – 2017); Collection Licenses # 40556 (2012 – 2013), 52108 (2013 – 2014), 52115 (2014 – 2015), 55567 (2015 – 2016), 56370 (2016 – 2017)].

ACKNOWLEDGEMENTS

This work would not have been possible without the financial and in-kind support from: Alberta Environment and Parks; Parks Canada; Natural Sciences and Engineering Research Council; University of Alberta; University of Montana; Alberta Conservation Association; Minister's Special License – Hunting for Tomorrow and Alberta Fish & Game Association; Rocky Mountain Elk Foundation; Safari Club International Foundation; Safari Club – Northern Alberta Chapter; CICan; Science Horizons; TD Friends of the Environment; Alberta Sport, Parks, Recreation & Wildlife Foundation; International Association for Bear Management; Wild Sheep Foundation Alberta; Center for Conservation Biology – University of Washington; Friends of the Eastern Slopes Association; Sundre Forest Products; fRI Research; NASA (USA, NNX11A047G to M. Hebblewhite); National Science Foundation (USA) Long-term Research in Environmental Biology grant (LTREB) to M. Hebblewhite and E. Merrill (1556248); and the Nestor and Sue Cebuliak, Bill Samuel, and William Wishart Graduate Awards.

I thank Parks Canada staff Blair Fyten, David Gummer, and Bill Hunt, among many others, for providing logistical, financial, and staff support, especially during the winter capture season. Jesse Whittington deserves recognition for continual maintenance of wolf databases. For their never-ending help, patience, and understanding, I especially thank the Ya Ha Tinda ranch staff: Rick and Jean Smith, Rob Jennings, and Tom McKenzie. The ranch would not have been a home away from home without sunset evenings on Rick and Jean's porch. And I surely wouldn't have survived (there were some close calls!) darting or navigating the backcountry on horseback without Tom and Rob's expertise. Anne Hubbs (AEP), Rachel Cook (NCASI), P.J. White (NPS), Bruce Johnson (OR DFW), Shannon Barber-Meyer (USGS), Holger Bohm (U Alberta), and Jon Horne (IDFG) all provided helpful advice and insight. Dr. Todd Shury (Parks Canada), Dr. Geoff Skinner (Parks Canada), Dr. Asa Fahlman, Dr. Rob McCorkell (U Calgary), and Dr. Owen Slater (U Calgary) gave their time, expert knowledge, and assistance during winter captures. Dr. Mark Boyce generously loaned us numerous GPS collars, allowing this project to a whole new level of data collection and analysis. Huge thanks to Antje Bohm for ensuring I hit the ground running by orienting me to the ins and outs of the ranch and the long-term monitoring protocols and databases – no small or easy task. Jan Vierck provided invaluable editing – thank you!

It takes a lot of hard work, dedication, and stamina to capture >100 elk calves in a place as rugged and remote as the eastern slopes of Banff National Park and the Ya Ha Tinda. This project would have been impossible without the numerous staff, volunteers, and interns who assisted for various lengths of time in various tasks surrounding the calf captures, monitoring, and logistics. Thank you all! Several folks couldn't get enough and returned for more: Bruce Wilson and Colleen Arnison deserve special thanks. I am forever indebted to Blair Fyten and 4 of the strongest women I know: Celie Intering, Sabrina Wales, Saakje Hazenberg, and Sarah Fassina. They might call me "Boss", but whether it was a cold, windy horse ride in the sun and snow, a night of music and dancing down at the campground in Old Tom's tent, or a rare night out in Banff, I realize now that they were the ones managing me (and my stress levels).

To fellow students in the ecology labs at U of A, thank you for the fun times, friendships, conversations, and support. I especially thank Eric Spilker, Andrew Ladle, Andrea Morehouse, Mel Dickie, Janet Ng, Kayla Deasley, Annie Loosen, Emily Blythe, Jody Reimer, Alex Beatty, and my accountabilibuddy-til-the-end, Kara MacAulay. Robin Steenweg and Hans Martin (for excellent crew leadership in my place!) should be mentioned as well. I thank my committee members Dr. Mark Hebblewhite and Dr. Colleen St. Clair for their thoughtful encouragement, constructive criticism, and insightful comments throughout the course of my PhD. Thanks also to my examiners Dr. Andy Derocher and Dr. Kevin Monteith for taking time out of their busy schedules to be part of this journey. I am extremely grateful for the opportunity to work on such an amazing project in such an incredible place. For that, I must thank my advisor, Dr. Evelyn Merrill. Evie is the most dedicated, passionate, and tireless scientist I know. She pushed me to push myself, and I am a better ecologist and critical thinker because of her.

Somehow this project turned into a family affair: from my dad braving a pounding hail and lightning storm in the almost-dark (without catching the calf and still a long ATV ride home!), my niece cheering me on while I crammed for the candidacy exam during our family ski vacation, my aunt helping feed all those hungry volunteers, to my mom who somehow ran the fieldhouse by rounding up volunteers of her own. I couldn't have done this without their love and support. I can't wait for the day I can stop using this dissertation as an excuse from joining in the family fun. Finally, thanks to Mark for believing in me, sticking by my side despite the distance, and enduring my focus on the PhD even through our most important moments. I'm excited for the next chapter in our adventure!

TABLE OF CONTENTS

Abstract ii

Preface v

Acknowledgements vi

Table of Contents viii

List of Tables xiii

List of Figures xix

Chapter 1. Introduction and Overview 1

Chapter 2. Mechanisms of migration: A review of partial migration in ungulates 6

- Introduction 6
- What is a Migrant? 7
- What Promotes Migration in Ungulates? 9
  - Genetically Based Migration 9
  - Learning, Culture, and Personality as a Basis for Migration 11
  - Migration in Relation to Age and Intrinsic Condition 12
  - Migration Based on Competition and Social Fences 13
  - Extrinsically Driven Migration 13
- Partial Migration and Its Maintenance within Populations 15
- Conclusions and Future Directions 18

Chapter 3. Mothers' movements: Shifts in calving area selection by partially migratory elk 32

- Introduction 32
- Study Area 35
- Methods 37
  - Elk Capture, Monitoring, and Migration 37

Modeling Calving Date 38

Calf-Rearing Areas 39

Elk Selection and Use during Calving 39

Environmental Covariates 40

Results 42

Parturition Dates 42

Calf-rearing Area Delineation and Size 43

Selection During Calving 43

Calving Areas of Migratory Tactics 44

Discussion 45

Chapter 4. Elk calf survival in a partially migratory elk population 57

Introduction 57

Study Area 61

Methods 63

Adult Elk Capture, Monitoring, and Migration 63

Calf Elk Capture, Monitoring, and Determining Cause-Specific Mortality 63

Modeling Risk of Mortality to Elk Calves 64

Results 69

Adult and Calf Elk Capture and Handling 69

Timing of Calving and Risk of Mortality 70

Modeling Factors Influencing Mortality 71

Discussion 72

Chapter 5. Conclusion 92

References 95

Appendix A. More on Partial Migration in Ungulates 132

Appendix B. Details of the Calf Ecology Component to the Ya Ha Tinda Long-term Elk Monitoring Project 136

- Study Area 136
- Methods 137
  - Adult Elk Capture and Handling 137
  - Nutritional Condition of Adult Female Elk 138
  - Calf Elk Capture and Handling 139
  - Calf Mortality 139
- Results 140
  - Adult Elk Capture and Handling 140
  - Calf Elk Capture and Handling 140
  - Calf Birth Sites 140
  - Calf Characteristics 141
  - Calf Mortality 141

Appendix C. R Code for Modeling Risk of Mortality 188

- Design matrix Z for splines 188

Appendix D. Details of Random Forest Model for Predicting Dates of Parturition 190

- Overview 190
- Methods 190

Appendix E. Land Cover and Accounting for Closed Canopy in NDVI 205

- Overview 205
- Methods 206
  - Calving Areas 206
  - Open-Habitat Mask 206
  - Regression 206

Results 207

Appendix F. Forage Biomass at Ya Ha Tinda 213

Overview 213

Appendix G. Predation Risk by Wolves, Bears, and Cougars for Elk at Ya Ha Tinda 215

Overview 215

Methods 216

Wolf Data 216

Bear Data 217

Resource Selection Component of Predation Risk by Wolves 217

Spatial Density Component of Predation Risk by Wolves 218

Resource Selection and Spatial Density Components of Predation Risk by Bears 219

Validation of the Wolf and Grizzly Predation Risk Models 220

Appendix H. Potential for Trade-offs between Forage and Predation Risk by Elk at Ya Ha Tinda 228

Methods 228

Results 228

Appendix I. Selection by Elk for Calf-rearing Areas at Ya Ha Tinda 237

Appendix J. Fine-scale Habitat Exposure for Elk Cow-calf Pairs 247

Methods 247

Location of Plots 247

Sampling 247

Appendix K. Selection by Adult Female Elk With and Without Calves 250

Overview 250

Results and Discussion 250

Appendix L. Estimating Age in Neonatal Elk: What to Measure? (Draft in Progress) 255

Introduction 255
Study Areas 256
Methods 257
    Calf Capture 257
    Calf Measurements 257
    Incisor Estimates 258
    Neonatal Age Model 259
Results 259
    Descriptive Statistics 259
    Incisor Estimates 259
    Neonatal Age Model 260

LIST OF TABLES

Table 2.1. Support (+ positive/likely, ? potentially but untested/suppositional, - negative/evidence against) for mechanisms explaining individual variation in partial migration, including genetics, learning, and state- or condition-dependence. 21

Table 2.2. State-dependent hypotheses to explain variation in migratory tendency..................... 25

Table 2.3. Reported rates of switching between migratory tactics in partially migratory populations of large ungulates. 26

Table 3.1. Number of collared elk used in comparing selection of calf-rearing and summer areas between 3 migratory tactics and 2 time periods (early: 2002 – 2006 and late: 2013 – 2016) in the Ya Ha Tinda elk population, Alberta, Canada, 2002 – 2016. 49

Table 3.2. Top models indicating latent selection differences between calf-rearing areas and areas used during summer by migrant and resident elk in the Ya Ha Tinda population during 2002 – 2006 and 2013 – 2016 in Alberta, Canada.. 50

Table 4.1. Hypotheses to explain elk calf survival in the partially migratory Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. 78

Table 4.2. Top 3 models for influence of intrinsic and maternal factors on daily risk of mortality through 3, 26, and 90 days of life in elk calves of the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016.. 79

Table 4.3. Parameter estimates of variables at birth or hiding sites associated with daily risk of mortality through 26 days of life in elk calves of the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016.. 80

Table 4.4. Parameter estimates for the effect of predation risk or refuge from predation (i.e., human infrastructure) at 2 spatial scales on daily risk of mortality through 26 days of life in elk calves of the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. 81

Table 4.5. Top 3 models at 3 spatial scales for influence of forage quality (NDVI) and forage biomass (g/m^2, FB) on daily risk of mortality through 26 days of life in elk calves of the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. 82

Table 4.6. Parameter estimates for models testing whether daily risk of mortality through 26 days of life in elk calves of the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016, depends on both lower risk of predation (or refuge from predation provided by higher human infrastructure) and higher available forage (FB). 83

Table A.1. Definitions of words used in discussion of animal migration 132

Table A.2. The different forms of migration in ungulates. 133

Table A.3. Additional state-dependent hypotheses to explain variation in migratory tendency that are less common in the ungulate literature. 134

Table A.4. Additional support (+ positive/likely, ? potentially but untested/suppositional, - negative/evidence against) for less-common, state- or condition-dependent mechanisms explaining individual variation in partial migration. 135

Table B.1. Adult female elk captured during February and March, 2013 – 2016, in the Ya Ha Tinda elk population, Alberta, Canada. 142

Table B.2. Body measurements taken on adult female elk in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016 149

Table B.3. Elk calf birth sites determined by location of VITs and/or neonatal calf in the Ya Ha Tinda elk population, Alberta, Canada 2013 – 2016. 156

Table B.4. Elk calves captured in the Ya Ha Tinda elk population, Alberta, Canada, 2013 - 2016. 162

Table B.5. Details of detected elk calf mortalities in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016... 167

Table B.6. Parameter estimates for the effect of intrinsic covariates on risk of mortality in elk calves in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. 171

Table B.7. Parameter estimates for the effect of intrinsic covariates on risk of mortality through 3 days of life in elk calves in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016.... 171

Table B.8. Parameter estimates for the effect of adult female body condition and migratory status on risk of mortality through 26 and 90 days of life in elk calves in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. 171

Table B.9. Parameter estimate for the effect of date of birth on risk of mortality through 26 days of life in elk calves in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. 172

Table B.10. Parameter estimates for the effect of available forage biomass (g/m^2) and NDVI on risk of mortality through 26 days of life in elk calves in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016... 172

Table B.11. Parameter estimates for the effect of predation risk or refuge from predation (i.e., human infrastructure) at 2 spatial scales on daily risk of mortality through 26 days of life in elk calves of the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. 173

Table D.1. Individuals in the Ya Ha Tinda elk population, Alberta, Canada, used for either model building or model prediction in a random forest analysis to identify date of parturition based on characteristics of movement data collected from 2002 - 2016. 191

Table D.2. Sample sizes of parturition events used to build random forest models and for predictions of parturition dates for elk following 3 migratory tactics in the Ya Ha Tinda elk population, Alberta, Canada, from 2002 – 2016. 197

Table D.3. Average importance of predictor variables, calculated from 1,000 random forest models used to predict dates of parturition of elk in the Ya Ha Tinda population, Alberta, Canada, 2002 – 2016. 198

Table D.4. Average importance of grouped predictor variables, calculated from 1,000 random forest models used to predict dates of parturition of elk in the Ya Ha Tinda population, Alberta, Canada, 2002 – 2016. 202

Table E.1. Land cover categories in the Ya Ha Tinda study area, Alberta, Canada, including open (0) and closed (1) habitat classification and the average percent (%) and range of each category within 26-day elk calving areas (*n* = 131). 208

Table G.1. Maximum number of wolves in each pack estimated from radiotelemetry, direct observations, snow tracking, and remote cameras during February and March 2002 - 2016 in the eastern slopes of Banff National Park, Alberta, Canada. 221

Table G.2. Number of GPS locations from collared wolves in the eastern slopes of Banff National Park, Alberta, Canada, 2002 - 2016. 221

Table H.1. Results from Pearson correlation analyses between predation and habitat characteristics of calving areas of western migrant elk by year and averaged across 2002 – 2006, in the Ya Ha Tinda study area, Alberta, Canada. 229

Table H.2. Results from Pearson correlation analyses between predation and habitat characteristics of calving areas of western migrant elk by year and averaged across 2013 – 2016, in the Ya Ha Tinda study area, Alberta, Canada. 230

Table H.3. Results from Pearson correlation analyses between predation and habitat characteristics of calving areas of resident elk by year and averaged across 2002 – 2006, in the Ya Ha Tinda study area, Alberta, Canada. The correlation coefficient, *r*, is displayed; bold marks significant correlation at least at the 0.05 level while values in red indicate a switch in the sign of the relationship from year to year. 231

Table H.4. Results from Pearson correlation analyses between predation and habitat characteristics of calving areas of resident elk by year and averaged across 2013 – 2016, in the Ya Ha Tinda study area, Alberta, Canada. The correlation coefficient, *r*, is displayed; bold marks significant correlation at least at the 0.05 level while values in red indicate a switch in the sign of the relationship from year to year. 232

Table H.5. Results from Pearson correlation analyses between predation and habitat characteristics of calving areas of eastern migrant elk by year and averaged across 2013 – 2016, in the Ya Ha Tinda study area, Alberta, Canada. 233

Table I.1. Results of fitting univariable conditional logistic regression models Results of fitting univariable conditional logistic regression models for selection of predation and habitat characteristics within calving areas relative to areas used during summer for migrant and resident elk in the Ya Ha Tinda population, Alberta, Canada. 237

Table I.2. Results of top models for selection of predation and habitat characteristics within calving areas relative to areas used during summer for migrant and resident elk in the Ya Ha Tinda population, Alberta, Canada. 239

Table I.3. Summary statistics for factors related to predation risk and habitat characteristics in calving areas of elk following 3 different migratory tactics and during 2 time periods (early: 2002 – 2006 and late: 2013 – 2016) in the Ya Ha Tinda elk population, Alberta, Canada. 241

Table K.1. Animals used to assess whether selection during calving differs between elk with calves that survived and elk with calves that died in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016.. 252

Table K.2. Results of models, with and without a categorical variable for calf survival, for selection of predation and habitat characteristics within calving areas for migrant and resident elk in the Ya Ha Tinda population, Alberta, Canada. 253

Table L.1. Mean measurements (range) taken on elk calves captured in the Ya Ha Tinda population, Alberta, Canada, 2013 - 2016. 261

LIST OF FIGURES

Figure 2.1. Example of classification of an animal as migrant and resident from Eggeman et al. (2016) and using the net-squared displacement method of Bunnefeld et al. (2011). The top row shows an elk in 2003 as resident, with movements within a 10-km^2 home range (coordinates are in meters, and the red square is the starting location while the blue triangle is the ending location), and NSD versus time with the model selection criteria for migrant, resident, and nomadic models. The bottom row shows the same elk in 2004, when she migrated 25 km from her winter range and was classified as a migrant. 27

Figure 2.2. On the left, Bayesian cluster analysis in STRUCTURE of microsatellite data from 93 elk belonging to the partially migratory Ya Ha Tinda elk population, Alberta, Canada. The continuous line represents a plot of mean *Ln P* (K) versus the number of clusters (K). K = 1 has the highest value and lowest variance, revealing that all 93 elk belonged to a single genetic unit. On the right, Principal Component Analysis of the microsatellite data, showing each individual classified according to status as migratory, resident, or unknown, also showed no difference between migratory and resident elk (Hebblewhite et al., unpubl. data). 28

Figure 2.3. The environmental-genetic threshold model assumes that a dichotomous trait is displayed as a result of an underlying continuous character or liability (i.e., migratory tendency) that is normally distributed within a population (Pulido 2011). The combined effects of genetic influences and environmental effects on the threshold position can push a facultative migrant (represented in gray), with a liability close to the threshold, to either migrate or remain resident, depending on the direction of the environmental shift. 29

Figure 2.4. Conceptual framework depicting how the density-dependent and density-independent factors may interact on the vital rates of migrants and residents to maintain partial migration within a population. 31

Figure 3.1. Calving areas of western migrant, resident, and eastern migrant elk in the Ya Ha Tinda population during 2002 – 2006 and 2013 – 2016 on the eastern slopes of Banff National

Park, Alberta, Canada. Calving areas were determined using GPS locations of maternal elk during the first 26 days after giving birth. 51

Figure 3.2. Total population and the estimated number of elk following each migratory tactic based on winter counts and movements of collared elk in the Ya Ha Tinda elk population, Alberta, Canada, during 2002 – 2006 and 2013 – 2016. 52

Figure 3.3. Known (black) vs. predicted (grey) parturition dates (n = 60) of elk in the Ya Ha Tinda population, Alberta, Canada, during 2013 – 2016. Predicted dates resulted from a random forest model that included variables related to movement: step length, turning angles, Euclidean displacement, and time of day. Grey bars denote the middle 2 quartiles of predicted dates. Results have been ordered along the x-axis by known parturition date for ease of figure interpretation. 53

Figure 3.4. Cumulative frequency of known (n = 73) and predicted (n = 58) parturition dates for elk following 3 migratory tactics and 2 time periods (early: 2002 - 2006 and late: 2013 - 2016) in the Ya Ha Tinda elk population, Alberta, Canada. Inset shows the distribution of the known and predicted dates of parturition. 54

Figure 3.5. Average area (km^2) used every 24 hr since day of parturition by maternal elk in the Ya Ha Tinda elk population, Alberta, Canada, 2002 – 2006 and 2013 – 2016. Left panel is the daily area used by elk since known (n = 73) dates of parturition, and right panel is the area used since both known and predicted (n = 131) dates of parturition. Both figures show a breakpoint at 26.0 (SE: 2.03) days. Lines represent a fitted segmented or piecewise regression model (R^2 = 0.91 and 0.88). 55

Figure 3.6. Comparison of predation risk and habitat characteristics in 26-day calving areas (n = 131) and summer areas of elk with 3 different migratory tactics and during 2 time periods (early: 2002 – 2006 and late: 2013 – 2016) in the Ya Ha Tinda elk population, Alberta, Canada. Small letters within each panel refer to differences of use during calving between migratory tactics and time periods. 56

Figure 4.1. Summer ranges of resident and eastern migrant female elk in the Ya Ha Tinda population during 2013 – 2016 on the eastern slopes of Banff National Park, Alberta, Canada. 84

Figure 4.2. Cumulative frequency of parturition dates for elk following 2 different migratory tactics (resident: *n* = 62, and eastern migrant: *n* = 32) in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. Inset shows the distribution of dates of parturition.................................. 85

Figure 4.3. Predicted daily hazard rates (solid line) from all causes of mortality for elk calves born to elk following 2 different migratory tactics (resident and eastern migrant) in the Ya Ha Tinda population, Alberta, Canada, 2013 – 2016. Dashed lines represent the variation in hazard rates (based on the estimated sigma) and are the bounds of the 95% cumulative distributions. The overall cumulative hazard rates were 0.69 for resident calves and 0.37 for eastern migrant calves. 86

Figure 4.4. Comparison of cumulative risk of mortality during the first 90 days of life for elk calves of elk following 2 different migratory tactics (on left, resident, and on right, eastern migrant) in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. 87

Figure 4.5. Daily cause-specific mortality rates for elk calves (*n* = 85) during the first 26 days following birth in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016.................... 88

Figure 4.6. In left panel, ingesta-free body fat (%) measured in late winter (Feb – Mar) for adult female elk following 2 different migratory tactics (resident: *n* = 53, and eastern migrant: *n* = 25). In right panel, weight at birth for calves (*n* = 94) captured in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016, in right panel. Letters indicate significant difference within each panel.. 89

Figure 4.7. Predicted probability of elk calf mortality with changes in ingesta-free body fat (%) and migratory tactic of adult females in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016.. 90

Figure 4.8. Effect of interaction between (scaled) human infrastructure and (scaled) forage biomass on daily mortality risk through 26 days of life in calves of eastern migrants in the left panel, and residents in the right panel, in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016.. 91

Figure B.1. Total population and the estimated number of elk within each migratory tactic in the Ya Ha Tinda elk population, Alberta, Canada, 2002 – 2016. 174

Figure B.2. Kill evaluation and categorization chart used to evaluate elk calf mortalities in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. Chart was adapted from Barber-Meyer (2006) and Hatter (1988). 175

Figure B.3. In the left panel, pregnancy rates for the Ya Ha Tinda elk population, Alberta, Canada, in late winter (Feb – Mar) across all years 2002 – 2016, except 2007 and 2010. In the right panel, pregnancy rates during the years 2013 – 2016, determined by rectal palpation...... 178

Figure B.4. In left panel, rump fat thickness (cm) regressed on body condition score (BCS) in adult females. In the right panel, Ingesta-Free Body Fat (IFBF, %) measured in late winter (Feb – Mar, 2014 – 2016) in relation to age (yr) of adult female elk in the Ya Ha Tinda elk population, Alberta, Canada... 179

Figure B.5. Ingesta-Free Body Fat (%, IFBF) measured in late winter (Feb – Mar, 2014 – 2016) for adult female elk following 3 migratory tactics (eastern, resident, and western) in the Ya Ha Tinda elk population, Alberta, Canada. 180

Figure B.6. Birth sites of elk calves located through use of vaginal implant transmitters (VITs) and/or neonatal elk calves in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. Based on known locations (*n* = 153), 12% of maternal elk gave birth in Banff National Park, 19% of elk gave birth to the north of the Ya Ha Tinda (YHT) ranch, mostly in the Bighorn Creek cut blocks and along Scalp Creek, 27% of elk gave birth to the east of YHT, 37% of elk gave birth in the vicinity of the ranch, and 4% gave birth to the south of the ranch.......................... 181

Figure B.7. Parturition dates (*n* = 147) determined through vaginal implant transmitters (VITs) or through age estimation of opportunistically caught calves in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. Known birth dates ranged from 9 May to 11 July. 182

Figure B.8. Body measurements of calves (*n* = 94 used in Chapter 4 survival analysis) captured and marked in the years 2013 – 2016 for monitoring survival in the Ya Ha Tinda elk population, Alberta, Canada... 183

Figure B.9. Weights at birth (kg) for elk calves captured (*n* = 102) in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. We used the estimated daily growth rate of the calves to back-calculate weight at birth from weight at capture... 184

Figure B.10. Raw frequencies for causes of death of elk calves (*n* = 105) in the Ya Ha Tinda elk population, Alberta, Canada, 2013 - 2016. Note that the chart ignores differences in timing of the different causes of mortality (i.e., predation by bears tends to occur earlier in the neonatal period compared to that of other predators), and that the cumulative incidence functions reported in Chapter 4 are a more appropriate and accurate method for presenting percent mortality by cause. 184

Figure B.11. Estimated age at death of elk calves (*n* = 105) in the Ya Ha Tinda elk population, Alberta, Canada, 2013 - 2016. 185

Figure B.12. In left panel, raw frequency, and in right panel, raw percent frequency, of mortality by cause in elk calves of elk following 2 migratory tactics (resident: *n* = 47, and eastern migrant: *n* = 10 used in Chapter 4 survival analysis) in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. Note that the cumulative incidence functions reported in Chapter 4 are a more appropriate and accurate method for presenting percent mortality by cause because of the timing of mortality by the different causes. 186

Figure B.13. Timing of mortality by cause in elk calves (*n* = 57 used in Chapter 4 survival analysis) in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016............................ 186

Figure B.14. Predicted daily hazard rates (solid line) of elk calves (*n* = 57 used in Chapter 4 survival analysis) in the Ya Ha Tinda population, Alberta, Canada, 2013 – 2016. Dashed lines represent the variation in hazard rate (based on the estimated sigma) and are the bounds of the 95% cumulative distribution. The overall cumulative hazard rate was 0.61. 187

Figure D.1. Step lengths (m) averaged across 3-day moving windows in 7 animals assumed to be pregnant in the Ya Ha Tinda elk population, Alberta, Canada, 2002 – 2016. Depressed movement rates in late May or early June could be indicative of an elk calving event. 203

Figure D.2. Size (km^2) of 26-day calving areas (*n* = 131) used by maternal elk in the Ya Ha Tinda elk population, Alberta, Canada, 2002 – 2006 and 2013 – 2016. 204

Figure E.1. Average area (km^2) used every 24 hr since day of parturition by maternal elk in the Ya Ha Tinda elk population, Alberta, Canada, 2002 – 2006 and 2013 – 2016. On left is the area used by elk since known (*n* = 73) days of parturition, and on right is the area used since both known and predicted (*n* = 131) days of parturition... 209

Figure E.2. Relationships between (a) the square transformation of NDVI at calving and the amount (%) of closed canopy, and (b) the cube transformation of NDVI at peak lactation and the amount (%) of closed canopy within 26-day elk calving areas in the Ya Ha Tinda population, Alberta, Canada, 2002-2006 and 2013-2016. 210

Figure E.3. NDVI at calving in open habitat (a), and (b) an index of NDVI after accounting for moderate and closed conifer (%) in calving sites (*n* = 131) of elk following 3 migratory tactics during 2 time periods (2002-2006 and 2013-2016) in the Ya Ha Tinda elk population, Alberta, Canada.. 211

Figure E.4. NDVI at peak lactation in open habitat (a), and (b) an index of NDVI at peak lactation after accounting for moderate and closed conifer (%) in calving sites (*n* = 131) of elk following 3 migratory tactics during 2 time periods (2002-2006 and 2013-2016) in the Ya Ha Tinda elk population, Alberta, Canada. 212

Figure G.1. 95% home range estimates for GPS-collared wolves during 2002 – 2006 (Panther-Cascade, Bow Valley, Red Deer, Ranch, and Wildhorse-James packs) and during 2013 – 2016 (Panther-Cascade and Bow Valley packs) on the eastern slopes of Banff National Park, Alberta, Canada.. 222

Figure G.2. Home ranges (95% Kernel Density Estimates) of 5 wolf packs in the eastern slopes of Banff National Park, Alberta, 2002 – 2016. 223

Figure G.3. Kernel Density Estimate of 5 wolf packs combined (top) and averaged Probability Density Function (PDF; bottom) from the eastern slopes of Banff National Park, Alberta, Canada, 2002 – 2016. Density functions were calculated separately for each wolf pack, then combined and weighted by the average size of each pack to create the PDF............................ 224

Figure G.4. Maps of predation risk by wolves for elk during the day in 2002 – 2006 (top) and 2013 – 2016 (bottom) created by combining pack size, spatial density of use, and pack-level resource selection in the eastern slopes of Banff National Park, Alberta, Canada.................... 225

Figure G.5. Grizzly bear Probability Density Function (PDF) used to create maps of resource selection and predation risk in the eastern slopes of Banff National Park, Alberta, Canada, 2002 – 2016... 226

Figure G.6. Maps of predation risk by bears for elk in 2002 – 2006 (top) and 2013 – 2016 (bottom) created by combining spatial density of use and resource selection in the eastern slopes of Banff National Park, Alberta, Canada. 227

Figure H.1. Predation characteristics of calving areas of elk with 3 different migratory tactics and 2 time periods (early: 2002 – 2006 and late: 2013 – 2016) in the Ya Ha Tinda elk population, Alberta, Canada... 234

Figure H.2. Mean rate of forage green-up on 26-day calving areas (*n* = 131) of elk with 3 different migratory tactics and during 2 time periods (early: 2002 – 2006 and late: 2013 – 2016) in the Ya Ha Tinda elk population herd, Alberta, Canada. 235

Figure H.3. Differences in forage greenness (NDVI) on 1 June (median date of calving) and 22 June (peak lactation) averaged across calving areas of elk with 3 different migratory tactics and 2 time periods (early: 2002 – 2006 and late: 2013 – 2016) in the Ya Ha Tinda elk population, Alberta, Canada. The mean for each migratory tactic-year is shown by the + symbol; there were very few eastern migrants during the early years, so we used the calving areas of eastern migrants from the later years to show what NDVI would've been in those same areas. 236

Figure I.1. Pairwise plot for early (2002 – 2006) western migrants in the Ya Ha Tinda elk population, Alberta, Canada. 242

Figure I.2. Pairwise plot for late (2013 – 2016) western migrants in the Ya Ha Tinda elk population, Alberta, Canada. 243

Figure I.3. Pairwise plot for early (2002 – 2006) residents in the Ya Ha Tinda elk population, Alberta, Canada... 244

Figure I.4. Pairwise plot for late (2013 – 2016) residents in the Ya Ha Tinda elk population, Alberta, Canada... 245

Figure I.5. Pairwise plot for eastern migrants (2013 – 2016) in the Ya Ha Tinda elk population, Alberta, Canada... 246

Figure J.1. Schematic diagram of sampling design for fine-scale habitat used by elk cow-calf pairs in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. 249

Figure K.1. Average area (km^2) used every 24 hr since day of parturition by maternal females in the Ya Ha Tinda elk population, Alberta, Canada, 2002 – 2006 and 2013 – 2016. On left is the area used by maternal females with known and predicted (*n* = 131) dates of parturition, and on right is the area used by females (*n* = 31) whose calves died within 26 days of parturition. The figure on left shows a breakpoint at 26.0 (SE: 2.03) days, and the figure on right shows a breakpoint at 25.0 (*SE*: 1.92) days. Lines represent a fitted segmented or piecewise regression model (R^2 = 0.88 and 0.86, respectively).. 254

Figure K.2. Distribution of mortality times for calves (*n* = 31) from the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. Five calves were offspring of elk with an eastern migratory tactic, and 26 calves were offspring of elk with a resident tactic. 254

CHAPTER 1. INTRODUCTION AND OVERVIEW

East of Banff National Park and western Alberta's Wapiti Mountain, at the end of a long dirt road that follows the Red Deer River, lies the Ya Ha Tinda. "Mountain prairie" in the Stoney-Sioux language, the Ya Ha Tinda is home to a rare, montane rough fescue (*Festuca campestris*) grassland, but also to a partially migratory elk (*Cervus canadensis*) population that winters there. The Ya Ha Tinda elk population is the focus of what is now the longest-running study on a partially migratory ungulate population, and one of the longest-running population studies on elk in a predator-prey-montane system that includes grizzly bears (*Ursus arctos*), wolves (*Canis lupus*), cougars (*Puma concolor*), and human hunting.

Since 1972, Alberta Environment and Parks has collected long-term population data on the population. Beginning in 2000, researchers at the Universities of Alberta and Montana, collaboratively with staff from Parks Canada, Alberta Environment and Parks, and other natural resource groups within Alberta, have been working to determine how changes in the Ya Ha Tinda (YHT) elk population, its trophic dynamics, and migratory behaviors are affected by both humans (harvest, recreation, habitat management) and natural factors (predation, climate, vegetation succession). Over the long-term Ya Ha Tinda elk project, data have been collected on adult female survival, pregnancy rates, elk calf-cow ratios and juvenile survival via mark-resight observations, grassland dynamics, and habitat use and selection with a focus on forage-predation trade-offs. Being partially migratory, determining the causes and consequences of migratory behavior by elk in this system has become a major focus in recent years (e.g., Eggeman et al. 2016, Killeen et al. 2016).

The Ya Ha Tinda population has declined by almost 70% over the past 2 decades from a maximum count of ~2,200 elk in the early 1990s (Morgantini 1995) to a recent low of <400 elk during the course of this study (Berg et al. 2016). Historically, the majority (~90%) of the YHT population migrated ~32 (25 – 80) km westward from the winter range to summer at high elevations (>2,000 m) in Banff National Park (BNP, Morgantini and Hudson 1988). But concurrent to the overall population decline, the number of elk migrating westward has declined, while there has been a proportional increase in elk remaining on winter range year-round. Over time, a new pattern of migration eastward to low-elevation (~1,400 m) industrial and recreational forest has emerged, and the ratio of western migrants to residents to eastern migrants is now ~1:10:5 (Berg et al. 2016).

Initial studies in 2002 – 2004 (Hebblewhite 2006) that focused on the western migrants and residents showed that by migrating to high-elevation summer range, elk were exposed to higher forage quality resulting in higher pregnancy rates and heavier calves in winter, and lower risk of predation from wolves except during migration itself (Hebblewhite and Merrill 2007, 2009, 2011, Hebblewhite et al. 2008). Resident elk were capable of lowering predation risk exposure from wolves by remaining on winter range close to humans, which wolves avoided primarily during the day, but resident elk experienced higher cause-specific mortality from First Nations harvest (Hebblewhite and Merrill 2007, 2009). In addition, migrants were not excluded on the winter range but stayed in smaller, less cohesive groups, while residents were better at balancing vigilance with foraging and remained in larger, cohesive groups (Robinson et al. 2010). Therefore, even though residents were at a nutritional disadvantage, population growth rates remained approximately equal to that of western migrants over time (Hebblewhite and Merrill 2011). Despite nearly equal demographic fitness, western migrants continued to decline 2-3% faster than residents, suggesting that the ability of the residents to take advantage of fine-scale refuge was underestimated. Alternatively, continued monitoring showed that western migrant and resident elk in the Ya Ha Tinda switch between migratory behaviors in a facultative, density-dependent manner, suggesting behavioral switching may be maintaining partial migration and equivalent fitness between tactics within the population (Eggeman et al. 2016).

Modelling efforts based on continued monitoring of elk demography through 2010 predicted that elk at Ya Ha Tinda would reach a low-density equilibrium at ~500 elk (Glines et al. 2011). In 2010, the population declined to <400 elk, and the population seemed in peril. A major assumption behind the projection for population stabilization was that predation by wolves was density-dependent, such that as the elk population declined, the predation rate also was expected to decline. However, Hebblewhite et al. (2018) found that through 2014, predation by wolves was the largest source of predator mortality, and it was density-independent, contributing to the continued decline of both western migrant and resident tactics. In contrast, predation rates by humans (First Nations) for residents and by grizzly bears for western migrants were weakly density-dependent. We hypothesized several reasons for why wolf predation was independent of elk density. First, consistent with the apparent competition hypothesis (DeCesare et al. 2010), an increasing white-tailed deer (*Odocoileus virginianus*) population may have maintained wolf densities, as supported by the increased prevalence of deer in wolf scats collected at Ya Ha Tinda later in this study compared to earlier efforts (unpublished data, Merrill, Hebblewhite, and Parks Canada, MacAulay 2018). Apparent competition has been reported to occur with moose (*Alces alces*)/deer and caribou (*Rangifer tarandus caribou*) in other parts of Alberta and British Columbia (e.g., Serrouya et al. 2015).

Secondly, because of the loss of western migrants, an aversive conditioning program was initiated to test the feasibility of pushing elk westward to re-establish their historical migratory patterns (Spaedtke 2009). Ultimately, the aversive conditioning was not successful, but about this time, the number of collared elk migrating eastward onto industrial forest lands increased (Killeen et al. 2016). One hypothesis for the eastward movement of elk was that elk were attracted to the developing forage in the Dogrib burn that covered 10,200 ha and occurred in 2001. Studies of initial vegetation recovery in 2003 across 3 different treatments indicated post-fire logging had transient effects on total herbaceous biomass; while forb biomass was reduced, increases in graminoid biomass more than compensated by the third year (Hebblewhite et al. 2009). However, ungulates initially avoided burned logged areas despite greater herbaceous biomass, and this was attributed to wolf selection for areas closer to roads where higher forage biomass occurred (Hebblewhite et al. 2009). Forage biomass of the same burned sites ($n = 60$) was re-sampled in 2012, and elk pellet counts show that elk appear to use the Dogrib area in spring (May – June) but less so in summer (July – Sept).

A second hypothesis for the increase in elk migration eastward was lower predation because wolves and cougars are hunted/trapped, and there is high density of human infrastructure and recreation during summer that indicates the spatial pattern of predation refuges created by humans could be shifting (Spilker 2018). Further, habitats in the area have also been subject to wild and prescribed fires (~7,000 ha) and an increase in forest cutting with over 3,000 ha cut since 2000, primarily at low elevations (Smolko et al., in prep.). Therefore, because of early summer maturation of forage and/or high predation risk created by the open habitat, elk may be moving through the burn to areas where they can take advantage of forest cover or human activity (both industrial and recreational) as refuge from predation.

Preliminary evidence (i.e., elk calf-cow ratios) indicated calf survival was not high enough to counter the population decline (Eggeman 2012). There is recent evidence that indicates a diverse predator community might render predation additive in causes of calf mortality, particularly as related to grizzly bear predation on neonates (Linnell et al. 1995, Griffin et al. 2011). Predator-caused mortality should be compensatory with other natural or climate-induced mortality in juvenile ungulates. However, Linnell et al. (1995) suggest a mix of predators might cause predation to be additive; therefore, predation would be expected to overwhelm natural mortality, and predation effects should increase with a greater number of predator species. If predation was compensatory, survival should stabilize with a greater number of predator species as one predator species replaces another in its effect on neonate survival. Alternatively, differences in spatial risk by multiple predator species and between migratory tactics, including the new eastern migrants, are supported by our most recent studies (MacAulay 2018, Spilker 2018). Yet up until the start of this calf survival study in 2013, detailed information on (1) reproductive success of individual adult elk, including survival and cause-specific mortality of calves, and (2) the emerging eastward migration, was lacking and continued to limit the conclusions regarding drivers of migratory behavior and the resulting consequences for the population. Indeed, population assessments indicate dynamics of the elk population at Ya Ha Tinda is driven by variability in calf survival (Gaillard et al. 2000, Raithel et al. 2007, Glines et al. 2011).

In this dissertation, I first review the literature for evidence of different mechanisms that promote migration and maintain partial migration (Chapter 2). In particular, I evaluate the evidence for switching between migratory tactics in ungulates to show that both migrant and resident individuals (i.e., partial migration) within a population can be maintained by density-dependent and/or -independent factors, in combination with genetic variation and state-dependent responses of individuals. In Chapter 3, I use long-term data from Ya Ha Tinda to compare habitat selection during the calving period to that in summer in the early (2002 – 2006) and late (2013 – 2016) years of the long-term monitoring. I do not include the period 2007 to 2012 because objectives of the aversive conditioning during this period focused the collaring efforts primarily on residents. I first delineate the area used by elk cow-calf pairs in the calf-rearing phase, then evaluate trade-offs in forage and predation risk made on calving areas and through time that might contribute to observed shifts in the number of individuals following each of the migratory tactics. In Chapter 4, I estimate the overall survival, timing and causes of mortality, and the spatiotemporal scales for which biological and environmental factors are related to risk of mortality for calves of elk following the resident and low-elevation eastern migrant tactics. Finally, in Chapter 5, I synthesize the findings of these studies and describe the implications for our understanding of the maintenance of partial migration and for the long-term viability of the Ya Ha Tinda elk population.

This calf survival study addresses whether the new migration of elk to recreational and industrial forest lands east of Ya Ha Tinda is related to elk density, maternal elk selection for improved forage from burning or timber harvest, or reduced calf mortality associated with predator exploitation or human disturbance (predator refuge). Until now, cause-specific calf survival and the mechanisms influencing calf survival at Ya Ha Tinda have not been addressed and were a missing link in the overall understanding of the role of predation and migration in the Ya Ha Tinda population dynamics. Given concern over declines in migratory behavior and migratory populations worldwide (Berger 2004, Wilcove and Wikelski 2008, Harris et al. 2009), but also interest from local management and the public in maintaining the Ya Ha Tinda elk population, the consequences of shifting migratory behavior for differential calf survival among migratory tactics is a timely conservation question.

CHAPTER 2. MECHANISMS OF MIGRATION: A REVIEW OF PARTIAL MIGRATION IN UNGULATES

INTRODUCTION

Dramatic declines in populations of migratory ungulates and the disappearance of migratory behavior in many ungulate species are now recognized as a global conservation challenge (Berger 2004, Bolger et al. 2008). Population reductions have been well-documented in migratory species ranging from antelope (*Antidorcas marsupialis*, Child and Le Riche 1969; *Saiga tatarica*, Milner-Gulland et al. 2001) and buffalo (*Syncerus caffer caffer*, Bennitt et al. 2016) to wildebeest (*Connochaetes taurinus*, Gasaway et al. 1996) and zebra (*Equus burchelli antiquorum*, Bartlam-Brooks et al. 2013). Loss of migratory ungulates is attributed primarily to human-induced changes to landscapes, which may be exacerbated by climate change (Lendrum et al. 2013). Loss of migration can have significant impacts, extending from alteration of plant composition and ecosystem processes such as grassland production and nitrogen mineralization (McNaughton et al. 1988, Frank 1998, Holdo et al. 2006), to declines in other species including apex predators (Packer et al. 2005, Lee et al. 2016), to the collapse of whole ecosystems as wildlife tourism-based incentives for environmental protection dissolve (Harris et al. 2009, Holdo et al. 2011*b*). Given the potential severity of these ecological impacts and their associated economic consequences, identifying the processes that lead to migratory behavior should be a primary focus of biodiversity research and conservation efforts to address the loss of migration in ungulate populations (Bolger et al. 2008).

Migratory movements of individuals are expected to arise in variable environments such that ungulates migrate to enhance lifetime reproductive fitness by gaining access to critical resources such as nutrients or water, reduce their likelihood of predation, or escape parasites (Fryxell and Sinclair 1988*a*, Mysterud et al. 2011, Qviller et al. 2013, Mysterud et al. 2016). However, anthropogenic disturbances and environmental changes have, in some cases, altered the relative benefits of migrating in large herbivores, so that residency becomes the favored tactic (Berger 2004, Hebblewhite et al. 2006, Jones et al. 2014). Trade-offs between the costs and benefits of migration lead to partial migration, a population-level phenomenon that is widespread across taxa, in which a population is comprised of both resident and migrant individuals

(Chapman et al. 2011*a*). The number of studies on partially migratory ungulate populations continues to grow, but they remain theoretical or empirically correlative because experimental manipulations needed to illustrate mechanisms driving migratory tendency in large mammals remain problematic. Nevertheless, there is an urgent need to better synthesize what theoretical and empirical information does exist on partial migration in ungulates to better understand what may be driving the worldwide decline in their migratory behavior and to offer directions for future studies (Bolger et al. 2008).

We start by reviewing the definition of a migrant and the issues related to defining the migrant and resident behavior for studying partial migration. Then we review mechanisms that might promote migration in individuals within partially migratory populations. We focus primarily on views of genetic variability, intrinsic factors such as age and condition, social interactions and cultural inheritance, and extrinic or environmental factors such as forage and predation risk. We then address the key mechanisms that maintain partial migration at the level of population in variable environments. We address how changes in proportions of migrants and residents might occur across generations through either a frequency- or density-dependent equilibrium in fitness, or even within generations via behavioral switching. We end by challenging researchers to collect the long-term data necessary to test the mechanisms underlying maintenance of partial migration to bring us closer to conserving ungulate populations in the face of ongoing environmental change.

WHAT IS A MIGRANT?

Migration is a phenomenon that is not easily defined because of variation in both terminology and types of animal movement among taxa (Sinclair 1983, Fryxell et al. 2011). When applied at the level of individual or at the level of population, it can offer different characterizations (Dingle 2014*a*). To call migration a trait or a syndrome, migration must respond to natural selection (Dingemanse et al. 2010, Sih et al. 2012, Dingle 2014*a*). Thus, despite often being used to describe a population process (Dingle and Drake 2007), we take the view that migration is one among 2 or more tactics that describes a movement behavior exhibited by individuals (see Appendix Table A.1 for more thorough definitions). For many taxa including ungulates, migration is most commonly defined as round-trip movement between discrete seasonal ranges (Fryxell & Sinclair 1988, Sinclair 1983). Thus, because of the emphasis placed on spatiotemporal separation between ranges and on return movement, migration differs from: (1) dispersal, a relatively short-term, one-time movement to a new population or a new range primarily for the purpose of reproduction; (2) nomadism, where animals move through different ranges with no distinct pattern; and (3) residency, where there is continuous, overlapping use of the same range (McPeek and Holt 1992, Hjeljord 2001, Abrahms et al. 2017). However, using seasonal ranges to distinguish between migratory tactics becomes problematic when individuals exhibit more idiosyncratic or mixed movements, such as returning to a seasonal range after initially leaving it (Dingle and Drake 2007, Dingle 2014*a*). The variation in migratory movement suggests that partial migration is not a simplistic dichotomy of migrant versus resident, or even that all migrants should be classified equally (e.g., short- versus long-distant migrant, Appendix Table A.2). That the choice to migrate reflects a continuum of movement responses that occur within multiple scales of spatiotemporal variability is now being proposed (Cagnacci et al. 2011).

Several quantitative methods have emerged to distinguish migration from other types of movements and to classify variation in migratory movements (Cagnacci et al. 2016, Singh et al. 2016, Abrahms et al. 2017, Peters et al. 2018). Migrants are often distinguished from residents based on criteria such as seasonal home range overlap (Mysterud 1999, Ball et al. 2001, Fieberg and Kochanny 2005), trajectory segmentation (Buchin et al. 2013), or algorithms that cluster seasonal locations (Cagnacci et al. 2011, Damiani et al. 2015, Cagnacci et al. 2016). A second approach is based on Correlated Random Walk (CRW) models (Bergman et al. 2000), including the recently popular Net Squared Displacement (NSD), measured as the cumulative squared displacement from a starting point (Meland 2014, Bastille-Rousseau et al. 2016, Peters et al. 2017). The drawback to NSD is that it can be computationally complex and often requires ad hoc reclassification of the migratory status of an individual (Spitz et al. 2017). On the other hand, this method is capable of objectively quantifying different types of movement along a continuum, overcoming the problem of simplistic dichotomies (Figure 2.1, Singh et al. 2016). Despite the limitations in methodologies, quantifying animal movements as migratory behavior is a first step in exploring how partial migration is maintained.

WHAT PROMOTES MIGRATION IN UNGULATES?

Migration reflects a balance between conflicting costs and benefits that leads to remaining in a range year-round, or moving to new areas. In this section we identify and assess the support for the most commonly hypothesized mechanisms shaping individual variation in migratory tendency in ungulates (Table 2.1). Many mechanistic hypotheses have been proposed to account for individual variation in migratory tendency where migration is dependent on individual state or environmental conditions and/or their interactions (Table 2.2), but here, we also consider a genetic basis and the emerging evidence for the role of learning and cultural transmission. We conducted the review based on the published literature for all ungulate species listed in Ultimate Ungulate (Huffman 2018), and Groves and Grubb's (2011) species within the orders Perissodactyla (odd-toed ungulates) and Cetartiodactyla (even-toed ungulates). We used 'Web of Science' and 'Google Scholar' search engines to find articles by the common and Latin name and/or genus in combination with 'migra*' or 'partia* migra*'. In particular, we focused on any article that described partial migration (i.e., the article needed to state that a portion of the population remained resident/sedentary) and addressed or speculated on the reasons behind the observed differences in migratory behavior. We chose not to include gray literature due to variability in robustness of data presented. The hypotheses we evaluated are not mutually exclusive and 2 or more proximate mechanisms could operate simultaneously (Avgar et al. 2014). Teasing apart their relative importance can be especially difficult because the predicted effects could be the same or at least partly overlapping (Ketterson and Nolan Jr. 1983, Smith and Nilsson 1987).

We focused on migration in female ungulates because adult female survival is thought to have the greatest influence on large ungulate population dynamics (Gaillard et al. 1998, Raithel et al. 2007), but included migratory tendency in males where new mechanisms arose and there were adequate data.

Genetically Based Migration

We found very little direct evidence for strictly controlled, genetically based migration in ungulate populations with partial migration (Bolger et al. 2008). The evidence did not say that genetic control of migratory tactic in ungulates may not exist, but that drawing direct inferences from the available data was challenging. Evidence for a genetic basis for migration would require that behavioral traits of migration were linked to specific alleles that differentiate groups or show heritability, as demonstrated for migratory restlessness in captive birds (Berthold and Querner 1982, Terrill 1987, Berthold 1991, Berthold and Pulido 1994). Such experiments showing restless behavior related to migration were not attempted and may not be feasible in ungulates. Instead, the limited number of studies on the genetic basis for migration in ungulates often used one of several primary sources of evidence.

First, GPS technologies were used to characterize migratory traits of individuals (migration status, timing, distances, switching) and then microsatellites were compared among the respective groups. Although successful in indicating spatial genetic structure in ungulates (e.g., Coltman et al. 2003, Colson et al. 2016), microsatellite analyses have not shown consistent evidence for distinguishing between individuals showing migrant and resident behavior. For example, migrant and resident elk (*Cervus canadensis*) in Ya Ha Tinda Alberta, Canada, were not genetically differentiated (Figure 2.2, Hebblewhite et al., unpubl. data), whereas some differentiation was found between migrant and resident pronghorn (*Antilocapra americana*) in Yellowstone (Barnowe-Meyer et al. 2013). Inferences from microsatellite differentiation based on a few multi-loci (typically <20) were limited. The approach might have been improved if the determinant gene of the trait of interest was known or if new genomics approaches, such as amplified fragment length polymorphism (AFLP) markers in whole genome scans, were used (Liedvogel et al. 2011).

A second approach for establishing a genetic link for the tendency to migrate has been related to lineages of subpopulations based on mtDNA analysis or trait heritability demonstrated by studies on parents and offspring/siblings. McDevitt et al. (2009) reported that in the Canadian Rockies, the probability of being migratory was higher in individual caribou (*Rangifer tarandus*) carrying a Beringian–Eurasian haplotype, which was mainly associated with the migratory, barren-ground subspecies, compared to the typically non-migratory woodland caribou. In contrast, microsatellite data did not support this distinction, which the authors suggested resulted from interbreeding between these diverged lineages since the last glaciation. Northrup et al. (2014) also found timing of migration of individual mule deer (*Odocoileus hemionus*) from 4 distinct winter ranges in the Piceance Basin of Colorado was more coincident as pairwise relatedness and similarity in mtDNA haploid group increased. They argued the mtDNA effect reflected either a confluence of several refugial lineages identified in northwestern Colorado or was related to mitochondrial introgression, resulting in differences in mitochondrial efficiency associated with metabolic demands of migration.

A third approach to identifying the genetic basis of any behavior would have been to compare parent-offspring pairs in longer-term studies with known individuals (e.g., Gaillard 2013). To our knowledge no authors have applied this technique to address migration in ungulates. Further, few of the studies we reviewed adequately addressed alternative explanations. In the case of timing of migration in mule deer, Northrup et al. (2014) rejected sociality being a key mechanism because in their analysis, they controlled for the source of the individual's winter range and showed little spatial clustering of haplotypes among the winter ranges. Even so, disentangling body condition and social/cultural factors, which we discuss next, in correlative studies to support a genetic component for migration would be challenging and typically would require cross-fostering experiments, which may not be practical in free-ranging ungulate populations.

Learning, Culture, and Personality as a Basis for Migration

The difficulty of studying mother-offspring pairs for long periods of time that has resulted in a rarity of studies on genetically based migration has also prevented researchers from discriminating genetic mechanisms from learning and cultural transmission. For migratory animals, it is likely that information about navigation and migratory routes are passed from more experienced, key individuals to those that are less experienced (Dodson 1988, Couzin et al. 2005, Fagan et al. 2012). For example, the cultural inheritance of summer feeding locations for migratory southern right whales (*Eubalaena australis*) has extended over generations with calves learning site fidelity from their mothers during their first migrations (Valenzuela et al. 2009). However, few studies investigated the role of learning and cultural inheritance in maintaining partial migration within ungulate populations (Sweanor and Sandegren 1988, Andersen 1991*a*, Nelson 1998). Residency or migration of the first year of life is dependent on the migratory status of the parent, and in a long-term study of white-tailed deer, fawns were shown to mimic the migratory behavior of their mothers (Nelson 1998). In the case of social learning, migration does not need to be heritable to evolve (Boyce 1991), although the ability to learn and mimic migratory behavior should be at least partially hereditary (Nelson 1998). Indeed, Found and St. Clair (2016, 2017) suggest that the combination of an animal's developmental environment and genetic hardwiring predetermine its personality as an adult, making bolder individuals most likely to express year-round residency and habituation, and ultimately influencing the proportion of migrants and residents within the population.

Migration in Relation to Age and Intrinsic Condition

The *Terminal Investment Hypothesis* states that older individuals are more likely to devote more resources towards ensuring successful reproduction than younger individuals because they anticipate fewer future reproductive events (Clutton-Brock 1984, Bercovitch et al. 2009). The prediction consistent with this theory is that ungulates have a propensity to remain resident while young (avoiding the risks of migration and prioritizing their own survival), but take risks to migrate as they age because they have fewer remaining reproductive events, and migration is expected to improve access to resources (Fryxell and Sinclair 1988*a*, Albon and Langvatn 1992). However, White et al. (2007) found that pronghorn became non-migratory as they aged, and Singh et al. (2012) found that younger moose (*Alces alces*) always migrated, whereas older moose were less likely to migrate with increasing snow and road density. Evidence to support predictions of the terminal investment hypothesis could be confounded with other factors. For example, increasing costs of movement are associated with age-related changes in physiological condition (Ericsson and Wallin 2001), and home ranges may become smaller with age due to experience gained (Allen et al. 2016).

Migration may also be state-dependent if animals in good condition are willing to take more risks (Visscher and Merrill 2018). Because ungulate survival and reproductive efforts are dependent on body reserves (Cook et al. 2004, Monteith et al. 2014, Cook et al. 2016), we would expect to see the propensity to migrate closely linked to nutritional state if condition buffers consequences (Spitz 2015). Alternatively, recent evidence shows that transfer of the nutritional benefits that are normally associated with migration to residents, as can occur when irrigated agriculture supplements elk feeding, can promote resident behavior (Jones et al. 2014, Barker 2018). If individuals are able to meet their nutritional demands satisfactorily without migrating, there may be no need to migrate if it would incur additional costs related to movement, predation risk, or social conflict (see below). In fact, reproducing and migrating every other year (Morrison and Bolger 2012) may be a better strategy for ensuring survival and lifetime reproduction, and decisions surrounding migration in ungulates might be driven almost primarily by nutrition and reproductive status (e.g., Festa-Bianchet, 1988, described below).

Migration Based on Competition and Social Fences

The *Dominance or Competitive Release Hypothesis* (Ketterson and Nolan Jr. 1976, Fudickar et al. 2013) is based on intraspecific competition, with an increasing proportion of individuals expected to migrate at higher density on sympatric ranges. Although competition for food on high-density sympatric winter range is likely, competition is difficult to demonstrate directly, but it might be inferred. For example, migrating white-tailed deer (*O. virginianus*) have shown a flexible strategy in which they migrate back to summer ranges during years of little snow and good weather (Nelson 1995). Similarly, the distance migrated by elk and red deer has been shown to increase with density, suggesting avoidance of competition (Mysterud et al. 2011, Eggeman et al. 2016). Sawyer et al. (2016) also speculated that long-distance migrants may have initiated spring migration 3 weeks earlier than moderate- or short-distance migrants to escape intraspecific competition on the winter range.

Foraging at high density on allopatric ranges, especially as high-quality forage begins to emerge, may also lead to a tendency to move, similar to density-dependent habitat selection (Fretwell and Lucas 1969). According to the *Social Fence Hypothesis,* if population densities increase, migration tendency can be altered due to competition and social aggression on allopatric ranges (Matthysen 2005). Mysterud et al. (2011) reported that a lower proportion of red deer migrated at a high density, consistent with the social fence hypothesis, but the authors only contrasted areas of differing densities and did not measure variation in habitat quality which is needed to determine the level of competition. Constraints on distribution and changes in sociality and aggressive behaviors of deer would need to be documented on both sympatric and allopatric ranges as deer densities increased to support these hypotheses.

Extrinsically Driven Migration

Though difficult to distinguish whether animals are escaping reduced fitness on shared ranges versus seeking resources, the *Forage Maturation Hypothesis* predicts that migration along phenological gradients of plant development maximizes energy intake, allowing animals the advantage of spatiotemporally varying resources over a larger area or when local resources have become depleted (Fryxell and Sinclair 1988*a*, Fryxell et al. 1988, Albon and Langvatn 1992, Hebblewhite et al. 2008). Support for this hypothesis is found across a number of systems. Whereas the classic example may be the Serengeti wildebeest (*Connochaetes taurinus*) following new green growth to the plains during the wet season (Holdo et al. 2009), many cervids in temperate systems show elevational migrations tied to green up (Sawyer and Kauffman 2011, Bischof et al. 2012, Merkle et al. 2016, Aikens et al. 2017). Migrants are predicted to be heavier and in better body condition than residents as a consequence of higher-quality forage (Albon and Langvatn 1992, Hebblewhite et al. 2008), but a study by Middleton et al. (2018) on elk is one of very few examples to support this. Middleton et al. (2018) verified that female elk were fatter when they were migratory and better timed their movements with green-up. However, their conclusion was driven largely by non-lactating females (mainly migratory) with no data on release from nutritional costs associated with calf loss. Though closely tracking green-up likely does contribute to fat accumulation, their results for lactating elk (mainly residents) remained inconclusive. Even fewer have linked migration tactic to life-time reproductive fitness, which would not only require long-term studies but additionally evaluating other costs or benefits of migration. For example, White et al. (2014) reported that migratory behavior did not increase body fat but did increase calf survival as a result of refuge from predation, which we address next.

The major alternative addressed in the ungulate literature is the *Predation Risk Hypothesis*, which proposes that ungulates migrate to escape or minimize predation or other risk factors (e.g., human hunting, parasites, Fryxell and Sinclair, 1988; Hebblewhite and Merrill, 2007). Evidence supports this hypothesis that migrating ungulates reduce predation risk by moving outside of predator ranges and denning territories (Bergerud 1988) or by using terrain where predators travel less frequently (Bergerud and Page 1987). For example, pregnant bighorn (*Ovis canadensis*) ewes in Alberta moved to high-elevation summer range earlier than non-pregnant ewes. Festa-Bianchet (1988) determined the reason was related to predator avoidance just prior to lambing, as opposed to being related to forage because the ewes moved from high-quality forage to harsher, more rugged terrain consisting of lower-quality, sparse vegetation. Migrant moose on the coast of Alaska showed improved calf survival by avoiding predation but did not obtain nutritional benefits in terms of accumulation of body fat (White et al. 2014). While this study represents an important first step to understanding the costs and benefits of migratory tactics, its application is limited because the authors framed migration as an ‘either-or’ situation, to be explained by only 2 hypotheses (predation risk avoidance vs. forage maturation). However, their results demonstrate that there may be no straightforward, easy answer because the top-down benefits of avoiding risk through migration may be complicated by life history trade-offs (the cost of rearing offspring to subsequent fecundity), which may be at odd with, or modulate, the bottom-up effects of increased access to forage.

PARTIAL MIGRATION AND ITS MAINTENANCE WITHIN POPULATIONS

Historically, partial migration was simply described as a kind of within-population variation in movement behavior in which just a part of the population migrates (Lack 1943) with speculation about causation (e.g., Lack, 1943; Lundberg, 1988). Modern assessments have since evolved to include theoretical frameworks for testing hypotheses with empirical data (Kokko 2007, 2011, Lundberg 2013). Both views assume that migration results from natural selection such that the occurrence of partial migration requires the long-term balancing of Darwinian fitness between migrant and resident strategies under different ecological conditions. Such polymorphisms in life history strategies are maintained over evolutionary time only if fitness varies with population densities, environmental conditions, or similar phenomena (Swingland and Lessells 1979). More specifically, natural selection could favor the maintenance of partial migration within a population via: (1) a frequency-dependent mixed evolutionarily-stable strategy (ESS; Dingle 2014b, Swingland 1983), (2) an environmental-genetic threshold, a variant of a gene-environment interaction that accommodates changing environments (Pulido 2011), or (3) a conditional strategy in which an individual’s choice of migratory tactic varies with other aspects of phenotype or individual state (Pulido 2011, Chapman et al. 2011b, 2012; Lundberg 1987). Each of these mechanisms might prevail under different environmental conditions.

A frequency-dependent evolutionarily-stable state (ESSt) assumes that migratory behavior is fixed, and residents are favored when migrants are at a high frequency and vice versa. At some specific equilibrium frequency, the migratory and non-migratory strategies should have the same average pay-off; that is, if one strategy increases in frequency, its pay-off should decrease (i.e., fitness is negatively frequency-dependent; Dingle, 2014a; Swingland, 1983). The evolution of partial migration has been examined using frequency-dependent ESS modeling especially in birds (Lundberg 1987, Kaitala et al. 1993, Kokko 2011). However, empirical support for frequency-dependent ESSts in most species is lacking (Chapman et al.

2011*b*, Lundberg 2013), perhaps because negative frequency-dependence may be observable only when the population is at or above the carrying capacity.

Nonetheless, that migration is a fixed trait is a common assumption in many studies of large ungulates (Hebblewhite and Merrill 2011, Gaillard 2013, Middleton et al. 2013*b*). If fixed, then this would necessarily mean that the ratio of migrants and residents in a population would need to be balanced by density- or frequency-dependence in a mixed-ESS at the population level (Lundberg 1988, Kaitala et al. 1993), as described above. That is, individuals cannot change their behavior, but the relative demographic success of each separate strategy determines the relative fitness of each strategy, which then changes in some stabilizing way as densities or frequencies change. Without such a stabilizing mechanism, a population would fixate 100% in one strategy. The rarity of 'pure' migrant or resident populations itself rejects this notion.

In fact, partial migration through an ESSt can happen only if there is no switching between tactics, but switching has been reported in deer (Nelson 1995), elk (Eggeman et al. 2016), impala (*Aepyceros melampus*, Gaidet and Lecomte 2013), moose (White et al. 2014), pronghorn (White et al. 2007), bighorn sheep (Spitz 2015), and Svalbard reindeer (*R. t. platyrhynchus*, Hansen et al. 2010, Meland 2014; Table 2.3). Across the studies reviewed, the average level of annual switching was ~ 20%, although most studies had low statistical power to detect switching due to limited monitoring over the course of an individual's life. Indeed, a recent modeling study showed a minimum sample size of tracked individuals over a minimum number of years and within a minimum number of populations is required to detect such transient coexistence (Singh and Leonardsson 2014). If the results of these few switching studies are representative of the many long-lived ungulates with lifespans >10 years, this means that individuals may switch tactics several times during their lifetime.

In contrast, the environmental-genetic threshold describes a mechanism in which a number of additive, environmental variables may interact with a number of genes to contribute towards expression of an underlying phenotypic, behavioral liability (i.e., migratory tendency), or trait that is normally distributed within a population (Figure 2.3, Pulido, 2011). According to the environmental-genetic threshold model (Figure 2.3), individuals have a genetically determined propensity for migration that is triggered, or not, by environmental conditions. A threshold exists below which individuals are sedentary, whereas those above the threshold are migratory (Berthold 1991, Pulido et al. 1996). Migratory traits may not be fixed, even under strong, directional selection, because as the distribution of migratory propensity shifts below the threshold, migratory traits will not be phenotypically expressed (Pulido 2011). Individuals whose liability lies well above the threshold will migrate, while individuals whose liability is well below the threshold will not. However, environmental variables such as food, social dominance, or body condition may affect individuals with liability values close to the threshold, causing them to change migratory tactic. This conceptual model has not been used to address partial migration in ungulates, and testing its predictions would require long-term studies once the genetic basis or a correlate for migration propensity was identified. For example, Found and St. Clair (2016, 2017) reported that reduced lateralization, which was detected based on front-limb bias and reflects cerebral specialization that is associated with expressions of behavioral plasticity, was associated with elk that were 3 times more likely to migrate. Even if further work identifies genetically-controlled, regulatory pathways of complex traits linked to migration, monitoring the interaction of these traits with environmental conditions over a sufficiently long period in free-ranging ungulates remains a formidable challenge (Pulido 2011).

The alternative to genetically fixed traits or liabilities is the possibility that migration varies between individuals as a function of state, such as age, condition, or other circumstances. As discussed in the previous section, state-dependent migration may be relatively fixed intrinsically (e.g., dependent on an individual's age or sex or personality), or highly plastic based on nutritional state (e.g., fat reserves or body condition) or extrinsic conditions (e.g., predation risk, parasite loads or climate). If fitness varies temporally with environmental conditions (Rolandsen et al. 2016), and migration is the "best of a bad job" (Lundberg 1987), then fitness balancing is not necessary over the short term. In this case, the condition-dependent strategy is a single conditional strategy resulting in 2 (or more) tactics, and each individual adopts the migratory tactic that is best for it at the time (Swingland 1983), but the relative pay-offs may not be equal. For example, dominant or more competitive individuals may optimize fitness by remaining resident, whereas less competitive or sub-dominant individuals may optimize fitness by trading the cost of migration in return for a habitat where there is less competition (Swingland 1983, Lundberg 1987, Chapman et al. 2011*b*).

Consequently, both migratory and non-migratory tactics may be maintained within a population due to differential density-dependent regulation of vital rates that must counteract each other over the long term, such that any differences in reproductive success between migrants and residents must be countered by differences in survival (Figure 2.4, Gillis et al., 2008). Hebblewhite and Merrill (2011) found that despite higher pregnancy rates and winter calf weights, migratory elk were more at risk during migration. Residents reduced predation risk by remaining in areas of human activity, and had lower pregnancy and calf weights, but slightly higher adult and calf survival. Similarly, White et al. (2014) found that calf survival was higher in migratory moose, but that there was no difference in body fat accumulation between residents and migrants. Both studies were suggestive of demographic balancing between the two tactics (Hebblewhite and Merrill, 2011; White et al., 2014). Peters et al. (2018) suggested that the probability of migrating should increase under high-density conditions; with increasing density, density-dependent or environmentally-driven switching between tactics would maintain partial migration within a population (Figure 2.5). Indeed, recent evidence from elk supports the notion of density-dependent migration being a potentially stabilizing mechanism regulating partial migration in populations (Eggeman et al. 2016). On the other hand, stochastic environmental events could cause mortality for individuals following the more successful tactic, independent of density, but if the decrease in mortality is only to the level of survival of the alternative behavior, partial migration can be maintained (Grayson et al. 2011).

CONCLUSIONS AND FUTURE DIRECTIONS

Although partial migration in ungulates is likely the rule, rather than the exception (Chapman et al. 2011*b*, Avgar et al. 2014), its potential importance in maintaining migratory behavior across populations has only recently gained recognition. Migration is a complex phenomenon (Alerstam et al. 2003) determined by a number of traits, in turn determined by a number of genes, most of which contain multiple alleles (Sutherland 1998). Our current understanding of what maintains partial migration is limited because experimental studies to assess potential mechanisms in ungulates are not feasible, and in our review, we found only a handful of studies that provide sufficient long-term data to address the alternative hypotheses reviewed here. Further, our ability to make progress in understanding migration is hindered by clear, universal definitions (Avgar et al. 2014, Cagnacci et al. 2016) and classification methods (e.g., Bunnefeld et al., 2011; Naidoo et al., 2012). In fact, the longer individual white-tailed deer were monitored, the more likely they were to be classified by researchers as conditional migrants as opposed to non-migratory or obligate migrants (Fieberg et al. 2008).

The decision to migrate or not is an individualistic one, but rarely do studies examine individual decision-making in partially migratory populations (Ball et al. 2001), although the characterization of multiannual movement patterns by more than 300 moose in 10 different populations by Allen et al. (2016) provides a good example of individual-level variation both within and between populations. Instead, we found migration was too often characterized simply dichotomously at a single population level (Cagnacci et al. 2016). Migration may be viewed as a continuum (Ball et al. 2001), both in behavior (e.g., individuals may exhibit intermediate tactics or variability in timing and distance) and literally (i.e., 1 to 99% of the population may be migratory); based on our review, this means the reasons for migration were often hard to detect and characterize (Cagnacci et al. 2016). Behavioral switching between migratory tactics was mostly viewed as confusing this gradient even more, making it difficult to characterize the demographic consequences of tactic choice, rather than viewed as a mechanism of maintaining partial migration.

Linking multiple, interacting intrinsic and extrinsic variables to the occurrence of migration when there is strong environmental variation is extremely difficult (Fieberg et al. 2008). In contrast to obligate migrants in other species that show predictable movements as a result of physiological processes (neuroendocrine and endocrine systems), linking environmental cues (day length, photoperiod) to the mechanisms controlling facultative migration in highly variable environments is challenging (Ramenofsky et al. 2012). Therefore, it is no surprise that our understanding remains limited for animals that are as long-lived and as difficult to study as ungulates. We found correlative support for state- or condition-dependent migration in ungulates in our review, but relatively little empirical data, despite several indirect lines of evidence. We know that differences in habitat quality lead to corresponding differences in physiology, body condition, and reproductive success in ungulates (Weber et al. 1984, Becker et al. 2010). A good place to start, then, would be to track how an individual's habitat use promotes survival and leads to nutritional acquisition, linked to measures of body condition and reproductive success to identify fitness consequences. But the questions then become when do we take these measurements and how many times per year? Despite the obstacles, to truly understand the mechanisms driving individual migratory behavior, we need studies that track migratory traits of mothers and their offspring to separate the genetic and learned components of migratory behavior from environmental effects.

Very few of the studies we found were set up to examine how density-dependent and -independent factors could lead to a long-term demographic balancing of migrants and residents within a population. Instead, most studies on partially migratory ungulates that we reviewed were not designed to address population-level mechanisms promoting partial migration (Table 2.1). In addition, few studies explicitly tested for a genetic basis for differences in migration in partially migratory populations, and what few studies mentioned learning or cultural inheritance (Singer et al. 1981, Sweanor and Sandegren 1988, Andersen 1991*b*, Barnowe-Meyer et al. 2013) did not conduct them with detailed behavioral observations or controlled experiments to test related hypotheses.

As technology continues to develop and become more cost-effective, the difficulties in tracking individual ungulates over the long term in space and time, and in remote environments, will be overcome so that the relative fitness-related consequences of partially migratory behavior may be integratively tested (Bolger et al. 2008, Gaillard 2013). Long-term, demographic studies and population models tracking the life-history traits of co-existing residents and migrants through the seasonal (i.e., migratory and non-migratory) parts of the year will allow for calculating the costs and benefits of migration (Bolger et al. 2008). Given the potential ecological and evolutionary significance of partial migration, and that ever-increasing anthropogenic disturbance and environmental change may alter or eliminate the benefits of migration altogether (Bischof et al. 2012), understanding the genetic, environmental, and density-driven trade-offs underlying partial migration is of the utmost importance.

Table 2.1. Support (+ positive/likely, ? potentially but untested/suppositional, - negative/evidence against) for mechanisms explaining individual variation in partial migration, including genetics, learning, and state- or condition-dependence.[a]

					State- or Condition-Dependent?				
Order	**Scientific name**	**Common name**	**Genetic?**	**Learning?**	**Dominance/ competitive release**	**Forage mat./ high-quality forage**	**Pred. risk**	**Social fence**	**Term. invest.**
Antilocapridae	*Antilocapra americana*	pronghorn	+ (Barnowe-Meyer et al. 2013)	+ (Barnowe-Meyer et al. 2013)	? (Kolar et al. 2011)		- (White et al. 2007) ? (Barnowe-Meyer et al. 2010)		? (White et al. 2007)
Bovidae	*Aepyceros melampus*	impala				+ (Gaidet and Lecomte 2013)			
	Antidorcas marsupialis	springbok			? (Child and Le Riche 1969)				
	Bison spp.	bison			+ (Bruggeman et al. 2008, Kowalczyk et al. 2013)				
	Budorcas taxicolor	takin				+ (Guan et al. 2013)			
	Connochaetes taurinus	gnu, wildebeest				? (Morrison and Bolger 2012)			
	Hemitragus jemlahicus	Himalayan tahr			+ (Forsyth 1999)				
	Naemorhedus	goral							

	Ovis canadensis	bighorn sheep				? (Spitz et al. 2018)	+ (Festa-Bianchet 1988)		
	Ovis dalli stonei	Stone's sheep				+ (Seip and Bunnell 1985)			
	Pantholops hodgsonii	chiru							
	Procapra gutturosa^{b}	Mongolian gazelle							
	Rupicapra spp.	chamois, isard		? (Crampe et al. 2007)	+ (Clarke and Frampton 1991, Crampe et al. 2007)	? (Crampe et al. 2007)			
	Syncerus caffer	African buffalo				+ (Naidoo et al. 2012)			
	Taurotragus oryx	common eland			- (Hillman 1988)	+ (Hillman 1988)			
Camelidae	*Lama guanicoe*	guanaco			? (Moraga et al. 2015)				
Cervidae	*Alces alces*	moose		+ (Sweanor and Sandegren 1988, Andersen 1991*a*) ? (Singh et al. 2012)	? (Singh et al. 2012)		+ (White et al. 2014)		- (Singh et al. 2012)

	Capreolus capreolus	roe deer		? (Lamberti et al. 2004)	? (Wahlström and Liberg 1995, Mysterud 1999)	? (Ramanzin et al. 2007)	? (Wahlström and Liberg 1995, Lamberti et al. 2004)		
	Cervus elaphus	elk/red deer		+ (Jones et al. 2014)		+ (Albon and Langvatn 1992, Hebblewhite et al. 2008, Bischof et al. 2012, Jones et al. 2014)		? (Mysterud et al. 2011)	+ (Eggeman et al. 2016)
	Cervus nippon	sika deer		+ (Sakuragi et al. 2003)	? (Sakuragi et al. 2003, Takii et al. 2012)	+ (Sakuragi et al. 2003) ? (Takii et al. 2012)			
	Odocoileus hemionus	mule deer	- (Nicholson et al. 1997)			+ (Nicholson et al. 1997)	+ (Nicholson et al. 1997)		
	Odocoileus virginianus	white-tailed deer	- (Nelson 1998)	+ (Nelson 1998)		? (Brinkman et al. 2005)	? (Grovenburg et al. 2011)		
	Rangifer tarandus	caribou/ reindeer	+ (McDevitt et al. 2009)	? (Hansen et al. 2010)		+ (Hansen et al. 2010)			
Equidae	*Equus burchelli*	zebra		- (Bartlam-Brooks et al. 2013)		+ (Bartlam-Brooks et al. 2013)			
	Equus hemonius[b]	khulan							

Giraffidae	*Giraffa camelopardalis*	giraffe		? (Le Pendu and Ciofolo 1999)
Suidae	*Sus scrofa*	boar	+ (Singer et al. 1981)	+ (Singer et al. 1981)

---

[a] See Appendix A for supporting evidence for less common hypotheses.

[b] Best described as nomadic.

Table 2.2. State-dependent hypotheses to explain variation in migratory tendency.

	Driver	References	Hypothesis	Prediction in ungulates
Intrinsic	Dominance; Competitive Release	(Gauthreaux Jr. 1982, Nelson 1995, Mysterud et al. 2011)	Intraspecific competition for food predicts subordinate individuals will migrate, while more dominant individuals remain sedentary.	Increase in proportion of migrants with higher density on shared range.
	Social Fence	(Matthysen 2005, Mysterud et al. 2011)	Social constraints at high densities predict a decrease in migratory behavior.	Less and shorter migrations with higher density.
	Terminal Investment	(Clutton-Brock 1984)	Age predicts migration to obtain resources for current reproduction at expense of survival.	Increase in proportion of older migrants with higher density.
Extrinsic	Forage Maturation/ High-quality Forage	(Fryxell and Sinclair 1988*b*, Hebblewhite et al. 2008)	Phenological gradients of plant development predict migration to maximize energy intake. Rainfall effects on vegetation predict migration.	Increase in proportion of migrants in areas with altitudinal variation, with higher density, and following severe winters or during dry summers.
	Predation (or Human) Risk	(Bergerud et al. 1990, Barten et al. 2001, Skov et al. 2011)	Seasonal predation risk predicts animals should move to minimize the ratio of predation risk to potential growth.	Individuals migrate to avoid predation on vulnerable offspring, with higher predator density, but irrespective of intraspecific density. Alternatively, a predator swamping tactic results in residency because migration is costly (inverse density dependence).

Table 2.3. Reported rates of switching between migratory tactics in partially migratory populations of large ungulates.

Species	**Study Years**	**Tot. # Animals**	**Rate of Switching**	**Study**
African buffalo (*S. caffer*)	2007, 2009, 2010	11	0%	(Naidoo et al. 2012)
Elk (*C. elaphus*)	2002-2012	223	15%	(Eggeman et al. 2016)[a]
Elk (*C. elaphus*)	1989-2009	90	0%	(Middleton et al. 2013*a*)
Impala (*A. melampus*)	2002-2003	61	11%	(Gaidet and Lecomte 2013)
Moose (*A. alces*)	2004-2010	67	21%	(White et al. 2014)
Moose (*A. alces*)	2006-2008	82	6%	(Rolandsen et al. 2016)
Moose (*A. alces*)	1980-1987	36	0%	(Sweanor and Sandegren 1988)
Mule deer (*O. hemionus*)	1989-1991	23	17%	(Nicholson et al. 1997)
Mule deer (*O. hemionus*)	2007-2017	312	0%	(Sawyer et al. 2018)
Pronghorn (*A. americana*)	1999-2005	44	10%	(White et al. 2007)
Red deer (*C. elaphus*)	1999-2014	264	< 1% of females 23% of males	(Peters et al. 2018)
Roe deer (*C. capreolus*)	1999-2014	273	8% of females 9% of males	(Peters et al. 2018)[b]
Sierra Nevada bighorn sheep (*O. c. sierrae*)	2005-2013	70	33%	(Spitz 2015)
Svalbard reindeer (*R. t. platyrynchus*)	1998-2000	34	35%	(Hansen et al. 2010)
Svalbard reindeer (*R. t. platyrynchus*)	2009-2013	27	41%	(Meland 2014)
White-tailed deer (*O. virginianus*)	1994-1998	54	39%	(Sabine et al. 2002)
White-tailed deer (*O. virginianus*)	1994-1998	51	8%	(Sabine et al. 2002)[c]
White-tailed deer (*O. virginianus*)	2001-2002	77	35%	(Brinkman et al. 2005)[c]
White-tailed deer (*O. virginianus*)	2000-2007	149	20%	(Grovenburg et al. 2011)[c]
White-tailed deer (*O. virginianus*)	1992-1995	83	7%	(Van Deelen et al. 1998)
White-tailed deer (*O. virginianus*)	1975-1996	97	7%	(Nelson 1998)

[a] See also (Hebblewhite and Merrill 2011).

[b] See also (Gurarie et al. 2017, Peters et al. 2017).

[c] Considered conditional migrants: they migrated at least once, but then failed to migrate during any 1 season, or they migrated briefly within 1 season.

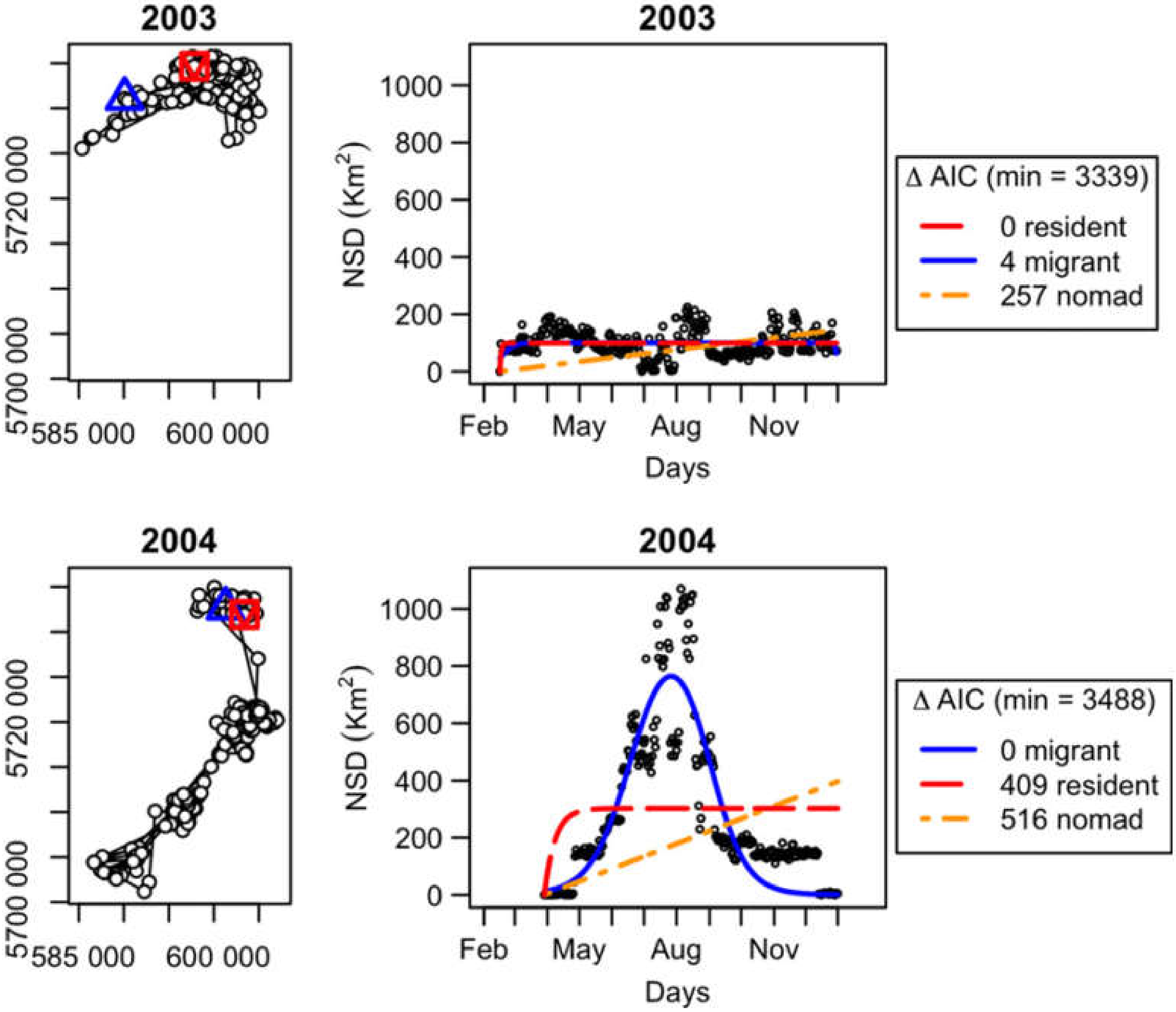


Figure 2.1. Example of classification of an animal as migrant and resident from Eggeman et al. (2016) and using the net-squared displacement method of Bunnefeld et al. (2011). The top row shows an elk in 2003 as resident, with movements within a 10-km^2 home range (coordinates are in meters, and the red square is the starting location while the blue triangle is the ending location), and NSD versus time with the model selection criteria for migrant, resident, and nomadic models. The bottom row shows the same elk in 2004, when she migrated 25 km from her winter range and was classified as a migrant.

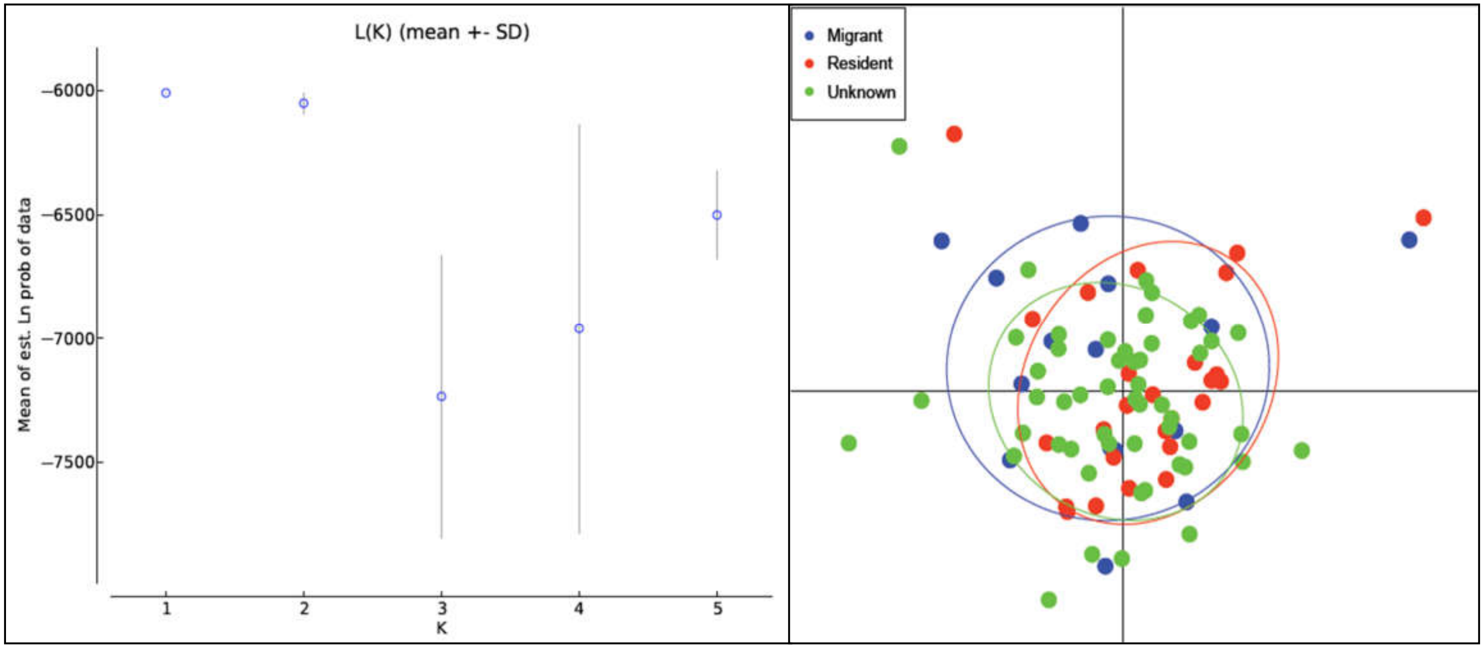


Figure 2.2. On the left, Bayesian cluster analysis in STRUCTURE of microsatellite data from 93 elk belonging to the partially migratory Ya Ha Tinda elk population, Alberta, Canada. The continuous line represents a plot of mean *Ln P* (K) versus the number of clusters (K). K = 1 has the highest value and lowest variance, revealing that all 93 elk belonged to a single genetic unit. On the right, Principal Component Analysis of the microsatellite data, showing each individual classified according to status as migratory, resident, or unknown, also showed no difference between migratory and resident elk (Hebblewhite et al., unpubl. data).

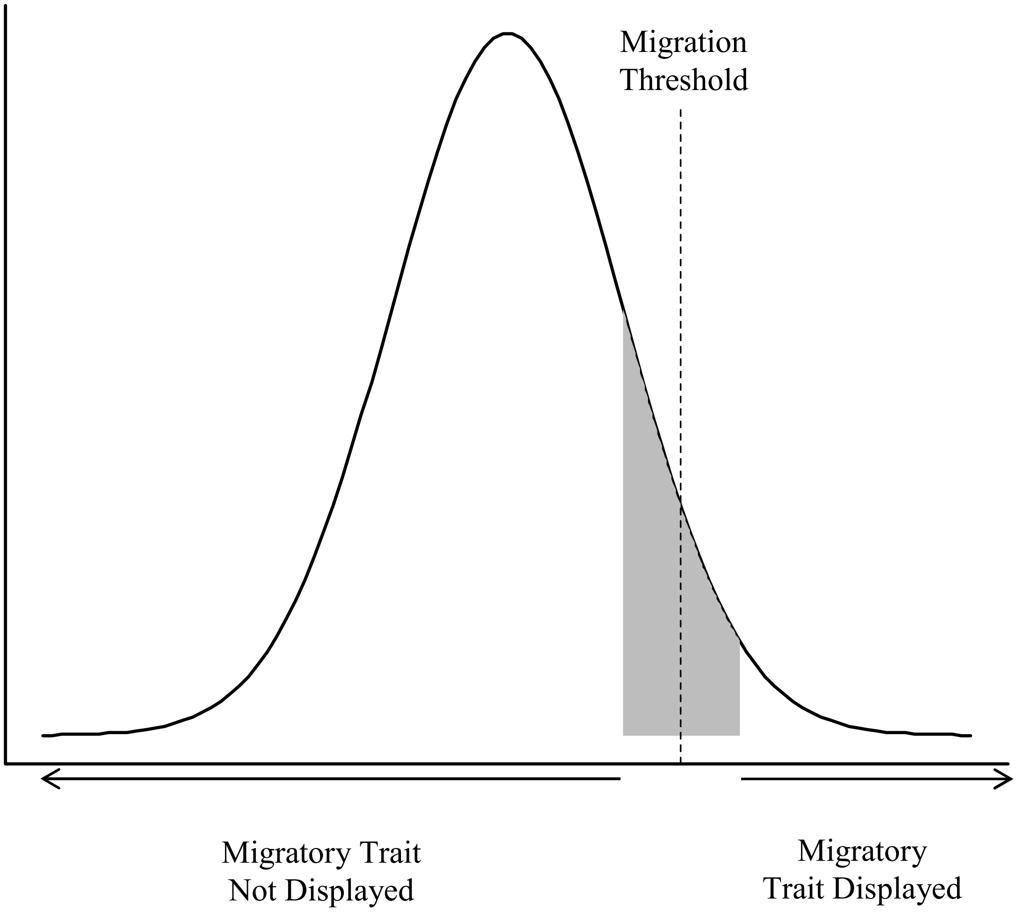


Figure 2.3. The environmental-genetic threshold model assumes that a dichotomous trait is displayed as a result of an underlying continuous character or liability (i.e., migratory tendency) that is normally distributed within a population (Pulido 2011). The combined effects of genetic influences and environmental effects on the threshold position can push a facultative migrant (represented in gray), with a liability close to the threshold, to either migrate or remain resident, depending on the direction of the environmental shift.

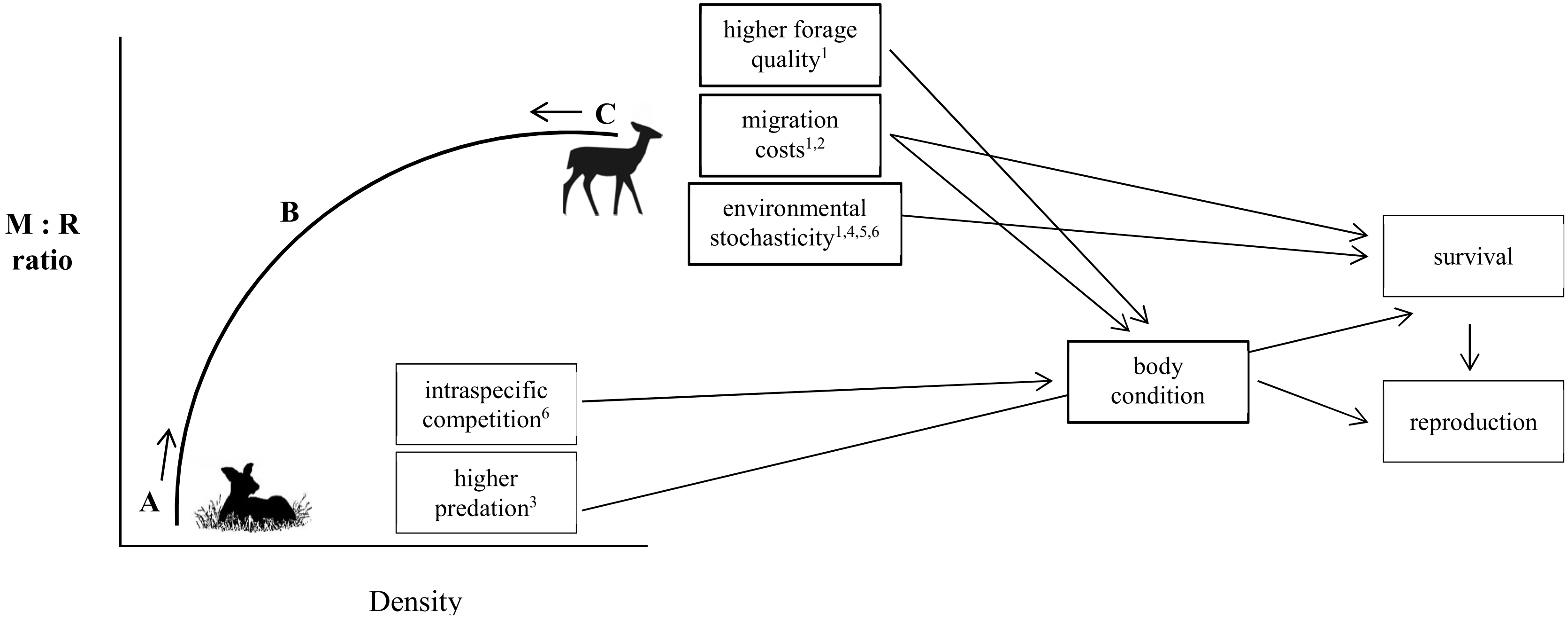


Figure 2.4. Conceptual framework depicting how the density-dependent and density-independent factors may interact on the vital rates of migrants and residents to maintain partial migration within a population. Migrants (M) may do better in one vital rate at high density, but residents (R) will do better in another vital rate at low density. This 'demographic balancing' may not happen every year, but will prevent fixation of the proportion of migrants at either 0 or 1, and provide the mechanism for the long-term average ratio of M:R in a population. **(A)** With each additional R individual, individual fitness for each R individual declines, and density dependence in predation or competition, or alternatively, stochastic climate events, shift the M:R ration back towards **(B)**, the point at which partial migration is maintained. **(C)** With each additional M individual, fitness for each M individual declines. However, very little empirical evidence to support demographic balancing is found in the partially migratory ungulate literature because most studies are not long-term, or examine only 1 or 2 vital rates: (1) Nicholson et al. 1997 found that though migratory female mule deer used higher-quality habitat than did residents, they were at higher risk of predation during migration, and had higher rates of mortality due to low precipitation (snow). (2) Hebblewhite and Merrill (2011) found that despite higher pregnancy rates and winter calf weights, migratory elk were more at risk during migration. (3) White et al. (2014) found that calf survival was higher in migratory moose, but that there was no difference in body fat accumulation between residents and migrants. (4) Middleton et al. (2013a) found that severe drought, coupled with large-carnivore recovery, reduced the migratory benefits in an elk population, while residents showed increasing recruitment and high rates of pregnancy. (5) Fieberg et al. (2008) found that the proportion of white-tailed deer migrating was positively related to winter severity. (6) Plumb et al. (2009) reported that migratory bison numbers increased with density, and annual variability in the proportion of migrants was explained by density-independent climate (snow) that limited access to forage.

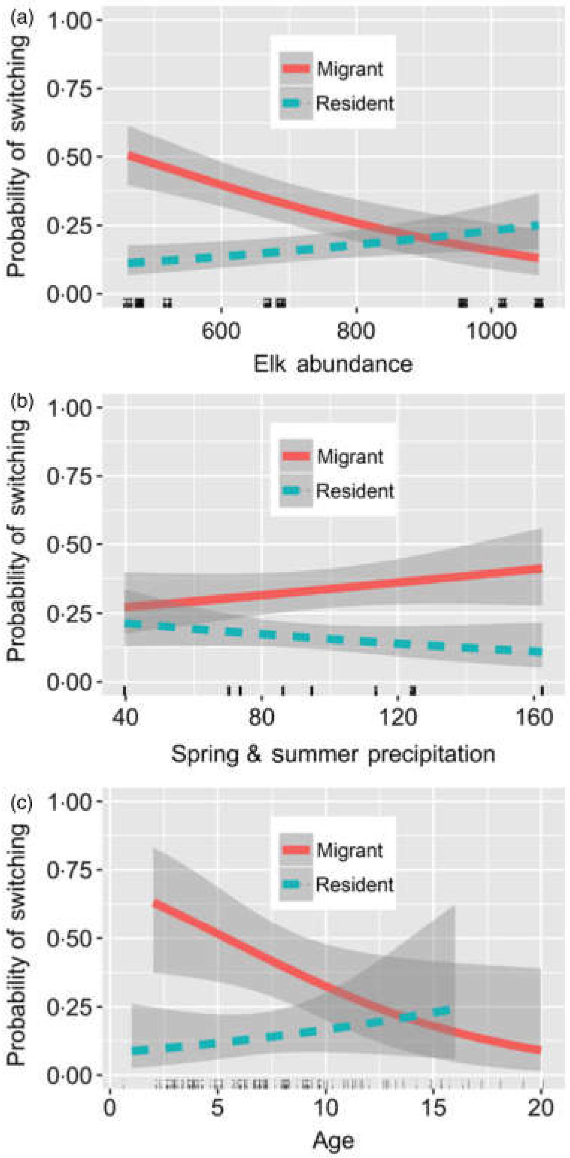


Figure 2.5. Probability of individual elk switching migratory tactics for elk in the Ya Ha Tinda elk herd, Alberta, Canada, 2002-2012 (reprinted from Eggeman et al. 2016). At top, density-dependent switching due to competition on the shared winter range occurs; at lower density, the probability of migrating decreases as more migrants (Ms) switch to resident (Rs), while Rs stay resident. At higher density, Ms tend to stay migrant, while the probability of migrating tends to increase for Rs. At middle, the probability of switching does not change for Ms with increasing precipitation as they already obtain high-quality forage, while the probability of switching for Rs decreases with increasing precipitation. At bottom, Ms are less likely to switch as they age, while Rs are more likely to maximize forage and reduce predation (terminal investment hypothesis) through migration. These opposing directions/rates of switching can lead to maintenance of partial migration within a population.

CHAPTER 3. MOTHERS' MOVEMENTS: SHIFTS IN CALVING AREA SELECTION BY PARTIALLY MIGRATORY ELK

INTRODUCTION

Migration in large herbivores is thought to be advantageous in seasonal environments when it affords prolonged access to high-quality forage and reduces predator exposure (Fryxell and Sinclair 1988*a*, Bolger et al. 2008, Mysterud et al. 2011), but in recent decades there have been dramatic declines in both migratory behavior and migratory wildlife populations across the globe (Wilcove and Wikelski 2008, Harris et al. 2009, Schuter et al. 2011). Where migration is lost, animals and their movements commonly become limited to a single seasonal range or are restricted by changes in land-use (Serneels and Lambin 2001), artificial feeding (Jones et al. 2014, Barker et al. 2018), or shifting resource availability (Post and Forchhammer 2008, Middleton et al. 2013*a*) related to habitat loss and fragmentation, which may be exacerbated by climate change (Holdo et al. 2011*b*, Tucker et al. 2018).

In the case of partial migration, a mix of residents and migrants within a population can be maintained over the long term if fitness is equal, or if individuals switch between migratory tactics (Chapter 2). However, environmental changes may alter the relative fitness and benefits to individuals following a particular existing migratory tactic or can promote new migratory patterns. For example, resident elk (*Cervus elaphus*) in the Clarks Fork population in Wyoming proportionally increased over a 21-year period due to more severe drought and predator recovery on migrant ranges (Middleton et al. 2013*a*), while long-distance migrants in the Jackson elk population decreased over a 35-year time period, likely due to changes in accessibility of hunters rather than switching between migratory tactics (Cole et al. 2015). The bighorn sheep (*Ovis canadensis*) population in the Teton Mountains of Wyoming, which was partially migratory before human development encroached on low-elevation winter ranges, has been able to persist as high-elevation residents (Courtemanch et al. 2017). Shifts in migratory behavior could result from animals following on migratory tactic dying out over time, individuals switching among tactics, or in the case of novel tactics, animals finding alternative resources that improve reproductive fitness (Cagnacci et al. 2011, Mysterud et al. 2011, Morrison and Bolger 2012, Gaillard 2013). Few studies have succeeded in directly linking underlying mechanisms to migratory shifts because long-term monitoring is required, yet an understanding of the behavioral changes that occur during these shifts could help prevent future losses in migratory behavior.

Environmental conditions of calf-rearing areas may play a key role in explaining shifts in migratory behavior of large herbivores. The large lifetime fitness costs that result from loss of offspring and the long-term cohort effects of early life development (Albon et al. 1987, Hamel et al. 2009, Douhard et al. 2013, Pigeon et al. 2017) suggest intense selection of behaviors during parturition (Bowyer et al. 1999, Bongi et al. 2008, Simard et al. 2014). Key to neonate survival is meeting necessary nutritional requirements while mitigating the risk of predation (Bowyer et al. 1999). Lactation is the most energetically demanding stage of reproduction for the mother, and cervids alter feeding behavior and activity budgets to meet nutritional demands (Clutton-Brock et al. 1982, Hamel and Côté 2008, Oftedal 2018). Daily food intake during lactation is known to influence milk production and composition (Oldham and Friggens 1989, Chan-McLeod et al. 1994, Landete-Castillejos et al. 2003). Where nutritional resources are inadequate to meet these requirements, maternal body stores can be depleted (Oftedal 2018) and calf growth depressed (Arman et al. 1974, Landete-Castillejos et al. 2001, 2003). At the same time, neonates are particularly vulnerable to predation due to their small size and limited mobility. Avoiding the risk of predation during parturition can trigger pronounced changes in behavior. For example, some species isolate themselves during parturition, which may avoid detection associated with conspecific-group detection (Vore and Schmidt 2001, Hudson et al. 2002), while others select for areas with cover to conceal their young (Bongi et al. 2008, Ciuti et al. 2009, Moorter et al. 2009, Roberts and Rubenstein 2014) or open areas with high visibility that promotes more efficient detection of predators (Poole et al. 2007, Pinard et al. 2012, Blank et al. 2015).

Selection at the scale of the calf-rearing area to balance the threat to young, while at the same time, meeting nutritional demands (Roff 1992, Stearns 1992, Bowyer et al. 1999), may be particularly important for species following the post-partum “hider strategy”. A hider neonate conceals itself away from the mother and the mother returns to feed and care for it (Lent 1974). A hider strategy is hypothesized to avoid aggressive interactions with conspecifics, improve pair bonding, and decrease detection by predators at a time when the neonate’s ability to escape is poor (Fitzgibbon 1990, Ebensperger 1998, Dwyer and Lawrence 2005). However, limited mobility also compromises the female’s ability to exploit a broader range of heterogeneity in forage conditions and makes the mother and neonate predictable in space for predators, without the associated group-benefits against predation (Lima and Bednekoff 1999, White and Berger 2001, Ciuti et al. 2009, Panzacchi et al. 2010). As a result, selection of areas that meet the requirements of both the mother and neonate would be expected to be more stringent during calving than later in the summer (Candolin 1998, Parker et al. 2009).

Because neonatal mortality in ungulates can be high, particularly when subject to predation (as much as 95%, Barber-Meyer et al. 2008), and calf mortality has a major influence on annual variation in population growth of many ungulates (Gaillard et al. 1998, Van Moorter et al. 2009), we hypothesized that differences among migrants and residents in habitat selection during the calving period may play a key role in changing patterns in migration. We tested this hypothesis with data from the Ya Ha Tinda elk population, a partially migratory population that winters adjacent to Banff National Park. The population has declined by 70% since the early 2000s and has exhibited concomitant changes in proportions of the population following different migratory tactics (Hebblewhite et al. 2006, Eggeman et al. 2016). In 2001 – 2004, the ratio of western migrants to elk remaining on the Ya Ha Tinda year-round was 3:1 (Hebblewhite et al. 2006), but over time, a new eastern migration to low-elevation (~1,400 m) industrial forest has emerged, and the ratio of western migrants to residents to eastern migrants is now ~1:10:5. Elk in this area are subject to a suite of predators. Wolves (*Canis lupus*) returned to Banff National Park in the mid-1980s (Morgantini 1995), and grizzly bear (*Ursus arctos*) populations have remained relatively stable for at least the last decade (Whittington and Sawaya 2015, Whittington et al. 2017). On provincial lands east of Banff National Park, wolves have maintained a presence but are liberally hunted and trapped, while grizzly bears were subject to limited hunting until 2008. Habitats in the area have also been subject to wild and prescribed fires (~7,000 ha) and to an increase in forest cutting with over 3,000 ha cut since 2000, primarily at low elevations (Smolko et al., in prep.).

We compared the selection patterns of migratory and resident GPS-collared elk during calving in 2002 – 2006 (early) and 2013 – 2016 (late) to assess 3 predictions related to varying forage resources and predation risk. First, we predicted that both migrants and resident elk would trade off foraging opportunities to avoid predators during calving more than during summer due to calf vulnerability. We predicted western migrants would avoid areas of high risk by grizzly bears because there is higher predation by bears on adult elk that migrate into Banff National

Park than on residents (Hebblewhite et al. 2018), whereas resident elk would avoid areas of high risk by wolves because of high year-round predation risk from wolves on the winter range (Hebblewhite and Merrill 2009). Second, because elk migrating into Banff National Park have decreased proportionally more than resident elk over the study period (Hebblewhite 2006, Eggeman et al. 2016) and grizzly bear predation appears to be density-dependent (Hebblewhite et al. 2018), we predicted that the western migrant elk would show more relaxed forage-predation trade-offs from the early period to the late period of our study than the residents. Finally, we predicted elk migrating eastward to calve on low-elevation, industrial forests are predicted to show the least trade-offs in selecting foraging areas (e.g., recent clear cut and burns) because predator scat surveys support a declining west-to-east gradient in summer predation risk for elk (Spilker 2018), which is supported by an increase in eastern migrants over time.

To test these predictions, we first modelled dates of parturition events based on elk movements, and then identified a threshold number of days post-partum that reflected an increase in the size of area used daily by elk cow-calf pairs. We used the threshold number of days since parturition date to delineate calf-rearing areas. We then compared characteristics of calf-rearing areas to 10 similar-sized areas centered on random locations of the same individual in summer. We assessed the effects of the areal extent of herbaceous-shrub cover and cut and burned land cover, mean forage abundance (g/m^2), and mean Normalized Difference Vegetation Index (NDVI) values within open areas as indices of forage abundance or quality. We used amount of forest edge and mean values of resource selection functions (RSFs) weighted by abundance of wolves and grizzly bears as measures of habitat security. If elk following different migratory tactics selected for forage resources or avoided risky areas during calving differently between the early and late time periods, this provided evidence that habitat selection during calving contributed to the observed shifts in migratory elk behaviour.

STUDY AREA

The ~7000-km^2 study area is in west-central Alberta, Canada (51º38’ N/-115º30’ W) and straddles the boundary between Banff National Park and adjacent provincial lands (Figure 3.1). Central to the study area is the Ya Ha Tinda ranch (44 km^2) that is administered by Parks Canada, though Alberta’s provincial government manages the natural resources. The Ya Ha Tinda is winter range for elk and consists of a large montane rough fescue (*Festuca campestris*) grassland (20 km^2), interspersed with bog birch (*Betula glandulosa*), shrubby cinquefoil (*Potentilla fruticosa*), and willow (*Salix* spp.) and surrounded by forest (McGillis 1977, Holland and Coen 1982). The rugged terrain of BNP lies to the west of the ranch, and across the study area, there is a west-to-east gradient that decreases in ruggedness, elevation, and predator occurrence but increases in anthropogenic activity (both industrial and recreational). The study area is a mixture of about 45% open, 15% burned, and 40% forested habitat, including lodgepole pine (*Pinus contorta*) and trembling aspen (*Populus tremuloides*) at low elevations, and Engelmann and white spruce (*Picea engelmannii and P. glauca*) and subalpine fir (*Abies lasiocarpa*) at higher elevations.

Elevations in the study area range from 1,400 – 3,500 m with long, snowy winters (Oct – Apr) and a short summer (May – Sep). Low precipitation and westerly winds (i.e., chinooks) keep the provincial lands in the eastern part of the study area mostly snow-free in winter (Holland and Coen 1982), with an average of 157 cm of snowfall. Temperatures in winter average -4.1°C and 9°C in May – September, with an average of 31.9 cm of precipitation, though during drought years, precipitation can be <10 cm in summer (Environment Canada Ya Ha Tinda weather station).

The Ya Ha Tinda elk population peaked from a maximum count of ~2,200 individuals in 1992 (Morgantini 1995), and the wintering population declined by 70% over the course of this study from 1,398 elk counted in 2002 to 450 elk in 2016 (Table 3.1, Figure 3.2). From 1977 to 1987, the majority (~90%) of the population migrated west from the Ya Ha Tinda winter range to summer at higher elevations in Banff National Park (Morgantini and Hudson 1988). However, the ratio of western migrants to residents to eastern migrants shifted from an average of 14:15:1 during the early period of 2002 – 2006 to 1:10:5 in the late period of 2013 – 2016 (Table 3.1, Figure 3.2).

Wolves recolonized the study area by the mid-1980s after extirpation by the 1950s (Morgantini 1995), and numbers have likely remained stable into the early 2000s (Hebblewhite 2006). Grizzly bear numbers range from ~5.25 bears/1000 km^2 outside Banff National Park (Alberta Environment and Parks 2016) to ~12.4 – 15.1 bears/1000 km^2 inside the park (Whittington and Sawaya 2015, Whittington et al. 2017) and keep black bears (*U. americanus*) at moderately low densities (Alberta Environmental Protection 1993). Other main predators of elk in this system include coyotes (*C. latrans*) and cougars (*Puma concolor;* Morgantini 1995), which have increased in the last several decades (Knopff et al. 2014). Ungulates other than elk include white-tailed (*Odocoileus virginianus*) and mule deer (*O. hemionus*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus*, though mostly in Banff National Park, Stelfox 1993, Morgantini 1995). Plains bison (*Bison bison*) were extirpated by the 1870s but were recently reintroduced in 2018 (Soper 1941, Parks Canada 2017).

METHODS

Elk Capture, Monitoring, and Migration

We captured and fit adult female elk with GPS radiocollars (Lotek Wireless, Inc., models 2200, 3300, 4400, or 7000) during winter from 15 January to 31 March from 2002 to 2016 on the Ya Ha Tinda winter range. We did not use data from elk collared during 2007 – 2012 because collaring focused on resident elk and the number of collared migrant elk was limited. We used corral traps baited with hay, helicopter net gunning, or ground darting from horseback to capture and collar elk (University of Alberta Animal Care Protocol nos. 353112, 611812, 611912, 611/11/11, 611/11/13, 00000624). We immobilized elk from horseback with medetomidine and Telazol® by riding into the population and darting at a distance of 20 – 25 m. At capture, we determined pregnancy through rectal palpation or from elk blood serum (Huang et al. 2000, Duquette et al. 2012).

Pregnant elk captured in 2013 – 2016 were fit with small vaginal implant transmitters (VITs; Advanced Telemetry Systems, Inc., model M3960) to allow birth sites to be precisely located. We used VHF telemetry to monitor maternal elk and their VITs ≥2 – 5 times daily mid-May to mid-July; when a VIT was expelled, a ground crew located the birth site and recorded GPS coordinates of the birth site. Time of birth was determined to the nearest half hour through a code emitted by a Precise Event Transmitter (PET).

We used a combination of net-squared displacement (Bunnefeld et al. 2011, Spitz et al. 2017) and spatial rules to classify GPS-collared elk as migrants or residents in a particular year. Elk were classified as resident only if they remained within 15 km of the YHT winter range during calving and summer, and elk were migrants if they spent a minimum of 30 days on summer range >15 km from the winter range and calved off the Ya Ha Tinda winter range. Western migrants were those elk that migrated from the winter range to summer at higher elevations adjacent to the winter range, or within BNP, either along the front ranges of the Dormer, Panther, Clearwater, and Red Deer River drainages or in the Lake Louise area of western BNP. Eastern migrants migrated to lower elevations along the Red Deer River east of the YHT winter range.

Modeling Calving Date

We used 60 elk birth events from 1 May to 15 July, 2013 – 2016, and the associated 2-hr movement data from GPS-collared, pregnant elk to build a model for predicting the date of parturition using a random forest (RF) algorithm in program R (rfUtilities package; Evans et al. 2011, R Core Team 2017). An advantage of the RF method is that it can grow an ensemble of many classification trees, each developed from predictor variables, improving predictive accuracy over an individual model (Hastie et al. 2009, Severson et al. 2017). We included 180 variables in the RF as possible covariates: 5 descriptive statistics (mean, median, standard deviation, maximum, and total sum) for each of 6 movement statistics (step lengths, relative turning angles, absolute turning angles, Euclidean displacement, and parallel and orthogonal variances) over 6 moving-time windows (4, 24, 48, 96, 192, and 216 hr). Parallel and orthogonal variance were calculated by constructing dynamic bivariate Gaussian bridges (DBGBs) using the R package move (Kranstauber and Smolla 2016). DBGBs relax assumptions of the standard Brownian Bridge Movement Models (BBMMs) by separating variance in movement into forward and right angle components, which can better capture changes in animal behavior (Kranstauber et al. 2014).

Our approach followed Evans and Cushman (2009) and Murphy et al. (2010) by first identifying the most informative candidate variables among the movement statistics calculated for the 60 calving events (rf.modelSel function in the rfUtilities package). We then produced the final predictive algorithm from 1000 bootstrapped RF models constructed from the covariates retained during the first stage of covariate selection. In each bootstrap iteration, 20% of the data (n = 12 elk-years; i.e., out-of-bag sample) were randomly selected and withheld to assess model robustness. A RF model using the remaining 80% (n = 48 elk-years) was constructed and used to predict a parturition date for the withheld 20%. After the 1000 iterations, a distribution of predicted parturition dates was obtained for each parturition event, and we used the median of this distribution to predict the final date of parturition.

We applied the final RF model to GPS data from 58 elk with unknown parturition dates; elk pregnancy was unknown for 7 of the predicted dates, but we assumed these elk were pregnant based on 86% pregnancy rates in 2002 – 2016. Eleven elk from early in the study period (2002 – 2006) had 6-hr instead of 2-hr fix rates in either early May or July (Appendix D). We removed GPS data from the first week of May for 4 of these elk, the first 2 weeks of May for 7 elk, and during at least one 24-hr period in July for 5 elk to prevent gaps in the data from creating spurious movement statistics.

Calf-Rearing Areas

We assessed selection by elk during calving compared to summer first by defining movement-based calf-rearing areas identified by a threshold in the length of time after birth that movements remained localized. We used 73 known and 58 predicted dates of calving (n = 131). We used the GPS locations of the elk to derive daily 95% utilization kernels using the plug-in method for the smoothing factor in the ks package in program R (Duong 2018). We plotted the average of the daily 95% UDs against the number of days since calving to identify a temporal breakpoint between the expanding size of the area used by elk cow-calf pairs as calves gained mobility and the asymptote of area used by elk cow-calf pairs daily throughout summer. The breakpoint and corresponding threshold of days were identified using a piecewise or broken stick regression model (Johnson et al. 2002) in the R package segmented (Muggeo 2008).

Elk Selection and Use during Calving

We assessed elk selection of calf-rearing areas by comparing characteristics of areas used by individual elk during calving to areas they used in summer (second order selection *sensu* (Johnson 1980) using a matched-case design within the same year. This approach is similar to a latent selection difference (LSD, Mueller et al. 2004, Latham et al. 2011, Erickson et al. 2014), where we interpret selection coefficients as the relative difference between the calving and post-calving (summer) periods (Latham et al. 2011). We matched an elk's calving area with 10 available circular areas of the same size that were centered on randomly selected GPS locations from the post-calving period (i.e., after the threshold number of days for calving up to 31 August). We derived beta coefficients for the exponential model (Fortin et al. 2005, Avgar et al. 2016) using conditional logistic regression within the survival package in R (Therneau 2015).

To avoid collinearity (correlation $|r| \geq 0.60$) and prevent overfitting, we followed the approach of Hosmer et al. (Hosmer et al. 2013) by assessing metrics for model inclusion with univariate analyses and considered further only covariates having a *P* value <0.250 when evaluated with likelihood ratio chi-square tests (Pinard et al. 2012, Hosmer et al. 2013, Appendix I). We ranked top models including covariates and their interactions based on Akaike's Information Criterion adjusted for small sample size (AICc) and model weight.

We then compared whether characteristics of calf-rearing areas found in the final top models differed between calf-rearing areas in the 3 regions of the study area and between the early and late time periods using Kruskal-Wallis with Dunn's (1961) Bonferroni adjustment for multiple comparisons.

Environmental Covariates

Covariates were measured on 30 x 30-m resolution and values averaged within a calving area. Prior to analysis, covariates were centered and standardized using the mean and SD across years and elk.

Forage greenness and forage biomass. — We used Normalized Difference Vegetation Index (NDVI) from a 250-m resolution MODIS platform to reflect greenness of herbaceous forage, which we interpreted as metric of forage quality in open-canopy areas (Appendix F) because these areas provide the greatest biomass in summer, and herbaceous biomass comprises the greatest proportion of elk diet until September (Hebblewhite 2006*a*: Tables A2.5a and A2.11). We used the NDVI values closest to the parturition date of individual elk and averaged the values across open habitat within the calving area.

Similarly, we used total forage biomass (g/m^2) in open-canopied areas at time of calving (Appendix F), which was averaged across open areas within the calving area. We estimated forage biomass spatially with the dynamic forage model of Hebblewhite et al. (2008). Hebblewhite et al. (2008) estimated forage biomass at the annual peak (~1 Aug) in 2002 – 2004 using a general linear model to estimate herbaceous and shrub biomass at a 30-m^2 resolution as a function of year, land cover type, elevation (m), aspect (°), and distance to the continental divide (km) based on field sampling along transects at 983 sites (Hebblewhite et al. 2008). We compared May – July precipitation for the years 2005 – 2016 to that which occurred in 2002 – 2004 because 2002 had average (180 mm) precipitation, 2003 had low (167 mm) precipitation, and 2004 had high (319 mm) precipitation, and we used the peak biomass estimate from the year that was most similar because there was a year effect of May – July precipitation on total biomass (herbaceous + shrub). Precipitation data were obtained from the Alberta Climate Information Service (ACIS, http://www.agric.gov.ab.ca). We adjusted annual changes in forage availability resulting within areas burnt or from timber harvested assuming biomass reached pre-disturbance after 15 years post-harvest or post-fire. We used forage growth models derived by Smolko (2014) in the study area for burned areas and by Visscher et al. (2009) for stands aged 1 – 20 years in an area immediately north of the YHT. Herbaceous and shrub biomass were estimated separately then summed to total biomass. Areas burned since 2002 with date of burn origin were obtained from Banff National Park's fire database and Sundre Forest Products, Sundre, AB.

The forage biomass available to a particular animal at the time of location was adjusted phenologically from peak biomass in a particular year using the ratio of $NDVI_i$ to the maximum mean ($NDVI_{max}$) from the nearest 16-day period to the peak NDVI in open-canopied areas (Hebblewhite et al. 2009).

Land cover types. — We used a land cover map derived from LANDSAT-TM (Franklin et al. 2001) to classify 16 vegetative land cover categories (Hebblewhite 2006). The land cover map was updated each year of our study with new burns and forest cuts, and old burns and cuts (>15 yr) were reclassified to moderate-cover conifer forest. We combined herbaceous, shrub, alpine herbaceous, and alpine shrub habitat into one category (Herb-Shrub), and burned forest, grassland, and shrub <15 yr into another category (Burn). We expressed the extent of these land cover types, the amount of regenerating forest <15 yr (Cut), and the amount of edge (Edge, defined by the linear border between open and closed habitats, buffered by 50 m to each side) as the percentage of each calving area.

Predation risk. — We modeled predation risk to elk by wolves (Wolf) based on the work of Hebblewhite and Merrill (2007) and by grizzly bears (Bear) based on the work of Nielsen (2005, 2007; Appendix G). Wolf predation risk was estimated by multiplying the population-level resource selection function (RSF) from collared wolves in 2002 – 2004 and the spatial density of wolves adjusted by kill rate/pack/day (Thurber et al. 1994) to derive annual probability density functions (PDFs). We extended the wolf RSF estimates to 2005 – 2016 by incorporating annual changes in land cover and distance to edge. Spatial density for each pack was calculated as the product of wolf distribution (KDE) and kill rate (Y). Kill rates were estimated from annual estimates of pack size (X) as: $Y = 0.385 \times [1.000 - 0.726^{X}]$, (Thurber et al. 1994). Where annual estimates of a pack size were missing in a certain year (n =18 pack size-years), we used the mean size of all wolf packs in 2002 – 2016 (i.e., 6.4 ± 1.4). We summed PDF values in areas where wolf packs overlapped, while for areas outside pack boundaries (<5%) that were used by elk, we assumed PDFs were the mean of those from the nearest wolf boundary. The final PDFs were multiplied by the wolf RSFs to create the population-level predation risk models for 2002 – 2016.

Grizzly bear predation risk to elk was estimated based on an RSF derived from location data of 11 GPS-collared bears from 1999 – 2006 during the hypophagia (1 May – 15 Jun) and early hyperphagia (16 Jun – 31 Jul) stages (Nielsen 2005, 2007). The RSF values were estimated based on forest canopy, land cover type, terrain features, and human use. Bear RSF values were predicted for 2013 – 2016 based on updated land cover layers (G. Stenhouse, pers. comm.). Spatial density of grizzly bears was based on density estimates inside BNP from 2006 – 2008 and 2012 – 2014 and on provincial lands outside BNP from 2005 that indicated grizzly bears in BNP were ~2.62 times higher than outside the park. We used a linear decline to smooth the density estimates along the park border with a moving window the same size as a female grizzly's average home range, 520 $\text{km}^2 \approx 12.9$-km radius, Stevens 2002) which was centered on the park border. We then multiplied the annual RSFs by the PDF.

Finally, we tested for correlation between the telemetry-based RSFs and RSFs created from wolf and bear scat locations (Spilker 2018), and also compared the predation risk values at 740 locations of wolf scat and 373 locations of grizzly bear scat with wolf and bear predation risk measured at 1,000 randomly-generated locations (Appendix G).

RESULTS

Parturition Dates

Step length over long time windows and parallel variance over shorter time windows had the greatest influence on determining parturition date based on importance values (Appendix D). The RF model predicted 31 of the 60 dates used for modeling birth date to the exact day, and 22 of the remaining 29 dates predicted within 1 day of the actual date of calving. The mean number of days between the calving dates predicted by the RF model and the observed day of calving was -1.43 ± 0.85 days ($n = 60$, Figure 3.3). Dates of parturition for the 73 known births occurred between 14 May and 11 July, and between 8 May and 29 June for the 58 predicted parturition dates (Figure 3.4). The median parturition date (including known and predicted) for eastern migrants (27 May, $n = 26$) was earlier than the median parturition date of western migrants during the early (6 June, $n = 17$, Kolmogorov-Smirnov $D = 0.44$, $P = 0.04$) and late periods (4 June, $n = 15$, K-S $D = 0.44$, $P = 0.05$), and residents in the early (5 June, $n = 18$, K-S $D = 0.54$, $P = 0.004$) but not the late period (30 May, $n = 55$, K-S $D = 0.16$, $P = 0.78$). The median parturition date did not differ between the early and late periods for western migrants (K-S $D = 0.24$, $P = 0.75$), but was earlier for residents in the late period compared to the early period (K-S $D = 0.42$, $P = 0.02$).

Calf-rearing Area Delineation and Size

We identified a 26-day (± 2.03 *SE*) period during which movements increased more dramatically after birth before reaching an asymptote (piecewise regression $R^2 = 0.91$, $n = 73$, Figure 3.5a). The 26-day threshold did not change when the predicted births were added ($R^2 = 0.88$, Figure 3.5b). We used this threshold to delineate 26-day calf-rearing areas that averaged 8.24 ± 4.67 km^2 for known births and 14.18 ± 10.98 km^2 for predicted births; the distributions did not differ between known and predicted births (K-S $D = 0.5$, $P = 0.39$) and the calf-rearing areas averaged 10.87 ± 8.59 km^2 (range 0.42 – 46.53 km^2) across all elk. Calving areas of resident elk in the early (14.68 ± 7.27 km^2) and late (10.80 ± 6.95 km^2) periods did not differ whereas calving areas of western migrants in the early (14.95 ± 14.87 km^2) period were larger than in the late (9.20 ± 9.57 km^2) period. Eastern migrants had the smallest calving areas (6.66 ± 2.93 km^2, Kruskal-Wallis $\chi^2 = 20.28$, $P = 0.0004$).

Selection During Calving

Forage variables that were linearly or non-linearly related that were not entered into the same models of selection included forage biomass and NDVI because forage biomass was adjusted for phenological changes based on NDVI, and forage biomass and extent of burn or herbaceous-shrub cover because non-forested areas had the highest forage biomass (Hebblewhite et al. 2008, Robinson et al. 2012).

Western migrants during the early period selected for calving areas with a large extent of herbaceous-shrub cover, particularly where NDVI values were high (i.e., positive herb-shrub × NDVI interaction, Table 3.2). In the late period, western migrants showed similar selection during calving compared to summer, except they increased their selection for areas with greater extents of burned land cover. During both periods, selection for these forage resources was associated with high predation risk by bears. Resident elk also selected for calving areas with a high extent of herbaceous-shrub cover and high mean NDVI values but avoided areas of high edge densities. Further, in the early period, elk were associated with areas selected by bears, whereas in the later period, elk also selected for forest clearcuts, which bears also selected for (Nielsen 2005, 2007).

Finally, elk that migrated east of the Ya Ha Tinda winter range in the later period also selected areas for calving areas with a larger extent of herbaceous-shrub cover and high NDVI values compared to summer ranges, in addition to burned and cut forest areas (Table 3.2). At the same time, eastern migrants avoided areas of high predation risk by wolves more strongly during calving than during summer, and as predation risk by wolves increased, selected for greater extents of cut forest (Table 3.2).

Calving Areas of Migratory Tactics

The amount of herbaceous and shrub cover used in calving areas differed between migratory tactics (Kruskal-Wallis $\chi^2_4 = 41.71$, $P < 0.0001$). There were higher amounts of herbaceous and shrub cover in areas used by resident elk in both the early and late periods than western migrants, whereas eastern migrants had the lowest amounts of herbaceous and shrub cover in calving areas (Dunn’s Bonferroni $P < 0.05$, Figure 3.6, Appendix I). In contrast, eastern migrants had the highest amount of edge habitat and cut forests comprising their calving areas, and elk using all 3 migratory tactics had a higher amount of burned habitat in their calving areas during the later period compared to the earlier period (Dunn’s Bonferroni $P < 0.05$, Figure 3.6, Appendix I). Differences in forage biomass in open areas used during calving by the different migratory tactics (Kruskal-Wallis $\chi^2_4 = 21.59$, $P = 0.0002$) were consistent with the extent of herbaceous and shrub areas, except forage biomass in calving areas also reflected greater use of cut forests and burns (Figure 3.6). NDVI values in calving areas of western migrants and residents did not differ in either time period but were higher during the early period than during the late period, respectively (Dunn's Bonferroni $P < 0.05$, Figure 3.6, Appendix I). During the late period, calving areas of eastern migrants had NDVI values that were non-significantly higher than both the western migrants and residents (Dunn's Bonferroni $P > 0.05$, Figure 3.6, Appendix I).

Predation risk in calving areas differed between migratory tactics for both wolves (Kruskal-Wallis $\chi^2_4 = 81.36$, $P < 0.0001$) and grizzly bears (Kruskal-Wallis $\chi^2_4 = 80.29$, $P < 0.0001$). Wolf risk was higher in calving areas of resident elk than western or eastern migrants in both time periods (Dunn's Bonferroni $P < 0.05$, Figure 3.6, Appendix I). Predation risk from bears was highest in the calving areas of western migrants during both time periods, followed by calving areas used by residents both in the early and late periods, and lowest in calving areas of eastern migrants (Dunn's Bonferroni $P < 0.05$, Figure 3.6, Appendix I).

DISCUSSION

As migratory behavior and migratory populations of ungulates across the globe continue to face challenges (Berger et al. 2008, Bolger et al. 2008, Harris et al. 2009), our comparison of elk using different migratory tactics indicates that differential exposure to factors on calving areas may play a key role in explaining these shifts. Between the 2 time periods of our study, we observed a decreasing shift in the proportion of elk migrating west (~45% decline) whereas residents (~5%) and eastern migrants (~70%) increased based on data of collared elk (Killeen et al. 2016: Table 1). We found strong patterns in habitat selection for forage resources during the critical time elk isolate themselves to calve that likely facilitated their ability to meet nutritional needs (Clutton-Brock et al. 1982, Hamel and Côté 2008, Oftedal 2018). At the same time, we found lack of support that elk traded forage resources within calving areas to avoid predation risk, despite elk calves being immobile and presumably vulnerable (Testa 2002).

Ungulate migration is thought to be advantageous when it affords access to high-quality forage (Sawyer and Kauffman 2011, Bischof et al. 2012, Merkle et al. 2016). In both the early and late periods of our study, maternal elk using all migratory tactics consistently selected more strongly for key metrics of forage resources during calving than summer. During calving, elk selected not only for high NDVI reflecting areas that were greening up early, but for large extents of open, non-forested habitat such as herbaceous-shrub cover, burned, and cut forests, regardless of migratory tactic. During the early growing season, there may be greater small-scale heterogeneity that elk following all migratory tactics can take advantage of compared to summer.

In contrast to patterns of selection during calving, early work from 2002 – 2004 that focused primarily on summer at Ya Ha Tinda showed that westward migration to high elevations increased the duration of access to higher-quality forage and resulted in higher pregnancy and calf weights in winter, but by remaining on winter range year-round, resident elk traded off the benefits of migration in terms of forage quality (Hebblewhite and Merrill 2011). However, using areas of higher forage biomass may have allowed residents to forage more selectively to meet nutritional requirements (Hebblewhite et al. 2008, Hebblewhite and Merrill 2009).

During calving, contrary to our predictions, we found only limited evidence that elk traded off forage to avoid predation risk. Instead, the strong selection for foraging areas may have exposed migratory tactics to different levels of predation risk. Western migrants were likely exposed to risk of bear predation because resource selection analyses indicated bears in the study area also selected for shrubby, herbaceous areas during May and early June (Nielsen 2005, 2007). By isolating themselves to calve, many resident elk used areas immediately adjacent to the Ya Ha Tinda ranch, which put them at higher risk from wolves and farther from the human-derived refuge associated with ranch activities that wolves avoided during the day (Hebblewhite and Merrill 2009). To potentially compensate, resident elk also avoided areas of forest edge, which both wolves and cougars are known to use to stalk their prey (Holmes and Laundre 2006).

Eastern migrants selected more strongly for burns and clearcuts during the calving period. Herbaceous forage after fires and forest cutting usually provides enhanced forage productivity (Sachro et al. 2005, Hebblewhite et al. 2009, Smolko 2014), although nutrient pulses may be short-lived (Singer and Harter 1996). Even if nutrient levels are unaffected, an earlier green-up in spring can result in better condition of elk (Singer and Harter 1996). For example, elk feeding (measured by bite count) was 3 times greater in burned than unburned aspen forest in southeastern Idaho (Canon et al. 1987). The positive interaction between selection for cuts, even under predation risk from wolves, may reflect that compared to herbaceous-shrub and burned areas, downed logs in clearcuts make travel more difficult for wolves compared to elk (Mao et al. 2005, Forester et al. 2007, Mech et al. 2015) or that regenerating vegetation provides the necessary cover for hiding elk. The active land management created cover-forage combinations that may have provided small-scale refuges from wolf predation compared to the more contiguous open areas that existed on the Ya Ha Tinda and within Banff National Park. The small predator refuges were possibly made more effective by human activity that increases each May, particularly on motorized trails (Hebblewhite and Merrill 2008, 2011, Rogala et al. 2011). In addition, direct, human-caused wolf mortality from legal trapping and hunting for up to 10 months each year and some illegal harvest the rest of the year (Hebblewhite 2006) may have strengthened wolf avoidance of the eastern study area (Theuerkauf et al. 2003). Indeed, past work and recent scat surveys indicated wolves avoided motorized roads and trails in the east (Hebblewhite and Merrill 2008, MacAulay 2018, Spilker 2018). In contrast, cougars used roads and trails and forest edge to take advantage of both adult and juvenile elk (Chapter 4, MacAulay 2018, Spilker 2018).

To understand patterns of selection during calving relative to summer, we used the knowledge that ungulates exhibit an abrupt drop in movement rates at parturition (Vore and Schmidt 2001, DeMars et al. 2013) to infer parturition dates. We found our approach accurately predicted parturition dates to within ~1.5 days (Figure 3.3), but our approach differed from other approaches by using data only from elk known to be pregnant, or assumed pregnant with convincing information, rather than predicting whether parturition occurred or not for all elk per se. Therefore, our approach and results are not directly comparable, but could be considered a "next step" to the parturition-prediction methods used on elk by Dzialak et al. (2011) and on woodland and barren-ground caribou (*Rangifer tarandus caribou* and *R. t. granti*) by DeMars et al. (2013), Bonar et al. (2018), and Cameron et al. (2018). The accuracy of our predictions is likely due to our use of VITs to determine the exact date of birth rather than aerial surveys and/or field observations (i.e., predictions are restricted to time intervals between observations that took place days apart), which can only coarsely determine when parturition occurred. The ability to predict parturition dates then allowed us to use movement data after parturition to define calf-rearing areas. We found elk used localized movement for ~26 days, which is approximately the time to peak lactation in elk (Carl and Robbins 1988, Oftedal 2018). As maternal females approach peak lactation, the demand for more forage resources to meet energetic demands may require increased movements by elk cow-calf pairs, which may also correspond to the need for social grouping to protect more active, mobile young (Altmann 1952, Lent 1974, Testa et al. 2000, Paquet and Brook 2004).

We did not study calf survival of western migrants directly due to the remoteness of the area (Chapter 4), but past data based on mark-resighting of individually-marked adult females with their calves indicated calf survival was lower for the western migratory tactic compared to residents (Hebblewhite and Merrill 2011, Eggeman 2012). In addition, Hebblewhite et al. (2018) reported that adult elk migrating into Banff National Park experienced higher mortality from grizzly bears but not wolves in summer during 2002 – 2014. We hypothesize that high predation on elk by bears early in the growing season in Banff National Park is contributing to the decline in western migrants and also that overlap in use may contribute to the fact that bear predation was found to be weakly density-dependent in the Ya Ha Tinda elk population, whereas wolf predation was not (Hebblewhite et al. 2018).

Migration is generally predicted to be a beneficial tactic for maximizing access to seasonally available forage, but the interaction between predation pressure and nutritional gain may alter the benefits of a particular movement tactic, rendering it no longer as favorable. Our results indicated that by migrating into Banff National Park to take advantage of high-quality forage during calving, elk predisposed their calves to higher predation when bear predation on elk calves appeared to be at its greatest (i.e., early in the calving period, Chapter 4). In contrast, the number of elk that migrated to low-elevation, industrial lands east of the Ya Ha Tinda increased since about 2011. Although eastern migrants also selected for forage resources, they directly avoided and experienced lower exposure to predation risk compared to the other migratory tactics, suggesting shifts in human-induced refuge from predation can contribute to emergent migratory behavior.

Table 3.1. Number of collared elk used in comparing selection of calf-rearing and summer areas between 3 migratory tactics and 2 time periods (early: 2002 – 2006 and late: 2013 – 2016) in the Ya Ha Tinda elk population, Alberta, Canada, 2002 – 2016.

Year	Western Migrants	Residents	Eastern Migrants
2002		1	
2003	5	1	
2004	7	5	
2005	1	5	
2006	4	6	
…			
2013	2	12	3
2014	3	13	7
2015	4	11	4
2016	6	19	12
Total	32	73	26

Table 3.2. Top models indicating latent selection differences between calf-rearing areas and areas used during summer by migrant and resident elk in the Ya Ha Tinda population during 2002 – 2006 and 2013 – 2016 in Alberta, Canada. Predation variables included wolf (Wolf) and bear (Bear) resource selection function values, and habitat characteristics included % herbaceous or shrub (Herb/Shrub), % edge (Edge), % burned (Burn), % cut (Cut), forage greenness measured by Normalized Vegetation Difference Index (NDVI), and forage biomass available (g/m^2; Forage).

Time Period	Migratory Tactic	Parameter ($\beta \pm SE$)	
2002 - 2006	Western	Bear	**2.48 ± 0.79**
		NDVI	**1.68 ± 0.55**
		Herb-Shrub	**2.87 ± 0.93**
		NDVI x Herb-Shrub	**1.88 ± 0.72**
	Resident	Bear	**2.21 ± 0.95**
		NDVI	**3.32 ± 1.23**
		Herb-Shrub	**1.50 ± 0.69**
		Edge	**-2.94 ± 1.25**
2013 - 2016	Western	Bear	**1.28 ± 0.47**
		NDVI	**1.06 ± 0.46**
		Herb-Shrub	**1.49 ± 0.69**
		Burn	1.20 ± 0.66
	Resident	NDVI	**2.10 ± 0.40**
		Herb-Shrub	**0.94 ± 0.23**
		Edge	**-0.88 ± 0.31**
		Cut	6.59 ± 3.59
	Eastern	Wolf	**-3.30 ± 1.63**
		NDVI	**1.51 ± 0.74**
		Herb-Shrub	**3.51 ± 0.81**
		Burn	**0.95 ± 0.42**
		Cut	**2.42 ± 0.84**
		Wolf × Cut	**2.19 ± 1.11**

Notes: Coefficients for which the 95% CI did not overlap zero are shown in bold.

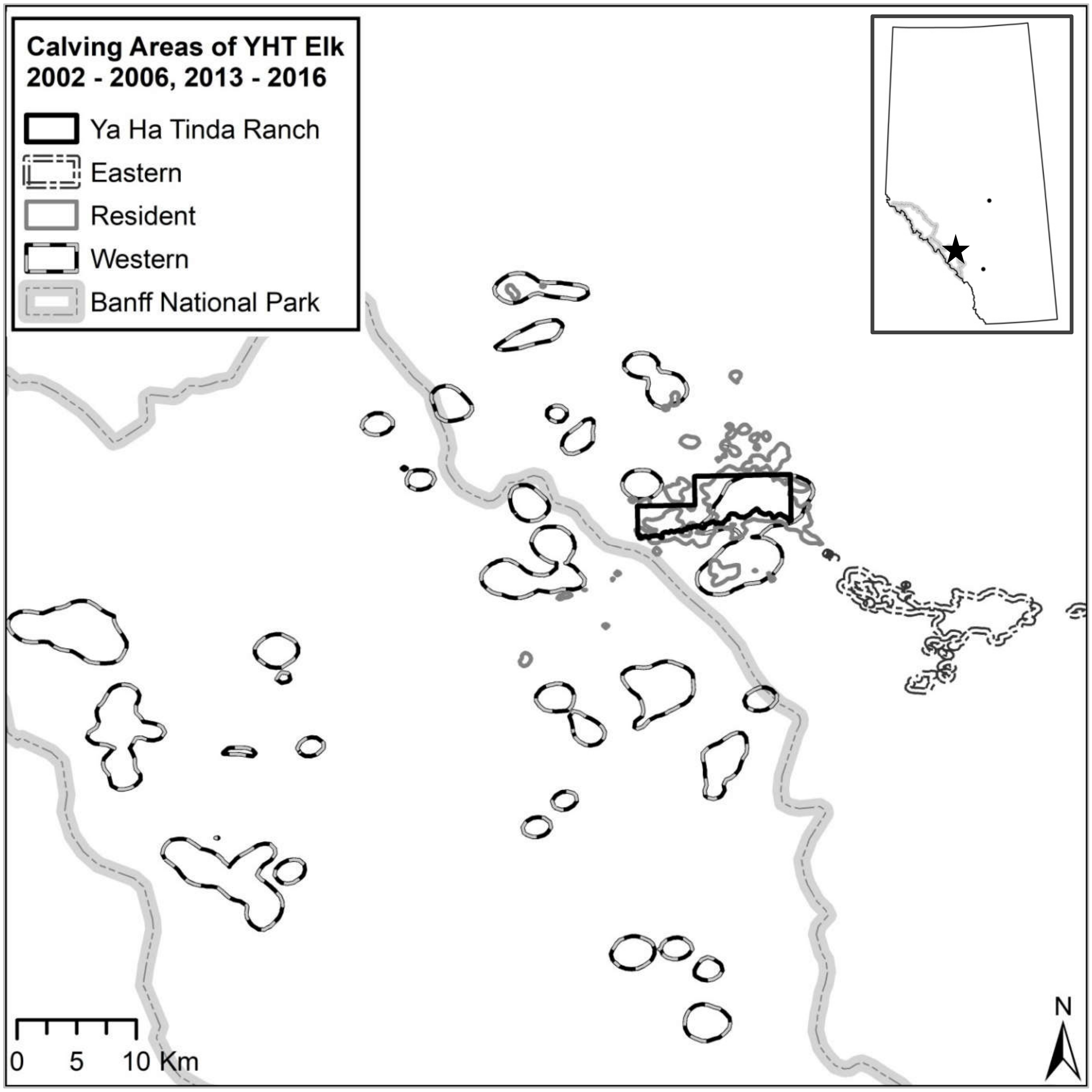


Figure 3.1. Calving areas of western migrant, resident, and eastern migrant elk in the Ya Ha Tinda population during 2002 – 2006 and 2013 – 2016 on the eastern slopes of Banff National Park, Alberta, Canada. Calving areas were determined using GPS locations of maternal elk during the first 26 days after giving birth.

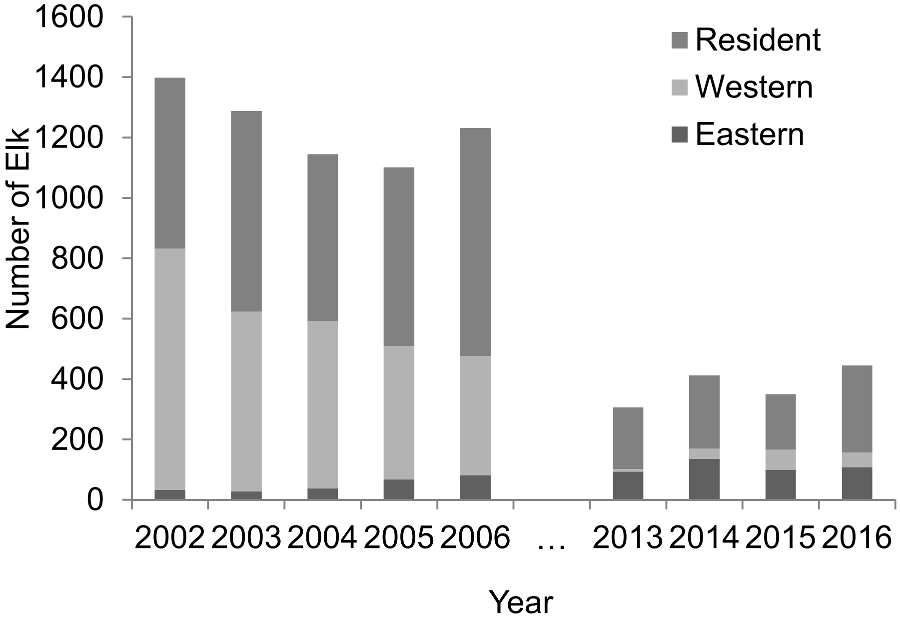


Figure 3.2. Total population and the estimated number of elk following each migratory tactic based on winter counts and movements of collared elk in the Ya Ha Tinda elk population, Alberta, Canada, during 2002 – 2006 and 2013 – 2016.

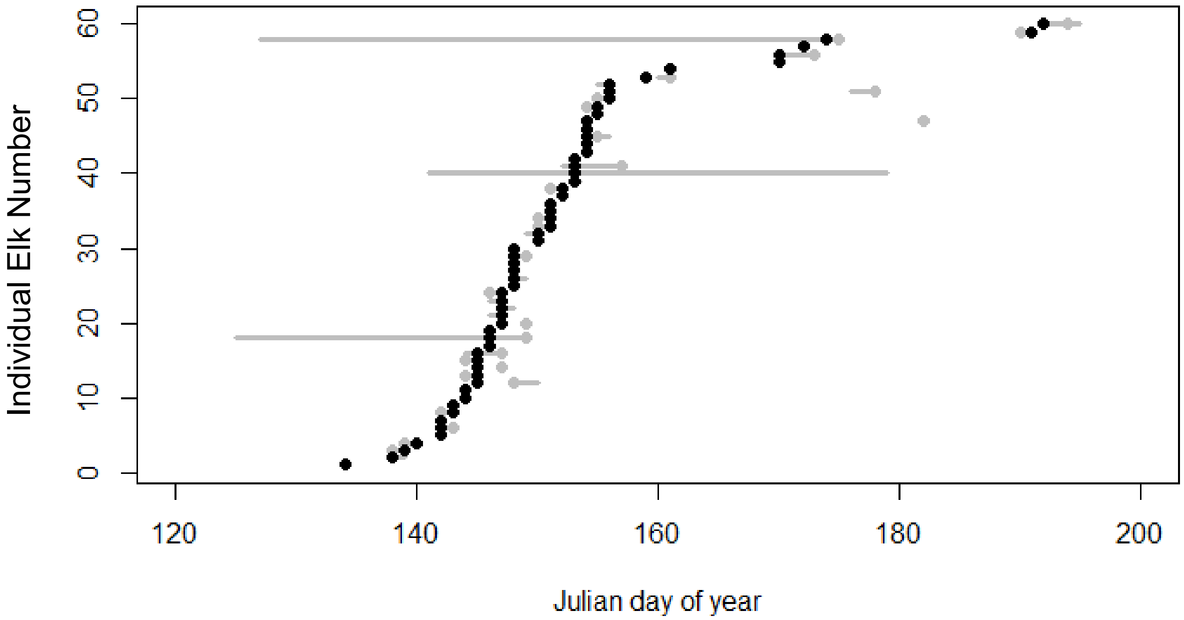


Figure 3.3. Known (black) vs. predicted (grey) parturition dates (*n* = 60) of elk in the Ya Ha Tinda population, Alberta, Canada, during 2013 – 2016. Predicted dates resulted from a random forest model that included variables related to movement: step length, turning angles, Euclidean displacement, and time of day. Grey bars denote the middle 2 quartiles of predicted dates. Results have been ordered along the x-axis by known parturition date for ease of figure interpretation.

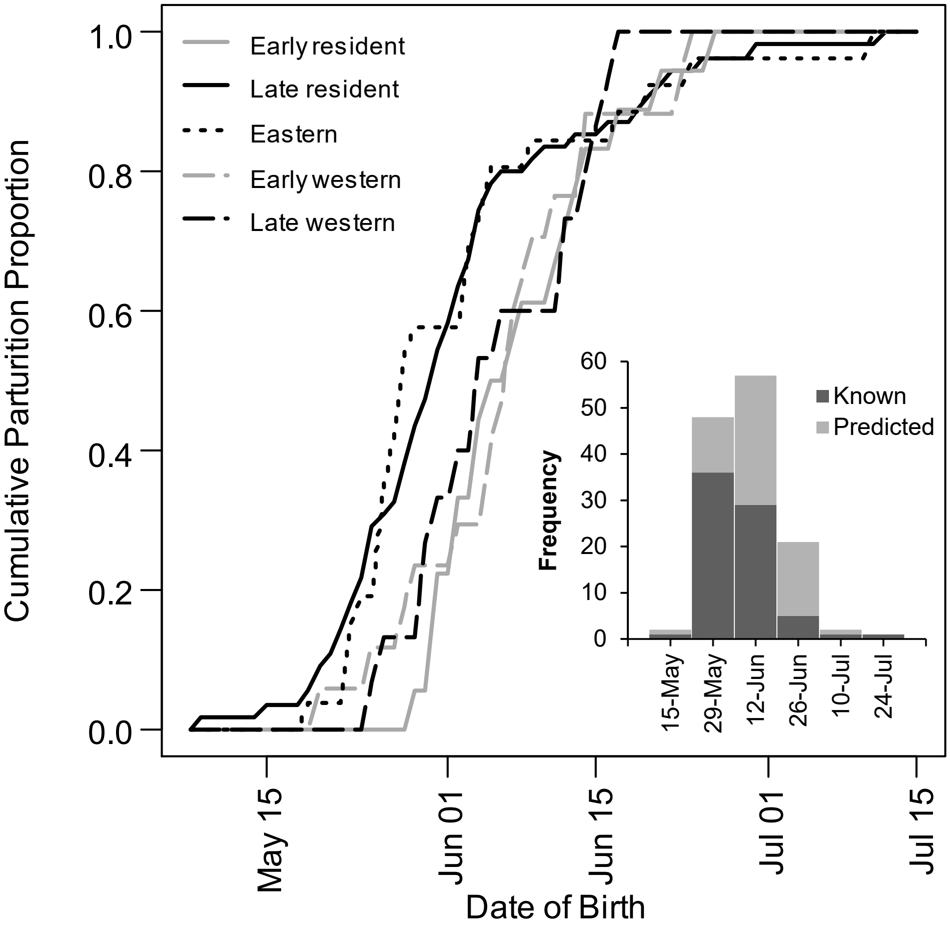


Figure 3.4. Cumulative frequency of known (*n* = 73) and predicted (*n* = 58) parturition dates for elk following 3 migratory tactics and 2 time periods (early: 2002 - 2006 and late: 2013 - 2016) in the Ya Ha Tinda elk population, Alberta, Canada. Inset shows the distribution of the known and predicted dates of parturition.

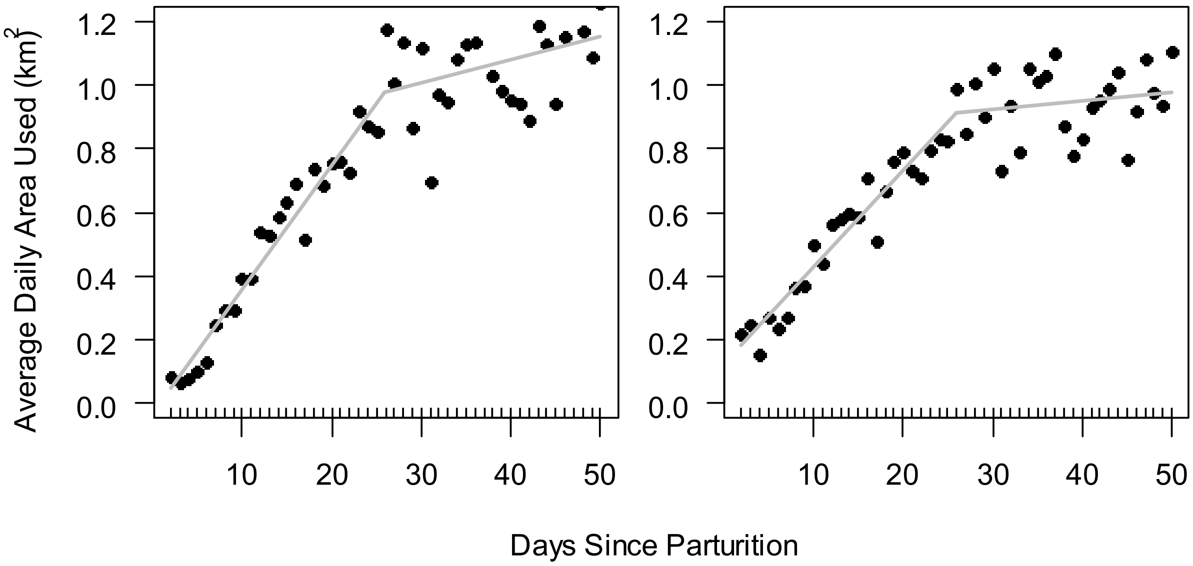


Figure 3.5. Average area (km^2) used every 24 hr since day of parturition by maternal elk in the Ya Ha Tinda elk population, Alberta, Canada, 2002 – 2006 and 2013 – 2016. Left panel is the daily area used by elk since known (*n* = 73) dates of parturition, and right panel is the area used since both known and predicted (*n* = 131) dates of parturition. Both figures show a breakpoint at 26.0 (SE: 2.03) days. Lines represent a fitted segmented or piecewise regression model (R^2 = 0.91 and 0.88).

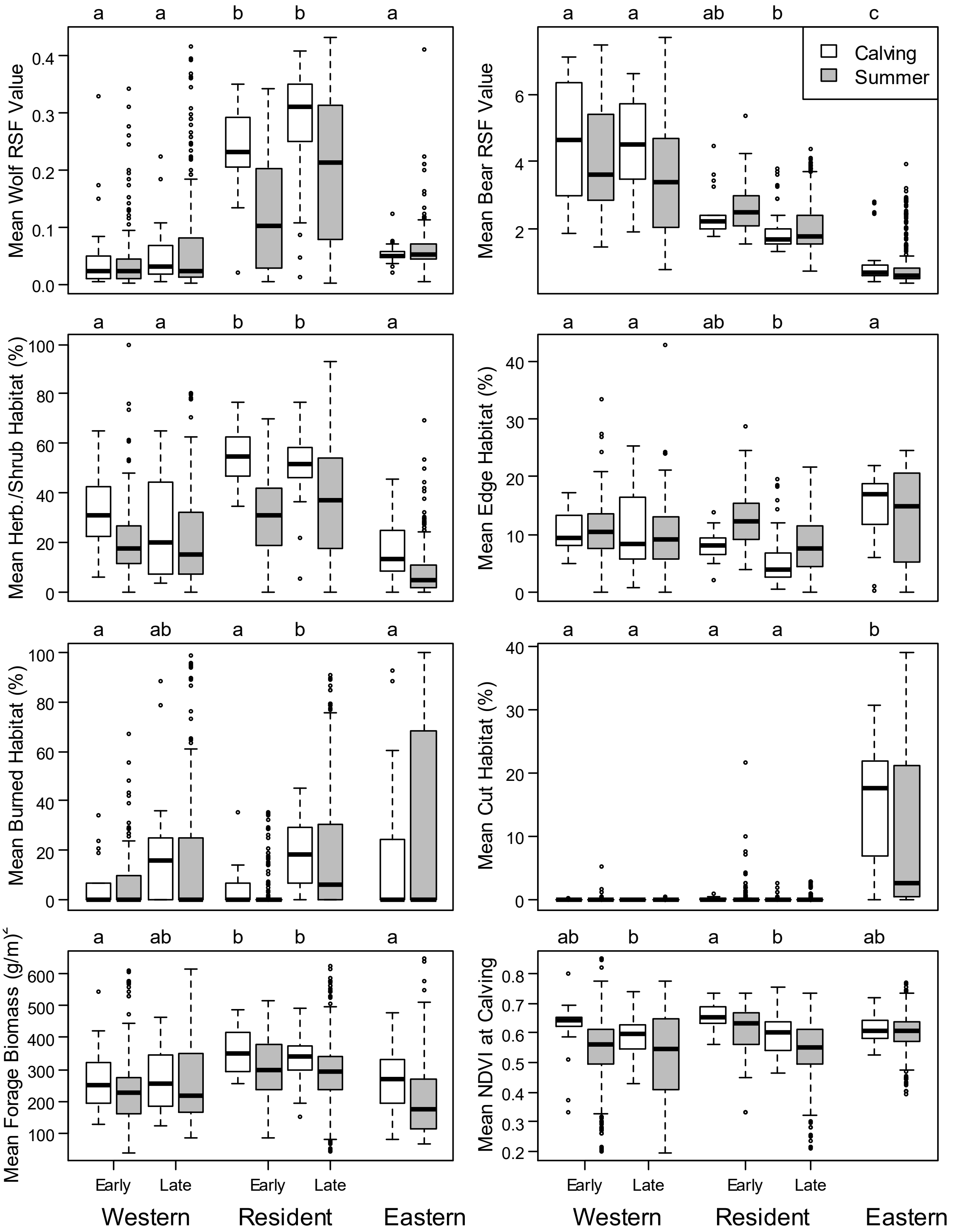


Figure 3.6. Comparison of predation risk and habitat characteristics in 26-day calving areas (*n* = 131) and summer areas of elk with 3 different migratory tactics and during 2 time periods (early: 2002 – 2006 and late: 2013 – 2016) in the Ya Ha Tinda elk population, Alberta, Canada. Small letters within each panel refer to differences of use during calving between migratory tactics and time periods.

CHAPTER 4. ELK CALF SURVIVAL IN A PARTIALLY MIGRATORY ELK POPULATION

INTRODUCTION

In variable environments, animals are predicted to distribute themselves seasonally in ways that maximize lifetime reproductive success through condition- or density-dependent habitat or resource selection (Fretwell and Lucas 1969, Rosenzweig 1981, McLoughlin et al. 2006, Morris 2006). Large ungulates use seasonal migration as a tactic to take advantage of bottom-up spatial changes in resource availability (i.e., higher-quality forage, Hebblewhite et al. 2008, Bischof et al. 2012), to avoid intraspecific competition (Nelson 1995, Matthysen 2005, Mysterud et al. 2011), and/or to avoid predation pressure (Fryxell and Sinclair 1988*a*). Migratory individuals thus are predicted to be more numerous and to experience increased fitness benefits over non-migratory conspecifics (Fryxell et al. 1988). Both the indirect and direct reasons why some individuals migrate seasonally while others within the same population remain resident year-round are becoming more evident. The benefits to residents can include avoidance of movements costs (Sandegren et al. 1985) or density-dependent competition elsewhere (Matthysen 2005), the ability to take advantage of familiarity on year-round ranges, and in some cases, avoidance of migratory corridors that are restricted or cut off completely (Kokko and Sutherland 2001, Holdo et al. 2011*a*, Sawyer et al. 2013). Less evident, though, are the mechanisms by which shifts in the relative benefits to the different migratory tactics drive changes in migratory behavior or the emergence of altogether completely new patterns of migration.

In what used to be a predominantly migratory elk (*Cervus canadensis*) population located in west-central Alberta, migratory behavior has shifted towards residency over the past 2 decades, and more recently, a new pattern of migration has emerged. The Ya Ha Tinda elk population historically migrated west from provincial lands to summer at high elevations in Banff National Park (Morgantini and Hudson 1988), but the population has declined in number from a maximum count of ~2,200 elk in 1992 (Morgantini 1995) to ~450 elk in 2016, with a proportional increase in elk remaining on the winter range year-round (Appendix B). Previous studies in 2002 – 2011 that compared western migrants to residents showed that migrant elk were exposed to higher forage quality, resulting in higher pregnancy rates and heavier calves, whereas resident elk reduced predation risk from wolves (*Canis lupus*) by remaining on low-elevation winter range close to human-based refuge from predation (Hebblewhite and Merrill 2009). Thus, the growth rates of the 2 tactics were similar (Hebblewhite and Merrill 2011) under what appeared to be density-independent predation by wolves (Hebblewhite et al. 2018). The new pattern emerging entails migration of elk to low elevations east of the Ya Ha Tinda winter range (Killeen et al. 2016). High calf recruitment (i.e., elk calf-cow ratios, Berg et al. 2016) of these elk supports evidence based on predator distribution that there is a west-to-east gradient from high predation risk for elk calves in Banff National Park where predators are protected, to lower risk east of the winter range where wolves and cougars (*Puma concolor*) are hunted and trapped (Spilker 2018). The appearance of this new migratory tactic presents a unique opportunity to understand the fitness consequences of a major shift in migratory behavior and its contribution to maintaining this, and other, partially migration populations of large herbivores.

Reproduction is a major determinant of fitness, and the migratory behavior used by female ungulates such as elk governs their ability to maximize their chances for successful reproduction (Raithel et al. 2007, Long et al. 2016). Because migrant and resident elk are exposed to similar habitat on their shared winter range, we would expect seasonal range use during summers to impart the greatest differences in survival between migratory tactics, especially during the critical perinatal period (which we define here as late pregnancy, parturition, and lactation through weaning). The nutritional status of the mother going into and coming out of winter can influence the amount of fat depletion during winter and fetal growth during late pregnancy, which then affects birth weight, lactation, and perinatal growth of offspring (Guinness et al. 1978, Clutton-Brock et al. 1987, Cook et al. 2004, 2016). Once a calf is born, maternal females must balance investment in current offspring with their own survival and future reproduction (Trivers 1974, Roff 1992, Stearns 1992). They are also faced with trading off the risk of predation to young with the nutritional requirements of lactation during current reproduction (Bergerud et al. 1984, Bowyer et al. 1999). If maternal females of different migratory tactics are unable to trade-off equally well across varying exposure to predation and forage, we would expect behavioral choices during the perinatal period to have major consequences for reproductive success and fitness balancing among migratory tactics (Hebblewhite and Merrill 2011, Middleton et al. 2013*a*, White et al. 2014). We hypothesize that differences in seasonal range use in response to forage resources and predation risk by maternal elk manifest themselves through maternal effects and exposure to environmental variables that promote survival of young.

Determining how and at which spatial scale maternal females select areas to meet nutritional requirements while protecting young is key to understanding and predicting the consequences of neonatal survival and recruitment to success of migratory tactics in the Ya Ha Tinda elk population. Rettie and Messier (2000) hypothesized that the spatiotemporal scales at which animals select resources reflects the relative importance of factors to individual fitness (i.e., hierarchical habitat selection, Basille et al. 2013). They hypothesized that predation was limiting at large scales and continues to influence behavior at successively finer scales, until another factor becomes more limiting. Thus, where predation risk is heterogeneous across large spatial scales, migration to ranges with lower risk of predation is likely to be a major impetus for migration (Fryxell and Sinclair 1988*a*, Hebblewhite and Merrill 2007, White et al. 2014). However, this implies that animals are not flexible enough in their behaviors to trade off large-scale constraints at multiple and/or smaller scales in either time or space. Yet, in the Jacques Cartier Park and Laurentides Wildlife Reserve of Canada, moose (*Alces alces*) traded off several limiting factors at both the landscape and the home-range scales by using high-snow areas that wolves avoided, but offset deep snow conditions with patches that provided shelter from snow and abundant food (Dussault et al. 2005).

The consequences to maternal females of multiple-scale selection may be particularly important because once parturition occurs, vulnerable young are relatively immobile, yet forage resources are soon needed to support lactation requirements. Migration to areas of high-quality forage that spatially overlap with areas of high predation risk may incur high offspring mortality unless animals are able to avoid predation at fine temporal and spatial scales. Predation may be avoided by being born either before (Testa 2002, Barber-Meyer et al. 2005) or during the peak birthing period (Barber-Meyer et al. 2008). Calves born early may be smaller and weaker so are more susceptible (Cook et al. 2004), or they could achieve the size and mobility needed before predators key into the seasonal availability of neonates as a food source (Testa 2002, Barber et al. 2005). Alternatively, it may be most advantageous to synchronize birthing times to swamp predators to dilute predation risk (Estes 1976, Rutberg 1987, Ims 1990*a*). Indeed, in Yellowstone National Park, calves born closest to the median birth date survived best (Barber-Meyer et al. 2008). In the case of elk at Ya Ha Tinda, parturition typically spans about an 8-week period (Chapter 3). Thus, if the timing of parturition differs among migratory tactics, they may be subject to differential predation depending on the predator community and distribution (Linnell et al. 1995, Griffin et al. 2011). Where bear (*Ursus* spp.) predation on ungulate neonates occurs, the pattern is clear that most bear predation occurs early and typically before that of other predators, especially wolves, as has been seen not only in elk, but moose and caribou (*Rangifer tarandus*) as well (Gasaway et al. 1992, Adams et al. 1995, Griffin et al. 2011). Thus, if one migratory tactic gives birth earlier, cause-specific mortality by bears could be higher for elk following that tactic.

Spatial isolation during parturition is hypothesized to promote formation of the mother-infant bond during the immediate post-partum period (Lent 1974, Vore and Schmidt 2001) but may also reduce encounters with predators (de Vos et al. 1967, Geist 1982, Rearden et al. 2011). Even with isolation, complete escape from wide-ranging predators in space is unlikely. Fine-scale habitat selection at parturition and during early calf-rearing may be critical for successful reproduction because neonatal calves are particularly vulnerable due to their small size and lack of coordination (Bleich 1999). Birthing and early hiding sites of neonates typically has not been associated with forage quality and abundance (Barbknecht et al. 2011, Rearden et al. 2011, Fogarty and Lehman 2016), which may indicate a relatively short amount of time spent feeding near the actual birthing site, and that maternal elk quickly move calves away from the immediate site (Berg et al. 2016). Instead, fine-scale characteristics reported at birthing sites include increased ground and shrub cover that was associated with improved survival when elk are very young (e.g., in Idaho, calves <2 wks old, White et al. 2010, Barbknecht et al. 2011, Rearden et al. 2011) but was speculated to be at the expense of a female’s ability to obtain abundant high-quality forage (Bergerud et al. 1984, Festa-Bianchet 1988) and may have limited a female’s ability to detect predators in thick vegetation (Underwood 1982). In contrast, during the calf-rearing stage, which lasts for several weeks (Chapter 3), calves are more mobile but still employ a hiding strategy in which they lay prone and immobile (Johnson 1951, Lent 1974). Selection for the overall calf-rearing areas compared to the birth site may be for meeting the nutritional requirements of the lactating female because calves can be moved among patches of hiding cover chosen by the mother (Chapter 3, Van Moorter et al. 2009, Pitman et al. 2014).

In this paper, we took advantage of the emerging pattern of migration in the Ya Ha Tinda elk population to compare a priori predictions for the effects of intrinsic (e.g., maternal body condition in winter, calf weight and size) and extrinsic (multi-species predation risk, forage availability, habitat cover, and human infrastructure) factors on daily risk of mortality to calves of elk following 2 different migratory tactics. We first determined the period during which calves are most vulnerable and most of mortality occurs, and the temporal scale at which intrinsic characteristics have the greatest effect on risk of mortality. We then focused on this critical period to associate risk of mortality with extrinsic factors measured at 3 spatial scales: (1) the fine-scale neonatal area around the birth site, (2) the calf-rearing area, measured by the area used from birth through day 26 (Chapter 3), and (3) the summer range, measured by the area used from birth through 90 days. We hypothesized that better maternal condition, earlier or calving outside peak of parturition, and greater access to forage resources and/or lower exposure to predation risk on summer range resulted in higher calf survival. Thus, we predicted higher calf survival in the eastern migrants that was associated with better maternal condition or potentially earlier calving (Chapter 3) and green-up on low-elevation summer range east of the Ya Ha Tinda (Killeen et al. 2016). We also expected lower exposure to predation for eastern migrants because predators have either not keyed into this new migration, or are hunted and trapped, or because there is high human activity that predators avoid. In addition, although bears would be an early source of calf mortality overall (Singer et al. 1997, Barber-Meyer et al. 2008, Griffin et al. 2011), we expected bear predation to be heavier for residents because of the predation gradient and earlier calving in eastern migrants, whereas wolf mortalities would be relatively constant over time. Finally, we expected calf mortality to be lowest where elk were exposed not only to low predation risk but where forage was also abundant (i.e., forage-predation interaction). We used a known-fate, continuous-time approach (Murray 2006) in a Bayesian framework to examine survival related to intrinsic and extrinsic covariates over time. We focused on calf survival because adult survival rates were similar among migrant and resident elk (Hebblewhite et al. 2018); declining summer calf survival was therefore implicated in contributing to the population’s shift in migratory behavior.

STUDY AREA

The study area was in west-central Alberta, Canada (51º38’ N/-115º30’ W), just east of the boundary of Banff National Park (BNP) on provincial lands (Figure 4.1). The winter range for the Ya Ha Tinda (YHT) elk population was the YHT ranch (44 km^2) that was administered by

Parks Canada, although Alberta's provincial government managed the natural resources. Open habitat (~45% of the study area) consisted of a large montane rough fescue (*Festuca campestris*) grassland (20 km^2) interspersed with bog birch (*Betula glandulosa*), shrubby cinquefoil (*Potentilla fruticosa*), and willow (*Salix* spp.), while closed habitat (~40%) was forest composed of lodgepole pine (*Pinus contorta*) and trembling aspen (Populus tremuloides) at low elevations and Engelmann and white spruce (*Picea engelmannii* and *P. glauca*) and subalpine fir (*Abies lasiocarpa*) at high elevations (McGillis 1977, Holland and Coen 1982). Starting from the ranch and heading east, there was a decrease in elevation and also predator occurrence, but an increase in both industrial and recreational activity.

Elevations ranged from 1,400 – 2,200 m. Low precipitation and westerly winds (i.e., chinooks) kept the grassland mostly snow-free in the long winters from October – April (Holland and Coen 1982). Temperatures in winter averaged -4.1ºC with approximately 157 cm of snowfall, while temperatures during the short summers in May – September averaged 9ºC with ~40 cm of precipitation. During drought years, precipitation was <10 cm in summer (Environment Canada Ya Ha Tinda weather station).

The YHT elk population peaked at a maximum count of ~2,200 individuals in 1992 (Morgantini 1995), and the population wintering at Ya Ha Tinda declined to 450 elk in 2016. Historically, ~90% of the population migrated westward to summer at high elevations in Banff National Park, but the ratio of western migrants to residents to eastern migrants shifted from an average of 14:15:1 during initial studies in 2002 – 2006 to an average of 1:10:5 in 2013 – 2016.

Wolves were extirpated by the 1950s (Morgantini 1995) but recolonized since then, and although heavily trapped, numbers likely remained stable into the early 2000s (Hebblewhite 2006). Grizzly bears (*U. arctos*) numbered ~5.25 bears/1000 km^2 outside BNP (Alberta Environment and Parks 2016) while black bear (*U. americanus*) numbers were moderately low (Alberta Environmental Protection 1993). Additional predators of elk in the study area included coyotes (*C. latrans*, Morgantini 1995) and cougars, which increased in the last several decades (Knopff et al. 2014). White-tailed and mule deer (*Odocoileus virginianus* and *O. hemionus*), moose, bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus*) though mostly in Banff National Park, Stelfox 1993, Morgantini 1995) also inhabited the study area.

METHODS

Adult Elk Capture, Monitoring, and Migration

We captured and collared adult female elk through ground darting from horseback in winter (15 Jan – 31 Mar, 2013 – 2016) on the Ya Ha Tinda winter range (University of Alberta Animal Care Protocol nos. 611/11/13, 00000624). Elk were immobilized with Telazol® and medetomidine and reversed with atipamezole by riding into the population and darting at a distance of 20 – 25 m. Elk were fitted with VHF or GPS radiocollars (Lotek Wireless, Inc., models 3300, 4400, 7000, Lifecycle, or LMRT-4). GPS collars recorded location every 15 min during May and June, and every 2 hr during other months of the year, and VHF collars were monitored daily for mortality. We extracted vestigial canines for aging, and determined pregnancy through rectal palpation. We fit all pregnant elk with small vaginal implant transmitters (VITs; Advanced Telemetry Systems, Inc., model M3960). When parturition occurred, VITs were expelled with the calf; a temperature-sensitive trigger doubled the pulse rate and a code was emitted that allowed time of birth to be determined to the nearest half hour through a Precise Event Transmitter (PET) and birth sites to be precisely located.

Radiocollared elk were classified as migrant or resident each year using a combination of net-squared displacement (Bunnefeld et al. 2011, Spitz et al. 2017) and visual inspection (Eggeman et al. 2016). Residents remained within approximately 15 km of the YHT winter range during the calving and summer periods, while migrants spent a minimum of 30 days on summer range >15 km from the winter range and calved on their summer range. Eastern migrants generally followed the Red Deer River to lower elevations east of the YHT winter range.

Calf Elk Capture, Monitoring, and Determining Cause-Specific Mortality

We used VHF telemetry to monitor maternal elk and their VITs multiple times daily during mid-May to mid-July. When a VIT was expelled, a ground crew located the birth site and recorded GPS coordinates. Birth sites were typically searched within 10.5 ± 11.2 (range: 0.5 – 52.0) hr of birth, and calves were captured from the ground. We blindfolded and restrained calves with hobbles to limit stimuli and reduce stress and weighed calves with a Pesola spring scale. We equipped calves with VHF radiotransmitting ear tags (Biotrack Ltd., model TW-5) to allow for regular relocation and monitoring and to locate calves when the signal indicated they remained unmoved for >4 hr. Calves were released at the capture location after no more than 10 ± 3 minutes of capture and handling, and all crew members wore gloves to minimize transfer of human scent to the calves. Although we opportunistically caught calves (*n* = 17; Appendix B), we did not include those in our analysis to avoid the bias that arises when calves are dead before detection and capture can occur (Gilbert et al. 2014, Chitwood et al. 2017, Tatman et al. 2018).

We used VHF signals to monitor calves 1 – 3x daily until 31 August each year. We immediately attempted to investigate mortality signals, typically arriving at mortality sites within 12 – 24 hr of death. We searched each site to assess the specific cause of mortality following established protocols (Hatter 1988, Barber-Meyer 2006, Knamiller 2011) and based on predation characteristics, presence of tracks, scat, puncture wounds, claw/bite marks, and site characteristics. We assumed that scat and sign at kill sites reflected the specific predator that made the kill because the low biomass and short handling times associated with calves are unlikely to provide scavenging by other predators (Kunkel and Mech 1994, Knopff et al. 2009, Knamiller 2011). In cases where cause of mortality was uncertain, we relied first on field evidence but supplemented our conclusions with carnivore hair found at the site (Normandeau et al. 2018) or swabs of predator saliva to determine predator species based on DNA analysis (Appendix B Table B.5, Wengert et al. 2013). If field evidence suggested predation but no hairs could be found or DNA could not reliably identify the predator species, we classified the cause as unknown predator. We submitted carcasses with no evidence of predation to a diagnostics laboratory for necropsy to screen for other causes of mortality.

Modeling Risk of Mortality to Elk Calves

We modeled risk of mortality to elk calves across different temporal and spatial scales. First, we verified whether calving occurred earlier for eastern migrants and if timing of birth influenced mortality (Table 4.1: H1a – b). We then modeled daily risk of mortality through 90 days to assess overall timing and differences in mortality between migratory tactics and also contrasted timing of predator-specific mortality (Table 4.1: H1c – d). Second, we examined the time period (3, 10, 26, or 90 days) for which intrinsic characteristics might have early or longer-term effects on the risk of mortality (Table 4.1: H2). Third, because 90% of the mortality occurred by 26 days after birth (see Results) and elk cow-calf pairs attained summer movement levels and re-joined larger groups of elk around this age (Chapter 3), we focused on this 26-day period to relate risk of mortality to extrinsic characteristics. We related risk of mortality to security cover measured at fine-scale birth and hiding sites (Table 4.1: H3a) and to predation risk, human infrastructure, and forage of the calf-rearing area and the summer range, respectively (Table 4.1: H3b – c, H4, H5).

We used a known-fate, continuous-time approach (Murray 2006) to model risk of mortality to calves. Because VITs aided in catching calves soon after birth (<24 hr), we modeled risk of mortality from date of birth (i.e., models were based on calf age and/or time since capture, rather than an approach that used staggered entry by date; (Pollock et al. 1989, Raithel 2005, Fieberg and DelGiudice 2009) through 3, 10, 26, or 90 days, depending on the hypothesis being tested (Table 4.1). We right censored calves that had tags which failed (*n* = 1) and all calves that survived past the time period in their year of birth (*n* = 36). We did not include 1 stillborn or 17 opportunistically caught and tagged calves in our analysis. We modeled whether or not individual *i* died during day *t* as a Bernoulli random variable with probability $\rho_{i,t}$, where $y_{i,t} = 1$ if the individual died and 0 otherwise, following Lehman et al. (2018):

$$y_{i,t} \sim Bernoulli[\rho_{i,t}]$$

We used generalized linear models with the logit link to estimate the effects of individual-level maternal or intrinsic characteristics and spatiotemporal covariates ($X_{i,t}$). We added a 5-knot spline function (Crainiceanu et al. 2005, Cross et al. 2015, Warbington et al. 2017) to smooth variability in daily hazards over time to allow for a clearer understanding of the pattern in mortality not accounted for by the covariates:

$$logit(\rho_{i,t}) = \beta' X_{i,t} + Time_{spline} + E_t$$

$$E_t \sim normal(0, \sigma^2)$$

where σ^2 represents the amount of process variation in mortality rate.

We used deviance information criterion (DIC; Van Der Linde 2005, Abadi et al. 2010, Spiegelhalter et al. 2014) to rank candidate models and selected the top model based on DIC. We fit our models using Bayesian Markov Chain Monte Carlo (MCMC) methods in program R (R Core Team 2017) using JAGS (Plummer 2003) and the R package JagsUI (Kellner 2017, Appendix C). We assigned uninformative priors, *normal* (0, 1.7), for the linear predictors and spline parameters, which translates to a uniform distribution from 0 to 1 (Eacker 2015). We ran MCMC chains for 100,000 iterations, using 20,000 for the adaptive phase and 80,000 as burn-in.

We ensured sufficient burn-in and convergence by visually inspecting trace plots for mixing in chains and evaluating the scale reduction factor ($\hat{R} \leq 1.1$; Gelman et al. 2014).

Similarly, we contrasted timing among predator-specific mortality through 26 days of calf life (Table 4.1: H1d) by defining a response variable as a vector of possible "states" that an individual could assume at time t, one for each cause of mortality (i.e., death by wolf, bear, cougar, or unknown predator) or the state of remaining alive. In this case, $c_{i,t,s}$ equaled 1 if individual i was in state s at time t and 0 otherwise. We modeled $c_{i,t}$ as a multinomial response with a vector of probabilities φ for each state (Servanty et al. 2010):

$$c_{i,t} \sim Multinomial[\varphi_{i,t}, 1]$$

and used DIC to rank and select the top candidate model.

However, because of small sample sizes within migratory tactic for each predator, we estimated cause-specific probability of mortality from birth (i.e., age- or time-since-capture-based, as described above) through 90 days of life (Table 4.1: H1c) using cumulative incidence functions (CIFs; Fine and Gray 1999, Heisey and Patterson 2006), calculated with the cmprsk package (Gray 2014) in program R (R Core Team 2017). We categorized the causes of mortality for elk calves as bear, cougar, wolf, unknown predator, and other (unknown causes and disease) and first tested for differences in mortality between calf sexes and among years. We pooled data across sexes and years when there was no effect to test for differences between migratory tactics with a modified χ^2 statistic (Fine and Gray 1999, Warbington et al. 2017). To relate risk of mortality to timing of birth, we considered calves born in the first and fourth quartiles of the distribution of birth dates as born outside the peak of parturition (Table 4.1: H1b).

We related intrinsic covariates including maternal effects of migratory tactic, nutritional condition, and age, and the calf characteristics of year of birth, sex, and birth weight, to daily risk of mortality through 3, 10, 26, and 90 days. We used the estimated percent of ingesta-free body fat (IFBF) as an indicator of adult female nutritional condition. Briefly, IFBF was determined through a visual and tactile body scoring system, combined with maximum rump and loin fat thicknesses (cm) measured with ultrasound (Sonovet system with 5.0- MHz, 7.0-cm probe, Universal Medical Systems, Bedford Hills, New York, USA), and body mass (kg) estimated with chest girth circumference (cm, see Appendix B and Cook et al. 2001*a*, 2010). We estimated ages of adult females using cementum of vestigial canines (Hamlin et al. 2000). We used calf mass at capture to represent the susceptibility of calves to mortality and estimated birth mass (kg) based on the age of calf in days and a 0.9 kg/day growth rate used by Johnson (1951) and Smith et al. (1997). We used DIC to rank and select the top candidate model.

To relate risk of mortality to security cover at hiding sites (Table 4.1: H3a), we returned to birth and/or capture sites at the end of the calving season to measure site-specific habitat characteristics (Appendix J). We visited all but 10 of the calf birth/capture sites ($n = 84$); for the 10 not visited, we used regression trees and the R package rpart (Therneau et al. 2017) in a machine learning framework to fill in missing values based on environmental variables extracted from GIS. At each site, we measured the mean amount of horizontal cover (%, i.e., hiding cover for calves) at the site using cover board estimates taken from distances of 10, 20, and 30 m from each of the 4 cardinal directions and at 2 heights (i.e., kneeling and standing) to approximate the average eye height of a large predator on 4 legs or a bear standing upright (i.e., 0.5 – 1 m and 2 – 2.5 m; Panzacchi et al. 2010). We recorded over-story canopy cover (%) and habitat type, estimated distance (m) to the nearest cover large enough to hide a calf laying prone (e.g., shrub, rock, log), and used 2 intersecting line transects stemming outward from plot center 15 m in each of the cardinal directions to record shrub and downed log cover intercepted by the transect tape. We estimated shrub cover in 2 categories, <1 m in height and between 1 and 2 m in height, and we excluded gaps in shrub cover <5 cm or shrubs <3 cm in height and gaps in log cover <5 cm or branches <2 cm in diameter. Before testing for the importance of security in the predation hypothesis, we first conducted a machine learning analysis with the R package randomForest (Liaw and Wiener 2002) among all cover variables to identify the variable(s) most important to security cover for calf survival using the rf.modelSel function in the rfUtilities package (Evans et al. 2011).

To evaluate the hypotheses related to extrinsic factors influencing calf daily risk of mortality through 26 days (Table 4.1), we measured predation risk, human infrastructure, and forage at the scales of the calf-rearing area (26 d) and summer range (90 d). We buffered each calf's birth or nearby capture site with the average size of area used during the calf-rearing period (i.e., 26 d, Chapter 3). We used telemetry locations to derive 95% utilization kernels for the summer range (i.e., 90 d) with the plug-in method for the smoothing factor in the ks package (Duong 2018). We then measured the following extrinsic characteristics by averaging their values across each area.

Indicators of predation risk to elk calves were derived from maps of resource selection function (RSF) values for cougars, wolves, and bears (Appendix G). The temporally static cougar RSF was developed at a 30-m resolution based on locations of cougar scat detected in the years 2014 – 2015 compared to random locations within a 100-m wide transect and using landscape variables hypothesized to influence cougar selection (e.g., % conifer forest and edge density, Spilker 2018). Similarly, we modeled the annual pack-level predation risk by wolves based on the work of Hebblewhite (Hebblewhite 2006) and Hebblewhite and Merrill (2007) who derived day and night population-level RSFs for collared wolves, weighted by spatial density of wolves and kill rate/pack/day (Thurber et al. 1994). We used the RSFs of Hebblewhite (2006) from 2002 – 2004 and updated the predictions to the years 2013 – 2016 by incorporating changes in land cover due to fire and clearcutting. We also modeled the spatial density of wolf use based on population-level kernel density estimates (KDEs) for each pack across all years and weighted by the kill rate/pack/day to create annual layers of total predation risk by wolves for elk. For the analysis, we assumed wolf selection did not change over time and wolf home ranges were stable, which was supported by movements of radiocollared wolves (Eggeman et al. 2016). We similarly updated summer predation risk by grizzly bears for elk in 2013 – 2016 using RSF maps developed with data of GPS-collared grizzly bears by applying annually changing landscape conditions. Based on available data from the study area (Whittington and Sawaya 2015, Alberta Environment and Parks 2016, Whittington et al. 2017), we incorporated differences in spatial density of grizzly bears into the RSFs because grizzly bears were 2.4 – 2.9 times more prevalent in Banff National Park compared to provincial lands outside the park. Finally, we evaluated the telemetry-based wolf and bear RSFs by comparing them to scat-based RSFs developed in 2014 – 2016 (Spilker 2018).

To understand whether human activity plays a role as refuge in the predation hypothesis (Table 4.1: H3b, H5), we used density of linear features as an indicator because both elk predators and prey have shown mutual avoidance, but the response by ungulate prey is more variable, and individuals may use areas near roads and trails for refuge (Rogala et al. 2011, Nelson et al. 2012, Lesmerises et al. 2016). We therefore extracted density (m/km^2) of linear features in the calf-rearing area and summer home range boundaries, including all classes of roads (unpaved gravel), trails, and cut lines.

We related calf survival to access to higher forage quality or higher forage biomass (Table 4.1: H4, H5) using greenness of herbaceous forage measured with Normalized Difference Vegetation Index (NDVI) and seasonal availability of forage (g/m^2, Appendix F). NDVI was extracted in open habitats using a land cover mask (Hebblewhite et al. 2008, Robinson et al. 2012) from a MODIS platform with 250-m resolution; NDVI varied temporally across the season in 16-day intervals. Hebblewhite et al. (2008) used a general linear model to estimate herbaceous and shrub biomass for the years 2002 – 2004 at a 30-m^2 resolution as a function of year, land cover type, elevation (m), aspect (^{o}), and distance (km) to the continental divide based on field sampling along transects at 983 sites (Hebblewhite et al. 2008). For the years 2013 – 2016, we compared May – July precipitation to that which occurred in 2002 – 2004 and used the peak biomass estimate from the year that was most similar because there was a year effect of May – July precipitation on total biomass (herbaceous + shrub); 2002 had average (180 mm), 2003 had low (167 mm), and 2004 had high (319 mm) precipitation (data obtained from Alberta Climate Information Service, http://www.agric.gov.ab.ca). We accounted for temporal changes in forage availability resulting from timber harvest or fire by modelling the changes up to 15 years, then assuming biomass reached pre-burn or pre-cut levels. We also adjusted forage biomass for plant growth within a season using remote sensing for open habitats and field-based models for closed habitats (Hebblewhite et al. 2008).

RESULTS

Adult and Calf Elk Capture and Handling

In February and March, 2013 – 2016, we darted a total of 184 adult female elk from horseback (Appendix B Table B.1). Of these, 181 elk were checked for pregnancy via rectal palpation and 172 elk were pregnant and implanted with VITs (21 in 2013, 47 in 2014, 60 in 2015, and 44 in 2016). Pregnancy rate averaged 94.7 ± 2.8% across years. Thirteen of the 172 VITs were never found, and 8 adult females with VITs died between winter capture and the calving period. Birth sites of the remaining elk ($n = 153$) were identified during the 4-yr period with all but 2 of the birth sites found using VITs; the remaining 2 were found opportunistically (Appendix B Table B.3, Figure B.6). Not all locations of VITs led to a calf capture because calves either could not be found, or maternal females moved long distances just prior to giving birth in remote areas where they could not be followed, including 28 elk (4 – 9 elk/yr) into Banff National Park. VITs that led to calf capture and that were used in this analysis included VITs from 62 residents (R) and 32 eastern migrants (EM, total *n* = 94). Maternal females of captured calves ranged from 3 to 18 years in age with a mean of 9.66 ± *SE* 0.39 (*n* = 90) and a median of 10; the ages of 4 females were unknown and the migratory-specific mean (R: 12.4, EM: 9.8) used instead.

Timing of Calving and Risk of Mortality

All models had $\hat{R}$ estimates < 1.1 and visual inspection of the chains showed ample mixing, indicating convergence.

Calving. — Peak of calving was similar between residents and eastern migrants (Kolmogorov-Smirnov *D* = 0.24, *P* = 0.19), and the median birth date of all individuals across years was 28 May (R: 30 May, EM: 26 May, Figure 4.2). Timing of birth (i.e., a birth date inside vs. outside the peak of parturition) did not influence the risk of mortality across migratory tactics through 26 days ($\beta = 0.05$, CI: -0.23, 0.34, Appendix B Table B.9).

Overall risk. — We documented 57 deaths (47 R, 10 EM, Figure 4.4), with females representing 55% of the calves that died (R: 27, EM: 6) and males representing 45% (R: 20, EM: 4). The overall mortality rate for calves from all causes through 90 days of life was 0.61 (95% CI: 0.52, 0.70, Appendix B Figure B.14). Mortality hazard peaked at ~3-7 days of life and remained high in the first 20 – 30 days of life when 90% of deaths occurred (Figure 4.3). Daily mortality rate for residents (0.69, 95% CI: 0.13, 0.99) was 86.5% higher than eastern migrants (0.37, CI: 0.03, 0.97, Figure 4.3).

Cause-specific mortality. — Predation was the single most frequent cause of mortality (*n* = 48, 84%). Two of 4 calves were found dead within 1 and 2 hr of birth with predators actually at the birth sites predating on the calves when we arrived, whereas the other 2 calves were killed by predators at their birth sites within 10 and 22 hrs after birth. We attributed 29 deaths (51.7%, 23 R, 6 EM) to bears, 7 deaths (11.7%, 4 R, 3 EM) to mountain lions, 4 deaths (6.7%, 4 R, 0 EM) to wolves, 8 deaths (15.0%, 7 R, 1 EM) to unknown predators, and 9 (15.0%, 9 R, 0 EM) to other causes (8 unknown and 1 to bacterial septicaemia related to a navel infection, Appendix B. Figure B.12). Resident calves had a cumulative risk of mortality from bears 2 times, and a cumulative risk from unknown/other causes 15 times, that of calves in the eastern migratory tactic ($\chi^2_1 = 3.35$, *P* = 0.07 and $\chi^2_1 = 5.67$, *P* = 0.02, respectively, Figure 4.4). Through 90 days since birth, the cumulative probability of death by bear predation for resident calves was 37% and the probability of death from unknown/other causes was 15%. Eastern calves had a 19% probability of death by bears and a 0% probability from unknown causes. Resident calves had 11%, 6%, and 6% probabilities of death from unknown predators, cougars, and wolves, whereas eastern calves had 3% and 9% probabilities of death from unknown predators and cougars but a 0% probability from wolves (Figure 4.4). Predation by bears across migratory tactics occurred early, exhibiting a clear peak ~3 – 7 days, while predation by other predators was relatively low and constant throughout the first 30 days (Figure 4.5).

Modeling Factors Influencing Mortality

Intrinsic factors. — Ingesta-free body fat (%, IFBF) was 23.8% higher in residents (12.05 ± *SE* 0.32) than in eastern migrants (9.73 ± *SE* 0.34, $n = 32$, Welch's $t_{59} = -3.97$, $P = 0.0002$, Figure 4.6). There was no relationship between IFBF and age of adult female ($r = -0.09$, $n = 78$, $P = 0.41$, Appendix B) or in IFBF between years ($F_{2,75} = 0.07$, $P = 0.94$, Figure 4.6). Of the 94 calves included in our analysis, 39 were male, and 51 were female ($n = 90$), while 4 were of unknown sex. The mean weight at birth was 17.5 ± 2.1 kg (range = 12.2 – 23.0). Weight at birth did not differ between males (17.7 ± 2.3 kg, $n = 39$) and females (17.3 ± 2.0 kg, $n = 55$, Welch's $t_{75} = -0.83$, $P = 0.41$) or between residents (17.6 ± 2.2 kg) and eastern migrants (17.2 ± 1.9 kg, Welch's $t_{71} = -0.92$, $P = 0.36$), but was higher in 2015 compared to 2016 only (Tukey's HSD $P = 0.03$, Figure 4.6). Chest girth adjusted for age at capture was also similar between sexes ($W = 988$, $P = 0.43$), migratory tactics ($W = 928.5$, $P = 0.53$), and years (Kruskal-Wallis $\chi^2_3 = 8.25$, $P = 0.04$, Dunn-Bonferroni post-hoc $P > 0.05$, Appendix B).

Calf sex and calf girth adjusted for age at capture negatively influenced risk of mortality in the first 3 days of life ($\beta = -1.13$, CI: -2.16, -0.18 and $\beta = -0.99$, CI: -2.12, -0.10, respectively, Table 4.2), but the effects were not observable by 26 days (Appendix B Table B.6). Risk of mortality through the first 26 and 90 days of life decreased with increasing IFBF, with evidence for an interaction between IFBF and migratory status ($\beta = 0.70$, CI: 0.08, 1.33, Table 4.2, Figure 4.7). With increasing IFBF, the probability of mortality decreased more for residents than it did for eastern migrants.

Security cover. — Cover provided by downed logs negatively influenced risk of mortality through the first 26 days of life (β = -0.39, CI: -0.78, -0.04, Table 4.3), though the effect was only marginal when migratory tactic was accounted for (β = -0.25, CI: -0.62, 0.07).

Calf-rearing area. — The best supported model that examined whether exposure to predator-specific or total risk by predators influenced risk of mortality in the first 26 days included the main effects of migratory status and amount of human infrastructure (Appendix B Table B.11). After accounting for migratory tactic, human infrastructure on the summer range decreased the risk of mortality (β = -0.98, CI: -1.97, -0.02), whereas there was little effect of either predator-specific or total risk by predators (Appendix B Table B.11). Negative interactions between migratory tactic and both cougar (β = -0.61, CI: -1.20, -0.03) and bear (β = -0.67, CI: -1.29, -0.05) indicated that as predation risk by both predators increased, the risk of mortality increased more for calves of eastern migrants (Table 4.4).

NDVI did not influence mortality through 26 days of life at the scale of the calf-rearing (β = -0.03, CI: -0.35, 0.29) or summer range areas (β = 0.02, CI: -2.76, 2.78, Appendix B Table B.10). However, the amount of forage biomass (g/m^2) available positively influenced the risk of mortality across all 3 scales, and after accounting for migratory tactic, forage biomass on the summer range had the greatest influence on variation in risk of mortality (β = 0.44, CI: 0.01, 0.88, Table 4.5).

We found no support for the hypothesis that high survival to 26 days occurred where both forage was high and predation was low nor was there evidence for an interaction between predation risk and forage resources indicating that predation risk modifies the beneficial effects of forage (Table 4.6). Instead, a model with the main effects of human infrastructure and amount of forage biomass best explained variation in the risk of mortality after accounting for migratory tactic (Table 4.6), with marginal evidence for an interaction between these 2 variables that positively influenced risk of mortality (β = 0.60, CI: -0.06, 1.29).

DISCUSSION

Our comparison of calf survival between the resident and eastern migrants in the Ya Ha Tinda elk population suggests that maternal decisions made during the critical reproductive period may play a role in shifting migration patterns as a consequence of exposure to extrinsic factors on summer range. The risk of mortality to calves of resident elk remaining on winter range year-round was over 80% higher than the risk of mortality to calves that migrated east to low-elevation summer range.

Risk of mortality was highest for both migratory tactics in the first 26 days of life, with over 90% of mortality taking place in the calf-rearing phase that occurs before elk cow-calf pairs re-join larger groups of elk for summer. Predation was the single most frequent cause of mortality (98% of all known-caused deaths). Mortality by wolves and cougars was relatively low and constant, while the high predation by bears in the first 20 – 30 days of life is well-supported and documented by multiple studies on neonatal ungulates (e.g., caribou in Alaska, Adams et al. 1995; elk in Yellowstone, Montana, and Idaho, Singer et al. 1997, Harris 2006, Barber-Meyer et al. 2008, Griffin et al. 2011; deer in Minnesota, Kunkel and Mech 1994). Despite the hiding strategy used by calves, bears are known for their efficient and active search and hunting efforts (Gunther and Renkin 1990). For example, bears in Yellowstone National Park chased groups of elk with calves for longer and over greater distances than groups of elk without calves (Gunther and Renkin 1990). Though variable in their foraging behavior, in some cases, bears may aggregate in calving areas and pass foraging behavior on to their young through social learning and rearing conditions (Zager and Beecham 2006, Mazur and Seher 2008, Rayl et al. 2015). Neonatal hiding ungulates must necessarily find suitable cover within the constraints of the habitat chosen by the mother (Van Moorter et al. 2009). However, if maternal elk are exposing their calves to greater biomass in order to meet nutritional needs of lactation (Rearden et al. 2011), this necessarily means elk cow-calf pairs are out in the open and away from forest cover. That fine-scale security cover provided by downed logs decreased the risk of mortality to some extent may not be enough to counter the effect of bears, particularly if bears also seek vegetated areas and given their efficient hunting strategies.

We predicted higher calf survival in the eastern migrants that was associated with better maternal condition or potentially earlier calving and/or green-up on low-elevation summer range. Though plasticity in gestation length of ungulates can exist when maternal females have the ability to adjust nutritionally (Verme 1965, Rachlow and Bowyer 1991, Rowell and Shipka 2009), calving within a population tends to be highly synchronized (Estes 1976). Though eastern migrants did gain access to earlier green-up compared to residents (Killeen et al. 2016), we found no evidence that eastern migrants calved earlier than residents. Our result contrasts the highly synchronized calving and plant phenology that occurred in 2 populations of caribou, even when phenology started earlier in one population (Post et al. 2003). Other studies have also suggested that synchronous parturition likely evolved to coincide with progressing forage or long-term patterns in climate (Rutberg 1987, Rachlow and Bowyer 1991, Bowyer et al. 1998), but age of breeding bulls (Noyes et al. 1996) or predation pressure might be additional factors influencing synchronization of parturition (Estes 1976, Ims 1990*b*). Long-term shifts in phenology may be causing a mismatch for residents, or perhaps being a relatively new migratory tactic, the eastern migrants might also have been slow to adjust the timing and synchrony of births to the onset of vegetation, as occurred in a reintroduced population of bighorn sheep in northern Utah (Whiting et al. 2011)

Timing of birth is also important because early-born young can experience quicker growth that lessens susceptibility (Landete-Castillejos et al. 2001), or birth during peak of parturition can dilute individual risk to predation leading to greater survival (Estes 1976, Rutberg 1987, Testa 2002). On the other hand, a birth date outside the peak of parturition can lead to increased predation pressure (Testa 2002, Barber-Meyer and Mech 2008), susceptibility from a mismatch in timing of birth to resource availability (Clutton-Brock et al. 1987, Rachlow and Bowyer 1994), or in some cases, have no effect at all (Bowyer et al. 1998, Feder et al. 2008). Similarly, we found no effect of birth date that might indicate timing of birth influences risk of mortality for calves at Ya Ha Tinda or that it alters calf vulnerability with longer growth.

In contrast to timing of birth, we found that individual calf characteristics (i.e., sex, girth) had only fleeting effects on survival, but that nutritional condition of the maternal female, as measured by ingesta-free body fat, decreased risk of mortality throughout summer. The brief effect of calf size on risk of mortality might be related to the vulnerability of calves when they are very young and that high, potentially additive predation on elk calves in multi-predator systems is likely condition-independent (Barber-Meyer et al. 2008, Monteith et al. 2014). Even the strongest of neonates are no match for the varied hunting tactics (cursorial, stalking, active searching) of large predators such as wolves, cougars, and bears (Kunkel and Mech 1994). Our results support a similar finding in mule deer, where an effect of birth mass in only the first 3 weeks of life shifted to an influence of maternal nutritional condition that was most evident at the onset of peak lactation (4 weeks, Monteith et al. 2014).

In general, there was no difference between the nutritional condition of lactating residents and eastern migrants in late winter (Appendix B. Figure B.5). Both groups of lactating elk had relatively lower nutritional condition compared to lactating elk from other parts of western North America (Cook et al. 2013). However, the nutritional condition of non-lactating residents was significantly higher than that of non-lactating eastern migrants. While the nutritional condition of non-lactating elk measured in late winter is likely not as indicative of summer range nutrition as that of lactating elk measured in autumn (Cook et al. 2004, 2013, Proffitt et al. 2016), we attribute our outcome to the higher forage biomass that was available on summer range of residents (Chapter 3), and that forage and predation risk overlapped spatially, i.e., they were positively correlated (Appendix H). Calf loss as a result of predation (or other factors) can release maternal elk from constraints of lactation, thus allowing regain of nutritional condition (Middleton et al. 2013*a*). The higher body condition was supported by lower calf survival among residents, but more work is needed to understand differences in forage quality between the 2 summer ranges and if any differences might interact with predation to affect survival.

Bottom-up forces on population productivity are largely the result of nutritional adequacy and forage availability for maintenance of body condition (Cook et al. 2004), mediated by the effects of climate. The effects of winter climate can operate directly on adult elk through steady decline in body condition (Loison and Langvatn 1998, Parker et al. 2009), nutritional stress, and overwinter depletion of maternal body reserves that can lead to lower birth mass (Post and Stenseth 1999) and lower neonatal survival (Thorne et al. 1976, Garrott et al. 2003). We did not directly look at the effects of winter weather on calf survival and instead relied on maternal nutritional status and calf characteristics as potential carryover effects. This could be a potential avenue for future analysis. However, the fleeting effect of calf size on risk of mortality, coupled with non-lactating females in good condition and low population density (Gaillard et al. 1998), make us suspect that winter severity would not be a big concern to summer calf survival in this population, especially when compared to the effects of predation.

The factors that most explained the risk of mortality to elk calves in the Ya Ha Tinda population involved a combination of refuge from predation and available forage on summer range. We found the lowest risk of mortality from predation was where human infrastructure was high on summer range. Indeed, escape from predation is a predicted benefit of migration in ungulates (Bergerud et al. 1990, Barten et al. 2001, Mysterud et al. 2011), which resulted in differential and higher survival for elk calves born to eastern migrants. Higher survival was apparently a consequence of lower exposure to predation risk due to human activity measured by density of roads/trails, which predators avoid (Berger 2007, Rogala et al. 2011, Shannon et al. 2014). In comparing 2 adjacent elk populations in Montana, one of which one was migratory, Eacker et al. (2016) found that migratory elk not only were exposed to higher forage biomass, but calves had higher survival because predation risk by cougars and wolves was lower. Although we found both resident and eastern migrants selected for forage resources during calving, elk that migrated to low-elevation summer ranges east of Ya Ha Tinda had lower risk but were exposed to slightly lower forage (Chapter 3). Therefore, the risk of mortality in areas of lower human infrastructure (i.e., less refuge/higher risk) was lessened to some degree for residents, but not for eastern migrants, only where forage was most available (Figure 4.8). In fact, Hebblewhite and Merrill (2009) previously showed that residents in the Ya Ha Tinda population were capable of reducing their risk to wolves by using areas close to human activity, which wolves avoided. However, although wolves may be the major source of mortality on adult elk (Hebblewhite et al. 2018), we found wolf predation on calves during the summer is relatively low compared to bears. Elk during calving may be predisposed to bear predation because they select areas of high forage value that bears may also select (Nielsen 2005, 2007). High spatial overlap in selection by bears and elk during calving may contribute to the additive effects of bear mortality (Griffin et al. 2011). Further, if bears overlap less with elk in these forage-value areas during calving as the elk population declines and adult elk protect their young, this may also contribute to the observed density-dependent effect of bear predation observed on elk in this system (Hebblewhite et al. 2018).

Low wolf densities contributed to low amounts of cause-specific mortality by wolves on elk calves in Wyoming (Smith et al. 2006), and we similarly found both wolf- and cougar-caused mortality to be low and relatively constant across time contrary to that caused by bears. In fact, there has been relatively little direct evidence of wolf predation on neonatal elk when part of a larger multi-predator system, leading to the generalization by others that wolf predation is most likely a compensatory source of mortality for elk calves (Raithel et al. 2007, Barber-Meyer et al. 2008, Griffin et al. 2011). The low mortality by wolves in our study area, particularly for the calves of eastern migrants, likely resulted from the relatively low density of predators encountered by elk the farther east they travel from Banff National Park because of human harvest (i.e., hunting and trapping) and human activity. Low numbers of wolves in the east relative to the west likely also contributed to the higher percentage of cougar-caused mortalities for calves of the eastern migrants (Figure B.12, Atwood et al. 2009). In multi-predator systems with both grizzly bears and wolves present, cougar-caused mortality on elk calves decreases (Griffin et al. 2011), suggesting cougars in our study area may have been taking advantage of lower interspecific competition in the east (Murphy et al. 1995, Bartnick et al. 2013). This conclusion is supported by the fact that cougar diets in the area are mainly composed of deer (Krawchuk 2014) and that we found evidence for an interaction between risk by cougars and migratory tactic, with a greater positive influence of risk by cougars on mortality for eastern migrants (Table 4.4). However, one limitation of our data on predators, and on cougars in particular, is that predators were not directly studied (e.g., through telemetry) concurrent with our study on calf survival. While our spatial layers of predation risk by bears and wolves were originally created with telemetry data, we could only update these layers with new data on land cover, and the static layer of risk by cougars was created from a scat-based resource selection function and tested with remote camera data, as opposed to telemetry. Nevertheless, the telemetry-based and scat-based predator layers provided a means to evaluate the layers against each other, and the spatiotemporal patterns in risk of mortality for calves between the predators should still hold (Spilker 2018). Thus, the spatial structure in predation risk, represented by heavier presence and risk by bears and wolves in the west, compared to cougars in the east, provides supporting evidence that differential predation could be playing a role in the shifting migratory behavior of the Ya Ha Tinda population.

The particular migratory tactic used by a maternal female ungulate comes with costs and benefits that ultimately affect life-history characteristics and maintenance of partial migration within a population. Differential mortality between migratory tactics of a population can result in poor recruitment and a decrease in the proportion of individuals using the more costly tactic, potentially with concurrent increases in the more successful tactic. In fact, we documented differences in exposure to forage resources and predation risk on summer ranges that resulted in variable predator-specific mortality leading to higher calf survival of one migratory tactic over another. Higher juvenile survival in the eastern migrants appears to be contributing to the shifting migratory behavior in the Ya Ha Tinda elk population. The appearance of the new eastern migratory tactic allowed a unique opportunity to increase understanding of the fitness consequences resulting from a major shift in migratory behavior and its contribution to maintaining this partially migration population.

Table 4.1. Hypotheses to explain elk calf survival in the partially migratory Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016.

Hypothesis		Expectation	Model Variables
Timing	**H1a**	Peak of calving occurs earlier in eastern migrants than residents.	Distribution of calving events
	H1b	Calves born outside peak of parturition have lower predation resulting in higher survival through the neonatal/calf-rearing (26 d) phases across migratory tactics, or in calves of eastern migrants if peak of calving occurs earlier.	Date of birth
	H1c	Resident calves are more vulnerable than migrant calves, especially during the neonatal/calf-rearing (26 d) phases as opposed to summer (90 d).	Overall and cumulative risk of mortality
	H1d	Predation-specific mortality varies during the neonatal/calf-rearing (26 d) phases of calf life with variable timing among predators.	Distribution of predation events
Intrinsic effects	**H2**	Chapter 2 Maternal and intrinsic calf factors influence survival during the neonatal (1 – 10 days) and calf-rearing (26 d) phases of calf life, but not through summer (90 d).	Adult IFBF, adult age, calf sex, calf body mass, calf chest girth
Predation	**H3a**	Increased fine-scale security cover improves calf survival during the first 3 days post-partum.	Birth site cover measurements
	H3b	Lower exposure to predator-specific or total predator risk on summer range results in higher calf survival during the neonatal/calf-rearing (26 d) phases.	RSFs, human infrastructure
	H3c	Spatial structure in predator risk on summer range results in differential predation-specific calf survival between migratory tactics through the neonatal/calf-rearing (26 d) phases.	RSFs × migratory tactic interaction
Forage	**H4**	Chapter 3 Calves of elk exposed to earlier high-quality forage or higher amounts of forage on summer range have higher survival through the neonatal/calf-rearing (26 d) phases.	NDVI, forage biomass
Trade-offs	**H5**	Higher calf survival through the neonatal/calf-rearing (26 d) phases requires both lower risk of predation and higher available forage on summer range.	RSFs or human infrastructure, forage biomass
Null	**H0**	Calf mortality is unrelated to intrinsic factors and is random in geographic and environmental space.	

Table 4.2. Top 3 models for influence of intrinsic and maternal factors on daily risk of mortality through 3, 26, and 90 days of life in elk calves of the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. Covariates considered included migratory tactic (eastern migrant as reference group, Mig), nutritional status (% Ingesta-Free Body Fat, IFBF), and age of the adult female, and calf sex (female as reference group), mass (kg), and chest girth (cm) at birth. Bold font indicates 90% credible intervals did not overlap zero.

	3-day Risk of Mortality				26-day Risk of Mortality				90-day Risk of Mortality			
Model	Sex	Girth	Sex × Girth	DIC	Mig	IFBF	Mig × IFBF	DIC	Mig	IFBF	Mig × IFBF	DIC
Sex + Girth	**-1.13**	**-0.99**		121.14								
Sex + Girth + (Sex × Girth)	**-1.18**	-0.99	-0.04	122.11								
Girth	**-1.02**			122.63								
Mig + IFBF + (Mig × IFBF)					**1.54**	-1.05	0.62	443.25	**1.59**	-1.17	**0.70**	546.09
Mig + IFBF					**1.22**	0.11		443.99	**1.25**	0.14		549.31
IFBF						0.30		454.00				
Mig					**1.31**			442.54	**1.36**			548.71
Null				124.68				455.87				565.44

Table 4.3. Parameter estimates of variables at birth or hiding sites associated with daily risk of mortality through 26 days of life in elk calves of the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. Covariates considered included cover provided by downed logs (%), overhead canopy (%), distance to the nearest edge (m), and migratory tactic (eastern migrant as reference group, Mig). Bold font indicates 90% credible intervals did not overlap zero.

	Mig	Log Cover	Canopy	Dist. Edge	Bear	FB[a]	Mig × Log Cover	DIC
Mig + Log Cover + Bear + FB	**1.11**	-0.24			-0.03	0.18		445.46
Mig + Log Cover + Bear + FB + (Mig × Log Cover)	**1.11**	-0.28			-0.02	0.18	-0.0002	447.02
Log Cover + Bear + FB		**-0.39**			**0.24**	0.25		448.79
Canopy + Bear + FB			0.09		**0.24**	**0.38**		451.32
Dist. Edge + Bear + FB				0.03	**0.23**	**0.36**		451.82

[a] FB = Forage Biomass (g/m^2)

Table 4.4. Parameter estimates for the effect of predation risk or refuge from predation (i.e., human infrastructure) at 2 spatial scales on daily risk of mortality through 26 days of life in elk calves of the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. The 2 spatial scales at which covariates were measured included the area used during the calf-rearing phase (26 days), and the annual summer range, defined by the adult female's migratory tactic (eastern migrant as reference group, Mig). Bold font indicates 90% credible intervals did not overlap zero.

	Calf-rearing Area							Summer Range						
Model	Mig	Human	Wolf	Bear	Cougar	Inter-action	DIC	Mig	Human	Wolf	Bear	Cougar	Inter-action	DIC
Mig + Cougar + (Mig × Cougar)	**1.36**				-0.08	0.10	446.16	**1.86**				**1.26**	**-0.61**	440.73
Mig + Human + (Mig × Human)	**1.35**	-0.55				0.35	445.03	-0.30	-1.88				0.63	441.80
Mig + Bear + (Mig × Bear)	0.82			0.83		-0.48	444.40	0.65			**1.13**		**-0.67**	442.79
Mig + Wolf + (Mig × Wolf)	**1.07**		0.20			-0.01	443.85	0.54		0.33			0.05	444.19

Table 4.5. Top 3 models at 3 spatial scales for influence of forage quality (NDVI) and forage biomass (g/m^2, FB) on daily risk of mortality through 26 days of life in elk calves of the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. The 2 spatial scales at which covariates were measured included the area used during the calf-rearing (26 days) phase, and the annual summer range, defined by the adult female's migratory tactic (eastern migrant as reference group, Mig). Bold font indicates 90% credible intervals did not overlap zero.

	Calf-rearing Area				Summer Range			
Model	Mig	FB	Mig × FB	DIC	Mig	FB	Mig × FB	DIC
Mig + FB + (Mig × FB)	**1.35**	-0.38	0.27	443.84	0.23	1.40	-0.50	441.80
Mig + FB	**1.19**	0.15		443.72	0.65	**0.44**		441.90
FB		**0.33**		452.67		**0.66**		441.81

Table 4.6. Parameter estimates for models testing whether daily risk of mortality through 26 days of life in elk calves of the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016, depends on both lower risk of predation (or refuge from predation provided by higher human infrastructure) and higher available forage (FB). Covariates were measured at the spatial scale of the annual summer range, defined by migratory tactic (eastern migrant as reference group, Mig). Bold font indicates 90% credible intervals did not overlap zero.

	Mig	Wolf	Bear	Coug.	Human	FB	Mig × Bear	Mig × Coug.	Human × FB	Wolf × FB	Bear × FB	Coug. × FB	DIC
Mig + Human + FB + (Human × FB)	-0.42				-0.41	**0.87**			0.60				438.19
Mig + Human + FB + (Mig × Human × FB)	-0.68				-0.59	**1.01**			0.38				439.46
Mig + Human + FB	-0.32				**-0.73**	**0.47**							440.18
Mig + Cougar + FB + (Mig × Cougar)	**1.19**			**1.33**		0.43		**-0.68**					440.47
Mig + Cougar + FB + (Mig × Coug.) + (Coug. × FB)	0.93			**1.93**		**0.53**		**-1.09**				0.26	441.55
Mig + Bear + FB + (Mig × Bear)	0.06		1.06			0.42	**-0.64**						441.92
Mig + Wolf + FB + (Wolf × FB)	-0.31	0.14				0.83				-0.42			443.26
Mig + Wolf + FB	0.63	0.02				0.42							443.37
Mig + Bear + FB + (Mig × Bear) + (Bear × FB)	0.09		0.99			0.41	-0.60				-0.02		443.18

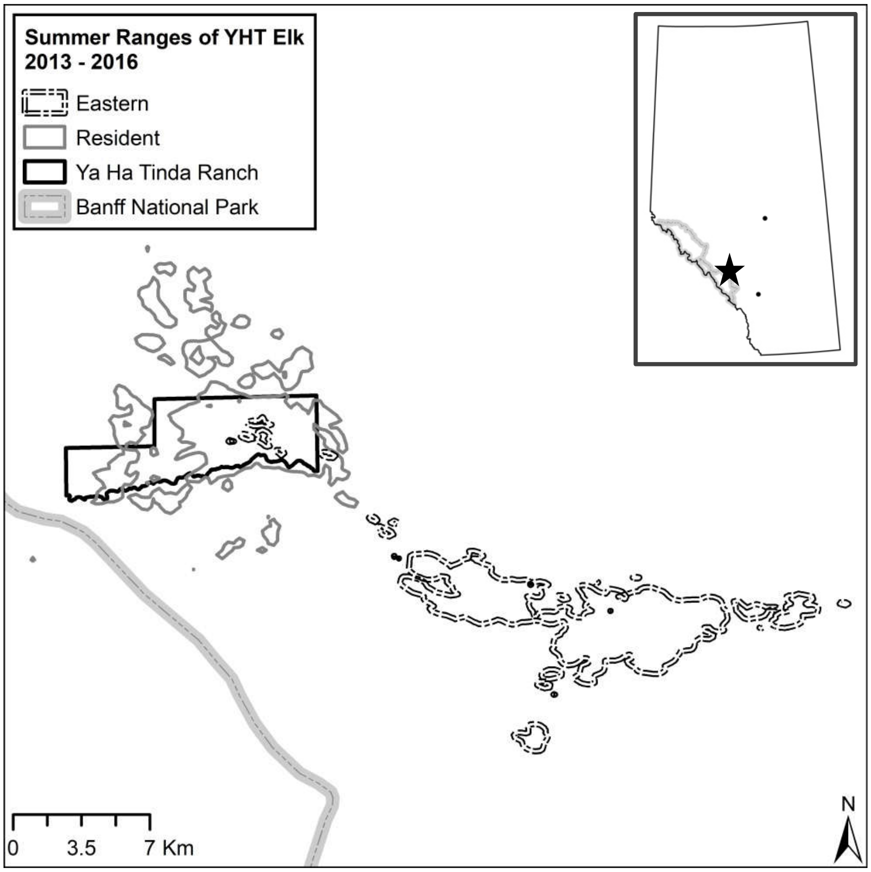


Figure 4.1. Summer ranges of resident and eastern migrant female elk in the Ya Ha Tinda population during 2013 – 2016 on the eastern slopes of Banff National Park, Alberta, Canada.

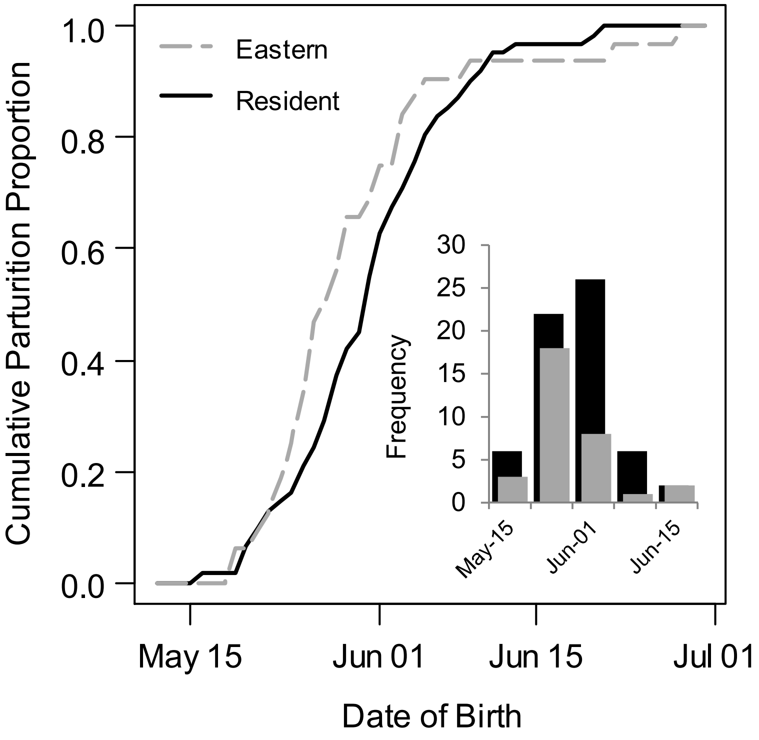


Figure 4.2. Cumulative frequency of parturition dates for elk following 2 different migratory tactics (resident: *n* = 62, and eastern migrant: *n* = 32) in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. Inset shows the distribution of dates of parturition.

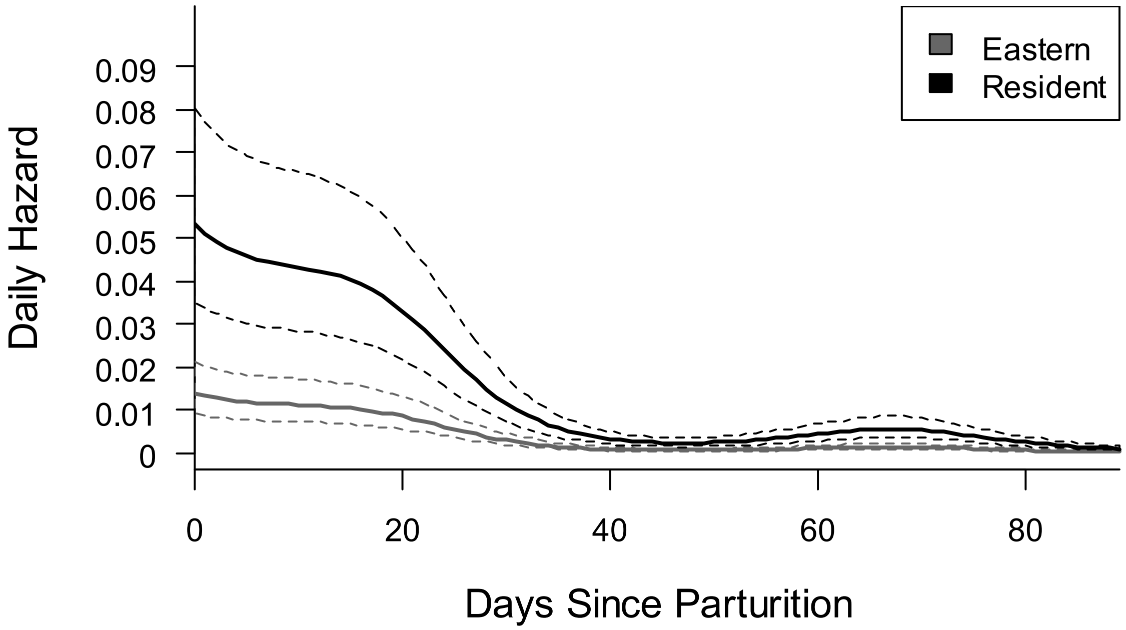


Figure 4.3. Predicted daily hazard rates (solid line) from all causes of mortality for elk calves born to elk following 2 different migratory tactics (resident and eastern migrant) in the Ya Ha Tinda population, Alberta, Canada, 2013 – 2016. Dashed lines represent the variation in hazard rates (based on the estimated sigma) and are the bounds of the 95% cumulative distributions. The overall cumulative hazard rates were 0.69 for resident calves and 0.37 for eastern migrant calves.

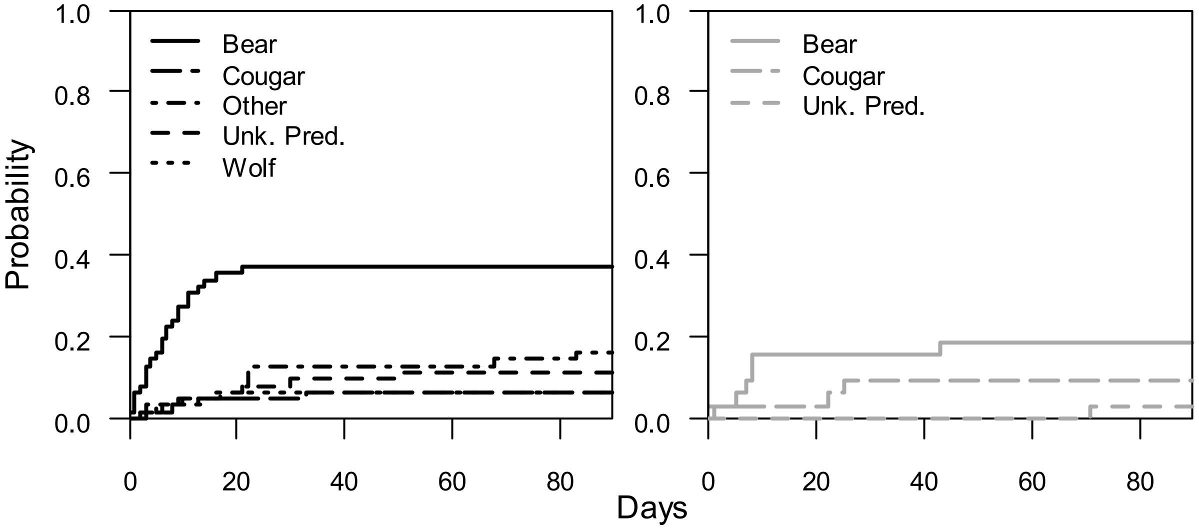


Figure 4.4. Comparison of cumulative risk of mortality during the first 90 days of life for elk calves of elk following 2 different migratory tactics (on left, resident, and on right, eastern migrant) in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016.

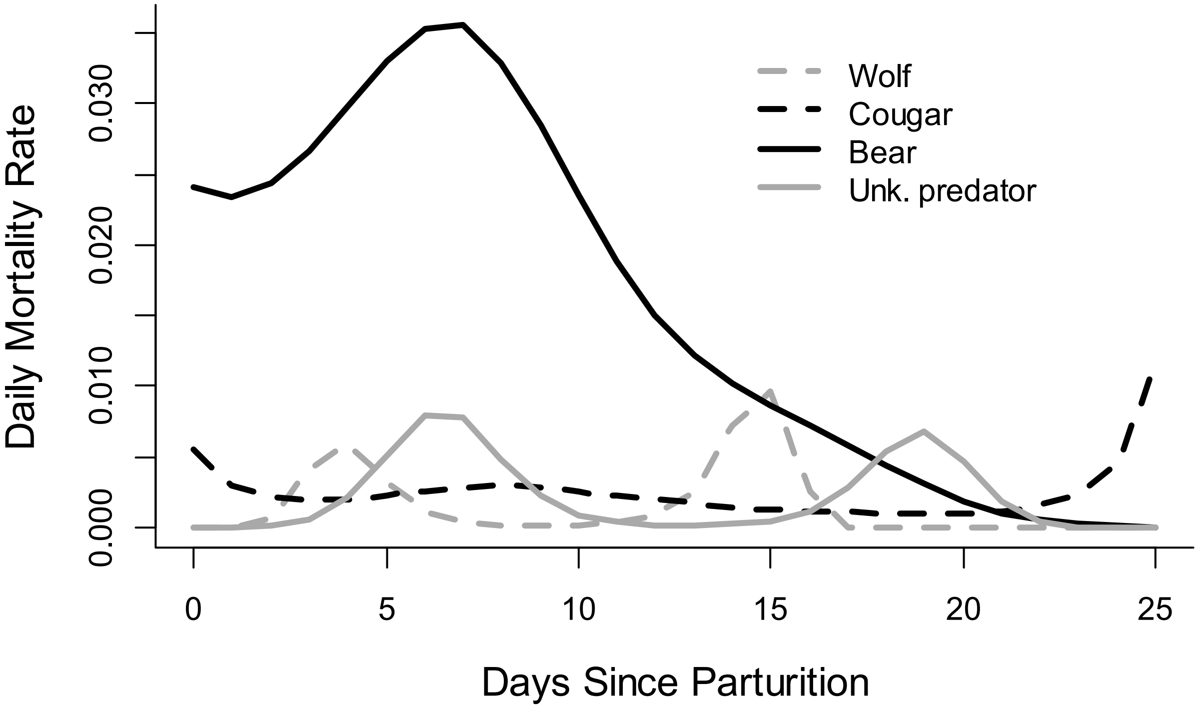


Figure 4.5. Daily cause-specific mortality rates for elk calves (*n* = 85) during the first 26 days following birth in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016.

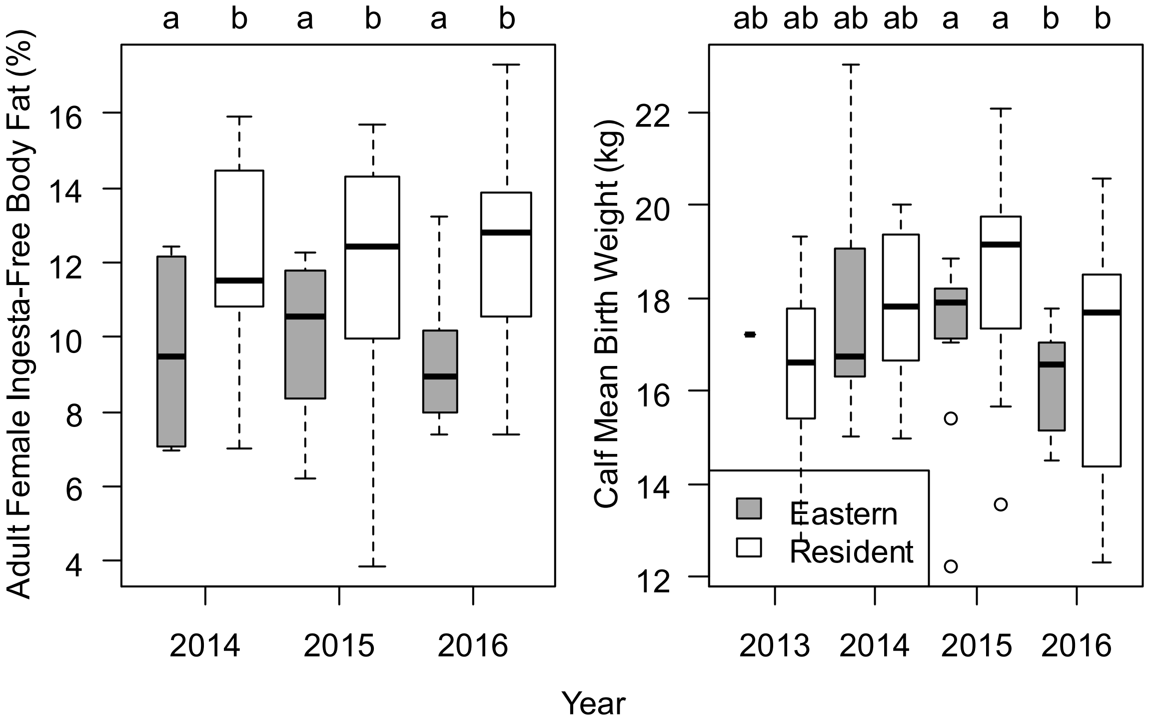


Figure 4.6. In left panel, ingesta-free body fat (%) measured in late winter (Feb – Mar) for adult female elk following 2 different migratory tactics (resident: *n* = 53, and eastern migrant: *n* = 25). In right panel, weight at birth for calves (*n* = 94) captured in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016, in right panel. Letters indicate significant difference within each panel.

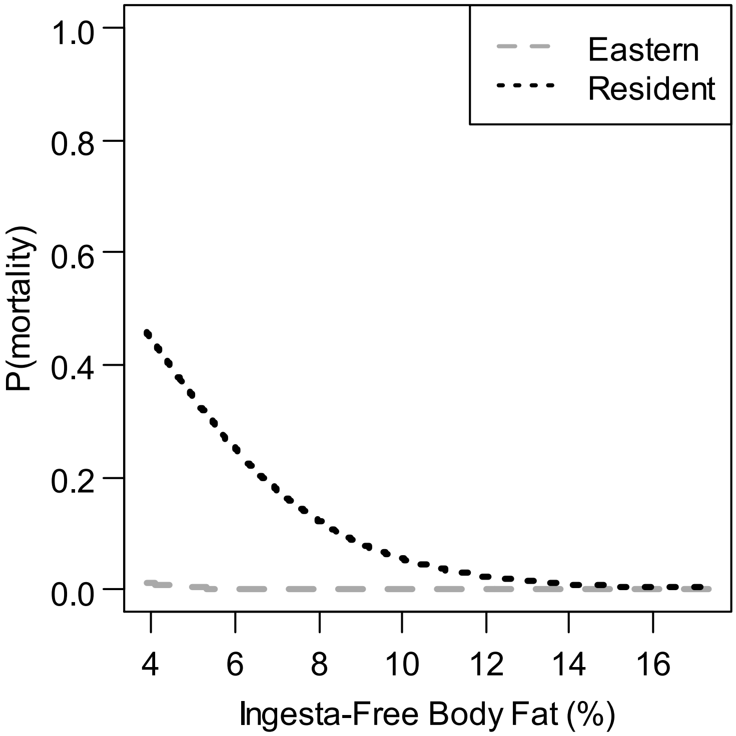


Figure 4.7. Predicted probability of elk calf mortality with changes in ingesta-free body fat (%) and migratory tactic of adult females in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016.

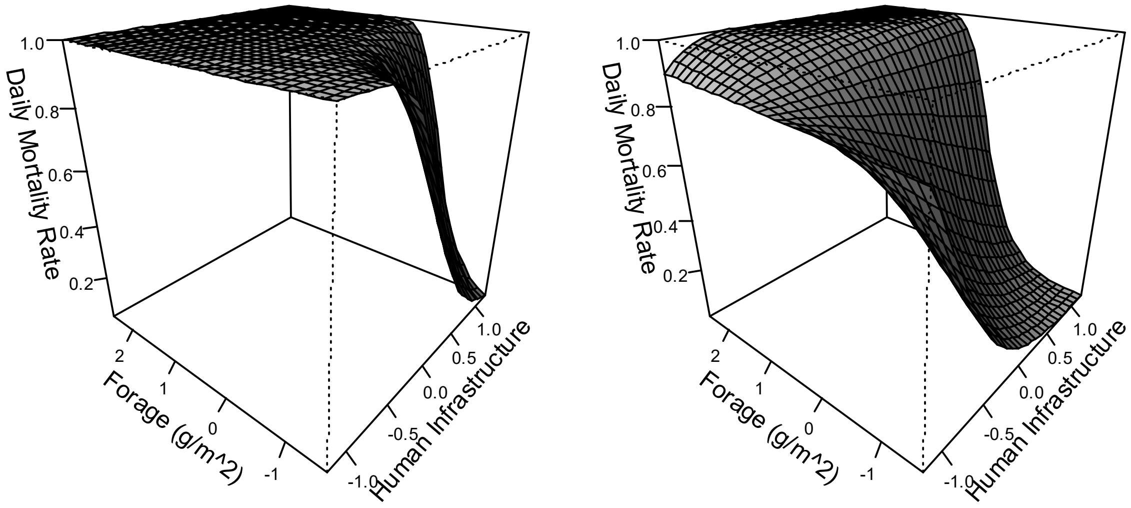


Figure 4.8. Effect of interaction between (scaled) human infrastructure and (scaled) forage biomass on daily mortality risk through 26 days of life in calves of eastern migrants in the left panel, and residents in the right panel, in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016.

CHAPTER 5. CONCLUSION

Migration is expected to arise in spatiotemporal environments such that ungulates migrate to enhance access to critical resources such as forage or water, lessen the likelihood of predation, or escape from parasites (Fryxell and Sinclair 1988*a*, Mysterud et al. 2011, 2016, Qviller et al. 2013). In moving across the landscape, large herbivores can have significant impacts on the systems they inhabit, from structuring plant communities, transferring nutrients, and altering ecosystem processes (McNaughton et al. 1988, Frank 1998, Holdo et al. 2006), to influencing distributions of apex predators (Packer et al. 2005, Lee et al. 2016). Yet anthropogenic influences, a shifting climate, and changing habitats are altering or reducing migratory behavior, and migratory populations of large ungulates are declining worldwide (Wilcove and Wikelski 2008, Harris et al. 2009). Loss of ungulate migration has been related to human effects on habitat that may be exacerbated by climate change, and which may have significant ecological impacts across trophic levels (Holdo et al. 2011*b*). In populations that are partially migratory (i.e., that consist of both resident and migratory individuals), these human-caused changes can alter the relative costs and benefits of migration to individuals so that residency may become the more favored tactic.

Across western North America, elk (*Cervus canadensis*) have widespread ecological, recreational, and socioeconomic importance (Fried et al. 1995, Hobbs 1996, Gordon et al. 2004, Schorr et al. 2014). However, in the Canadian Rockies, declines in some elk populations and changes in migratory behavior over the last several decades have become evident. For example, non-migratory elk appeared to proportionally increase relative to migrants in the 2000s in the East Kootenay of British Columbia; management concerns arose over elk crowding and overgrazing on public land along with crop depredation on private land (Phillips and Szkorupa 2011). These shifts in migratory behavior by elk in the East Kootenay were consistent with declines in other parts of British Columbia and Alberta; in the Slocan and Elk Valleys in the early 2000s, over 20% and 45% of collared elk, respectively, were determined to be non-migratory (Gibson and Sheets 1997, DeGroot and Woods 2006). Given the perceived changes in migrant-to-resident ratios, management agencies realized the need for updated information on elk movements, habitat use, and population dynamics. Still, because of the difficulty in conducting the long-term monitoring of marked individuals required to address the maintenance of long-distance animal migration (Gaillard 2013, Festa-Bianchet et al. 2017), detailed information relating intrinsic factors and vital rates (age, condition, reproductive history), and in particular, extrinsic factors (predation, vegetation), to migratory behavior remained largely lacking. In the Bow River Valley of Alberta, recolonizing wolves (*Canis lupus*) were implicated in the decline of migrant to resident elk and migration, yet the exact mechanisms behind the shifts in migratory behavior were unknown (Woods 1991, Hebblewhite 2007).

On the other hand, wolves and the mechanisms leading to migratory changes were central to studies on the partially migratory elk at Ya Ha Tinda (e.g., Hebblewhite 2006, Hebblewhite and Merrill 2007). Twenty years after recolonization of wolves, Hebblewhite (2006) showed that the decline of migratory behavior since the 1970s was largely due to a shift in the spatial distribution of elk to winter range year-round related to the consequences of selection for forage and predation risk by western migrants and residents on their summer ranges.

We sought to expand on the results of the work by Hebblewhite et al. at Ya Ha Tinda by focusing on calf survival to examine the ways that predation and other factors can differentially affect migrants and residents within a population or lead to new patterns of migration. Broad-scale, long-term decreases in recruitment have been a big focus of both management and research in recent decades (Lukacs et al. 2018), in large part because of recolonizing large carnivores. Preliminary evidence indicated recruitment at Ya Ha Tinda was in decline, or at least not increasing and not enough to counter adult mortality (Eggeman 2012). However, elk at Ya Ha Tinda face not just wolves, but a suite of predators that also includes coyotes (*Canis latrans*), grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), and cougars (*Puma concolor*). In multi-predator systems containing wolves and bears, mortality by cougars and wolves is often lower, and predation by bears is the dominant source of mortality (Griffin et al. 2011). Indeed, in Chapter 4, we found that the majority of mortality on elk calves occurred early on and through bears, and calves of residents were over 80% more at risk than calves of eastern migrants.

We further showed that exposure to environmental factors (predation, forage, human activity) on summer ranges resulted in differential survival between the migratory tactics, with higher calf survival for eastern migrants that is consistent with the shifts in migratory behavior. Maternal elk following all 3 migratory tactics consistently selected for forage resources during calving more than during summer, with limited evidence for trading off forage due to predation risk. This result was somewhat surprising, given the high amount of predation in this multi-predator system, but consistent with the recent decline in western migrants and the increase in eastern migrants. Only the eastern migrants appear able to escape predation as a benefit to migration, and conditions on calving areas seem to have contributed to the observed changes in migration behavior and promotion of the new migration.

Given that grizzly bears are protected within Banff National Park, that there is evidence for only weak density-dependent bear predation (Hebblewhite et al. 2018), and that selection for foraging areas during calving exposed western migrants to high risk of bear predation, we suggest that the western portion of the population is likely to continue to decline. On the other hand, because eastern migrants experienced lower predation as a result of risk avoidance through use of high human activity areas, higher calf survival is likely to continue in this portion of the population. Alternatively, as we reviewed in Chapter 2, elk may shift back towards a resident or western tactic if there is a perceived benefit to doing so; switching could occur, for example, with increasing conspecific or predator densities or further habitat changes (cuts or burns that could alter the current state of predator-prey dynamics) on the eastern summer range.

Our research provides site-specific information for elk management that contributes to an understanding of the population's migratory behaviors and produces guidelines for the dynamic value of burns and timber harvest in elk and habitat management. Results of this research lend a broader understanding to density-dependent predation, mechanisms of cause-specific calf mortality, loss and alteration of migratory behaviour, and elk habitat selection during calving in areas with burns and/or timber harvests. By monitoring intrinsic factors such as age, reproductive history and density, as well as extrinsic variation in forage and predation risk, we gained an understanding of how flexible partially migratory large ungulates can be when faced with environmental change. Yet still, there is a paucity of long-term, individually-based studies on ungulates, and on partially migratory ungulates in particular. We recommend continuing the long-term monitoring at Ya Ha Tinda in hopes of gaining further insight into the new eastward migration (e.g., adult survival and cause-specific mortality of eastern migrants) and how this new tactic fits within the population's demographic dynamics and population persistence.

REFERENCES

Abadi, F., O. Gimenez, B. Ullrich, R. Arlettaz, and M. Schaub. 2010. Estimation of immigration rate using integrated population models. Journal of Applied Ecology 47:393–400.

Abrahms, B., D. P. Seidel, E. Dougherty, E. L. Hazen, S. J. Bograd, A. M. Wilson, J. Weldon McNutt, D. P. Costa, S. Blake, J. S. Brashares, and W. M. Getz. 2017. Suite of simple metrics reveals common movement syndromes across vertebrate taxa. Movement Ecology 5:12.

Adams, L. G., F. J. Singer, and B. W. Dale. 1995. Caribou calf mortality in Denali National Park, Alaska. Journal of Wildlife Management 59:584–594.

Aikens, E. O., M. J. Kauffman, J. A. Merkle, S. P. H. Dwinnell, G. L. Fralick, and K. L. Monteith. 2017. The greenscape shapes surfing of resource waves in a large migratory herbivore. Ecology Letters 20:741–750.

Alberta Environment and Parks. 2016. Alberta grizzly bear (*Ursus arctos*) recovery plan. Edmonton, AB, Canada.

Alberta Environmental Protection. 1993. Management plan for black bears in Alberta. Edmonton, AB, Canada.

Albon, S. D., T. H. Clutton-Brock, and F. E. Guinness. 1987. Early development and population dynamics in red deer II. Density-independent effects and cohort variation. Journal of Animal Ecology 56:69–81.

Albon, S. D., and R. Langvatn. 1992. Plant phenology and the benefits of migration in a temperate ungulate. Oikos 65:502–513.

Alerstam, T., A. Hedenström, and S. Åkesson. 2003. Long-distance migration: Evolution and determinants. Oikos 103:247–260.

Allen, A. M., J. Månsson, H. Sand, J. Malmsten, G. Ericsson, and N. J. Singh. 2016. Scaling up movements: From individual space use to population patterns. Ecosphere 7:e01524.

Altmann, M. 1952. Social behavior of elk, *Cervus canadensis Nelsoni*, in the Jackson Hole area of Wyoming. Behaviour 4:116–143.

Andersen, R. 1991*a*. Habitat deterioration and the migratory behaviour of moose (*Alces alces* L.) in Norway. Journal of Applied Ecology 28:102–108.

Andersen, R. 1991*b*. Habitat changes in moose ranges: Effects on migratory behavior, site fidelity and size of summer home-range. Alces 27:85–92.

Arman, P., R. N. B. Kay, E. D. Goodall, and G. A. M. Sharman. 1974. The composition and yield of milk from captive red deer (*Cervus elaphus* L.). Journal of Reproductive Fertility 37:67–84.

Atwood, T. C., E. M. Gese, and K. E. Kunkel. 2009. Spatial partitioning of predation risk in a multiple predator–multiple prey system. Journal of Wildlife Management 73:876–884.

Avgar, T., J. R. Potts, M. A. Lewis, and M. S. Boyce. 2016. Integrated step selection analysis: Bridging the gap between resource selection and animal movement. Methods in Ecology and Evolution 7:619–630.

Avgar, T., G. Street, and J. M. Fryxell. 2014. On the adaptive benefits of mammal migration. Canadian Journal of Zoology 92:481–490.

Ball, J. P., C. Nordengren, and K. Wallin. 2001. Partial migration by large ungulates: Characteristics of seasonal moose *Alces alces* ranges in northern Sweden. Wildlife Biology 7:39–47.

Barber-Meyer, S. M. 2006. Elk calf mortality following wolf restoration to Yellowstone National Park. PhD Dissertation, University of Minnesota, Minneapolis, MN, USA.

Barber-Meyer, S. M., and L. D. Mech. 2008. Factors influencing predation on juvenile ungulates and natural selection implications. Wildlife Biology in Practice 4:8–29.

Barber-Meyer, S. M., L. D. Mech, and P. J. White. 2005. Bears remain top summer predators. Yellowstone Science 13:37–44.

Barber-Meyer, S. M., L. D. Mech, and P. J. White. 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. Wildlife Monographs 169:1–30.

Barbknecht, A. E., W. S. Fairbanks, J. D. Rogerson, E. J. Maichak, B. M. Scurlock, and L. L. Meadows. 2011. Elk parturition site selection at local and landscape scales. Journal of Wildlife Management 75:646–654.

Barker, K. J. 2018. Home is where the food is: Causes and consequences of partial migration in elk. MSc Thesis, University of Montana, Missoula, MT, USA.

Barker, K. J., M. S. Mitchell, K. M. Proffitt, and J. D. Devoe. 2018. Land management alters traditional nutritional benefits of migration for elk. Journal of Wildlife Management 83:167–174.

Barnowe-Meyer, K. K., P. J. White, T. L. Davis, D. W. Smith, R. L. Crabtree, and J. A. Byers.

2010. Influences of wolves and high-elevation dispersion on reproductive success of pronghorn (*Antilocapra americana*). Journal of Mammalogy 91:712–721.

Barnowe-Meyer, K. K., P. J. White, L. P. Waits, and J. A. Byers. 2013. Social and genetic structure associated with migration in pronghorn. Biological Conservation 168:108–115.

Barten, N. L., R. T. Bowyer, and K. J. Jenkins. 2001. Habitat use by female caribou: Tradeoffs associated with parturition. Journal of Wildlife Management 65:77–92.

Bartlam-Brooks, H. L. A., P. S. A. Beck, G. Bohrer, and S. Harris. 2013. In search of greener pastures: Using satellite images to predict the effects of environmental change on zebra migration. Journal of Geophysical Research: Biogeosciences 118:1427–1437.

Bartnick, T. D., T. R. Van Deelen, H. B. Quigley, and D. Craighead. 2013. Variation in cougar (*Puma concolor*) predation habits during wolf (*Canis lupus*) recovery in the southern Greater Yellowstone Ecosystem. Canadian Journal of Zoology 91:82–93.

Basille, M., B. Van Moorter, I. Herfindal, J. Martin, J. D. C. Linnell, J. Odden, R. Andersen, and J.-M. Gaillard. 2013. Selecting habitat to survive: The impact of road density on survival in a large carnivore. PLoS ONE 8:e65493.

Bastille-Rousseau, G., J. R. Potts, C. B. Yackulic, J. L. Frair, E. H. Ellington, and S. Blake. 2016. Flexible characterization of animal movement pattern using net squared displacement and a latent state model. Movement Ecology 4:15.

Becker, S. A., M. J. Kauffman, and S. H. Anderson. 2010. Nutritonal condition of adult female Shiras moose in northwest Wyoming. Alces 46:151–166.

Bennitt, E., M. C. Bonyongo, and S. Harris. 2016. Effects of divergent migratory strategies on access to resources for Cape buffalo (*Syncerus caffer caffer*). Journal of Mammalogy 97:1682–1698.

Bercovitch, F. B., C. P. Loomis, and R. G. Rieches. 2009. Age-specific changes in reproductive effort and terminal investment in female Nile lechwe. Journal of Mammalogy 90:40–46.

Berg, J., E. Spilker, J. Killeen, E. H. Merrill, and M. Hebblewhite. 2016. Ya Ha Tinda elk & predator study. Annual report 2015-2016. University of Alberta, Edmonton, AB, Canada.

Berger, J. 2004. The last mile: How to sustain long-distance migration in mammals. Conservation Biology 18:320–331.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letters 3:620–623.

Berger, J., J. K. Young, and K. M. Berger. 2008. Protecting migration corridors: Challenges and optimism for Mongolian saiga. PLoS Biology 6:1365–1367.

Bergerud, A. T. 1988. Caribou, wolves and man. Trends in Ecology & Evolution 3:68–72.

Bergerud, A. T., H. E. Butler, and D. R. Miller. 1984. Antipredator tactics of calving caribou: Dispersion in mountains. Canadian Journal of Zoology 62:1566–1575.

Bergerud, A. T., R. Ferguson, S. E. Butler, and H. E. Butler. 1990. Spring migration and dispersion of woodland caribou at calving. Animal Behaviour 39:360–368.

Bergerud, A. T., and R. E. Page. 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. Canadian Journal of Zoology 65:1597–1606.

Bergman, C. M., J. A. Schaefer, and S. N. Luttich. 2000. Caribou movement as a correlated random walk. Oecologia 123:364–374.

Berthold, P. 1991. Genetic control of migratory behaviour in birds. Trends in Ecology & Evolution 6:254–257.

Berthold, P., and F. Pulido. 1994. Heritability of migratory activity in a natural bird population. Proceedings of the Royal Society B: Biological Sciences 257:311–315.

Berthold, P., and U. Querner. 1982. Partial migration in birds: Experimental proof of polymorphism as a controlling system. Experimentia 38:20–21.

Bischof, R., L. E. Loe, E. L. Meisingset, B. Zimmermann, B. Van Moorter, and A. Mysterud. 2012. A migratory northern ungulate in the pursuit of spring: Jumping or surfing the green wave? American Naturalist 180:407–424.

Blank, D. A., K. Ruckstuhl, and W. Yang. 2015. Antipredator strategy of female goitered gazelles (*Gazella subgutturosa* Guld., 1780) with hiding fawn. Behavioural Processes 119:44–49.

Bleich, V. C. 1999. Mountain sheep and coyotes: Patterns of predator evasion in a mountain ungulate. Journal of Mammalogy 80:283–289.

Bolger, D. T., W. D. Newmark, T. A. Morrison, and D. F. Doak. 2008. The need for integrative approaches to understand and conserve migratory ungulates. Ecology Letters 11:63–77.

Bonar, M., E. H. Ellington, K. P. Lewis, and E. Vander Wal. 2018. Implementing a novel movement-based approach to inferring parturition and neonate calf survival. PLoS ONE 13:e0192204.

Bongi, P., S. Ciuti, S. Grignolio, M. Del Frate, S. Simi, D. Gandelli, and M. Apollonio. 2008.

Anti-predator behaviour, space use and habitat selection in female roe deer during the fawning season in a wolf area. Journal of Zoology 276:242–251.

Börger, L., J. Matthiopoulos, R. M. Holdo, J. M. Morales, I. D. Couzin, and E. McCauley. 2011. Migration quantified: Constructing models and linking them with data. Pages 111–128 *in*. Animal Migration: A Synthesis. Oxford University Press, Oxford, UK.

Bowyer, R. T., V. Van Ballenberghe, and J. G. Kie. 1998. Timing and synchrony of parturition in Alaskan moose: Long-term versus proximal effects of climate. Journal of Mammalogy 79:1332–1344.

Bowyer, R. T., V. van Ballenberghe, J. G. Kie, and J. A. K. Maier. 1999. Birth-site selection by Alaskan moose: Maternal strategies for coping with a risky environment. Journal of Mammalogy 80:1070–1083.

Boyce, M. S. 1991. Migratory behavior and management of elk (*Cervus elaphus*). Applied Animal Behaviour Science 29:239–250.

Brinkman, T. J., C. S. Deperno, J. A. Jenks, B. S. Haroldson, and R. G. Osborn. 2005. Movement of female white-tailed deer: Effects of climate and intensive row-crop agriculture. Journal of Wildlife Management 69:1099–1111.

Brinkman, T. J., K. L. Monteith, J. A. Jenks, and C. S. Deperno. 2004. Predicting neonatal age of white-tailed deer in the northern Great Plains. Prairie Naturalist 36:75–82.

Brown, C. G. 1992. Movement and migration patterns of mule deer in southeastern Idaho. Journal of Wildlife Management 56:246–253.

Bruggeman, J. E., P. J. White, R. A. Garrott, and F. G. R. Watson. 2008. Partial migration in central Yellowstone bison. R. A. Garrott, P. J. White, and F. G. R. Watson, editors. The ecology of large mammals in central Yellowstone: Sixteen years of integrated field studies. Academic Press, San Diego, CA, USA.

Buchin, M., H. Kruckenberg, and A. Kolzsch. 2013. Segmenting trajectories by movement states. Pages 15–25 *in* S. Timpf and P. Laube, editors. Advances in spatial data handling: Geospatial dynamics, geosimulation and exploratory visualization. Springer-Verlag Berlin Heidelberg, Heidelberg, Germany.

Bunnefeld, N., L. Börger, B. van Moorter, C. M. Rolandsen, H. Dettki, E. J. Solberg, and G. Ericsson. 2011. A model-driven approach to quantify migration patterns: Individual, regional and yearly differences. Journal of Animal Ecology 80:466–476.

Cagnacci, F., S. Focardi, A. Ghisla, B. van Moorter, E. H. Merrill, E. Gurarie, M. Heurich, A. Mysterud, J. D. C. Linnell, M. Panzacchi, R. May, T. Nygård, C. M. Rolandsen, and M. Hebblewhite. 2016. How many routes lead to migration? Comparison of methods to assess and characterize migratory movements. Journal of Animal Ecology 85:54–68.

Cagnacci, F., S. Focardi, M. Heurich, A. Stache, A. J. M. Hewison, N. Morellet, P. Kjellander, J. D. C. Linnell, A. Mysterud, M. Neteler, L. Delucchi, F. Ossi, and F. Urbano. 2011. Partial migration in roe deer: Migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. Oikos 120:1790–1802.

Callaghan, C. J. 2002. The ecology of gray wolf (*Canis lupus*) habitat use, survival, and persistence in the central Rocky Mountains, Canada. PhD Dissertation, University of Guelph, Guelph, ON, Canada.

Cameron, M. D., K. Joly, G. A. Breed, L. S. Parrett, and K. Kielland. 2018. Movement-based methods to infer parturition events in migratory ungulates. Canadian Journal of Zoology 96:1187–1195.

Candolin, U. 1998. Reproduction under predation risk and the trade-off between current and future reproduction in the threespine stickleback. Proceedings of the Royal Society B: Biological Sciences 265:1171–1175.

Canon, S. K., P. J. Urness, and N. V. DeByle. 1987. Habitat selection, foraging behavior, and dietary nutrition of elk in burned aspen forest. Journal of Range Management 40:433–438.

Caratti, J. F. 2006. Line intercept (LI) sampling method. USDA Forest Service Gen. Tech. Rep. RMRS-GTR-164-CD. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.

Carl, G. R., and C. T. Robbins. 1988. The energetic cost of predator avoidance in neonatal ungulates: Hiding versus following. Canadian Journal of Zoology 66:239–246.

Chan-McLeod, A. C. A., R. G. White, and D. F. Holleman. 1994. Effects of protein and energy intake, body condition, and season on nutrient partitioning and milk production in caribou and reindeer. Canadian Journal of Zoology 72:938–947.

Chapman, B. B., C. Bronmark, J.-Å. Nilsson, and L.-A. Hansson. 2011*a*. Partial migration: An introduction. Oikos 120:1761–1763.

Chapman, B. B., C. Bronmark, J.-Å. Nilsson, and L.-A. Hansson. 2011*b*. The ecology and evolution of partial migration. Oikos 120:1764–1775.

Chapman, B. B., K. Hulthen, J. Brodersen, P. A. Nilsson, C. Skov, L.-A. Hansson, and C. Bronmark. 2012. Partial migration in fishes: Causes and consequences. Journal of Fish Biology 81:456–478.

Chen, X., L. Vierling, E. Rowell, and T. DeFelice. 2004. Using lidar and effective LAI data to evaluate IKONOS and Landsat 7 ETM+ vegetation cover estimates in a ponderosa pine forest. Remote Sensing of Environment 91:14–26.

Child, G., and J. D. Le Riche. 1969. Recent springbok treks (mass movements) in south-western Botswana. Mammalia 33:499–504.

Chitwood, M. C., M. A. Lashley, C. S. DePerno, and C. E. Moorman. 2017. Considerations on neonatal ungulate capture method: Potential for bias in survival estimation and cause-specific mortality. Wildlife Biology 17:wlb.00250.

Ciuti, S., A. Pipia, S. Grignolio, F. Ghiandai, and M. Apollonio. 2009. Space use, habitat selection and activity patterns of female Sardinian mouflon (*Ovis orientalis musimon*) during the lambing season. European Journal of Wildlife Research 55:589–595.

Clarke, C. M. H., and C. M. Frampton. 1991. Structural changes in an apparently stable chamois population in Basin Creek, Canterbury, New-Zealand. New Zealand Journal of Zoology 18:233–241.

Clutton-Brock, T. H. 1984. Reproductive effort and terminal investment in iteroparous animals. American Naturalist 123:212–229.

Clutton-Brock, T. H., G. R. Iason, S. D. Albon, and F. E. Guinness. 1982. Effects of lactation on feeding behavior in wild red deer hinds. Journal of Zoology 198:227–236.

Clutton-Brock, T. H., M. Major, S. D. Albon, and F. E. Guinness. 1987. Early development and population dynamics in red deer I. Density-dependent effects on juvenile survival. Journal of Animal Ecology 56:53–67.

Cole, E. K., A. M. Foley, J. M. Warren, B. L. Smith, S. R. Dewey, D. G. Brimeyer, W. S. Fairbanks, H. Sawyer, and P. C. Cross. 2015. Changing migratory patterns in the Jackson elk population. Journal of Wildlife Management 79:877–886.

Colson, K. E., K. S. White, and K. J. Hundertmark. 2016. Parturition site selection in moose (*Alces alces*): Evidence for social structure. Journal of Mammalogy 97:788–797.

Coltman, D. W., J. G. Pilkington, and J. M. Pemberton. 2003. Fine-scale genetic structure in a free-living ungulate population. Molecular Ecology 12:733–742.

Conn, P. B., and D. R. Diefenbach. 2007. Adjusting age and stage distributions for misclassification errors. Ecology 88:1977–1983.

Cook, J. G., R. C. Cook, R. W. Davis, and L. L. Irwin. 2016. Nutritional ecology of elk during summer and autumn in the Pacific Northwest. Wildlife Monographs 195:1–81.

Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 155:1–61.

Cook, R. C., J. G. Cook, and L. L. Irwin. 2003. Estimating elk body mass using chest-girth circumference. Wildlife Society Bulletin 31:536–543.

Cook, R. C., J. G. Cook, D. L. Murray, P. Zager, B. K. Johnson, and M. W. Gratson. 2001*a*. Development of predictive models of nutritional condition for Rocky Mountain elk. Journal of Wildlife Management 65:973–987.

Cook, R. C., J. G. Cook, D. L. Murray, P. Zager, B. K. Johnson, and M. W. Gratson. 2001*b*. Nutritional condition models for elk: Which are the most sensitive, accurate, and precise? Journal of Wildlife Management 65:988–997.

Cook, R. C., J. G. Cook, T. R. Stephenson, W. L. Myers, S. M. Mccorquodale, D. J. Vales, L. L. Irwin, P. B. Hall, R. D. Spencer, S. L. Murphie, K. A. Schoenecker, and P. J. Miller. 2010. Revisions of rump fat and body scoring indices for deer, elk, and moose. Journal of Wildlife Management 74:880–896.

Cook, R. C., J. G. Cook, D. J. Vales, B. K. Johnson, S. M. McCorquodale, L. A. Shipley, R. A. Riggs, L. L. Irwin, S. L. Murphie, B. L. Murphie, K. A. Schoenecker, F. Geyer, P. B. Hall, R. D. Spencer, D. A. Immell, D. H. Jackson, B. L. Tiller, P. J. Miller, and L. Schmitz. 2013. Regional and seasonal patterns of nutritional condition and reproduction in elk. Wildlife Monographs 184:1–45.

Courtemanch, A. B., M. J. Kauffman, S. Kilpatrick, and S. R. Dewey. 2017. Alternative foraging strategies enable a mountain ungulate to persist after migration loss. Ecosphere 8:e01855.

Couzin, I. D., J. Krause, N. R. Franks, and S. A. Levin. 2005. Effective leadership and decision-making in animal groups on the move. Nature 433:513–516.

Cowan, I. M. 1947. The timber wolf in the Rocky Mountain national parks of Canada. Canadian Journal of Research 25d:139–174.

Crainiceanu, C. M., D. Ruppert, and M. P. Wand. 2005. Bayesian analysis for penalized spline regression using WinBUGS. Journal of Statistical Software 14:1–24.

Crampe, J.-P., R. Bon, J.-F. Gerard, E. Serrano, P. Caens, E. Florence, and G. Gonzalez. 2007. Site fidelity, migratory behaviour, and spatial organization of female isards (*Rupicapra pyrenaica*) in the Pyrenees National Park, France. Canadian Journal of Zoology 85:16–25.

Cross, P. C., E. J. Maichak, J. D. Rogerson, K. M. Irvine, J. D. Jones, D. M. Heisey, W. H. Edwards, and B. M. Scurlock. 2015. Estimating the phenology of elk brucellosis transmission with hierarchical models of cause-specific and baseline hazards. Journal of Wildlife Management 79:739–748.

Damiani, M. L., H. Issa, G. Fotino, M. Heurich, and F. Cagnacci. 2015. Introducing 'presence' and 'stationarity index' to study partial migration patterns: An application of a spatio-temporal clustering technique. International Journal of Geographical Information Science 8816:1–22.

Van Deelen, T. R., H. Campa III, M. Hamady, and J. B. Haufler. 1998. Migration and seasonal range dynamics of deer using adjacent deeryards in northern Michigan. Journal of Wildlife Management 62:205–213.

DeGroot, L., and G. Woods. 2006. Elk movement patterns, distribution, survival rates, and problem elk in the Slocan Valley – Castlegar area of the West Kootenay, British Columbia, 2003 - 2005. Ministry of Environment, Nelson, BC, Canada.

DeMars, C. A., M. Auger-Méthé, U. E. Schlägel, and S. Boutin. 2013. Inferring parturition and neonate survival from movement patterns of female ungulates: A case study using woodland caribou. Ecology and Evolution 3:4149–4160.

Dingemanse, N. J., A. J. N. Kazem, D. Réale, and J. Wright. 2010. Behavioural reaction norms: Animal personality meets individual plasticity. Trends in Ecology and Evolution 25:81–89.

Dingle, H. 2014*a*. Migration: Definition and scope. Pages 13–23 *in*. Migration: The biology of life on the move. Second. Oxford University Press, Oxford, UK.

Dingle, H. 2014*b*. Behavioral and life-history variability in migration. Pages 211–230 *in*. Migration: The biology of life on the move. Second. Oxford University Press, Oxford, UK.

Dingle, H., and V. A. Drake. 2007. What is migration? BioScience 57:113–121.

Dodson, J. J. 1988. Nature and role of learning in the orientation and migratory beahvior of fishes. Environmental Biology of Fishes 23:161–182.

Douhard, M., J.-M. Gaillard, D. Delorme, G. Capron, P. Duncan, F. Klein, and C. Bonenfant.

2013. Variation in adult body mass of roe deer: Early environmental conditions influence early and late body growth of females. Ecology 94:1805–1814.

Dunn, O. J. 1961. Multiple comparisons among means. Journal of the American Statistical Association 56:52–64.

Duong, T. 2018. ks: Kernel smoothing. R package version 1.11.0.

Duquette, J. F., J. L. Belant, D. E. Beyer, and N. J. Svoboda. 2012. Comparison of pregnancy detection methods in live white-tailed deer. Wildlife Society Bulletin 36:115–118.

Dussault, C., J. P. Quellet, R. Courtois, J. Huot, L. Breton, and H. Jolicoeur. 2005. Linking moose habitat selection to limiting factors. Ecography 28:619–628.

Dwyer, C. M., and A. B. Lawrence. 2005. A review of the behavioural and physiological adaptations of hill and lowland breeds of sheep that favour lamb survival. Applied Animal Behaviour Science 92:235–260.

Dzialak, M. R., S. M. Harju, R. G. Osborn, J. J. Wondzell, L. D. Hayden-Wing, J. B. Winstead, and S. L. Webb. 2011. Prioritizing conservation of ungulate calving resources in multiple-use landscapes. M. Somers, editor. PLoS ONE 6:e14597.

Eacker, D. R. 2015. Linking the effects of risk factors on annual calf survival to elk population dynamics in the Bitterroot Valley, Montana. MSc Thesis, University of Montana, Missoula, MT, USA.

Eacker, D. R., M. Hebblewhite, K. M. Proffitt, B. S. Jimenez, M. S. Mitchell, and H. S. Robinson. 2016. Annual elk calf survival in a multiple carnivore system. Journal of Wildlife Management 80:1345–1359.

Ebensperger, L. A. 1998. Strategies and counterstrategies to infanticide in mammals. Biological Reviews 73:321–346.

Eggeman, S. L. 2012. Migratory behavior and survival of adult female elk in a partially migratory population. MSc Thesis, University of Montana, Missoula, MT, USA.

Eggeman, S. L., M. Hebblewhite, H. Bohm, J. Whittington, and E. H. Merrill. 2016. Behavioural flexibility in migratory behaviour in a long-lived large herbivore. Journal of Animal Ecology 85:785–797.

Erickson, M. E., C. Found-Jackson, and M. S. Boyce. 2014. Using latent selection difference to model persistence in a declining population. PLoS ONE 9:e98126.

Ericsson, G., and K. Wallin. 2001. Age-specific moose (*Alces alces*) mortality in a predator-free environment: Evidence for senescence in females. Ecoscience 8:157–163.

Estes, R. D. 1976. The significance of breeding synchrony in the wildebeest. African Journal of Ecology 14:135–152.

Evans, J. S., and S. A. Cushman. 2009. Gradient modeling of conifer species using random forests. Landscape Ecology 24:673–683.

Evans, J. S., M. A. Murphy, Z. A. Holden, and S. A. Cushman. 2011. Modeling species distribution and change using random forests. Pages 139–159 *in* C. A. Drew, Y. F. Wiersma, and F. Huettmann, editors. Predictive species and habitat modeling in landscape ecology: Concepts and applications. Springer, New York, NY, USA, USA.

Fagan, W. F., R. S. Cantrell, C. Cosner, T. Mueller, and A. E. Noble. 2012. Leadership, social learning, and the maintenance (or collapse) of migratory populations. Theoretical Ecology 5:253–264.

Feder, C., J. G. A. Martin, M. Festa-Bianchet, C. Bérubé, and J. Jorgenson. 2008. Never too late? Consequences of late birthdate for mass and survival of bighorn lambs. Oecologia 156:773–781.

Festa-Bianchet, M. 1988. Seasonal range selection in bighorn sheep: Conflicts between forage quality, forage quantity, and predator avoidance. Oecologia 75:580–586.

Festa-Bianchet, M., M. Douhard, J.-M. Gaillard, and F. Pelletier. 2017. Successes and challenges of long-term field studies of marked ungulates. Journal of Mammalogy 98:612–620.

Fieberg, J., and G. D. DelGiudice. 2009. What time is it? Choice of time origin and scale in extended proportional hazards models. Ecology 90:1687–1697.

Fieberg, J. R., and C. O. Kochanny. 2005. Quantifying home-range overlap: The importance of the utilization distribution. Journal of Wildlife Management 69:1346–1359.

Fieberg, J. R., D. W. Kuehn, and G. D. DelGiudice. 2008. Understanding variation in autumn migration of northern white-tailed deer by long-term study. Journal of Mammalogy 89:1529–1539.

Fine, J. P., and R. J. Gray. 1999. Proportional hazards model for the subdistribution of a competing risk. Journal of the American Statistical Association 94:496–509.

Fitzgibbon, C. D. 1990. Anti-predator strategies of immature Thomson's gazelles: Hiding and the prone response. Animal Behaviour 40:846–855.

Fogarty, D. T., and C. P. Lehman. 2016. Do female elk select hiding cover for their calves at birth sites? Western North American Naturalist 76:367–373.

Forester, J. D., A. R. Ives, M. G. Turner, D. P. Anderson, D. Fortin, H. L. Beyer, D. W. Smith, and M. S. Boyce. 2007. State-space models link elk movement patterns to landscape characteristics in Yellowstone National Park. Ecological Monographs 77:285–299.

Forsyth, D. M. 1999. Long-term harvesting and male migration in a New Zealand population of Himalayan tahr Hemitragus jemlahicus. Journal of Applied Ecology 36:351–362.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320–1330.

Found, R., and C. C. St. Clair. 2016. Behavioural syndromes predict loss of migration in wild elk. Animal Behaviour 115:35–46.

Found, R., and C. C. St. Clair. 2017. Ambidextrous ungulates have more flexible behaviour, bolder personalities and migrate less. Royal Society Open Science 4:160958.

Frank, D. A. 1998. Ungulate regulation of ecosystem processes in Yellowstone National Park: Direct and feedback effects. Wildlife Society Bulletin 26:410–418.

Franklin, S. E., G. B. Stenhouse, M. J. Hansen, C. C. Popplewell, J. A. Dechka, and D. R. Peddle. 2001. An Integrated Decision Tree Approach (IDTA) to mapping landcover using satellite remote sensing in support of grizzly bear habitat analysis in the Alberta Yellowhead Ecosystem. Canadian Journal of Remote Sensing 27:579–592.

Fretwell, S. D., and H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–36.

Fried, B. M., R. M. Adams, R. P. Berrens, and O. Bergland. 1995. Willingness to pay for a change in elk hunting quality. Wildlife Society Bulletin 23:680–686.

Fritts, S. H., E. E. Bangs, J. A. Fontaine, M. R. Johnson, M. K. Phillips, E. D. Koch, and J. R. Gunson. 1997. Planning and implementing a reintroduction of wolves to Yellowstone National Park and central Idaho. Restoration Ecology 5:7–27.

Fryxell, J. M., J. Greever, and A. R. E. Sinclair. 1988. Why are migratory ungulates so abundant? American Naturalist 131:781–798.

Fryxell, J. M., E. J. Milner-Gulland, and A. R. E. Sinclair. 2011. Introduction. Pages 1–3 *in* E. J. Milner-Gulland, J. M. Fryxell, and A. R. E. Sinclair, editors. Animal Migration: A Synthesis. Oxford University Press, Oxford, UK.

Fryxell, J. M., and A. R. E. Sinclair. 1988*a*. Causes and consequences of migration by large herbivores. Trends in Ecology & Evolution 3:237–241.

Fryxell, J. M., and A. R. E. Sinclair. 1988*b*. Seasonal migration by white-eared kob in relation to resources. African Journal of Ecology 26:17–31.

Fudickar, A. M., A. Schmidt, M. Hau, M. Quetting, and J. Partecke. 2013. Female-biased obligate strategies in a partially migratory population. Journal of Animal Ecology 82:863–871.

Gaidet, N., and P. Lecomte. 2013. Benefits of migration in a partially-migratory tropical ungulate. BMC Ecology 13:1–13.

Gaillard, J.-M. 2013. Assessing fitness consequences of migratory tactics requires long-term individually based monitoring. Ecology 94:1261–1264.

Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: Variable recruitment with constant adult survival. Trends in Ecology & Evolution 13:58–63.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Garrott, R. A., L. L. Eberhardt, P. J. White, and J. Rotella. 2003. Climate-induced variation in vital rates of an unharvested large-herbivore population. Canadian Journal of Zoology 81:33–45.

Gasaway, W. C., R. D. Boertje, D. V. Grangaard, D. G. Kelleyhouse, R. O. Stephenson, and D. G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs 120:3–59.

Gasaway, W. C., K. T. Gasaway, and H. H. Berry. 1996. Persistent low densities of plains ungulates in Etosha National Park, Namibia: Testing the food-regulating hypothesis. Canadian Journal of Zoology 74:1556–1572.

Gauthreaux Jr., S. A. 1982. The ecology and evolution of avian migration systesm. Pages 93–168 *in* D. S. Farner, J. R. King, and K. C. Parkes, editors. Avian Biology. Volume VI. Academic Press, Inc., Orlando, FL, USA.

Geist, V. 1982. Adaptive behavioral strategies. Pages 219–277 *in* J. W. Thomas and D. E. Toweill, editors. Elk of North America: Ecology and management. Stackpole Books, Harrisburg, PA, USA.

Gibson, C., and D. Sheets. 1997. Natal Ridge elk study. Summerland, BC, Canada.

Gilbert, S. L., M. S. Lindberg, K. J. Hundertmark, and D. K. Person. 2014. Dead before detection: Addressing the effects of left truncation on survival estimation and ecological inference for neonates. Methods in Ecology and Evolution 5:992–1001.

Gillis, E. A., D. J. Green, H. A. Middleton, and C. A. Morrissey. 2008. Life history correlates of alternative migratory strategies in American Dippers. Ecology 89:1687–1695.

Glines, L. M., A. Bohm, H. R. Spaedtke, E. H. Merrill, S. L. Eggeman, A. Deedy, and M. Hebblewhite. 2011. Ya Ha Tinda elk population and Red Deer River valley ecotone study: Final report. University of Alberta, Edmonton, AB, Canada.

Gordon, I. J., A. J. Hester, and M. Festa-Bianchet. 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. Journal of Applied Ecology 41:1021–1031.

Gray, B. 2014. cmprsk: Subdistribution analysis of competing risks. R package version 2.2-7.

Grayson, K. L., L. L. Bailey, and H. M. Wilbur. 2011. Life history benefits of residency in a partially migrating pond-breeding amphibian. Ecology 92:1236–1246.

Green, H. U. 1951. The wolves of Banff National Park. Canada Department of Resources and Development, National Parks Branch, National Parks and Historic Sites Service, Ottawa, ON, Canada.

Griffin, K. A., M. Hebblewhite, H. S. Robinson, P. Zager, S. M. Barber-Meyer, D. A. Christianson, S. Creel, N. C. Harris, M. A. Hurley, and D. W. H. Jackson. 2011. Neonatal mortality of elk driven by climate, predator phenology and predator community composition. Journal of Animal Ecology 80:1246–1257.

Grovenburg, T. W., C. N. Jacques, R. W. Klaver, C. S. DePerno, T. J. Brinkman, C. C. Swanson, and J. A. Jenks. 2011. Influence of landscape characteristics on migration strategies of white-tailed deer. Journal of Mammalogy 92:534–543.

Groves, C., and P. Grubb. 2011. Ungulate taxonomy. Johns Hopkins University Press, Baltimore, MD, USA.

Guan, T. P., B. M. Ge, W. J. McShea, S. Li, Y. L. Song, and C. M. Stewart. 2013. Seasonal migration by a large forest ungulate: A study on takin (*Budorcas taxicolor*) in Sichuan Province, China. European Journal of Wildlife Research 59:81–91.

Guinness, F. E., T. H. Clutton-Brock, and S. D. Albon. 1978. Factors affecting calf mortality in red deer (*Cervus elaphus*). Journal of Animal Ecology 47:817–832.

Gunther, K. A., and R. A. Renkin. 1990. Grizzly bear predation on elk calves and other fauna of Yellowstone National Park. Ursus 8:329–334.

Gurarie, E., F. Cagnacci, W. E. Peters, C. H. Fleming, J. M. Calabrese, T. Mueller, and W. F. Fagan. 2017. A framework for modelling range shifts and migrations: Asking when, whither, whether and will it return. Journal of Animal Ecology 86:943–959.

Hamel, S., and S. D. Côté. 2008. Trade-offs in activity budget in an alpine ungulate: Contrasting lactating and nonlactating females. Animal Behaviour 75:217–227.

Hamel, S., J.-M. Gaillard, M. Festa-Bianchet, and S. D. Côté. 2009. Individual quality, early life conditions, and reproductive success in contrasted populations of large herbivores. Ecology 90:1981–1995.

Hamlin, K. L., D. F. Pac, C. A. Sime, R. M. DeSimone, and G. L. Dusek. 2000. Evaluating the accuracy of ages obtained by two methods for Montana ungulates. Journal of Wildlife Management 64:441–449.

Hansen, B. B., R. Aanes, and B.-E. Sæther. 2010. Partial seasonal migration in high-arctic Svalbard reindeer (*Rangifer tarandus platyrhynchus*). Canadian Journal of Zoology 88:1202–1209.

Harris, G., S. Thirgood, J. G. C. Hopcraft, J. P. G. M. Cromsigt, and J. Berger. 2009. Global decline in aggregated migrations of large terrestrial mammals. Endangered Species Research 7:55–76.

Harris, N. C. 2006. Monitoring survival of young in ungulates: A case study with Rocky Mountain elk. MSc Thesis, University of Montana, Missoula, MT, USA.

Hastie, T., R. Tibshirani, and J. Friedman. 2009. The elements of statistical learning: Data mining, inference, and prediction. Second. Springer, New York, NY, USA.

Hatter, I. W. 1988. Effects of wolf predation on recruitment of black-tailed deer on northeastern Vancouver Island. Wildlife Report. Volume R-23. Victoria, B.C., Canada.

Haugen, A. O., and D. W. Speake. 1958. Determining age of young fawn white-tailed deer. Journal of Wildlife Management 22:319–321.

Hebblewhite, M. 2000. Wolf and elk predator-prey dynamics in Banff National Park. MSc Thesis, University of Montana, Missoula, MT, USA.

Hebblewhite, M. 2006. Linking predation risk and forage to ungulate population dynamics. PhD Dissertation, University of Alberta, Edmonton, AB, Canada.

Hebblewhite, M. 2007. Predator-prey management in the national park context: Lessons from a transboundary wolf, elk, moose, and caribou system. Pages 348–365 *in*. Transactions of the 72nd North American Wildlife and Natural Resources Conference.

Hebblewhite, M., D. R. Eacker, S. L. Eggeman, H. Bohm, and E. H. Merrill. 2018. Density-independent predation affects migrants and residents equally in a declining partially migratory elk population. Oikos.

Hebblewhite, M., and E. H. Merrill. 2007. Multiscale wolf predation risk for elk: Does migration reduce risk? Oecologia 152:377–387.

Hebblewhite, M., and E. H. Merrill. 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. Journal of Applied Ecology 45:834–844.

Hebblewhite, M., and E. H. Merrill. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90:3445–3454.

Hebblewhite, M., and E. H. Merrill. 2011. Demographic balancing of migrant and resident elk in a partially migratory population through forage–predation tradeoffs. Oikos 120:1860–1870.

Hebblewhite, M., E. H. Merrill, and G. McDermid. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. Ecological Monographs 78:141–166.

Hebblewhite, M., E. H. Merrill, L. E. Morgantini, C. A. White, J. R. Allen, E. Bruns, L. Thurston, and T. E. Hurd. 2006. Is the migratory behavior of montane elk populations in peril? The case of Alberta's Ya Ha Tinda elk population. Wildlife Society Bulletin 34:1280–1294.

Hebblewhite, M., R. H. Munro, and E. H. Merrill. 2009. Trophic consequences of postfire logging in a wolf-ungulate system. Forest Ecology and Management 257:1053–1062.

Hebblewhite, M., C. A. White, and M. Musiani. 2010. Revisiting extinction in national parks: Mountain caribou in Banff. Conservation Biology 24:341–344.

Heisey, D. M., and B. R. Patterson. 2006. A review of methods to estimate cause-specific mortality in presence of competing risks. Journal of Wildlife Management 70:1544–1555.

Hillman, J. C. 1988. Home range and movement of the common eland (*Taurotragus oryx* Pallas

1766) in Kenya. African Journal of Ecology 26:135–148.

Hjeljord, O. 2001. Dispersal and migration in northern forest deer-are there unifying concepts? Alces. Volume 37.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60:695–713.

Holdo, R. M., J. M. Fryxell, A. R. E. Sinclair, A. Dobson, and R. D. Holt. 2011*a*. Predicted impact of barriers to migration on the Serengeti wildebeest population. PLoS ONE 6:e16370.

Holdo, R. M., R. D. Holt, M. B. Coughenour, and M. E. Ritchie. 2006. Plant productivity and soil nitrogen as a function of grazing, migration and fire in an African savanna. Journal of Ecology 95:115–128.

Holdo, R. M., R. D. Holt, and J. M. Fryxell. 2009. Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. American Naturalist 173:431–445.

Holdo, R. M., R. D. Holt, A. R. E. Sinclair, B. J. Godley, and S. Thirgood. 2011*b*. Migration impacts on communities and ecosystems: Empirical evidence and theoretical insights. Pages 131–143 *in* E. J. Milner-Gulland, J. M. Fryxell, and A. R. E. Sinclair, editors. Animal Migration: A Synthesis. Oxford University Press, Oxford, UK.

Holland, W. D., and G. M. Coen. 1982. Ecological (biophysical) land classification of Banff and Jasper National Parks volume II: Soil and vegetation resources. Publication No. SS-82-44. Alberta Institute of Pedology, Edmonton, AB, Canada.

Holmes, B. R., and J. W. Laundre. 2006. Use of open, edge and forest areas by pumas (*Puma concolor*) in winter: Are pumas foraging optimally? Wildlife Biology 12:201–209.

Hosmer, D. W., S. Lemeshow, and R. X. Sturdivant. 2013. Applied logistic regression. Third. John Wiley & Sons, Hoboken, NJ, USA.

Huang, F., D. C. Cockrell, T. R. Stephenson, J. H. Noyes, and R. G. Sasser. 2000. A serum pregnancy test with a specific radioimmunoassay for moose and elk pregnancy-specific protein B. Journal of Wildlife Management 64:492.

Hudson, R. J., J. C. Haigh, and A. B. Bubenik. 2002. Physical and physiological adaptations. Pages 199–257 *in*. North American elk: Ecology and management. Smithsonian Institution Press, Washington, DC, USA.

Huffman, B. 2018. Ultimate ungulate. www.ultimateungulate.com.

Igota, H., M. Sakuragi, H. Uno, K. Kaji, M. Kaneko, R. Akamatsu, and K. Maekawa. 2004. Seasonal migration patterns of female sika deer in eastern Hokkaido, Japan. Ecological Research 19:169–178.

Ims, R. A. 1990*a*. On the adaptive value of reproductive synchrony as a predator-swamping strategy. American Naturalist 136:485–498.

Ims, R. A. 1990*b*. The ecology and evolution of reproductive synchrony. Trends in Ecology & Evolution 5:135–140.

Jacques, C. N., J. A. Jenks, and R. W. Klaver. 2009. Seasonal movements and home-range use by female pronghorns in sagebrush-steppe communities of western South Dakota. Journal of Mammalogy 90:433–441.

Jędrzejewska, B., W. Jędrzejewski, A. N. Bunevich, L. Miłkowski, and Z. A. Krasiński. 1997. Factors shaping population densities and increase rates of ungulates in Białowieża Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. Acta Theriologica 42:399–451.

Jevons, S. 2001. Human use digital atlast of the Canadian central Rockies ecosystem. Miistakis Institute, Calgary, AB, Canada.

Johnson, C. J., K. L. Parker, D. C. Heard, and M. P. Gillingham. 2002. Movement parameters of ungulates and scale-specific responses to the environment. Journal of Animal Ecology 71:225–235.

Johnson, D. E. 1951. Biology of the elk calf, *Cervus canadensis nelsoni*. Journal of Wildlife Management 15:396–410.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Jones, J. D., M. J. Kauffman, K. L. Monteith, B. M. Scurlock, S. E. Albeke, and P. C. Cross. 2014. Supplemental feeding alters migration of a temperate ungulate. Ecological Applications 24:1769–1779.

Kaitala, A., V. Kaitala, and P. Lundberg. 1993. A theory of partial migration. American Naturalist 142:59–81.

Kellner, K. 2017. jagsUI: A wrapper around "rjags" to streamline "JAGS" analyses. R package version 1.4.9.

Ketterson, E. D., and V. Nolan Jr. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern-wintering dark-eyed juncos (*Junco hyemalis hyemalis*). Ecology 57:679–693.

Ketterson, E. D., and V. Nolan Jr. 1983. The evolution of differential bird migration. Current Ornithology 357–402.

Kie, J. G. 2013. A rule-based ad hoc method for selecting a bandwidth in kernel home-range analyses. Animal Biotelemetry 1:13.

Killeen, J., E. H. Merrill, H. Bohm, J. Berg, S. L. Eggeman, and M. Hebblewhite. 2016. Migration of the Ya Ha Tinda elk population 2002 - 2014. Final report. Contract no. 5P421-15-0423. University of Alberta, Edmonton, AB, Canada.

Knamiller, P. T. 2011. Seasonal wolf predation in a multi-prey system in west-central Alberta. MSc Thesis, University of Alberta, Edmonton, AB, Canada.

Knopff, K. H., A. A. Knopff, M. B. Warren, and M. S. Boyce. 2009. Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. Journal of Wildlife Management 73:586–597.

Knopff, K. H., N. F. Webb, and M. S. Boyce. 2014. Cougar population status and range expansion in Alberta during 1991-2010. Wildlife Society Bulletin 38:116–121.

Kokko, H. 2007. Modelling for field biologists and other interesting people. Cambridge University Press, Cambridge, UK.

Kokko, H. 2011. Directions in modelling partial migration: How adaptation can cause a population decline and why the rules of territory acquisition matter. Oikos 120:1826–1837.

Kokko, H., and W. J. Sutherland. 2001. Ecological traps in changing environments: Ecological and evolutionary consequences of a behaviourally mediated Allee effect. Evolutionary Ecology Research 3:537–551.

Kolar, J. L., J. J. Millspaugh, and B. A. Stillings. 2011. Migration patterns of pronghorn in southwestern North Dakota. Journal of Wildlife Management 75:198–203.

Koper, N., F. K. A. Schmiegelow, and E. H. Merrill. 2007. Residuals cannot distinguish between ecological effects of habitat amount and fragmentation: Implications for the debate. Landscape Ecology 22:811–820.

Kowalczyk, R., M. Krasińska, T. Kamiński, M. Górny, P. Struś, E. Hofman-Kamińska, and Z. a. Krasiński. 2013. Movements of European bison (*Bison bonasus*) beyond the Białowieża Forest (NE Poland): Range expansion or partial migrations? Acta Theriologica 58:391–401.

Kranstauber, B., K. Safi, and F. Bartumeus. 2014. Bivariate Gaussian bridges: Directional factorization of diffusion in Brownian bridge models. Movement Ecology 2:5.

Kranstauber, B., and M. Smolla. 2016. move: Visualizing and analyzing animal track data. R package version 1.6.541.

Krawchuk, K. E. 2014. Is niche separation between wolves and cougars realized in the Rocky Mountains? MSc Thesis, University of Alberta, Edmonton, AB, Canada.

Kunkel, K. E., and L. D. Mech. 1994. Wolf and bear predation on white-tailed deer fawns in northeastern Minnesota. Canadian Journal of Zoology 72:1557–1565.

Lack, D. 1943. The problem of partial migration. British Birds 37:122–130.

Lamberti, P., L. Mauri, and M. Apollonio. 2004. Two distinct patterns of spatial behaviour of female roe deer (*Capreolus capreolus*) in a mountainous habitat. Ethology Ecology & Evolution 16:41–53.

Landete-Castillejos, T., A. Garcia, and L. Gallego. 2001. Calf growth in captive Iberian red deer (*Cervus elaphus hispanicus*): Effects of birth date and hind milk production and composition. Journal of Animal Science 79:1085–1092.

Landete-Castillejos, T., A. García, J. Á. Gómez, and L. Gallego. 2003. Lactation under food constraints in Iberian red deer *Cervus elaphus hispanicus*. Wildlife Biology 9:131–139.

Latham, A. D. M., M. C. Latham, and M. S. Boyce. 2011. Habitat selection and spatial relationships of black bears (*Ursus americanus*) with woodland caribou (*Rangifer tarandus caribou*) in northeastern Alberta. Canadian Journal of Zoology 89:267–277.

Lee, D. E., B. M. Kissui, Y. A. Kiwango, and M. L. Bond. 2016. Migratory populations of wildebeests and zebras indirectly affect calf survival of giraffes. Ecology and Evolution 6:8402–8411.

Lehman, C. P., C. T. Rota, J. D. Raithel, and J. J. Millspaugh. 2018. Pumas affect elk dynamics in absence of other large carnivores. Journal of Wildlife Management 82:344–353.

Lendrum, P. E., C. R. Anderson Jr., K. L. Monteith, J. A. Jenks, and R. T. Bowyer. 2013. Migrating mule deer: Effects of anthropogenically altered landscapes. PLoS ONE 8:e64548.

Lent, P. C. 1974. Mother-infant relationships in ungulates. Pages 14–55 *in* V. Geist and F. Walther, editors. The behaviour of ungulates and its relation to management. Volume I. International Union for Conservation of Nature and Natural Resources, Morges, Switzerland.

LeResche, R. E. 1974. Moose migrations in North America. Naturaliste Canadien 101:393–415.

Lesmerises, F., C. J. Johnson, and M.-H. St-Laurent. 2016. Refuge or predation risk? Alternate ways to perceive hiker disturbance based on maternal state of female caribou. Ecology and Evolution 7:845–854.

Liaw, A., and M. Wiener. 2002. Classification and regression by randomForest. R News 2:18–22.

Liedvogel, M., S. Åkesson, and S. Bensch. 2011. The genetics of migration on the move. Trends in Ecology & Evolution 26:561–569.

Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. American Naturalist 153:649–659.

Van Der Linde, A. 2005. DIC in variable selection. Statistica Neerlandica 59:45–56.

Linnell, J. D. C., R. Aanes, and R. Andersen. 1995. Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. Wildlife Biology 1:209–223.

Loison, A., and R. Langvatn. 1998. Short- and long-term effects of winter and spring weather on growth and survival of red deer in Norway. Oecologia 116:489–500.

Long, R. A., R. T. Bowyer, W. P. Porter, P. Mathewson, K. L. Monteith, S. L. Findholt, B. L. Dick, and J. G. Kie. 2016. Linking habitat selection to fitness-related traits in herbivores: The role of the energy landscape. Oecologia 181:709–720.

Looman, J. 1969. The fescue grasslands of western Canada. Vegetatio 19:128–145.

Luccarini, S., L. Mauri, S. Ciuti, P. Lamberti, and M. Apollonio. 2006. Red deer (*Cervus elaphus*) spatial use in the Italian Alps: Home range patterns, seasonal migrations, and effects of snow and winter feeding. Ethology Ecology & Evolution 18:127–145.

Lukacs, P. M., M. S. Mitchell, M. Hebblewhite, B. K. Johnson, H. Johnson, M. J. Kauffman, K. M. Proffitt, P. Zager, J. Brodie, K. Hersey, A. A. Holland, M. A. Hurley, S. Mccorquodale, A. D. Middleton, M. Nordhagen, J. J. Nowak, D. P. Walsh, and P. J. White. 2018. Factors influencing elk recruitment across ecotypes in the Western United States. Journal of Wildlife Management 82:698–710.

Lundberg, P. 1987. Partial bird migration and evolutionarily stable strategies. Journal of Theoretical Biology 125:351–360.

Lundberg, P. 1988. The evolution of partial migration in birds. Trends in Ecology & Evolution 3:172–175.

Lundberg, P. 2013. On the evolutionary stability of partial migration. Journal of Theoretical Biology 321:36–39.

MacAulay, K. 2018. Spatial mortality risk for elk (Cervus elaphus) in a multi-predator community on the Rocky Mountain east slopes, Alberta. MSc Thesis, University of Alberta, Edmonton, AB, Canada.

Mao, J. S., M. S. Boyce, D. W. Smith, F. J. Singer, D. J. Vales, J. M. Vore, and E. H. Merrill. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. Journal of Wildlife Management 69:1691–1707.

Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. Ecography 28:403–416.

Mazur, R., and V. Seher. 2008. Socially learned foraging behaviour in wild black bears, *Ursus americanus*. Animal Behaviour 75:1503–1508.

McDevitt, A. D., S. Mariani, M. Hebblewhite, N. J. DeCesare, L. E. Morgantini, D. R. Seip, B. V. Weckworth, and M. Musiani. 2009. Survival in the Rockies of an endangered hybrid swarm from diverged caribou (*Rangifer tarandus*) lineages. Molecular Ecology 18:665–679.

McGillis, J. R. W. 1977. Range management of the Ya Ha Tinda ranch. Canadian Wildlife Service, Edmonton, AB, Canada.

McLoughlin, P. D., M. S. Boyce, T. Coulson, and T. H. Clutton-Brock. 2006. Lifetime reproductive success and density-dependent, multi-variable resource selection. Proceedings of the Royal Society B: Biological Sciences 273:1449–1454.

McNaughton, S. J., R. W. Ruess, and S. W. Seagle. 1988. Large mammals and process dynamics in African ecosystems. BioScience 38:794–800.

McPeek, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. American Naturalist 140:1010–1027.

Mech, L. D., D. W. Smith, and D. R. MacNulty. 2015. Wolves on the hunt: The behavior of wolves hunting wild prey. University of Chicago Press, Chicago, IL, USA.

Meland, M. 2014. Partial migration as a response to ground icing events in a high arctic ungulate. MSc Thesis, Norwegian University of Life Sciences, As, Norway.

Merkle, J. A., K. L. Monteith, E. O. Aikens, M. M. Hayes, K. R. Hersey, A. D. Middleton, B. A. Oates, H. Sawyer, B. M. Scurlock, and M. J. Kauffman. 2016. Large herbivores surf waves of green-up during spring. Proceedings of the Royal Society B: Biological Sciences

283:20160456.

Mickle, D., R. Kunelius, and G. Fortin. 1986. The status of wolves in Banff National Park. Canada Department of Resources and Development, National Parks Branch, National Parks and Historic Sites Service, Ottawa, ON, Canada.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, J. G. Cook, R. C. Cook, A. A. Nelson, M. D. Jimenez, and R. W. Klaver. 2013*a*. Animal migration amid shifting patterns of phenology and predation: Lessons from a Yellowstone elk population. Ecology 94:1245–1256.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, M. D. Jimenez, R. C. Cook, J. G. Cook, S. E. Albeke, H. Sawyer, and P. J. White. 2013*b*. Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. Ecology Letters 16:1023–1030.

Middleton, A. D., J. A. Merkle, D. E. McWhirter, J. G. Cook, R. C. Cook, P. J. White, and M. J. Kauffman. 2018. Green-wave surfing increases fat gain in a migratory ungulate. Oikos 127:1060–1068. Blackwell Publishing Ltd.

Milner-Gulland, E. J., M. V. Kholodova, A. Bekenov, O. M. Bukreeva, I. A. Grachev, L. Amgalan, and A. A. Lushchekina. 2001. Dramatic declines in saiga antelope populations. Oryx 35:340–345.

Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, J. G. Kie, and R. T. Bowyer. 2014. Life-history characteristics of mule deer: Effects of nutrition in a variable environment. Wildlife Monographs 186:1–62.

Montgomery, D. M. 2005. Age estimation and growth of Rocky Mountain elk calves and proximate factors influencing hunting mortality of elk in Idaho. MSc Thesis, University of Idaho, Moscow, ID, USA.

Van Moorter, B., J.-M. Gaillard, P. D. McLoughlin, D. Delorme, F. Klein, and M. S. Boyce. 2009. Maternal and individual effects in selection of bed sites and their consequences for fawn survival at different spatial scales. Oecologia 159:669–678.

Moraga, C., M. C. Funes, J. C. Pizarro, C. Briceño, and A. J. Novaro. 2015. Effects of livestock on guanaco density, movements and habitat selection in a forest-grassland mosaic in Tierra del Fuego, Chile. Oryx 49:30–41.

Morgantini, L. E. 1995. The Ya Ha Tinda: An ecological overview. Prepared for Parks Canada, Alberta Region, Calgary. Wildlife Resources Consulting, Ltd., Edmonton, AB, Canada.

Morgantini, L. E., and R. J. Hudson. 1988. Migratory patterns of the wapiti, *Cervus elaphus*, in Banff National Park, Alberta. Canadian Field Naturalist 102:12–19.

Morris, D. W. 2006. Moving to the ideal free home. Nature 443:645–646.

Morrison, T. A., and D. T. Bolger. 2012. Wet season range fidelity in a tropical migratory ungulate. Journal of Animal Ecology 81:543–52.

Mueller, C., S. Herrero, and M. L. Gibeau. 2004. Distribution of subadult grizzly bears in relation to human development in the Bow River watershed, Alberta. International Association for Bear Research and Management 15:35–47.

Mueller, T., K. A. Olson, G. Dressler, P. Leimgruber, T. K. Fuller, C. Nicolson, A. J. Novaro, M. J. Bolgeri, D. Wattles, S. Destefano, J. M. Calabrese, and W. F. Fagan. 2011. How landscape dynamics link individual- to population-level movement patterns: A multispecies comparison of ungulate relocation data. Global Ecology and Biogeography 20:683–694.

Muggeo, V. M. R. 2008. segmented: An R package to fit regression models with broken-line relationships. R News 8/1.

Murphy, K. M., G. S. Felzien, M. G. Hornocker, and T. K. Ruth. 1995. Encounter competition between bears and cougars: Some ecological implications. Ursus 10:55–60.

Murphy, M. A., J. S. Evans, and A. Storfer. 2010. Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. Ecology 91:252–261.

Murray, D. L. 2006. On improving telemetry-based survival estimation. Journal of Wildlife Management 70:1530–1543.

Mysterud, A. 1999. Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. Journal of Zoology 247:479–486.

Mysterud, A., L. E. Loe, B. Zimmermann, R. Bischof, V. Veiberg, and E. L. Meisingset. 2011. Partial migration in expanding red deer populations at northern latitudes – a role for density dependence? Oikos 120:1817–1825.

Mysterud, A., L. Qviller, E. L. Meisingset, and H. Viljugrein. 2016. Parasite load and seasonal migration in red deer. Oecologia 180:401–407.

Naidoo, R., P. Du Preez, G. Stuart-Hill, M. Jago, and M. Wegmann. 2012. Home on the range: Factors explaining partial migration of African buffalo in a tropical environment. PLoS ONE 7:e36527.

Nelson, A. A., M. J. Kauffman, A. D. Middleton, M. D. Jimenez, D. E. McWhirter, J. Barber, and K. Gerow. 2012. Elk migration patterns and human activity influence wolf habitat use in the Greater Yellowstone Ecosystem. Ecological Applications 22:2293–2307.

Nelson, M. E. 1995. Winter range arrival and departure of white-tailed deer in northeastern Minnesota. Canadian Journal of Zoology 73:1069–1076.

Nelson, M. E. 1998. Development of migratory behavior in northern white-tailed deer. Canadian Journal of Zoology 76:426–432.

Nicholson, M. C., R. T. Bowyer, and J. G. Kie. 1997. Habitat selection and survival of mule deer: Tradeoffs associated with migration. Journal of Mammalogy 78:483–504.

Nielsen, S. E. 2005. Habitat ecology, conservation and projected population viability of grizzly bears (Ursus arctos L.) in west-central Alberta, Canada. PhD Dissertation, University of Alberta, Edmonton, AB, Canada.

Nielsen, S. E. 2007. Seasonal resource selection function (RSF) models for grizzly bears in the Clearwater region of Alberta. Conservation Analytics, Inc., Edmonton, AB, Canada.

Normandeau, J., K. MacAulay, J. Berg, and E. H. Merrill. 2018. Identifying guard hairs of Rocky Mountain carnivores. Wildlife Society Bulletin 1–7.

Northrup, J. M., A. B. A. Shafer, C. R. Anderson, D. W. Coltman, and G. Wittemyer. 2014. Fine-scale genetic correlates to condition and migration in a wild cervid. Evolutionary Applications 7:937–948.

Noyes, J. H., B. K. Johnson, L. D. Bryant, S. L. Findholt, and J. W. Thomas. 1996. Effects of bull age on conception dates and pregnancy rates of cow elk. Journal of Wildlife Management 60:508–517.

Oftedal, O. T. 2018. Pregnancy and lactation. Pages 215–238 *in* R. J. Hudson and R. G. White, editors. Bioenergetics of wild herbivores. CRC Press, Taylor & Francis Group, Boca Raton, FL, USA.

Oldham, J. D., and N. C. Friggens. 1989. Sources of variability in lactational performance. Proceedings of the Nutrition Society 48:33–43.

Olson, K. A., T. K. Fuller, T. Mueller, M. G. Murray, C. Nicolson, D. Odonkhuu, S. Bolortsetseg, and G. B. Schaller. 2010. Annual movements of Mongolian gazelles: Nomads in the Eastern Steppe. Journal of Arid Environments 74:1435–1442.

Ortega, I. M., and W. L. Franklin. 1995. Social organization, distribution and movements of a migratory guanaco population in the Chilean Patagonia. Revista Chilena de Historia Natural 68:489–500.

Packer, C., D. Ikanda, B. M. Kissui, and H. Kushnir. 2005. Conservation biology: Lion attacks on humans in Tanzania. Nature 436:927–928.

Panzacchi, M., I. Herfindal, J. D. C. Linnell, M. Odden, J. Odden, and R. Andersen. 2010. Trade-offs between maternal foraging and fawn predation risk in an income breeder. Behavioral Ecology and Sociobiology 64:1267–1278.

Paquet, P. C. 1993. Summary reference document - ecological studies of recolonizing wolves in the central Canadian Rocky Mountains. Canada Department of Resources and Development, National Parks Branch, National Parks and Historic Sites Service, Ottawa, ON, Canada.

Paquet, P. C., and R. K. Brook. 2004. From the field: Island use as an anti-predator tactic by parturient elk and nursery populations in Riding Mountain National Park, Manitoba. Wildlife Society Bulletin 32:1321–1324.

Paquet, P. C., J. Wierzchowski, and C. J. Callaghan. 1996. Summary report on the effects of human activity on gray wolves in the Bow River Valley, Banff National Park, Alberta. Page 7.1-7.74 *in* J. Green, C. Pacas, L. Cornwell, and S. Bayley, editors. Ecological outlooks project. A cumulative effects assessment and futures outlook of the Banff Bow Valley: Final report. Department of Canadian Heritage, Ottawa, ON, Canada.

Parker, K. L., P. S. Barboza, and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology 23:57–69.

Parks Canada. 2017. Plains bison reintroduction. <https://www.pc.gc.ca/en/pn-np/ab/banff/info/gestion-management/bison>. Accessed 30 Jan 2019.

Le Pendu, Y., and I. Ciofolo. 1999. Seasonal movements of giraffes in Niger. Journal of Tropical Ecology 15:341–353.

Perveen, F., and A. Khan. 2013. Migratory status of the goral, *Naemorhedus goral* (Hardwicke) (Artiodactyla: Bovidae) in Kohistan, Pakistan. International Journal of Biodiversity and Conservation 5:671–677.

Peters, W. E., M. Hebblewhite, A. Mysterud, D. R. Eacker, A. J. M. Hewison, J. D. C. Linnell, S. Focardi, F. Urbano, J. De Groeve, B. Gehr, M. Heurich, A. Jarnemo, P. Kjellander, M. Kröschel, N. Morellet, L. Pedrotti, H. Reinecke, R. Sandfort, L. Sönnichsen, P. Sunde, and

F. Cagnacci. 2018. Large herbivore migration plasticity along environmental gradients in Europe: Life-history traits modulate forage effects. Oikos 00:1–14.

Peters, W. E., M. Hebblewhite, A. Mysterud, D. B. Spitz, S. Focardi, F. Urbano, N. Morellet, M. Heurich, P. Kjellander, J. D. C. Linnell, and F. Cagnacci. 2017. Migration in geographic and ecological space by a large herbivore. Ecological Monographs 87:297–320.

Pettorelli, N., J. O. Vik, A. Mysterud, J.-M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology & Evolution 20:503–510.

Phillips, B., and T. Szkorupa. 2011. East Kootenay elk monitoring project. Final report 2011. Fish and Wildlife Branch, Province of British Columbia, Cranbrook, BC, Canada.

Pigeon, G., M. Festa-Bianchet, and F. Pelletier. 2017. Long-term fitness consequences of early environment in a long-lived ungulate. Proceedings of the Royal Society B: Biological Sciences 284:20170222.

Pinard, V., C. Dussault, J.-P. Ouellet, D. Fortin, and R. Courtois. 2012. Calving rate, calf survival rate, and habitat selection of forest-dwelling caribou in a highly managed landscape. Journal of Wildlife Management 76:189–199.

Pitman, J. W., J. W. Cain, S. G. Liley, W. R. Gould, and N. T. Quintana. 2014. Post-parturition habitat selection by elk calves and adult female elk in New Mexico. Journal of Wildlife Management 78:1216–1227.

Plard, F., J.-M. Gaillard, T. Coulson, A. J. M. Hewison, M. Douhard, F. Klein, D. Delorme, C. Warnant, and C. Bonenfant. 2015. The influence of birth date via body mass on individual fitness in a long-lived mammal. Ecology 96:1516–1528.

Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Page 125 *in*. 3rd International Workshop on Distributed Statistical Computing (DSC 2003). Vienna, Austria.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: The staggered entry design. Journal of Wildlife Management 53:7–15.

Poole, K. G., R. Serrouya, and K. Stuart-Smith. 2007. Moose calving strategies in interior montane ecosystems. Journal of Mammalogy 88:139–150.

Poor, E. E., C. Loucks, A. Jakes, and D. L. Urban. 2012. Comparing habitat suitability and connectivity modeling methods for conserving pronghorn migrations. PLoS ONE 7:e49390.

Post, E., P. S. Bøving, C. Pedersen, and M. A. MacArthur. 2003. Synchrony between caribou calving and plant phenology in depredated and non-depredated populations. Canadian Journal of Zoology 81:1709–1714.

Post, E., and M. C. Forchhammer. 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. Philosophical Transactions of the Royal Society B: Biological Sciences 363:2369–2375.

Post, E., and N. C. Stenseth. 1999. Climatic variability, plant phenology, and northern ungulates. Ecology 80:1322–1339.

Proffitt, K. M., M. Hebblewhite, W. Peters, N. Hupp, and J. Shamhart. 2016. Linking landscape-scale differences in forage to ungulate nutritional ecology. Ecological Applications 26:2156–2174.

Pulido, F. 2011. Evolutionary genetics of partial migration - the threshold model of migration revis(it)ed. Oikos 120:1776–1783.

Pulido, F., P. Berthold, and A. J. van Noordwijk. 1996. Frequency of migrants and migratory activity are genetically correlated in a bird population: Evolutionary implications. Proceedings of the National Academy of Sciences of the United States of America 93:14642–14647.

Qviller, L., N. Risnes-Olsen, K. M. Bærum, E. L. Meisingset, L. E. Loe, B. Ytrehus, H. Viljugrein, and A. Mysterud. 2013. Landscape level variation in tick abundance relative to seasonal migration in red deer. PLoS ONE 8:e71299.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rachlow, J. L., and R. T. Bowyer. 1991. Interannual variation in timing and synchrony of parturition in Dall's sheep. Journal of Mammalogy 72:487–492.

Rachlow, J. L., and R. T. Bowyer. 1994. Variability in maternal behavior by Dall's sheep: Environmental tracking or adaptive strategy? Journal of Mammalogy 75:328–337.

Raithel, J. D. 2005. Impact of calf survival on elk population dynamics in west-central Montana.

Raithel, J. D., M. J. Kauffman, and D. H. Pletscher. 2007. Impact of spatial and temporal variation in calf survival on the growth of elk populations. Journal of Wildlife Management 71:795–803.

Ramanzin, M., E. Sturaro, and D. Zanon. 2007. Seasonal migration and home range of roe deer

(*Capreolus capreolus*) in the Italian eastern Alps. Canadian Journal of Zoology 85:280–289.

Ramenofsky, M., J. M. Cornelius, and B. Helm. 2012. Physiological and behavioral responses of migrants to environmental cues. Journal of Ornithology 153:181–191.

Rayl, N. D., T. K. Fuller, J. F. Organ, J. E. Mcdonald, R. D. Otto, G. Bastille-Rousseau, C. E. Soulliere, and S. P. Mahoney. 2015. Spatiotemporal variation in the distribution of potential predators of a resource pulse: Black bears and caribou calves in Newfoundland. Journal of Wildlife Management 79:1041–1050.

Rearden, S. N., R. G. Anthony, and B. K. Johnson. 2011. Birth-site selection and predation risk of Rocky Mountain elk. Journal of Mammalogy 92:1118–1126.

Rettie, W. J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: Its relationship to limiting factors. Ecography 23:466–478.

Rice, C. G. 2008. Seasonal altitudinal movements of mountain goats. Journal of Wildlife Management 72:1706–1716.

Roberts, B. A., and D. I. Rubenstein. 2014. Maternal tactics for mitigating neonate predation risk during the postpartum period in Thomson's gazelle. Behaviour 151:1229–1248.

Robinette, W. L., C. H. Baer, R. E. Pillmore, and C. E. Knittle. 1973. Effects of nutritional change on captive mule deer. Journal of Wildlife Management 37:312–326.

Robinson, B. G., M. Hebblewhite, and E. H. Merrill. 2010. Are migrant and resident elk (*Cervus elaphus*) exposed to similar forage and predation risk on their sympatric winter range? Oecologia 164:265–275.

Robinson, H. S., M. Hebblewhite, N. J. DeCesare, J. Whittington, L. Neufeld, M. Bradley, and M. Musiani. 2012. The effect of fire on spatial separation between wolves and caribou. Rangifer 32:277.

Roff, D. A. 1992. The evolution of life histories: Theory and analysis. Chapman & Hall, New York, NY, USA.

Rogala, J. K., M. Hebblewhite, J. Whittington, C. A. White, J. Coleshill, and M. Musiani. 2011. Human activity differentially redistributes large mammals in the Canadian Rockies National Parks. Ecology and Society 16:16.

Rolandsen, C. M., E. J. Solberg, B.-E. Saether, B. Van Moorter, I. Herfindal, and K. Bjorneraas. 2016. On fitness and partial migration in a large herbivore – migratory moose have higher reproductive performance than residents. Oikos 126:547–555.

Rosenzweig, M. L. 1981. A theory of habitat selection. Ecology 62:327–335.

Rowell, J. E., and M. P. Shipka. 2009. Variation in gestation length among captive reindeer (*Rangifer tarandus tarandus*). Theriogenology 72:190–197.

Ruffell, J., C. Banks-Leite, and R. K. Didham. 2016. Accounting for the causal basis of collinearity when measuring the effects of habitat loss versus habitat fragmentation. Oikos 125:117–125.

Rutberg, A. T. 1987. Adaptive hypotheses of birth synchrony in ruminants: An interspecific test. American Naturalist 130:692–710.

Sabine, D. L., S. F. Morrison, H. A. Whitlaw, W. B. Ballard, G. J. Forbes, and J. Bowman. 2002. Migration behavior of white-tailed deer under varying winter climate regimes in New Brunswick. Journal of Wildlife Management 66:718–728.

Sachro, L. L., W. L. Strong, and C. C. Gates. 2005. Prescribed burning effects on summer elk forage availability in the subalpine zone, Banff National Park, Canada. Journal of Environmental Management 77:183–193.

Sakuragi, M., H. Igota, H. Uno, K. Kaji, M. Kaneko, R. Akamatsu, and K. Maekawa. 2003. Benefit of migration in female sika deer population in eastern Hokkaido, Japan. Ecological Research 18:347–354.

Sams, M. G., R. L. Lochmiller, E. C. Hellgren, W. D. Warde, and L. W. Varner. 1996. Morphometric predictors of neonatal age for white-tailed deer. Wildlife Society Bulletin 24:53–57.

Sandegren, F., R. Bergstrom, and P. Y. Sweanor. 1985. Seasonal moose migration related to snow in Sweden. Alces 21:321–338.

Sawyer, H., and M. J. Kauffman. 2011. Stopover ecology of a migratory ungulate. Journal of Animal Ecology 80:1078–1087.

Sawyer, H., M. J. Kauffman, A. D. Middleton, T. A. Morrison, R. M. Nielson, and T. B. Wyckoff. 2013. A framework for understanding semi-permeable barrier effects on migratory ungulates. Journal of Applied Ecology 50:68–78.

Sawyer, H., J. A. Merkle, A. D. Middleton, S. P. H. Dwinnell, and K. L. Monteith. 2018. Migratory plasticity is not ubiquitous among large herbivores. Journal of Animal Ecology 1–11.

Sawyer, H., A. D. Middleton, M. M. Hayes, M. J. Kauffman, and K. L. Monteith. 2016. The extra mile: Ungulate migration distance alters the use of seasonal range and exposure to anthropogenic risk. Ecosphere 7:1–11.

Schorr, R. A., P. M. Lukacs, and J. A. Gude. 2014. The Montana deer and elk hunting population: The importance of cohort group, license price, and population demographics on hunter retention, recruitment, and population change. Journal of Wildlife Management 78:944–952.

Schuter, J. L., A. C. Broderick, D. J. Agnew, N. Jonzén, B. J. Godley, E. J. Milner-Gulland, and S. Thirgood. 2011. Conservation and management of migratory species. Pages 172–206 *in* E. J. Milner-Gulland, J. M. Fryxell, and A. R. E. Sinclair, editors. Animal migration: A synthesis, Oxford University Press, Oxford, UK.

Seip, D. R., and F. L. Bunnell. 1985. Foraging behaviour and food habits of Stone's sheep. Canadian Journal of Zoology 63:1638–1646.

Serneels, S., and E. F. Lambin. 2001. Impact of land-use changes on the wildebeest migration in the northern part of the Serengeti-Mara ecosystem. Journal of Biogeography 28:391–407.

Serrouya, R., M. J. Wittmann, B. N. McLellan, H. U. Wittmer, and S. Boutin. 2015. Using predator-prey theory to predict outcomes of broadscale experiments to reduce apparent competition. American Naturalist 185:665–679.

Servanty, S., R. Choquet, É. Baubet, S. Brandt, J.-M. Gaillard, M. Schaub, C. Toïgo, J.-D. Lebreton, M. Buoro, and O. Giménez. 2010. Assessing whether mortality is additive using marked animals: A Bayesian state-space modeling approach. Ecology 91:1916–1923.

Severson, J. P., C. A. Hagen, J. D. Maestas, D. E. Naugle, J. T. Forbes, and K. P. Reese. 2017. Effects of conifer expansion on greater sage-grouse nesting habitat selection. Journal of Wildlife Management 81:86–95.

Shannon, G., L. S. Cordes, A. R. Hardy, L. M. Angeloni, and K. R. Crooks. 2014. Behavioral responses associated with a human-mediated predator shelter. PLoS ONE 9:e94630.

Sih, A., J. Cote, M. Evans, S. Fogarty, and J. Pruitt. 2012. Ecological implications of behavioural syndromes. Ecology Letters 15:278–289.

Simard, M. A., J. Huot, S. De Bellefeuille, and S. D. Côté. 2014. Linking conception and weaning success with environmental variation and female body condition in a northern ungulate. Journal of Mammalogy 95:311–327.

Sinclair, A. R. E. 1983. The function of distance movement in vertebrates. Pages 248–258 *in* I. R. Swingland and P. J. Greenwood, editors. Ecology of Animal Movement. Clarendon Press, Oxford, UK.

Singer, F. J., and M. K. Harter. 1996. Comparative effects of elk herbivory and 1988 fires on northern Yellowstone National Park grasslands. Ecological Applications 6:185–199.

Singer, F. J., A. Harting, K. K. Symonds, and M. B. Coughenour. 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. Journal of Wildlife Management 61:12–25.

Singer, F. J., D. K. Otto, A. R. Tipton, and C. P. Hable. 1981. Home ranges, movements, and habitat use of European wild boar in Tennessee. Journal of Wildlife Management 45:343–353.

Singh, N. J., A. M. Allen, and G. Ericsson. 2016. Quantifying migration behaviour using net squared displacement approach: Clarifications and caveats. PLoS ONE 11:e0149594.

Singh, N. J., L. Börger, H. Dettki, N. Bunnefeld, G. Ericsson, L. Borger, and H. Dettki. 2012. From migration to nomadism: Movement variability in a northern ungulate across its latitudinal range. Ecological Applications 22:2007–2020.

Singh, N. J., and K. Leonardsson. 2014. Partial migration and transient coexistence of migrants and residents in animal populations. PLoS ONE 9:1–7.

Skov, C., H. Baktoft, J. Brodersen, C. Bronmark, B. B. Chapman, L.-A. Hansson, and P. A. Nilsson. 2011. Sizing up your enemy: Individual predation vulnerability predicts migratory probability. Proceedings of the Royal Society B: Biological Sciences 278:1414–1418.

Skrondal, A., and S. Rabe-Hesketh. 2004. Generalized latent variable modeling: Multilevel, longitudinal, and structural equation models. Chapman & Hall/CRC Press LLC, Boca Raton, FL, USA.

Smith, B. L., R. L. Robbins, and S. H. Anderson. 1997. Early development of supplementally fed, free-ranging elk. Journal of Wildlife Management 61:26–38.

Smith, B. L., E. S. Williams, K. C. McFarland, T. L. McDonald, G. Wang, and T. D. Moore. 2006. Neonatal mortality of elk in Wyoming: Environmental, population, and predator effects. Biological Technical Publication BTP-R6007-2006. US Department of Interior, US Fish and Wildlife Service, Washington, DC, USA.

Smith, D. W., W. G. Brewster, and E. E. Bangs. 1999. Wolves in the Greater Yellowstone

Ecosystem: Restoration of a top carnivore in a complex management environment. Pages 103–125 *in* T. W. Clark, editor. Carnivores in ecosystems: The Yellowstone experience. Yale University Press, New Haven, CT, USA.

Smith, H. G., and J.-Å. Nilsson. 1987. Intraspecific variation in migratory pattern of a partial migrant, the blue tit (*Parus caeruleus*): An evaluation of different hypotheses. Auk 104:109–115.

Smolko, P. 2014. Ecology of partially migratory elk populations (Cervus elaphus). PhD Dissertation, Technicka Univerzita vo Zvolene, Zvolen, Slovakia.

Smolko, P., E. H. Merrill, J. Berg, S. L. Eggeman, H. Bohm, R. Kropil, and M. Hebblewhite. n.d. In prep. Elk habitat selection: Facing fires and predators in the eastern slopes of the Rocky Mountains, Canada.

Soper, J. D. 1941. History, range, and home life of the northern bison. Ecological Monographs 11:347–412.

Spaedtke, H. R. 2009. Aversive conditioning on horseback: A management alternative for grassland systems threatened by sedentary elk populations. MSc Thesis, University of Alberta, Edmonton, AB, Canada.

Spiegelhalter, D. J., N. G. Best, B. P. Carlin, and A. Van Der Linde. 2014. The deviance information criterion: 12 years on (with discussion). Journal of the Royal Statistical Society: Series B 64:485–493.

Spilker, E. 2018. Spatial predation risk and interactions with a predator community on the Rocky Mountain east slopes, Alberta. MSc Thesis, University of Alberta, Edmonton, AB, Canada.

Spitz, D. B. 2015. Does migration matter? Causes and consequences of migratory behavior in Sierra Nevada bighorn sheep. PhD Dissertation, University of Montana, Missoula, MT.

Spitz, D. B., M. Hebblewhite, and T. R. Stephenson. 2017. ‘MigrateR’: Extending model-driven methods for classifying and quantifying animal movement behavior. Ecography 40:788–799.

Spitz, D. B., M. Hebblewhite, T. R. Stephenson, and D. W. German. 2018. How plastic is migratory behavior? Quantifying elevational movement in a partially-migratory alpine ungulate, the Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*). Canadian Journal of Zoology 96:1385–1394.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.

Steenweg, R., J. Whittington, and M. Hebblewhite. 2015. Canadian Rockies remote camera multi-species occupancy project: Examining trends in carnivore populations and their prey using remote cameras in Banff, Jasper, Kootenay, Yoho and Waterton Lakes National Parks. Final report. University of Montana, Missoula, MT, USA.

Stelfox, J. B. 1993. Hoofed mammals of Alberta. Lone Pine Publishers, Edmonton, AB, Canada.

Stephenson, T. R., K. J. Hundertmark, C. C. Schwartz, and V. Van Ballenberghe. 1998. Predicting body fat and body mass in moose with ultrasonography. Canadian Journal of Zoology 76:717–722.

Stevens, S. 2002. Landsat TM-based greenness as a surrogate for grizzly bear habitat quality in the central Rockies ecosystem. MSc Thesis, University of Calgary, Calgary, AB, Canada.

Sutherland, W. J. 1998. Evidence for flexibility and constraint in migration systems. Journal of Avian Biology 29:441–446.

Sweanor, P. Y., and F. Sandegren. 1988. Migratory behavior of related moose. Holarctic Ecolgy 11:190–193.

Swingland, I. R. 1983. Intraspecific differences in movement. Pages 102–115 *in* I. R. Swingland and P. J. Greenwood, editors. The Ecology of Animal Movement. Clarendon Press, Oxford, UK.

Swingland, I. R., and C. M. Lessells. 1979. The natural regulation of giant tortoise populations on Aldabra Atoll. Movement polymorphism, reproductive success and mortality. Journal of Animal Ecology 48:639–654.

Takii, A., S. Izumiyama, and M. Taguchi. 2012. Partial migration and effects of climate on migratory movements of sika deer in Kirigamine Highland, central Japan. Mammal Study 37:331–340.

Tatman, N. M., S. G. Liley, J. W. Cain, and J. W. Pitman. 2018. Effects of calf predation and nutrition on elk vital rates. Journal of Wildlife Management 82:1417–1428.

Terrill, S. B. 1987. Social dominance and migratory restlessness in the dark-eyed junco (Junco hyemalis). Behavioral Ecology and Sociobiology 21:1–11.

Testa, J. W. 2002. Does predation on neonates inherently select for earlier births? Journal of Mammalogy 83:699–706.

Testa, J. W., E. F. Becker, and G. R. Lee. 2000. Movements of female moose in relation to birth and death of calves. Alces 36:155–162.

Therneau, T. 2015. A package for survival analysis in S. version 2.38.

Therneau, T., B. Atkinson, and B. Ripley. 2017. Recursive partitioning and regression trees. R package version 4.1-11.

Theuerkauf, J., W. Jedrzejewski, K. Schmidt, and R. Gula. 2003. Spatiotemporal segregation of wolves from humans in the Bialowieza Forest (Poland). Journal of Wildlife Management 67:433–438.

Thorne, E. T., R. E. Dean, and W. G. Hepworth. 1976. Nutrition during gestation in relation to successful reproduction in elk. Journal of Wildlife Management 40:330–335.

Thurber, J. M., R. O. Peterson, T. D. Drummer, and S. A. Thomasma. 1994. Gray wolf response to refuge boundaries and roads in Alaska. Wildlife Society Bulletin 22:61–68.

Trivers, R. L. 1974. Parent-offspring conflict. American Zoologist 14:249–264.

Tucker, M. A., K. Böhning-gaese, W. F. Fagan, J. M. Fryxell, B. Van Moorter, S. C. Alberts, A. H. Ali, A. M. Allen, N. Attias, A. Bertassoni, D. Beyer, L. Bidner, F. M. van Beest, C. Fichtel, W. Fiedler, C. Fischer, I. Fischhoff, J. R. Goheen, E. Gurarie, M. Hebblewhite, M. Heurich, F. Jeltsch, P. Kaczensky, A. Kane, P. Kappeler, M. J. Kauffman, R. Kays, D. Kimuyu, F. Koch, B. Kranstauber, S. Lapoint, J. Mattisson, E. P. Medici, U. Mellone, E. H. Merrill, T. A. Morrison, S. L. Díaz-muñoz, A. Mysterud, D. Nandintsetseg, R. Nathan, A. Niamir, J. Odden, R. B. O. Hara, L. G. R. Oliveira-santos, K. A. Olson, B. D. Patterson, R. C. De Paula, L. Pedrotti, B. Reineking, and M. Rimmler. 2018. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. Science 359:466–469.

Underwood, R. 1982. Vigilance behaviour in grazing African antelopes. Behaviourr 79:81–107.

Valenzuela, L. O., M. Sironi, V. J. Rowntree, and J. Seger. 2009. Isotopic and genetic evidence for culturally inherited site fidelity to feeding grounds in southern right whales (*Eubalaena australis*). Molecular Ecology 18:782–791.

Verme, L. J. 1965. Reproduction studies on penned white-tailed deer. Journal of Wildlife Management 29:74–79.

Visscher, D. R., and E. H. Merrill. 2009. Temporal dynamics of forage succession for elk at two scales: Implications of forest management. Forest Ecology and Management 257:96–106.

Visscher, D. R., and E. H. Merrill. 2018. Functional connectivity in ruminants: A generalized state-dependent modelling approach. PLoS ONE 13:e0199671.

Vore, J. M., and E. M. Schmidt. 2001. Movements of female elk during calving season in northwest Montana. Wildlife Society Bulletin 29:720–725.

de Vos, A., P. Brokx, and V. Geist. 1967. A review of social behavior of the North American cervids during the reproductive period. American Midland Naturalist 77:390–417.

Wahlström, L. K., and O. Liberg. 1995. Patterns of dispersal and seasonal migration in roe deer (*Capreolus capreolus*). Journal of Zoology 235:455–467.

Warbington, C. H., T. R. Van Deelen, A. S. Norton, J. L. Stenglein, D. J. Storm, and K. J. Martin. 2017. Cause-specific neonatal mortality of white-tailed deer in Wisconsin, USA. Journal of Wildlife Management 81:824–833.

Weber, B. J., M. L. Wolfe, G. C. White, and M. M. Rowland. 1984. Physiologic response of elk to differences in winter range quality. Journal of Wildlife Management 48:248–253.

Wengert, G. M., M. W. Gabriel, J. E. Foley, T. Kun, and B. N. Sacks. 2013. Molecular techniques for identifying intraguild predators of fishers and other North American small carnivores. Wildlife Society Bulletin 37:659–663.

White, C. G., P. Zager, and M. W. Gratson. 2010. Influence of predator harvest, biological factors, and landscape on elk calf survival in Idaho. Journal of Wildlife Management 74:355–369.

White, K. S., N. L. Barten, S. Crouse, and J. Crouse. 2014. Benefits of migration in relation to nutritional condition and predation risk in a partially migratory moose population. Ecology 95:225–237.

White, K. S., and J. Berger. 2001. Antipredator strategies of Alaskan moose: Are maternal trade-offs influenced by offspring activity? Canadian Journal of Zoology 79:2055–2062.

White, P. J., T. L. Davis, K. K. Barnowe-Meyer, R. L. Crabtree, and R. A. Garrott. 2007. Partial migration and philopatry of Yellowstone pronghorn. Biological Conservation 135:502–510.

Whiting, J. C., R. T. Bowyer, J. T. Flinders, and D. L. Eggett. 2011. Reintroduced bighorn sheep: Fitness consequences of adjusting parturition to local environments. Journal of Mammalogy 92:213–220.

Whittington, J., M. Hebblewhite, and R. B. Chandler. 2017. Generalized spatial mark-resight models with an application to grizzly bears. Journal of Applied Ecology 1–12.

Whittington, J., and M. A. Sawaya. 2015. A comparison of grizzly bear demographic parameters estimated from non-spatial and spatial open population capture-recapture models. PLoS

ONE 10:e0134446.

Wilcove, D. S., and M. Wikelski. 2008. Going, going, gone: Is animal migration disappearing? PLoS biology 6:e188.

Willoughby, M. G., M. J. Alexander, and B. W. Adams. 2005. Range plant community types and carrying capacity for the montane subregion: Sixth approximation. Publication No. T/071. Sustainable Resource Development, Public Lands Dvision, Edmonton, AB, Canada.

Woods, J. G. 1991. Ecology of a partially migratory elk population. PhD Dissertation, University of British Columbia, Vancouver, BC, Canada.

Zager, P., and J. Beecham. 2006. The role of American black bears and brown bears as predators on ungulates in North America. Ursus 17:95–108.

Zager, P., D. M. Montgomery, and S. Hayes. 2008. Elk data analysis project: Progress Report, Project W-160-R-35. Idaho Department of Fish and Game, Boise, ID, USA.

APPENDIX A. MORE ON PARTIAL MIGRATION IN UNGULATES

Table A.1. Definitions of words used in discussion of animal migration.

Dispersal	movement of individuals between populations (McPeek and Holt 1992)
Frequency-dependence	a phenotype's fitness depends on its frequency and those of the other phenotypes within the population
Migratory	individuals that undertake regular, long-distance movements, usually as round-trips and often in systems with predictable spatiotemporal variation in resources
Net Squared Displacement	distinguishes migration from other movement by measuring the straight line distance between animal's point of departure and subsequent locations (Börger et al. 2011, Bunnefeld et al. 2011, Singh et al. 2016)
Nomadism	broad-scale, temporally unpredictable landscapes (Mueller et al. 2011, Singh et al. 2012) support animals moving through or occupying different ranges with no distinct pattern. Mongolian gazelles take advantage of changing conditions through lack of consistent range use (Olson et al. 2010)
Partial Migration	demonstrated by within-population behavioral dimorphism in migratory tendency, so one fraction of the population is migratory while the other is sedentary (Lundberg 1988, Chapman et al. 2011*a*)
Residency	individuals reside in areas that are small compared to the population range (Mueller et al. 2011); seasonal ranges overlap or are immediately adjacent
Strategy	set of rules or adaptations governing a range of behaviors an organism may employ; a ***pure strategy*** uses a single tactic without any alternative (e.g., only migrate, never resident); a ***mixed strategy*** can use more than one probabilistically preset tactic (e.g., either genotype determines migration 70% of time and residing 30%, or 70% of a species always migrates, while 30% always resides); an organism's environment and conditions determine the tactic used in a ***conditional strategy***
Tactic	individual action or behavior (e.g., migrate or reside) used within a strategy

Table A.2. The different forms of migration in ungulates. Note that populations exhibiting these non-exclusive forms may also be described as partially migratory.

Seasonal	Perhaps the most documented form of short-distance migration, seasonal migration is a round trip between non-overlapping ranges. Temperate cervids, such as elk, mule deer, and red deer are well-known for migrating seasonally between discrete, high-elevation summer ranges and low-elevation winter ranges; hypothesized triggers are snow and lowering temperatures in fall (Sabine et al. 2002, Brinkman et al. 2005), and competition avoidance and phenological tracking in spring (Albon and Langvatn 1992, Hebblewhite et al. 2008).
Altitudinal	Some mountainous herbivores use different elevations in different times of the year. We differentiate altitudinal from short-distance seasonal migration because in this case, migration is still achieved through movement across an 'ecological distance' (LeResche 1974, Peters et al. 2017), but may have no relationship with horizontal movement, as in mountain goats (Rice 2008) and bighorn sheep (Spitz 2015).
Long-distance	The definition may be subjective, dependent on species or population, but some suggest long-distance migration includes movements that are greater than 10-12 km (Berger 2004), or even 50 km (Poor et al. 2012). The best-known examples are barren-ground caribou and wildebeest.

Table A.3. Additional state-dependent hypotheses to explain variation in migratory tendency that are less common in the ungulate literature.

	Driver	**References**	**Hypothesis**	**Prediction in ungulates**	**Observed in lit.?**
Intrinsic	Arrival Time	(Ketterson & Nolan Jr. 1976)	Intraspecific competition for high quality resources predicts particular individuals should benefit by remaining at, or arriving earlier to, those resources.	(1) Territorial males remain resident or migrate earlier. (2) If high-quality parturition sites are limited, dominant females migrate to arrive at sites earlier.	**YES**
	Body Size; Thermal Tolerance	(Ketterson & Nolan Jr. 1976)	Cost of enduring thermal extremes or higher risk predicts migration in smaller individuals because larger individuals have greater body reserves relative to their metabolic rate.	Deep snow, severe temperatures, etc., causes migration in smaller individuals even in areas without altitudinal variation, irrespective of density.	NO
	Fasting Endurance/ Limited Foraging	(Boyle 2008, Ketterson & Nolan Jr. 1976)	Seasonal reduction in foraging opportunities or harsh environmental conditions predicts migration in individuals less able to cope.	Deep snow, severe temperatures, etc., causes migration even in areas without altitudinal variation, irrespective of density.	**YES**
	Sexual Conflict	(Grayson & Wilbur 2009)	Costly sexual harassment or breeding predicts migration in one sex- or age-class.	Females migrate while males remain resident; dependent on sex ratio rather than density.	**YES**
	Trophic or Resource-based Polymorphism	(Smith & Skulason 1996, Svanbäck et al. 2008, Werner & Gilliam 1984)	Individual variation predicts migration in those individuals asymmetrically affected by seasonal changes in resources.	Increase in migration with temporal/spatial variation in availability of preferred resources.	NO

Table A.4. Additional support (+ positive/likely, ? potentially but untested/suppositional, - negative/evidence against) for less-common, state- or condition-dependent mechanisms explaining individual variation in partial migration.

Order	Scientific name	Common name	Arrival time	Fasting endurance/ limited foraging	Sexual conflict
Antilocapridae	Antilocapra americana	pronghorn		? (White et al. 2007, Jacques et al. 2009, Kolar et al. 2011)	
Bovidae	Bison spp.	bison		+ (Bruggeman et al. 2008) ? (Kowalczyk et al. 2013)	
	Naemorhedus	goral		? (Perveen and Khan 2013)	
	Rupicapra spp.	chamois, isard		+ (Clarke and Frampton 1991)	
	Syncerus caffer	African buffalo		+ (Naidoo et al. 2012)	
Camelidae	Lama guanicoe	guanaco	? (Moraga et al. 2015)	? (Ortega and Franklin 1995)	
Cervidae	Alces alces	moose		+ (Sweanor and Sandegren 1988, Singh et al. 2012) ? (Ball et al. 2001)	
	Capreolus capreolus	roe deer		+ (Ramanzin et al. 2007), ? (Lamberti et al. 2004, Cagnacci et al. 2011)	
	Cervus elaphus	red deer		+ (Luccarini et al. 2006)	
	Cervus nippon	sika deer		+ (Igota et al. 2004)	
	Odocoileus hemionus	mule deer		? (Brown 1992)	
	Odocoileus virginianus	white-tailed deer		+ (Nelson 1995, 1998, Sabine et al. 2002, Brinkman et al. 2005, Grovenburg et al. 2011)	

APPENDIX B. DETAILS OF THE CALF ECOLOGY COMPONENT TO THE YA HA TINDA LONG-TERM ELK MONITORING PROJECT

STUDY AREA

The study area is situated in the upper foothill, montane, subalpine, and lower alpine ecoregions of west-central Alberta, Canada (51º38’ N/-115º30’ W). The area measures approximately 7,000 km^2 and straddles the boundary between Banff National Park (BNP) and adjacent provincial lands, including Parks Canada’s Ya Ha Tinda (YHT) ranch (44 km^2). Though owned and run by Parks Canada, the ranch’s natural resources are under management by Alberta’s provincial government. The vegetation at the ranch consists partly of montane rough fescue (*Festuca campestris*) grasslands (20 km^2) where the YHT elk population winters. Other common grasses include junegrass (*Koeleria macrantha*), Hooker’s oatgrass (*Helictotrichon hookeri*), and smooth brome (*Bromus inermis*; Looman 1969, Willoughby et al. 2005). Common trees include lodgepole pine (*Pinus contorta*), and trembling aspen (*Populus tremuloides*), interspersed with Engelmann and white spruce (*Picea engelmannii and P. glauca*) and subalpine fir (*Abies lasiocarpa*) at higher elevations, and shrubs include bog birch (*Betula glandulosa*), shrubby cinquefoil (*Potentilla fruticose*), and willow (*Salix* spp.; McGillis 1977, Holland and Coen 1982).

Elevations in the study area range from 1,400 – 3,500 m with long, snowy winters (Oct – Apr) and a short summer (May – Sep). Low precipitation and westerly winds (i.e., chinooks) keep the provincial lands in the eastern part of the study area mostly snow-free in winter (Holland and Coen 1982), with an average of 157 cm of snowfall. Temperatures in winter average -4.1ºC, and 9ºC in May – September, with an average of 31.9 cm of precipitation though during drought years, precipitation can be <10 cm in summer (Environment Canada Ya Ha Tinda weather station).

Wolves (*Canis lupus*) recolonized the study area by the mid-1980s after extirpation by the 1950s (Morgantini 1995). Other main predators of elk in this system include coyotes (*C. latrans*), grizzly and black bears (though rarer than grizzly bears; *Ursus arctos* and *U. americanus*), and cougars (*Puma concolor*) which have increased in the last several decades (Morgantini 1995, Knopff et al. 2014). Ungulates other than elk include white-tailed and mule deer (*Odocoileus virginianus* and *O. hemionus*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), and mountain goats (though mostly in BNP; *Oreamnos americanus;* Stelfox 1993, Morgantini 1995). Woodland caribou (*Rangifer tarandus caribou*) in BNP numbered ~30 – 40 individuals in 1980s but are now completely gone from the park (Hebblewhite et al. 2010), while plains bison (*Bison bison bison*) were extirpated by the 1870s but have recently been reintroduced (Soper 1941, Parks Canada 2017).

The elk population that winters at YHT grew over the 1900s to peak at a maximum count ~2,200 individuals in 1992 (Morgantini 1995, Glines et al. 2011), and historically almost the entire YHT elk population migrated west from the winter range to summer in BNP (Morgantini and Hudson 1988). However, the YHT elk population declined by 68% over the course of this study, from 1216 elk counted in 2002 to 391 elk in 2016 (Figure B.1). The ratio of western migrants to residents to eastern migrants averaged 14:15:1 during the early period of 2002 – 2006, whereas during the late period (2013 – 2016), the ratio averaged 1:10:5. This represents a significant loss in the proportion of the total population comprised of western migrants and a noticeable shift in migration towards the east. Past studies focused on western migrants and residents showed higher pregnancy rates and winter calf weights in western migrants, with cause-specific mortality dominated by wolves and grizzly bears, particularly during migration. On the other hand, by remaining close to human activity, residents reduced their risk of predation to achieve only marginally higher survival than that of migrants, with cause-specific mortality dominated by First Nations harvest (Hebblewhite and Merrill 2011).

METHODS

Adult Elk Capture and Handling

We captured and collared adult female elk through ground darting from horseback in winter (15 Jan – 31 Mar, 2013 – 2016) on the Ya Ha Tinda winter range (University of Alberta Animal Care Protocol no. 00000624). Elk were immobilized with Telazol® and medetomidine (with atipamezole as an antagonist) by riding into the population and darting at a distance of 20 – 25 m. We blindfolded and restrained elk with hobbles before giving them 2 ALL-flex cattle ear tags with a unique color-number combination. We drew blood samples and extracted vestigial canines for aging. Elk were fit with GPS or VHF radiocollars (Lotek Wireless, Inc., models

3300, 4400, 7000, Lifecycle, or LMRT-4); GPS collars recorded location every 15 min during May and June, and every 2 hr during other months of the year.

We determined pregnancy through rectal palpation. We collared and fit all pregnant elk with vaginal implant transmitters (VITs; Advanced Telemetry Systems, Inc., model M3960). When parturition occurred, VITs expelled with the calf; a temperature-sensitive trigger doubled the pulse rate and a code emitted that allowed time of birth to be determined to the nearest half hour through a Precise Event Transmitter (PET) and birth sites to be precisely located. From a distance, we used telemetry to locate and/or observe maternal elk from a distance multiple times daily during the calving season (mid-May to mid-July); when a VIT expelled or we observed solitary behavior from maternal elk, a ground crew attempted to locate the birth site and capture the calf (methods described below). The time of VIT expulsion to the nearest half hour was determined through a code emitted by a Precise Event Transmitter (PET) and we recorded GPS coordinates of the site.

Nutritional Condition of Adult Female Elk

To estimate nutritional condition of adult female elk while anesthetized, we used a combination of visual and tactile assessment and ultrasonography (portable Sonovet ultrasound system with a 5.0- MHz, 7.0-cm probe; Universal Medical Systems, Bedford Hills, New York, USA) with clear ultrasound gel. We used a body condition score (BCS) system (Cook et al. 2001, modified from Gerhardt et al. 1996) by combining separate scores derived from palpation of the ribs, withers, and rump areas. To obtain a clear ultrasound image, we plucked elk hair over the point of maximum rump fat, an area roughly the width of the probe and 12-15 cm long, along a line between the spine at the point closes to the coxal tuber (hip bone) and the ischial tuber (pin bone; Stephenson et al. 1998), in addition to measuring the longissimus dorsi muscle thickness between the 12th and 13th ribs directly beneath the backbone (Herring et al. 1995, Cook et al. 2001). We then estimated ingesta-free body fat (IFBF) percentage using the scaled LIVINDEX, which combines the rump BCS and maximum rump fat thickness (cm), scaled by body mass (kg) estimated with chest girth circumference (cm, Cook et al. 2001, 2010). In 2013, we measured chest girth circumference and estimated body mass, but did not take BCS or measure fat levels because we did not have adequate training or an ultrasound system. In 2014, we measured chest girth and estimated body mass and BCS, but did not measure fat levels. In 2015 and 2016, we took all measurements and were then able to use the BCS data from these years in linear regression to predict rump fat levels and IFBF for 2014. We used Kruskal-Wallis and Dunn-Bonferroni post-hoc tests to determine if IFBF differed among migratory tactics across all years.

Calf Elk Capture and Handling

Field crews captured calves on the ground opportunistically, or by using VITs to locate calves at or near their birth sites. Once calves were captured, blindfolded, and hobbled, the body measurements were taken (Appendix L). Calves were equipped with VHF radiotransmitting ear tags (Biotrack Ltd., model TW-5) to allow for regular relocation and monitoring, and to locate calves when the signal indicates they have remained unmoved for >4 hr. Calves were released after no more than 10 ± 3 minutes of capture and handling, and all crew members wore gloves to minimize transfer of human scent to the calves.

Calf Mortality

We used VHF signals to monitor calves 1-3x daily from a distance from birth through September, and monthly thereafter. When we detected a mortality signal, we immediately attempted to investigate the signal, usually within 12 – 24 hr of death. We searched each site to assess the specific cause of mortality following established protocols (Hatter 1988, Barber-Meyer 2006, Knamiller 2011) and based on predation characteristics, presence of tracks, scat, puncture wounds, claw/bite marks, and site characteristics (Figure B.2). We assumed that scat and sign at kill sites reflected the specific predator that made the kill, because the low biomass and short handling times associated with calves is unlikely to provide scavenging by other predators (Kunkel and Mech 1994, Knopff et al. 2009, Knamiller 2011). In cases where cause of mortality was uncertain, we relied first on field evidence, but supplemented our conclusions with carnivore hair found at the site (Normandeau et al. 2018) or swabs of predator saliva to determine predator species based on DNA analysis (Table 0.8, Wengert et al. 2013). If field evidence suggested predation but no hairs could be found or DNA could not reliably identify the predator species, we classified the cause as unknown predator. We submitted carcasses with no evidence of predation to a diagnostics laboratory for necropsy and concluded calf monitoring on 31 August 2016.

RESULTS

Adult Elk Capture and Handling

In February and March, 2013 – 2016, we free-range darted a total of 184 adult female elk from horseback; we darted 26 elk in 2013, 48 in 2014, 64 in 2015, and 46 in 2016 (Table B.1). Of these, we checked 181 elk for pregnancy via rectal palpation; 172 elk were pregnant, with the pregnancy rate averaging 94.7% across the 4 years and 81.9% across our long-term monitoring (2002 – 2016, Figure B.3). We implanted VITs in 21 females in 2013 (1 elk suffered from capture-related mortality; the VIT was re-deployed leaving $n = 20$), 47 in 2014 (1 elk was poached during capture; the VIT was not re-deployed leaving $n = 46$), 60 in 2015, and 44 in 2016 (Table B.1). Adult females ranged in age from 2 to 21 with a mean of 9.7 and a median of 10 (n =180, Figure B.4). The average estimated body weight of adult females was 257.0 kg ($n = 176$, range: 205.1 – 306.5). The average rump fat thickness measured 1.73 cm ($n = 107$, range: 0 – 3.6), while the average BCS was 3.5 ($n = 150$, range: 1.5 – 5). Based on BCS from 2015 and 2016, BCS explains 71% of the total variation in rump fat thickness and the average ingesta-free body fat (IFBF) was 10.7 ($n = 106$, range: 1.5 – 17.3, Figure B.4). IFBF differed significantly between eastern migrants (9.62 ± *SE* 0.37) and residents (11.59 ± 0.35, Dunn-Bonferroni P = 0.001), but did not differ between eastern and western migrants (10.68 ± 0.84, P = 0.398), or between residents and western migrants (P = 0.654, Figure B.5).

Calf Elk Capture and Handling

From 2013 – 2016, 90 calves were captured from the ground through use of VITs, another 4 calves had already been predated upon by the time of arrival at the VIT site, 1 calf was aborted, 1 was stillborn, and 17 calves were captured opportunistically, for a total of 113 calves (Table B.4). Another 8 calves were opportunistically discovered dead throughout the calving seasons. Sixteen calves were captured in 2013, 33 in 2014, 34 in 2015, and 29 in 2016.

Calf Birth Sites

As a result of VIT monitoring and calf capture efforts, 153 total birth sites were identified during the 4-yr study period (Table B.3, Figure B.6). All but 2 of the birth sites were found through use of the VITs, while the remaining 2 were identified by opportunistically finding a newborn calf. Thirteen of the 172 total VITs were never found, and the remaining 8 VITs were from elk that died between winter capture and the calving period. Based on the known birth site locations (*n* = 153), 12% of elk gave birth in Banff National Park, 19% of elk gave birth to the north of the Ya Ha Tinda ranch, mostly in the Bighorn Creek cut blocks and along Scalp Creek, 27% of elk gave birth to the east of YHT, 37% of elk gave birth in the vicinity of the ranch, and 4% gave birth to the south of the ranch.

Calf Characteristics

Of the 107 calves (*n* = 90 + 17 opportunistically caught calves) captured and tagged, 47 were male, and 59 were female, while 1 was of unknown sex.

Parturition dates (*n* = 147) determined through VITs or through age estimation of opportunistically caught calves ranged from 9 May to 11 July (Figure B.7). The median birth date for calves (*n* = 113) born in 2013 – 2016 was 29 May.

The mean weight at birth was 17.7 ± 2.2 kg (range = 12.3 - 21.0, *n* = 102, Figure B.9). There was no difference (t_{100} = 1.98, p = 0.13) between weight at birth for males (18.0 ± 2.4 kg, *n* = 44) and females (17.4 ± 2.1 kg, *n* = 58).

Calf Mortality

Of 105 calves and the known mortality causes in 2013 - 2017, most were attributed to bears (raw frequency = 32%), followed by cougars (13%), and wolves (9%, Figure B.10). Most calves died in the first 20 days of life (Figure B.11).

Table B.1. Adult female elk captured during February and March, 2013 – 2016, in the Ya Ha Tinda elk population, Alberta, Canada.

Date	Year	Animal ID	Method	Blood	Hair	Tooth	Preg Check	Pregnant	VIT	Collar
23/Mar/2013	2013	OR100	Ground Dart	Yes	Yes	Yes	NO	NA	NO	Lotek Lifecycle prototype
22/Mar/2013	2013	OR41	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
17/Feb/2013	2013	OR76	Ground Dart	Yes	Yes	Yes	Yes	NO	NO	VHF
18/Feb/2013	2013	OR77	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 3300
17/Feb/2013	2013	OR78	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
18/Feb/2013	2013	OR79	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 3300
18/Feb/2013	2013	OR80	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
18/Feb/2013	2013	OR81	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
19/Feb/2013	2013	OR82	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 3300
2/Mar/2013	2013	OR84	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
4/Mar/2013	2013	OR85	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
4/Mar/2013	2013	OR86	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Mortality
5/Mar/2013	2013	OR88	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
5/Mar/2013	2013	OR89	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
5/Mar/2013	2013	OR90	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	ATS GPS
5/Mar/2013	2013	OR91	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	VHF
6/Mar/2013	2013	OR92	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 7000
7/Mar/2013	2013	OR93	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 7000
7/Mar/2013	2013	OR94	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 7000
8/Mar/2013	2013	OR95	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	VHF
8/Mar/2013	2013	OR96	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	VHF
22/Mar/2013	2013	OR97	Ground Dart	Yes	Yes	Yes	Yes	NO	NO	Lotek Lifecycle satellite
22/Mar/2013	2013	OR98	Ground Dart	Yes	Yes	Yes	NO	NA	NO	Lotek Lifecycle satellite
22/Mar/2013	2013	OR99	Ground Dart	Yes	Yes	Yes	NO	NA	NO	Lotek Lifecycle prototype
2/Mar/2013	2013	YL116_OR83	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
4/Mar/2013	2013	YL133_OR87	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	ATS GPS
16/Mar/2014	2014	BL268	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
23/Mar/2014	2014	OR100	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek Lifecycle prototype

27/Feb/2014	2014	OR23	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
11/Mar/2014	2014	OR24	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	VHF
25/Feb/2014	2014	OR39	Ground Dart	Yes	NO	NO	Yes	Yes	Yes	Lotek GPS 4400
26/Feb/2014	2014	OR40	Ground Dart	Yes	NO	NO	Yes	Yes	Yes	Lotek GPS 4400
4/Mar/2014	2014	OR55_OR15	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 7000
7/Mar/2014	2014	OR59_BL259	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	VHF
20/Mar/2014	2014	OR60_BL288	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
5/Mar/2014	2014	OR77	Ground Dart	Yes	NO	NO	Yes	Yes	Yes	Lotek GPS 3300
23/Mar/2014	2014	OR78	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
17/Mar/2014	2014	OR79	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
25/Mar/2014	2014	OR84	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
29/Mar/2014	2014	OR85	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
17/Mar/2014	2014	OR91	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
5/Mar/2014	2014	OR96	Ground Dart	Yes	NO	NO	Yes	Yes	Yes	VHF
31/Mar/2014	2014	OR97	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek Lifecycle satellite
24/Feb/2014	2014	OR98	Ground Dart	Yes	NO	NO	Yes	Yes	Yes	Lotek GPS 4400
3/Mar/2014	2014	YL100	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
4/Mar/2014	2014	YL101	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
5/Mar/2014	2014	YL102	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	VHF
6/Mar/2014	2014	YL103_GR183	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	VHF
7/Mar/2014	2014	YL104	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	VHF
11/Mar/2014	2014	YL105	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	VHF
13/Mar/2014	2014	YL106	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400 ARGOS
13/Mar/2014	2014	YL107	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400 ARGOS
20/Mar/2014	2014	YL108_BL236	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
6/Mar/2014	2014	YL109_OR35	Ground Dart	Yes	NO	NO	Yes	Yes	Yes	Lotek GPS 4400
17/Mar/2014	2014	YL110_OR29	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
12/Mar/2014	2014	YL111_OR6	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400 ARGOS
26/Feb/2014	2014	YL113_OR31	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	VHF
27/Feb/2014	2014	YL114_BL274	Ground Dart	Yes	NO	NO	Yes	Yes	Yes	Lotek GPS 4400

22/Feb/2014	2014	YL115_OR34	Ground Dart	Yes	NO	NO	Yes	Yes	Yes	Lotek GPS 4400
3/Mar/2014	2014	YL119_BL245	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	VHF
4/Mar/2014	2014	YL123_OR7	Ground Dart	Yes	NO	NO	Yes	Yes	Yes	Lotek GPS 4400
31/Mar/2014	2014	YL128_BL261	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	VHF
10/Mar/2014	2014	YL131_OR32	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
30/Mar/2014	2014	YL132_OR2	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
6/Mar/2014	2014	YL136_BL284	Ground Dart	Yes	NO	NO	Yes	Yes	Yes	Lotek GPS 4400
5/Mar/2014	2014	YL138_BL295	Ground Dart	Yes	NO	NO	Yes	Yes	Yes	Lotek GPS 4400
18/Mar/2014	2014	YL140_BL257	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
15/Mar/2014	2014	YL151_YL87	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 3300
29/Mar/2014	2014	YL155_OR16	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
12/Mar/2014	2014	YL157_OR37	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400 ARGOS
3/Mar/2014	2014	YL160_OR12	Ground Dart	Yes	Yes	Yes	Yes	NO	NO	Lotek GPS 4400
31/Mar/2014	2014	YL165_OR17	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	VHF
18/Mar/2014	2014	YL167_OR10	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 3300
14/Mar/2014	2014	YL25	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
27/Feb/2015	2015	GR513	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
24/Feb/2015	2015	OR51_OR19	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	VHF
19/Feb/2015	2015	OR52_OR28	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
26/Feb/2015	2015	OR53_OR22	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
26/Feb/2015	2015	OR54_BL260	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
27/Feb/2015	2015	OR55_OR15	Ground Dart	NO	Yes	NO	Yes	Yes	Yes	VHF
1/Mar/2015	2015	OR56_BL251	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 7000 ARGOS
1/Mar/2015	2015	OR57_OR27	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
4/Mar/2015	2015	OR58_BL292	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
4/Mar/2015	2015	OR59_BL259	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
5/Mar/2015	2015	OR60_BL288	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
5/Mar/2015	2015	OR61	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	VHF
5/Mar/2015	2015	OR63_BL242	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	VHF
7/Mar/2015	2015	OR65_BL265	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 3300

7/Mar/2015	2015	OR66_BL293	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
7/Mar/2015	2015	OR78	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400 ARGOS
4/Mar/2015	2015	OR79	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
27/Feb/2015	2015	OR80	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400 ARGOS
15/Feb/2015	2015	OR81	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
15/Feb/2015	2015	OR82	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
1/Mar/2015	2015	OR88	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
13/Feb/2015	2015	OR89	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
12/Feb/2015	2015	OR91	Ground Dart	Yes	Yes	NO	Yes	NO	NO	VHF
13/Feb/2015	2015	OR92	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
24/Feb/2015	2015	OR96	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
4/Mar/2015	2015	OR97	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek Lifecycle satellite
19/Feb/2015	2015	OR99	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
26/Feb/2015	2015	YL100	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
26/Feb/2015	2015	YL102	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
19/Feb/2015	2015	YL105	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
11/Feb/2015	2015	YL107	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 3300
5/Mar/2015	2015	YL108_BL236	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
10/Feb/2015	2015	YL109_OR35	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
10/Feb/2015	2015	YL110_OR29	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
11/Feb/2015	2015	YL111_OR6	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400 ARGOS
11/Feb/2015	2015	YL112_OR38	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 3300
11/Feb/2015	2015	YL113_OR31	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
11/Feb/2015	2015	YL114_BL274	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
12/Feb/2015	2015	YL115_OR34	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
12/Feb/2015	2015	YL116_OR83	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
12/Feb/2015	2015	YL117_OR3	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
13/Feb/2015	2015	YL118_OR8	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
13/Feb/2015	2015	YL119_BL245	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
13/Feb/2015	2015	YL120_BL290	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400

13/Feb/2015	2015	YL121_BL250	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
14/Feb/2015	2015	YL122_BL244	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	VHF
14/Feb/2015	2015	YL123_OR7	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
14/Feb/2015	2015	YL124	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400 ARGOS
15/Feb/2015	2015	YL125_BL286	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
15/Feb/2015	2015	YL126_OR20	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	VHF
15/Feb/2015	2015	YL127	Ground Dart	Yes	Yes	Yes	Yes	NO	NO	Lotek GPS 4400
15/Feb/2015	2015	YL128_BL261	Ground Dart	Yes	Yes	NO	Yes	NO	NO	VHF
16/Feb/2015	2015	YL129_OR11	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
16/Feb/2015	2015	YL130_OR9	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
16/Feb/2015	2015	YL131_OR32	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
17/Feb/2015	2015	YL132_OR2	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
17/Feb/2015	2015	YL133_OR87	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
17/Feb/2015	2015	YL134_BL262	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
17/Feb/2015	2015	YL135_BL222	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
18/Feb/2015	2015	YL136_BL284	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
18/Feb/2015	2015	YL137_BE13	Ground Dart	Yes	Yes	NO	Yes	NO	NO	VHF
18/Feb/2015	2015	YL138_BL295	Ground Dart	NO	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
18/Feb/2015	2015	YL139_BL220	Ground Dart	NO	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
24/Feb/2015	2015	YL140_BL257	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	VHF
11/Feb/2016	2016	OR100	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
22/Feb/2016	2016	OR52_OR28	Ground Dart	Yes	Yes	NO	Yes	NO	NO	Lotek GPS 4400
17/Feb/2016	2016	OR54_BL260	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
20/Feb/2016	2016	OR56_BL251	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 7000
11/Feb/2016	2016	OR60_BL288	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
19/Feb/2016	2016	OR61	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
18/Feb/2016	2016	OR65_BL265	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
26/Feb/2016	2016	OR66_BL293	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
20/Feb/2016	2016	OR78	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
26/Feb/2016	2016	OR81	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400

14/Feb/2016	2016	OR89	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
20/Feb/2016	2016	OR97	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
21/Feb/2016	2016	OR99	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
17/Feb/2016	2016	YL100	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
12/Feb/2016	2016	YL107	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
15/Feb/2016	2016	YL112_OR38	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 7000
13/Feb/2016	2016	YL114_BL274	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 7000
19/Feb/2016	2016	YL115_OR34	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
13/Feb/2016	2016	YL118_OR8	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
18/Feb/2016	2016	YL120_BL290	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
19/Feb/2016	2016	YL124	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
16/Feb/2016	2016	YL133_OR87	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 7000
27/Feb/2016	2016	YL134_BL262	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
22/Feb/2016	2016	YL137_BE13	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
11/Feb/2016	2016	YL151_YL87	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
12/Feb/2016	2016	YL152_YL63	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
12/Feb/2016	2016	YL153	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
12/Feb/2016	2016	YL154	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
13/Feb/2016	2016	YL155_OR16	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 7000
14/Feb/2016	2016	YL156	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 7000
14/Feb/2016	2016	YL157_OR37	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
14/Feb/2016	2016	YL158_OR21	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
16/Feb/2016	2016	YL159	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
16/Feb/2016	2016	YL160_OR12	Ground Dart	Yes	NO	NO	Yes	NO	NO	Lotek GPS 4400
16/Feb/2016	2016	YL161	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
16/Feb/2016	2016	YL162_BC13	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
17/Feb/2016	2016	YL163	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
17/Feb/2016	2016	YL164_BL255	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 7000
19/Feb/2016	2016	YL165_OR17	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Mortality
21/Feb/2016	2016	YL166	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400

21/Feb/2016	2016	YL167_OR10	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400
22/Feb/2016	2016	YL168	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
26/Feb/2016	2016	YL169	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 7000
26/Feb/2016	2016	YL170	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
27/Feb/2016	2016	YL171	Ground Dart	Yes	Yes	Yes	Yes	Yes	Yes	Lotek GPS 4400
27/Feb/2016	2016	YL172	Ground Dart	Yes	Yes	NO	Yes	Yes	Yes	Lotek GPS 4400S

Table B.2. Body measurements taken on adult female elk in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016.

Animal ID	**Year**	**Girth (cm)**	**Pregnant**	**Lactating**	**BCS**	**Rump (cm)**	**Body Mass (kg)**	**IFBF (%)**	**Migratory Status**	**Age**
OR100	2013	164	Yes	NA	NA	NA	262.0	NA	Resident	5
OR41	2013	169	Yes	NA	NA	NA	275.9	NA	Resident	5
OR76	2013	169	NO	NA	NA	NA	275.9	NA	Resident	19
OR77	2013	152	Yes	NA	NA	NA	228.7	NA	Resident	16
OR78	2013	154	Yes	NA	NA	NA	234.2	NA	Western	4
OR79	2013	163	Yes	NA	NA	NA	259.2	NA	Resident	9
OR80	2013	159	Yes	NA	NA	NA	248.1	NA	Resident	4
OR81	2013	161	Yes	NA	NA	NA	253.7	NA	Eastern	9
OR82	2013	166	Yes	NA	NA	NA	267.6	NA	Resident	14
OR84	2013	168	Yes	NA	NA	NA	273.1	NA	Resident	9
OR85	2013	171	Yes	NA	NA	NA	281.5	NA	Resident	12
OR86	2013	166	Yes	NA	NA	NA	267.6	NA	NA	9
OR88	2013	167	Yes	NA	NA	NA	270.3	NA	Resident	5
OR89	2013	154	Yes	NA	NA	NA	234.2	NA	Resident	4
OR90	2013	165	Yes	NA	NA	NA	264.8	NA	Resident	10
OR91	2013	166	Yes	NA	NA	NA	267.6	NA	Resident	13
OR92	2013	170	Yes	NA	NA	NA	278.7	NA	Eastern	4
OR93	2013	172	Yes	NA	NA	NA	284.2	NA	Resident	13
OR94	2013	168	Yes	NA	NA	NA	273.1	NA	Eastern	8
OR95	2013	176	Yes	NA	NA	NA	295.3	NA	Southern	10
OR96	2013	NA	Yes	NA	NA	NA	NA	NA	Resident	11
OR97	2013	164	NO	NA	NA	NA	262.0	NA	Resident	7
OR98	2013	175	NA	NA	NA	NA	292.6	NA	Resident	4
OR99	2013	155	NA	NA	NA	NA	237.0	NA	Resident	11
YL116_OR83	2013	170	Yes	NA	NA	NA	278.7	NA	Resident	7
YL133_OR87	2013	167	Yes	NA	NA	NA	270.3	NA	Resident	4
BL268	2014	149.7	Yes	NA	NA	NA	222.3	NA	Eastern	11
OR100	2014	NA	Yes	NA	3.75	2.0	NA	NA	Resident	6

OR23	2014	161	Yes	NA	3.75	2.0	253.7	11.9	Eastern	6
OR24	2014	157	Yes	NA	4.75	3.1	242.6	16.1	Resident	12
OR39	2014	158.5	Yes	NA	3.25	1.5	246.7	10.0	Eastern	14
OR40	2014	NA	Yes	NA	4.25	2.6	NA	NA	Resident	6
OR55_OR15	2014	164	Yes	NA	4.5	2.8	262.0	14.7	Western	8
OR59_BL259	2014	160	Yes	NA	NA	NA	250.9	NA	Eastern	13
OR60_BL288	2014	158	Yes	NA	3.5	1.7	245.4	11.0	Resident	11
OR77	2014	155	Yes	NA	4.5	2.8	237.0	15.2	Resident	17
OR78	2014	156	Yes	NA	3	1.2	239.8	9.1	Western	5
OR79	2014	NA	Yes	NA	2.5	0.6	NA	NA	Resident	10
OR84	2014	165.5	Yes	NA	4.25	2.6	266.2	13.6	NA	10
OR85	2014	161.5	Yes	NA	3.75	2.0	255.1	11.9	Resident	13
OR91	2014	161.5	Yes	NA	3	1.2	255.1	8.9	Resident	14
OR96	2014	158	Yes	NA	4.25	2.6	245.4	14.0	Resident	12
OR97	2014	159	Yes	NA	4.5	2.8	248.1	15.0	Resident	8
OR98	2014	162	Yes	NA	3.5	1.7	256.5	10.9	Resident	5
YL100	2014	158	Yes	NA	3.5	1.7	245.4	11.0	Resident	5
YL101	2014	162.5	Yes	NA	4.25	2.6	257.9	13.8	Resident	NA
YL102	2014	159.5	Yes	NA	4.75	3.1	249.5	15.9	Resident	5
YL103_GR183	2014	154	Yes	NA	NA	NA	234.2	NA	Eastern	13
YL104	2014	162	Yes	NA	NA	NA	256.5	NA	Western	9
YL105	2014	156.5	Yes	NA	4.25	2.6	241.2	14.1	Resident	6
YL106	2014	157.5	Yes	NA	2.75	0.9	244.0	8.0	Western	12
YL107	2014	157.5	Yes	NA	3.5	1.7	244.0	11.1	Resident	9
YL108_BL236	2014	162	Yes	NA	4	2.3	256.5	12.8	Resident	10
YL109_OR35	2014	157.5	Yes	NA	NA	NA	244.0	NA	Eastern	5
YL110_OR29	2014	162.3	Yes	NA	2.75	0.9	257.3	7.9	Resident	6
YL111_OR6	2014	155	Yes	NA	3.75	2.0	237.0	12.2	Eastern	9
YL113_OR31	2014	161	Yes	NA	4.5	2.8	253.7	14.8	Resident	5
YL114_BL274	2014	150.4	Yes	NA	3.75	2.0	224.3	12.4	Eastern	7

YL115_OR34	2014	160	Yes	NA	3.75	2.0	250.9	11.9	Resident	14
YL119_BL245	2014	155	Yes	NA	3.5	1.7	237.0	11.2	Resident	13
YL123_OR7	2014	161.5	Yes	NA	3.75	2.0	255.1	11.9	Eastern	11
YL128_BL261	2014	156	Yes	NA	2.5	0.6	239.8	7.1	Eastern	10
YL131_OR32	2014	160	Yes	NA	3.75	2.0	250.9	11.9	Resident	6
YL132_OR2	2014	160	Yes	NA	2.5	0.6	250.9	7.0	Resident	12
YL136_BL284	2014	163	Yes	NA	NA	NA	259.2	NA	Eastern	8
YL138_BL295	2014	163.5	Yes	NA	3.5	1.7	260.6	10.8	Resident	8
YL140_BL257	2014	162	Yes	NA	2.5	0.6	256.5	7.0	Eastern	10
YL151_YL87	2014	160	Yes	NA	3.5	1.7	250.9	11.0	Resident	14
YL155_OR16	2014	152.5	Yes	NA	2.5	0.6	230.1	7.1	Eastern	NA
YL157_OR37	2014	164	Yes	NA	3.5	1.7	262.0	10.8	Resident	14
YL160_OR12	2014	163	NO	NA	3.75	2.0	259.2	11.8	Resident	19
YL165_OR17	2014	164.5	Yes	NA	3.25	1.5	263.4	9.8	Western	7
YL167_OR10	2014	152	Yes	NA	4.25	2.6	228.7	14.4	Resident	11
YL25	2014	164.5	Yes	NA	2.5	0.6	263.4	6.9	Western	14
GR513	2015	156	Yes	NO	3	2.3	239.8	13.2	Western	7
OR51_OR19	2015	166	Yes	NO	4.25	2.8	267.6	14.4	Western	10
OR52_OR28	2015	163	Yes	NO	3.5	1.8	259.2	11.0	Eastern	7
OR53_OR22	2015	162	Yes	NO	2.5	0.9	256.5	7.9	Eastern	7
OR54_BL260	2015	162	Yes	NO	4.5	3.1	256.5	15.7	Resident	9
OR55_OR15	2015	NA	Yes	Yes	2.75	0.9	NA	NA	Western	9
OR56_BL251	2015	167	Yes	NO	4.25	2.3	270.3	12.6	Southern	11
OR57_OR27	2015	167	Yes	NO	3.5	1.7	270.3	10.5	Eastern	8
OR58_BL292	2015	161	Yes	NO	2.5	1.2	253.7	9.0	Resident	15
OR59_BL259	2015	159	Yes	NO	3	2.1	248.1	12.3	Eastern	14
OR60_BL288	2015	167	Yes	NO	3.5	1.5	270.3	9.9	Western	12
OR61	2015	158	Yes	NO	3.5	1.7	245.4	10.9	Resident	14
OR63_BL242	2015	164	Yes	NO	NA	2.8	262.0	14.5	Resident	10
OR65_BL265	2015	166	Yes	NO	2.75	1.5	267.6	9.9	Southern	12

OR66_BL293	2015	161	Yes	NO	3.5	2.1	253.7	12.2	Resident	9
OR78	2015	172	Yes	NO	2.75	1.3	284.2	9.0	Western	6
OR79	2015	156	Yes	NO	3.75	2.8	239.8	15.0	Resident	11
OR80	2015	167	Yes	Yes	2.75	0.7	270.3	7.1	Resident	6
OR81	2015	169	Yes	NO	2.75	1.0	275.9	8.1	Eastern	11
OR82	2015	164	Yes	Yes	2.5	0.6	262.0	6.8	Resident	16
OR88	2015	175	Yes	NO	4.5	2.8	292.6	13.9	Resident	7
OR89	2015	158	Yes	NO	4.25	3.3	245.4	16.7	Southern	6
OR91	2015	157.5	NO	NA	2.5	0.4	244.0	6.1	Resident	15
OR92	2015	162	Yes	NO	3.25	2.0	256.5	11.8	Eastern	6
OR96	2015	162.5	Yes	NO	3	2.2	257.9	12.5	Resident	13
OR97	2015	159.5	Yes	NO	4.5	2.3	249.5	13.0	Resident	9
OR99	2015	164	Yes	NO	3.75	2.5	262.0	13.5	Resident	13
YL100	2015	162.5	Yes	NO	3.25	1.8	257.9	11.1	Resident	6
YL102	2015	160	Yes	NO	4	2.8	250.9	14.8	Resident	6
YL105	2015	160.5	Yes	Yes	2	0.0	252.3	3.9	Resident	7
YL107	2015	163	Yes	NO	4	2.3	259.2	12.8	Resident	10
YL108_BL236	2015	167.5	Yes	NO	4	1.7	271.7	10.5	Resident	11
YL109_OR35	2015	162	Yes	NO	3.25	2.0	256.5	11.8	Eastern	6
YL110_OR29	2015	167	Yes	NA	3.75	2.8	270.3	14.3	Resident	7
YL111_OR6	2015	155	Yes	NO	3.25	1.9	237.0	11.7	Eastern	10
YL112_OR38	2015	160.5	Yes	NO	3.75	2.8	252.3	14.7	Resident	7
YL113_OR31	2015	157	Yes	NO	3.75	1.3	242.6	9.4	Resident	6
YL114_BL274	2015	161.5	Yes	NO	2.75	1.1	255.1	8.6	Eastern	8
YL115_OR34	2015	NA	Yes	NO	4	2.3	NA	NA	Resident	15
YL116_OR83	2015	161	Yes	Yes	2.75	0.5	253.7	6.5	Resident	9
YL117_OR3	2015	156	Yes	NO	3.75	2.1	239.8	12.4	Resident	14
YL118_OR8	2015	161	Yes	NO	3.5	2.0	253.7	11.8	Eastern	10
YL119_BL245	2015	156	Yes	NO	2.75	1.2	239.8	9.1	Resident	14
YL120_BL290	2015	169	Yes	NO	4.5	2.8	275.9	14.2	Resident	9

YL121_BL250	2015	156.5	Yes	NO	2.75	0.7	241.2	7.3	Resident	10
YL122_BL244	2015	149	Yes	NO	2.5	0.4	220.4	6.2	Eastern	16
YL123_OR7	2015	164	Yes	NO	3.5	1.3	262.0	9.2	Eastern	12
YL124	2015	168	Yes	NO	3.75	2.0	273.1	11.5	Resident	10
YL125_BL286	2015	160.5	Yes	NO	3.25	1.0	252.3	8.3	Resident	20
YL126_OR20	2015	159.5	Yes	NO	3.75	2.1	249.5	12.3	Eastern	6
YL127	2015	153.5	NO	NO	2.75	0.8	232.9	7.7	Eastern	2
YL128_BL261	2015	159	NO	Yes	2	0.0	248.1	3.9	Eastern	11
YL129_OR11	2015	164	Yes	NO	4.75	2.9	262.0	14.9	Western	9
YL130_OR9	2015	162	Yes	NO	2.75	0.0	256.5	7.4	Eastern	12
YL131_OR32	2015	164	Yes	NO	3	1.4	262.0	9.6	Western	7
YL132_OR2	2015	170	Yes	NO	3.75	2.3	278.7	12.5	Resident	13
YL133_OR87	2015	173	Yes	NO	4.75	2.3	287.0	12.4	Resident	6
YL134_BL262	2015	NA	Yes	NO	4	3.1	NA	NA	Eastern	10
YL135_BL222	2015	172	Yes	NO	4	2.3	284.2	12.4	NA	11
YL136_BL284	2015	NA	Yes	NO	NA	NA	NA	NA	Eastern	9
YL137_BE13	2015	143.5	NO	NO	4	0.7	205.1	7.5	Resident	2
YL138_BL295	2015	171	Yes	NA	4	2.3	281.5	12.4	Eastern	9
YL139_BL220	2015	168	Yes	NO	3	1.7	273.1	10.5	Eastern	15
YL140_BL257	2015	166	Yes	NO	3.75	1.6	267.6	10.2	Eastern	11
OR100	2016	169	Yes	NO	4.25	2.8	275.9	14.2	Resident	7
OR52_OR28	2016	160	NO	Yes	2.5	0.7	250.9	7.2	Eastern	8
OR54_BL260	2016	155	Yes	NO	4.5	3.4	237.0	17.3	Resident	10
OR56_BL251	2016	159	Yes	Yes	2	0.0	248.1	3.9	Western	12
OR60_BL288	2016	165	Yes	NO	3.75	1.9	264.8	11.3	Western	13
OR61	2016	168	Yes	NO	3.75	1.2	273.1	8.8	Resident	15
OR65_BL265	2016	161	Yes	Yes	2.25	0.0	253.7	5.0	Western	13
OR66_BL293	2016	167	Yes	NO	3.5	0.7	270.3	7.1	Resident	10
OR78	2016	162	Yes	NO	3.25	1.0	256.5	8.2	Western	7
OR81	2016	166	Yes	NO	3.5	1.7	267.6	10.6	Eastern	12

OR89	2016	160	Yes	NO	4.5	3.4	250.9	16.9	Western	7
OR97	2016	163	Yes	NO	4.25	2.3	259.2	12.8	Resident	10
OR99	2016	156	Yes	NO	4.25	2.4	239.8	13.5	Resident	14
YL100	2016	169	Yes	Yes	3.25	0.8	275.9	7.4	Resident	7
YL107	2016	163	Yes	NO	4	2.7	259.2	14.2	Resident	11
YL112_OR38	2016	165	Yes	NO	5	3.5	264.8	16.9	Resident	8
YL114_BL274	2016	160	Yes	NO	3.5	1.1	250.9	8.6	Eastern	9
YL115_OR34	2016	169	Yes	NO	3.75	2.7	275.9	13.9	Resident	16
YL118_OR8	2016	168	Yes	NO	2.75	0.8	273.1	7.4	Eastern	11
YL120_BL290	2016	180	Yes	NO	4.25	2.6	306.5	13.0	Resident	10
YL124	2016	159	Yes	NO	4	2.1	248.1	12.3	Resident	11
YL133_OR87	2016	168	Yes	NO	4.25	2.9	273.1	14.6	Resident	7
YL134_BL262	2016	169	Yes	Yes	2.75	0.0	275.9	7.4	Eastern	11
YL137_BE13	2016	161	Yes	NO	3.5	1.1	253.7	8.6	Resident	3
YL151_YL87	2016	177	Yes	NO	3.5	2.3	298.1	12.2	Resident	16
YL152_YL63	2016	166	Yes	NO	3.75	1.7	267.6	10.6	Resident	18
YL153	2016	164	Yes	NO	4.25	3.6	262.0	17.3	Southern	10
YL154	2016	155	Yes	NO	3	0.7	237.0	7.3	Eastern	9
YL155_OR16	2016	165	Yes	NO	3.5	1.1	264.8	8.5	Eastern	NA
YL156	2016	158	Yes	NO	4	2.3	245.4	13.1	Resident	4
YL157_OR37	2016	159	Yes	NO	2.75	0.9	248.1	7.9	Resident	16
YL158_OR21	2016	154	Yes	Yes	2	0.4	234.2	6.2	Eastern	16
YL159	2016	162	Yes	NO	3.75	1.3	256.5	9.3	Eastern	4
YL160_OR12	2016	161	NO	Yes	1.5	0.0	253.7	1.5	Resident	21
YL161	2016	156	Yes	NO	4.25	2.6	239.8	14.3	Resident	4
YL162_BC13	2016	155	Yes	NO	4.25	3.1	237.0	16.2	Resident	3
YL163	2016	163	Yes	NO	3.75	1.2	259.2	8.9	Resident	7
YL164_BL255	2016	159	Yes	Yes	3.5	1.0	248.1	8.3	Resident	11
YL165_OR17	2016	158	Yes	Yes	2.75	0.6	245.4	6.9	Western	8
YL166	2016	159	Yes	NO	3.25	1.6	248.1	10.5	Eastern	6

YL167_OR10	2016	176	Yes	NO	2	0.0	295.3	3.9	Western	13
YL168	2016	168	Yes	NO	4	2.6	273.1	13.6	Southern	8
YL169	2016	166	Yes	NO	3.75	1.9	267.6	11.3	Resident	17
YL170	2016	155	Yes	NO	4	2.5	237.0	14.0	Eastern	4
YL171	2016	155	Yes	NO	4	2.3	237.0	13.2	Eastern	3
YL172	2016	169	Yes	NO	4	1.5	275.9	9.8	Eastern	NA

Table B.3. Elk calf birth sites determined by location of VITs and/or neonatal calf in the Ya Ha Tinda elk population, Alberta, Canada 2013 – 2016.

Adult Female ID	**Year**	**Mig. Status**	**Date VIT Retrieved**	**General Birth Site**	**Birth Site Easting**	**Birth Site Northing**	**Calf Cap-tured?**	**Calf ID**	**Survive to Recruit?**	**Notes**
GR127	2013	Resident	NA	YHT	NA	NA	Y	BN13	Y	
OR100	2013	Resident	NA	YHT	599080	5733475	Y	BR13	Y	
OR41	2013	Resident	25-Oct-13	BNP	587697	5722393	N			
OR77	2013	Resident	5-May-13	North of YHT	602473	5737241	Y	BH13	N	
OR78	2013	Western	27-Sep-13	BNP	562904	5712358	N			
OR79	2013	Resident	25-May-13	YHT	603552	5732450	Y	BC13	Y	
OR80	2013	Resident	3-Jun-13	YHT	597853	5735585	Y	BJ13	N	
OR81	2013	Eastern	29-Jun-13	East of YHT	619082	5723446	N			
OR82	2013	Resident	1-Jun-13	BNP/YHT	591802	5728800	N			
OR84	2013	Resident	27-May-13	North of YHT	601172	5738472	Y	BS13	N	
OR85	2013	Resident	2-Jun-13	North of YHT	592930	5740667	N			
OR86	2013	NA	NA	NA	NA	NA	NA			Elk mortality
OR88	2013	Resident	9-Jun-13	YHT	598669	5735027	Y	BT13	N	
OR89	2013	Resident	29-Sep-13	BNP	583227	5716632	N			
OR90	2013	Resident	1-Jun-13	North of YHT	593765	5741419	N			
OR91	2013	Resident	19-May-13	YHT	601815	5731854	Y	BE13	Y	
OR92	2013	Eastern	19-Jun-13	East of YHT	617092	5722446	N			
OR93	2013	Resident	28-May-13	North of YHT	600297	5737401	N			
OR94	2013	Eastern	26-May-13	East of YHT	617866	5723815	Y	BD13	Y	
OR95	2013	Southern	Not found	NA	NA	NA	NA			Elk mortality
OR96	2013	Resident	30-May-13	YHT	601222	5733283	Y	BG13	N	
Untagged	2013	Resident	NA	YHT	UNK	UNK	Y	BB13	N	
YL111_OR6	2013	Eastern	NA	East of YHT	616454	5720289	Y	BA13	N	
YL116_OR83	2013	Resident	28-May-13	YHT	600699	5734631	Y	BL13	N	
YL117_OR3	2013	Resident	NA	YHT	NA	NA	Y	BF13	UNK	
YL120_BL290	2013	Resident	NA	North of YHT	NA	NA	Y	OR43	N	
YL133_OR87	2013	Resident	27-May-13	YHT	598696	5732592	Y	BI13	N	
BL268	2014	Eastern	22-Jun-14	East of YHT	620593	5722395	Y	UN06	N	
OR100	2014	Resident	18-May-14	YHT	599555	5734202	N			
OR23	2014	Eastern	10-Jul-14	East of YHT	619628	5719993	N			
OR24	2014	Resident	28-May-14	BNP	583957	5724309	N			
OR39	2014	Eastern	23-May-14	East of YHT	621468	5723849	N			

OR40	2014	Resident	23-Jul-14	BNP	580797	5719396	N			
OR55_OR15	2014	Western	Not found	BNP	NA	NA	N			
OR59_BL259	2014	Eastern	30-May-14	East of YHT	619816	5721498	Y	BQ14	N	
OR60_BL288	2014	Resident	14-Jul-14	BNP	593180	5728801	N			
OR77	2014	Resident	4-Jun-14	North of YHT	602353	5737468	Y	YX14	Y	
OR78	2014	Western	8-Jul-14	BNP	545350	5720688	N			
OR79	2014	Resident	26-May-14	YHT	597540	5735192	N			
OR80	2014	Resident	NA	YHT	NA	NA	Y	BK14	Y	
OR84	2014	NA	NA	NA	NA	NA	NA			Elk mortality
OR85	2014	Resident	31-May-14	North of YHT	592749	5740895	Y	YZ14	N	
OR91	2014	Resident	27-May-14	YHT	599963	5733421	Y	C114	Y	
OR96	2014	Resident	7-Jun-14	YHT	599477	5732269	Y	RD14	N	
OR97	2014	Resident	6-Jun-14	YHT	600458	5734492	Y	YT14	N	
OR98	2014	Resident	3-Jun-14	YHT	601034	5734566	Y	RG14	N	
UNK	2014	Resident	NA	YHT	NA	NA	Y	YP14	N	
Untagged	2014	Resident	NA	YHT	NA	NA	Y	YF14	N	
Untagged	2014	Resident	NA	YHT	NA	NA	Y	YB14	N	
Untagged	2014	NA	NA	BNP	NA	NA	Y	KK14	UNK	Failed/dropped tag
YL100	2014	Resident	26-May-14	YHT	598789	5734447	Y	RA14	N	
YL101	2014	Resident	28-May-14	YHT	598101	5732139	Y	YA14	N	
YL102	2014	Resident	31-May-14	YHT	601142	5732678	N	UN07	N	Predated at birth site
YL103_GR183	2014	Eastern	1-Jun-14	East of YHT	NA	NA	Y	RF14	UNK	Failed/dropped tag
YL104	2014	Western	2-Jul-14	BNP	546986	5715368	N			
YL105	2014	Resident	4-Jun-14	North of YHT	602689	5735655	Y	YW14	Y	
YL106	2014	Western	2-Jul-14	BNP	547101	5716749	N			
YL107	2014	Resident	2-Jul-14	YHT	597409	5735286	N			
YL108_BL236	2014	Resident	13-Jul-14	YHT	600224	5729921	N			
YL109_OR35	2014	Eastern	22-May-14	East of YHT	620538	5722037	Y	B114	Y	
YL110_OR29	2014	Resident	31-May-14	YHT	597264	5733157	Y	A114	N	
YL111_OR6	2014	Eastern	18-May-14	East of YHT	619017	5724287	Y	YM14	N	
YL113_OR31	2014	Resident	25-May-14	YHT	599996	5732661	Y	YY14	N	
YL114_BL274	2014	Eastern	28-May-14	East of YHT	620939	5722004	Y	YJ14	Y	
YL115_OR34	2014	Resident	29-Jun-14	North of YHT	600652	5738437	N			
YL119_BL245	2014	Resident	30-May-14	North of YHT	603012	5736867	Y	RH14	UNK	Failed/dropped tag
YL123_OR7	2014	Eastern	27-May-14	East of YHT	617249	5722451	Y	YU14	N	
YL128_BL261	2014	Eastern	24-May-14	East of YHT	620630	5724025	Y	YO14	Y	

YL131_OR32	2014	Resident	Not found	BNP	NA	NA	N			
YL132_OR2	2014	Resident	3-Jun-14	YHT	602798	5731827	Y	YV14	N	
YL136_BL284	2014	Eastern	25-May-14	East of YHT	618828	5723730	Y	YC14	N	
YL138_BL295	2014	Resident	10-Aug-14	North of YHT	598771	5742856	N			
YL140_BL257	2014	Eastern	24-May-14	East of YHT	618050	5722276	Y	YD14	N	
YL151_YL87	2014	Resident	15-May-14	North of YHT	601765	5736704	Y	YE14	Y	
YL155_OR16	2014	Eastern	23-May-14	East of YHT	616547	5724831	Y	YK14	Y	
YL157_OR37	2014	Resident	31-May-14	YHT	598071	5733393	Y	YQ14	N	
YL165_OR17	2014	Western	Not found	BNP	NA	NA	N			
YL167_OR10	2014	Resident	17-May-14	YHT	601302	5734191	N	UN08	N	Stillborn
YL25	2014	Western	NA	NA	NA	NA	NA			Elk mortality
GR513	2015	Western	28-Aug-15	BNP	596363	5689234	N			
OR51_OR19	2015	Western	1-Aug-15	BNP	591263	5713091	N			
OR52_OR28	2015	Eastern	24-May-15	East of YHT	623437	5723834	Y	YR15	N	
OR53_OR22	2015	Eastern	NA	NA	NA	NA	NA			Elk mortality
OR54_BL260	2015	Resident	31-May-15	North of YHT	595791	5737283	Y	RW15	N	
OR55_OR15	2015	Western	Not found	BNP	NA	NA	N			
OR56_BL251	2015	Southern	28-Aug-15	BNP	589784	5695183	N			
OR57_OR27	2015	Eastern	31-May-15	East of YHT	615057	5725962	Y	RB15	N	
OR58_BL292	2015	Resident	27-May-15	YHT	599541	5733969	Y	YO15	Y	
OR59_BL259	2015	Eastern	29-May-15	East of YHT	619764	5721646	Y	RI15	N	
OR60_BL288	2015	Western	20-Jul-15	BNP	581546	5732200	N			
OR61	2015	Resident	8-Jun-15	YHT	598297	5733791	Y	SS15	N	
OR63_BL242	2015	Resident	14-Mar-15	YHT	597809	5734572	NA	UN09	N	Aborted
OR65_BL265	2015	Southern	10-Jul-15	South of YHT	598563	5726977	N			Site est. by flight
OR66_BL293	2015	Resident	1-Jun-15	North of YHT	596411	5738460	N			
OR78	2015	Western	13-Sep-15	BNP	542737	5721577	N			
OR79	2015	Resident	1-Jun-15	YHT	600802	5734856	Y	YI15	Y	
OR80	2015	Resident	19-Jun-15	North of YHT	599082	5736350	Y	RY15	Y	
OR81	2015	Eastern	2-Jun-15	East of YHT	617288	5723271	Y	E115	N	
OR82	2015	Resident	28-May-15	YHT	601090	5734803	N			
OR88	2015	Resident	2-Jun-15	YHT	602889	5734950	N			
OR89	2015	Southern	Not found	BNP	NA	NA	N			
OR92	2015	Eastern	2-Jul-15	East of YHT	617069	5722437	Y	RU15	N	
OR96	2015	Resident	10-Jun-15	YHT	603517	5732358	Y	RP15	Y	
OR97	2015	Resident	24-Jun-15	North of YHT	598253	5739418	N			

OR99	2015	Resident	7-Jun-15	YHT	598879	5734094	Y	RC15	N	
Untagged	2015	Resident	NA	YHT	NA	NA	Y	RJ15	N	
Untagged	2015	Resident	NA	YHT	NA	NA	Y	RN15	N	
YL100	2015	Resident	30-May-15	YHT	601737	5733728	Y	RL15	UNK	Failed/dropped tag
YL102	2015	Resident	5-Jun-15	YHT	591173	5730230	Y	I115	N	
YL105	2015	Resident	10-Jun-15	North of YHT	603469	5735541	Y	K115	N	
YL107	2015	Resident	24-May-15	North of YHT	599999	5736695	Y	YS15	N	
YL108_BL236	2015	Resident	25-May-15	YHT	598427	5732898	Y	BM15	N	
YL109_OR35	2015	Eastern	13-May-15	East of YHT	620577	5724783	N			
YL110_OR29	2015	Resident	6-Jul-15	YHT	596379	5730522	Y	RM15	N	
YL111_OR6	2015	Eastern	NA	NA	NA	NA	NA			Elk mortality
YL112_OR38	2015	Resident	2-Jun-15	YHT	601744	5732683	Y	RV15	N	
YL113_OR31	2015	Resident	28-May-15	North of YHT	601000	5734427	Y	RR15	N	
YL114_BL274	2015	Eastern	22-May-15	East of YHT	624188	5725458	Y	YG15	Y	
YL115_OR34	2015	NA	Not found	NA	NA	NA	N			
YL116_OR83	2015	Resident	2-Jun-15	North of YHT	599620	5737380	N			
YL117_OR3	2015	Resident	6-Aug-15	South of YHT	596728	5727335	N			
YL118_OR8	2015	Eastern	29-May-15	East of YHT	613139	5723702	Y	BP15	N	
YL119_BL245	2015	Resident	4-Jun-15	North of YHT	603197	5737032	Y	RT15	Y	
YL120_BL290	2015	Resident	1-Jun-15	North of YHT	594422	5737896	Y	RQ15	N	
YL121_BL250	2015	Resident	10-Jul-15	North of YHT	598815	5739758	N			Site est. by flight
YL122_BL244	2015	Eastern	8-Jun-15	East of YHT	617110	5720984	Y	RX15	N	
YL123_OR7	2015	Eastern	NA	NA	NA	NA	NA			Elk mortality
YL124	2015	Resident	27-May-15	YHT	597806	5734578	Y	RE15	N	
YL125_BL286	2015	Resident	14-Jun-15	North of YHT	601156	5740447	N			
YL126_OR20	2015	Eastern	19-May-15	East of YHT	608884	5726471	Y	YN15	Y	
YL129_OR11	2015	Western	31-May-15	BNP	545091	5721105	N			
YL130_OR9	2015	Eastern	27-Jun-15	East of YHT	608258	5725560	Y	G115	Y	
YL131_OR32	2015	Western	18-Jul-15	BNP	573503	5711951	N			
YL132_OR2	2015	Resident	7-Jun-15	YHT	600891	5732040	Y	RO15	N	
YL133_OR87	2015	Resident	28-May-15	YHT	600022	5734776	Y	RK15	N	
YL134_BL262	2015	Eastern	12-Jul-15	East of YHT	613906	5716968	N			
YL135_BL222	2015	NA	NA	NA	NA	NA	NA			Elk mortality
YL136_BL284	2015	Eastern	28-May-15	East of YHT	616081	5720801	Y	L115	N	
YL138_BL295	2015	Eastern	24-Aug-15	North of YHT	598451	5743519	N			
YL139_BL220	2015	Eastern	23-Jun-15	East of YHT	617308	5722831	N			

YL140_BL257	2015	Eastern	28-May-15	East of YHT	617973	5724442	Y	YH15	N	
OR100	2016	Resident	25-May-16	YHT	594371	5729964	Y	YQ16	N	
OR54_BL260	2016	Resident	28-May-16	North of YHT	596640	5737765	Y	YP16	N	
OR56_BL251	2016	Western	5-Sep-16	BNP	590400	5694100	N			
OR60_BL288	2016	Western	Not found	BNP	NA	NA	N			
OR61	2016	Resident	20-Jun-16	YHT	601716	5732651	Y	YG16	N	
OR65_BL265	2016	Western	19-Jun-16	BNP	587415	5725399	N			
OR66_BL293	2016	Resident	18-May-16	YHT	599199	5733716	N			
OR78	2016	Western	6-Sep-16	BNP	545110	5721152	N			
OR81	2016	Eastern	30-May-16	East of YHT	620726	5723252	Y	YB16	Y	
OR89	2016	Western	Not found	BNP	NA	NA	N			
OR97	2016	Resident	24-May-16	YHT	602550	5733967	N	UN11	N	Predated at birth site
OR99	2016	Resident	19-May-16	YHT	597877	5730843	Y	YN16	N	
Untagged	2016	Resident	NA	YHT	NA	NA	Y	RJ16	N	
Untagged	2016	Resident	NA	YHT	NA	NA	Y	YD16	Y	
YL100	2016	Resident	30-May-16	YHT	592761	5731152	Y	RM16	N	
YL101	2016	Resident	NA	YHT	NA	NA	Y	RK16	N	
YL107	2016	Resident	Not found	NA	NA	NA	N			
YL112_OR38	2016	NA	8-Sep-16	North of YHT	586918	5747659	N			
YL114_BL274	2016	Eastern	26-May-16	East of YHT	627350	5723875	Y	YT16	N	
YL115_OR34	2016	Resident	9-Jun-16	YHT	595693	5730078	Y	YS16	N	
YL118_OR8	2016	Eastern	7-Jul-16	East of YHT	610410	5725560	Y	RO16	N	
YL120_BL290	2016	Resident	30-May-16	YHT	593777	5732975	Y	YK16	N	
YL124	2016	Resident	21-May-16	YHT	597981	5731900	Y	YE16	N	
YL131_OR32	2016	Resident	NA	North of YHT	NA	NA	Y	RV16	N	
YL133_OR87	2016	Resident	23-May-16	YHT	597704	5733051	Y	YF16	N	
YL134_BL262	2016	Eastern	2-Jun-16	East of YHT	614326	5717207	Y	D116	N	
YL137_BE13	2016	Resident	2-Jun-16	YHT	601867	5731945	Y	RN16	N	
YL151_YL87	2016	Resident	24-May-16	North of YHT	601188	5736340	Y	YR16	N	
YL152_YL63	2016	Resident	30-May-16	South of YHT	601152	5728522	Y	YH16	N	
YL153	2016	Southern	14-Jun-16	South of YHT	597295	5733199	N			
YL154	2016	Eastern	5-Jun-16	East of YHT	607939	5725739	N			
YL155_OR16	2016	Eastern	23-May-16	East of YHT	615744	5722719	N	UN12	N	Predated at birth site
YL156	2016	Resident	15-Jun-16	YHT	600226	5731542	Y	YA16	N	
YL157_OR37	2016	Resident	22-Jun-16	South of YHT	597699	5726573	N			
YL158_OR21	2016	Eastern	Not found	NA	NA	NA	N			

YL159	2016	Eastern	2-Jun-16	East of YHT	608268	5726653	Y	RC16	N	
YL161	2016	Resident	22-May-16	YHT	604427	5732448	Y	YU16	N	
YL162_BC13	2016	Resident	24-May-16	YHT	602856	5730841	N			
YL163	2016	Resident	29-May-16	YHT	602740	5733258	Y	YO16	Y	
YL164_BL255	2016	Resident	2-Aug-16	YHT	596689	5727231	N			
YL165_OR17	2016	Western	NA	NA	NA	NA	NA			Elk mortality
YL166	2016	Eastern	26-May-16	East of YHT	616090	5718017	N			
YL167_OR10	2016	Western	Not found	BNP	NA	NA	N			
YL168	2016	Southern	30-Jul-16	South of YHT	604300	5726158	N			
YL169	2016	Resident	25-May-16	North of YHT	599497	5738969	Y	YC16	N	
YL170	2016	Eastern	28-May-16	East of YHT	609226	5724972	N			
YL171	2016	Eastern	29-May-16	East of YHT	622368	5723434	Y	YM16	UNK	
YL172	2016	Eastern	22-May-16	East of YHT	615466	5721069	Y	YJ16	Y	

Table B.4. Elk calves captured in the Ya Ha Tinda elk population, Alberta, Canada, 2013 - 2016.

Calf ID	Freq.	Adult Female ID	Birth Site Easting	Birth Site Northing	Capture Date	Cap. Site Easting	Cap. Site Northing	Est. Age at Capture(hr)
A114	149.222	YL110_OR29	597264	5733157	31-May-14	597264	5733157	1.5
B114	149.744	YL109_OR35	620538	5722037	22-May-14	620546	5722024	7.0
BA13	152.582	YL111_OR6	616454	5720289	27-May-13	616439	5720282	14.5
BB13	152.253	Untagged	UNK	UNK	6-Jun-13	601092	5733345	59.4
BC13	152.623	OR79	603552	5732450	25-May-13	603555	5732530	27.5
BD13	152.273	OR94	617866	5723815	26-May-13	618113	5723798	24.0
BE13	152.612	OR91	601815	5731854	19-May-13	601815	5731854	2.5
BF13	152.293	YL117_OR3	UNK	UNK	23-May-13	600982	5733228	33.5
BG13	152.313	OR96	601222	5733283	30-May-13	601022	5733283	3.5
BH13	152.401	OR77	602473	5737241	5-Jun-13	602446	5737197	3.5
BI13	152.161	YL133_OR87	598696	5732592	27-May-13	598696	5732592	5.0
BJ13	152.563	OR80	597853	5735585	3-Jun-13	597845	5735609	15.0
BK14	152.142	OR80	UNK	UNK	6-Jun-14	600405	5733089	74.1
BL13	152.201	YL116_OR83	600699	5734631	28-May-13	600699	5734631	2.0
BM15	149.262	YL108_BL236	598427	5732898	20-May-15	598439	5732908	3.5
BN13	152.523	GR127	UNK	UNK	26-May-13	599602	5732534	14.9
BP15	148.922	YL118_OR8	613139	5723702	25-May-15	613153	5723700	3.0
BQ14	152.253	OR59_BL259	619816	5721498	30-May-14	619816	5721498	0.5
BR13	152.462	OR100	599080	5733475	27-May-13	599080	5733475	1.0
BS13	152.644	OR84	601172	5738472	27-May-13	600315	5733172	192.0
BT13	152.353	OR88	598669	5735027	9-Jun-13	598891	5735090	22.5
C114	149.242	OR91	599963	5733421	27-May-14	599358	5733588	7.0
D116	150.711	YL134_BL262	614326	5717207	2-Jun-16	614326	5717207	4.0
E115	152.503	OR81	617288	5723271	2-Jun-15	617288	5723271	2.5
G115	149.682	YL130_OR9	608258	5725560	27-Jun-15	608273	5725530	3.5
I115	152.313	YL102	591173	5730230	6-Jun-15	591172	5730029	20.0

K115	149.262	YL105	603469	5735541	10-Jun-15	603498	5735554	4.5
KK14	148.209	Untagged	UNK	UNK	25-May-14	580417	5724241	7.3
L115	149.763	YL136_BL284	616081	5720801	28-May-15	616081	5720801	4.5
OR43	NA	YL120_BL290	UNK	UNK	30-May-13	600441	5734634	30.4
RA14	152.644	YL100	598789	5734447	26-May-14	598755	5734344	1.0
RB15	148.582	OR57_OR27	615057	5725962	31-May-15	615057	5725962	1.0
RC15	149.513	OR99	598879	5734094	1-Jun-15	598879	5734094	2.5
RC16	150.522	YL159	608268	5726653	2-Jun-16	608268	5726653	2.0
RD14	152.313	OR96	599477	5732269	7-Jun-14	599477	5732269	2.5
RE15	152.042	YL124	597806	5734578	27-May-15	592340	5730343	11.0
RF14	152.094	YL103_GR183	UNK	UNK	1-Jun-14	613482	5723797	15.0
RG14	152.503	OR98	601034	5734566	3-Jun-14	601118	5734664	1.5
RH14	148.110	YL119_BL245	603012	5736867	30-May-14	603088	5736839	24.0
RI15	149.252	OR59_BL259	619764	5721646	29-May-15	619812	5721790	19.0
RJ15	148.872	Untagged	UNK	UNK	30-May-15	600355	5733217	12.5
RJ16	148.872	Untagged	UNK	UNK	31-May-16	600024	5733171	9.9
RK15	148.938	YL133_OR87	600022	5734776	28-May-15	599988	5734661	16.0
RK16	149.406	YL101	UNK	UNK	16-Jun-16	601492	5733250	31.0
RL15	148.522	YL100	601737	5733728	30-May-15	601737	5733728	3.8
RM15	148.368	YL110_OR29	596379	5730522	4-Jun-15	596580	5730406	10.5
RM16	148.427	YL100	592761	5731152	30-May-16	592761	5731152	4.0
RN15	148.703	Untagged	UNK	UNK	29-May-15	601341	5734650	12.6
RN16	148.852	YL137_BE13	601867	5731945	1-Jun-16	601867	5731945	3.0
RO15	148.341	YL132_OR2	600891	5732040	28-May-15	600891	5732040	3.0
RO16	148.180	YL118_OR8	610410	5725560	4-Jun-16	610426	5725589	3.5
RP15	148.982	OR96	603517	5732358	10-Jun-15	603370	5732259	5.0
RQ15	148.743	YL120_BL290	594422	5737896	1-Jun-15	594483	5737823	11.0
RR15	149.461	YL113_OR31	601000	5734427	30-May-15	600451	5736755	104.5
RT15	149.482	YL119_BL245	603197	5737032	4-Jun-15	603294	5737226	18.5
RU15	149.602	OR92	617069	5722437	3-Jun-15	617055	5722417	2.0

RV15	152.400	YL112_OR38	601744	5732683	2-Jun-15	601744	5732683	3.0
RV16	148.938	YL131_OR32	UNK	UNK	5-Jun-16	597869	5741746	39.0
RW15	152.200	OR54_BL260	595791	5737283	31-May-15	595203	5737216	20.5
RX15	149.622	YL122_BL244	617110	5720984	8-Jun-15	617110	5720984	2.5
RY15	152.582	OR80	599082	5736350	19-Jun-15	599088	5736412	5.5
SS15	149.853	OR61	598297	5733791	9-Jun-15	598307	5733661	30.5
UN01	NA	UNK	UNK	UNK	18-Jun-13	619861	5724902	9.5
UN02	NA	UNK	UNK	UNK	9-Jun-13	601424	5732514	68.1
UN03	NA	UNK	UNK	UNK	8-Oct-13	599092	5733038	9.5
UN04	NA	UNK	UNK	UNK	27-May-14	600357	5734012	17.6
UN05	NA	UNK	UNK	UNK	16-Jun-14	617882	5724815	76.1
UN06	NA	BL268	620593	5722395	22-Jun-14	620593	5722395	12.0
UN07	NA	YL102	601142	5732678	31-May-14	601142	5732678	6.0
UN08	NA	YL167_OR10	601302	5734191	17-May-14	601302	5734191	0.0
UN09	NA	OR63_BL242	597809	5734572	14-Mar-15	597809	5734572	0.0
UN10	NA	UNK	UNK	UNK	12-May-15	620513	5724795	9.5
UN11	NA	OR97	602550	5733967	20-May-16	602550	5733967	2.0
UN12	NA	YL155_OR16	615744	5722719	23-May-16	615744	5722719	1.0
UN13	NA	OR98	UNK	UNK	3-Jun-16	600441	5732685	9.5
UN14	NA	UNK	UNK	UNK	15-Oct-16	599872	5732712	9.5
YA14	149.482	YL101	598101	5732139	28-May-14	598101	5732139	2.0
YA16	149.893	YL156	600226	5731542	12-Jun-16	600207	5731527	4.0
YB14	149.682	Untagged	UNK	UNK	25-May-14	600280	5732319	24.0
YB16	149.922	OR81	620726	5723252	26-May-16	620731	5723257	1.5
YC14	149.512	YL136_BL284	618828	5723730	26-May-14	619240	5723659	29.5
YC16	149.781	YL169	599497	5738969	25-May-16	599400	5738841	35.0
YD14	149.622	YL140_BL257	618050	5722276	24-May-14	618038	5722300	6.0
YD16	148.633	Untagged	UNK	UNK	5-Jun-16	597809	5734569	15.2
YE14	149.311	YL151_YL87	601765	5736704	15-May-14	601775	5736639	6.0
YE16	148.427	YL124	597981	5731900	21-May-16	597977	5731924	5.0

YF14	149.374	Untagged	UNK	UNK	23-May-14	599668	5733152	10.4
YF16	148.723	YL133_OR87	597704	5733051	24-May-16	597732	5733348	20.0
YG15	149.092	YL114_BL274	624188	5725458	22-May-15	624349	5725574	25.0
YG16	149.781	OR61	601716	5732651	22-Jun-16	601387	5732504	45.5
YH15	149.422	YL140_BL257	617973	5724442	21-May-15	618033	5724432	12.0
YH16	148.452	YL152_YL63	601152	5728522	31-May-16	600841	5728311	24.5
YI15	149.012	OR79	600802	5734856	1-Jun-15	600243	5734939	22.0
YJ14	149.444	YL114_BL274	620939	5722004	28-May-14	620939	5722004	6.0
YJ16	149.863	YL172	615466	5721069	22-May-16	615466	5721069	3.0
YK14	149.552	YL155_OR16	616547	5724831	23-May-14	616547	5724831	6.0
YK16	148.551	YL120_BL290	593777	5732975	30-May-16	593750	5733009	8.0
YM14	149.703	YL111_OR6	619017	5724287	18-May-14	618990	5724328	5.0
YM16	148.490	YL171	622368	5723434	28-May-16	622438	5723421	17.5
YN15	149.111	YL126_OR20	608884	5726471	19-May-15	608840	5726644	23.5
YN16	148.852	OR99	597877	5730843	21-May-16	598564	5730592	51.5
YO14	152.183	BL261	620630	5724025	24-May-14	620630	5724025	0.5
YO15	149.333	OR58_BL292	599541	5733969	27-May-15	599541	5733969	5.5
YO16	148.082	YL163	602740	5733258	29-May-16	602805	5733217	6.5
YP14	149.151	UNK	UNK	UNK	1-Jun-14	600130	5734267	10.0
YP16	150.973	OR54_BL260	596640	5737765	28-May-16	597122	5737775	46.5
YQ14	149.834	OR37	598071	5733393	31-May-14	598259	5733000	2.0
YQ16	150.892	OR100	594371	5729964	25-May-16	594273	5729817	13.0
YR15	149.132	OR52_OR28	623437	5723834	24-May-14	623485	5723842	11.0
YR16	150.522	YL151_YL87	601188	5736340	24-May-16	601191	5736153	3.5
YS15	149.853	YL107	599999	5736695	22-May-15	599999	5736695	4.0
YS16	150.912	YL115_OR34	595693	5730078	10-Jun-16	595631	5730072	21.0
YT14	149.602	OR97	600458	5734492	6-Jun-14	600458	5734492	1.5
YT16	150.163	YL114_BL274	627350	5723875	26-May-16	627357	5723890	27.5
YU14	149.811	YL123_OR7	617249	5722451	27-May-14	617249	5722451	2.0
YU16	150.711	YL161	604427	5732448	22-May-16	604427	5732448	25.5

YV14	149.531	YL132_OR2	602798	5731827	3-Jun-14	602790	5731845	2.5
YW14	149.352	YL105	602689	5735655	4-Jun-14	602689	5735655	3.5
YX14	149.052	OR77	602353	5737468	4-Jun-14	602344	5737471	5.0
YY14	149.641	YL113_OR31	599996	5732661	25-May-14	599984	5732665	4.0
YZ14	149.461	OR85	592749	5740895	31-May-14	592749	5740895	1.0

Table B.5. Details of detected elk calf mortalities in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. Listed is the source of evidence used to determine cause-specific mortality based on field sign, identification of predator species by hair or through DNA swab of predator saliva.

Calf ID	**Date Found**	**Easting**	**Northing**	**Est. Time Since Death (days)**	**Est. Age (days)**	**Cause of Death**	**Source of Evidence**
A114	19-Jun-14	595693	5732244	0	19	Unknown	Field
B114	NA	NA	NA	NA	360	Unknown	Field
BA13	7-Jun-13	615832	5722111	3	8	Bear	Field
BB13	8-Jun-13	601113	5734678	0	8	Cougar	Field
BD13	NA	NA	NA	NA	376	Failed/Dropped Tag	Field
BF13	NA	NA	NA	NA	82	Unknown	Field
BG13	31-May-13	601048	5733560	0	1	Bear	Field
BH13	14-Jun-13	602163	5737099	0	9	Bear	Field
BI13	13-Jun-13	598642	5734924	0	17	Unk. pred. - likely bear	Field
BJ13	23-Jun-13	602176	5732400	0	21	Unk. pred. - likely wolf	Field
BK14	18-May-16	601032	5733215	0	715	Failed/Dropped Tag	Field
BL13	7-Jun-13	600919	5734059	0	10	Bacterial septicaemia	Field
BM15	2-Jun-15	598522	5732877	6	7	Bear	Field
BN13	27-Jun-14	NA	NA	NA	368	Failed/Dropped Tag	Field
BP15	NA	NA	NA	NA	308	Failed/Dropped Tag	Field
BQ14	4-Jun-14	619814	5723735	0	5	Bear	Field
BR13	21-Sep-14	601064	5734866	NA	482	Failed/Dropped Tag	Field
BS13	28-May-13	600617	5732737	0	9	Unk. pred. - likely bear	Field
BT13	27-Jun-13	596019	5732609	4	15	Wolf	Field
D116	10-Sep-16	615428	5724937	3	98	Cougar	Field
E115	17-Aug-15	621299	5722510	5	71	Unknown Predator	Field
I115	12-Jun-15	590783	5730863	1	6	Canid	Field
K115	19-Jun-15	603004	5733748	1	8	Bear	Field
KK14	13-Jun-14	587642	5725932	NA	18	Failed/Dropped Tag	Field
L115	28-Jan-16	600430	5732979	75	170	Unknown	Field
OR43	NA	NA	NA	NA	3	Unknown	Field

RA14	29-May-14	599618	5732305	0	3	Wolf	Field
RB15	27-Mar-16	602015	5732907	58	243	Wolf	Hair
RC15	16-Jun-15	596077	5734390	2	13	Cougar	Field
RC16	27-Jun-16	610207	5724492	0	25	Cougar	Field
RD14	14-Jun-14	601977	5731869	0	7	Bear	Field
RE15	12-Oct-15	601485	5734811	115	23	Unknown	Field
RF14	20-Sep-14	613070	5726523	1	111	Failed/Dropped Tag	Field
RG14	7-Jun-14	600639	5734550	0	4	Unk. pred. - likely cougar	Field
RH14	20-Jun-14	597728	5733899	NA	22	Failed/Dropped Tag	Field
RI15	NA	NA	NA	NA	209	Unknown	Field
RJ15	7-Jun-15	600048	5732944	4	5	Bear	Field
RJ16	11-Jun-16	601979	5731739	0	11	Drowned	Field
RK15	5-Jun-15	600902	5734075	0	9	Bear	Field
RK16	9-Sep-16	601130	5734472	10	76	Wolf	Field
RL15	15-Feb-16	600047	5734203	7	254	Unknown	Field
RM15	11-Jul-15	599738	5736655	4	33	Cougar	Hair
RM16	21-Jun-16	592472	5730247	1	21	Bear	Field
RN15	2-Jul-15	598868	5735994	0	34	Cougar	Field
RN16	3-Jun-16	601919	5731902	1	1	Bear	Field
RO15	28-Jun-15	605109	5729692	17	14	Wolf	Field
RO16	13-Jun-16	610305	5725821	1	8	Bear	Field
RQ15	15-Jun-15	594558	5738073	1	13	Bear	Field
RR15	15-Oct-15	603295	5735017	33	109	Unknown	Field
RU15	30-Mar-16	599782	5733518	54	247	Unknown	Field
RV15	7-Jun-15	599828	5733127	2	3	Bear	Field
RV16	23-Jun-16	595607	5741417	2	18	Wolf	Field
RW15	15-Jun-15	594558	5738073	0	16	Bear	Field
RX15	27-Mar-16	600311	5734656	51	242	Unknown	Field
SS15	12-Jun-15	599153	5734048	1	3	Bear	Field
UN01	18-Jun-13	619861	5724902	0	NA	Unknown Predator	Field

UN02	9-Jun-13	601424	5732514	0	NA	Unknown	Field
UN03	8-Oct-13	599092	5733038	0	NA	Human-caused	Field
UN04	27-May-14	600357	5734012	0	NA	Cougar	Field
UN05	16-Jun-14	617882	5724815	0	NA	Cougar	Field
UN06 (BL268)	22-Jun-14	620638	5722423	0	1	Cougar	DNA
UN07 (YL102)	31-May-14	601142	5732678	0	1	Bear	Field
UN08 (OR10)	17-May-14	601302	5734191	0	0	Stillborn	Field
UN09 (OR63)	14-Mar-15	597809	5734572	1	0	Aborted	Field
UN10 (YL109)	12-May-15	620513	5724795	0	NA	Bear	Field
UN11 (OR97)	20-May-16	602550	5733967	0	0	Bear	Field
UN12 (YL155)	23-May-16	615744	5722719	0	1	Bear	Field
UN13 (OR98)	3-Jun-16	600441	5732685	0	NA	Cougar	DNA
UN14	15-Oct-16	599872	5732712	3	NA	Wolf	Field
YA14	3-Jun-14	598034	5733441	0	6	Bear	Field
YA16	22-Sep-16	601044	5735590	80	21	Unknown	Field
YB14	29-May-14	600410	5732669	0	4	Wolf	Field
YC14	16-Jun-14	617882	5724815	0	22	Cougar	Field
YC16	1-Jun-16	600818	5736506	2	6	Bear	DNA
YD14	1-Jun-14	618816	5723156	0	8	Bear	Field
YE14	6/6/2015	NA	NA	NA	388	Failed/Dropped Tag	Field
YE16	23-May-16	598127	5731867	0	2	Cougar	DNA
YF14	25-May-14	598734	5732917	0	2	Cougar	Field
YF16	NA	NA	NA	NA	85	Unknown	Field
YG16	27-Sep-16	595767	5730672	29	68	Unknown	Field
YH15	2-Jul-15	612118	5724454	0	42	Bear	Field
YH16	13-Jun-16	600489	5727185	2	12	Bear	Field
YJ14	16-May-16	NA	NA	NA	719	Failed/Dropped Tag	Field
YK14	11-May-16	620396	5723614	96	623	Human-caused	Field
YK16	13-Jun-16	593816	5734709	0	14	Bear	Field
YM14	11-Sep-14	610673	5723918	4	112	Bear	Field

YM16	19-Feb-17	600884	5733449	9	259	Unknown	Field
YN16	25-May-16	599017	5731484	1	5	Bear	Field
YO14	7-Jul-16	NA	NA	NA	775	Failed/Dropped Tag	Field
YP14	13-Jun-14	600020	5732205	0	12	Bear	Field
YP16	4-Jun-16	597291	5739419	1	8	Cougar	DNA
YQ14	5-Jun-14	595688	5732024	2	3	Unknown	Field
YQ16	21-Jul-16	602622	5730805	6	51	Unknown Predator	Field
YR15	29-Mar-15	602336	5733657	53	257	Unknown	Field
YR16	28-May-16	600661	5733927	2	2	Canid	Field
YS15	24-May-15	599967	5736564	0	2	Bear	Field
YS16	9-Jul-16	595025	5730611	0	30	Unk. pred. - likely canid	Field
YT14	10-Jun-14	601028	5734146	0	4	Bear	Field
YT16	1-Jun-16	626890	5723556	0	7	Bear	Field
YU16	26-May-16	604436	5732566	2	3	Bear	Field
YV14	NA	NA	NA	NA	22	Unknown	Field
YW14	12-Jun-16	612989	5723660	26	728	Human-caused	Field
YX14	24-May-16	NA	NA	NA	720	Failed/Dropped Tag	Field
YY14	30-May-14	599954	5732551	0	5	Wolf	Field
YZ14	11-Jun-14	595791	5736825	0	11	Bear	Field

Table B.6. Parameter estimates for the effect of intrinsic covariates on risk of mortality in elk calves in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. We considered nutritional status of the adult female (% Ingesta-Free Body Fat, IFBF), age of adult female, calf sex, calf mass and chest girth at birth, and year of birth in models of daily survival through 3, 10, 26, and 90 days of life. Bold font indicates the 90% credible intervals did not overlap 0.

	3-day Survival		10-day Survival		26-day Survival		90-day Survival	
Model	*β*	DIC	*β*	DIC	*β*	DIC	*β*	DIC
% IFBF	0.29	125.21	0.28	278.97	**0.30**	454.00	**0.34**	560.04
Female Age	-0.10	126.29	0.01	281.03	-0.11	457.47	-0.04	565.24
Calf Sex	**-1.13**	122.88	**-0.74**	277.30	-0.33	456.35	-0.17	566.23
Calf Mass	0.14	125.97	-0.13	280.39	-0.14	457.02	-0.15	564.91
Calf Girth	**-1.02**	122.63	0.01	281.10	-0.05	457.83	0.03	566.77
Year	0.00	124.59	0.00	279.98	0.00	457.07	0.00	566.09
Null		124.68		279.15		455.87		565.44

Table B.7. Parameter estimates for the effect of intrinsic covariates on risk of mortality through 3 days of life in elk calves in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. Bold font indicates the 90% credible intervals did not overlap 0.

	3-day Survival			
Model	Sex	Girth	Sex × Girth	DIC
Sex + Girth	**-1.13**	**-0.99**		121.14
Sex + Girth + (Sex × Girth)	**-1.18**	-0.99	-0.04	122.11
Girth	**-1.02**			122.63
Sex	**-1.13**			122.88

Table B.8. Parameter estimates for the effect of adult female body condition and migratory status on risk of mortality through 26 and 90 days of life in elk calves in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. Bold font indicates the 90% credible intervals did not overlap 0.

	26-day Survival				90-day Survival			
	Mig	IFBF	Mig × IFBF	DIC	Mig	IFBF	Mig × IFBF	DIC
Mig + IFBF + (Mig × IFBF)	**1.54**	-1.05	0.62	443.25	**1.59**	-1.17	**0.70**	546.09
Mig + IFBF	**1.22**	0.11		443.99	**1.25**	0.14		549.31
IFBF		0.30		454.00				

Table B.9. Parameter estimate for the effect of date of birth on risk of mortality through 26 days of life in elk calves in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016.

	26-day	
Model	Date	DIC
Null		455.87
Date	0.05	457.78

Table B.10. Parameter estimates for the effect of available forage biomass (g/m^2) and NDVI on risk of mortality through 26 days of life in elk calves in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. The 2 spatial scales at which covariates were measured included the area used during the calf-rearing phase (26 days), and the annual summer range, defined by the adult female's migratory tactic. Bold font indicates the 90% credible intervals did not overlap 0.

	Hiding Area		Summer Range	
Model	β	DIC	β	DIC
Biomass	**0.33**	452.67	**0.66**	441.81
NDVI	-0.03	457.92	0.02	455.99
Null		455.87		455.87

Table B.11. Parameter estimates for the effect of predation risk or refuge from predation (i.e., human infrastructure) at 2 spatial scales on daily risk of mortality through 26 days of life in elk calves of the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. The 2 spatial scales at which covariates were measured included the area used during the calf-rearing phase (26 days), and the annual summer range, defined by the adult female's migratory tactic (eastern migrant as reference group, Mig). Bold font indicates 90% credible intervals did not overlap zero.

	Hiding Area						Summer Range					
Model	Mig	Human	Wolf	Bear	Cougar	DIC	Mig	Human	Wolf	Bear	Cougar	DIC
Mig + Human	**1.32**	0.00				444.65	-0.46	**-0.98**				441.17
Human		**-0.31**				453.81		**-0.75**				441.16
Wolf			**0.37**			448.56			**0.64**			442.39
Mig + Cougar	**1.34**				0.08	445.03	**1.52**				0.22	443.13
Mig + Wolf	**1.07**		0.18			443.21	0.51		0.42			443.51
Mig + Bear	**1.33**			-0.02		444.42	**1.37**			-0.04		444.51
Wolf + Bear + Cougar			**0.40**	0.24	-0.14	448.25			**0.62**	0.08	0.08	446.57
Bear				**0.32**		452.71				**0.37**		451.96
Null						455.87						455.87
Cougar					0.03	457.95					-0.07	457.96

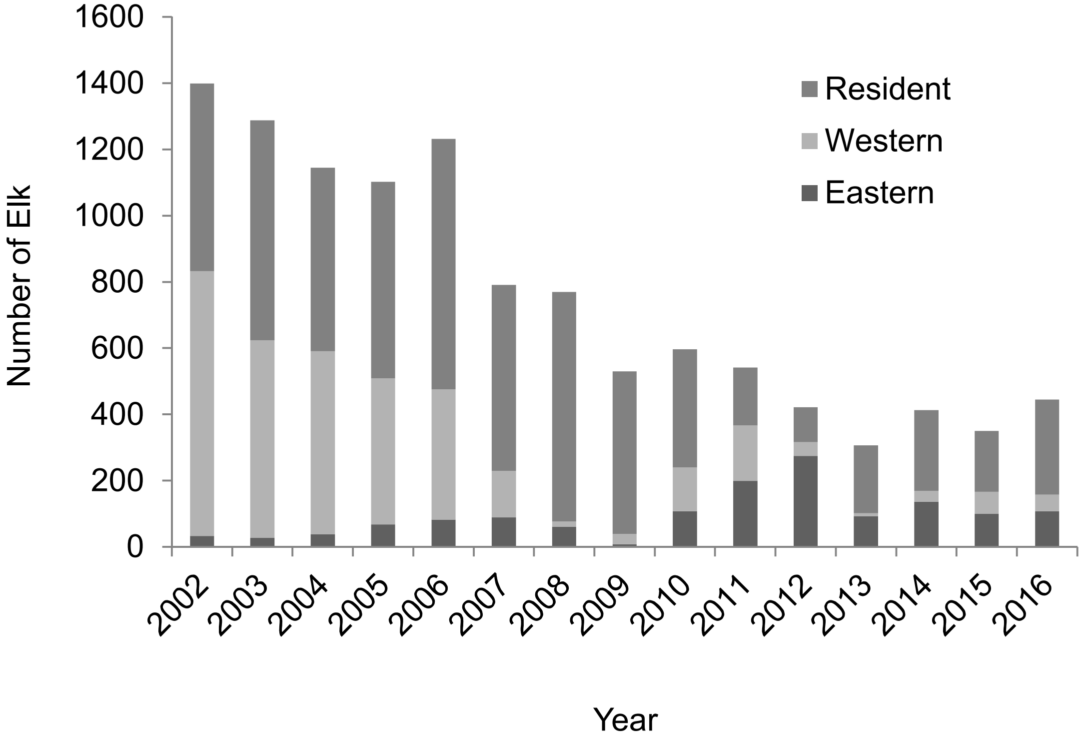


Figure B.1. Total population and the estimated number of elk within each migratory tactic in the Ya Ha Tinda elk population, Alberta, Canada, 2002 – 2016.

Figure B.2. Kill evaluation and categorization chart used to evaluate elk calf mortalities in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. Chart was adapted from Barber-Meyer (2006) and Hatter (1988).

KILL EVALUATION AND CATEGORIZATION CHART Frequency___________ Date____________ Mortality #__________

Some criteria implicate more than one predator, so mortalities should be evaluated using all of the available evidence. Circle anything that applies and attach this sheet to the mortality / necropsy data form.

Characteristics of wounds or death site:

A.	Sign of a struggle: scuff or track evidence of chase, blood on ground from pursuit, broken branches, blood on trees	predator involved
B.	Subcutaneous hemorrhaging on hide / carcass	predator involved
C.	Calf observed within 48 hrs prior and appeared in good physical condition	predator involved
D.	Carcass retrieved within 12-24 hrs of death and partially / totally consumed	predator involved
E.	Blood around wounds; aspirated blood in trachea, mouth, nose.	predator involved
F.	Blood not around wounds; no evidence of bruises/hemorrhaging	predator scavenged
G.	Carcass lacks signs of being bitten	predator not involved

Carcass disposition

A.	Laying in open, no concealment attempt, remains not scattered	unknown predator
B.	Laying in open, no concealment attempt, remains scattered	unknown predator
C.	Carcass partially or completely covered by litter	cougar or bear
D.	Partially or completely buried	*Lynx* sp., cougar, bear, wolf, or coyote

Carcass consumption

A.	All consumed	unknown predator
B.	All consumed except hide and larger leg bones left intact	unknown predator
C.	Hide inverted	bear

If a predator has scavenged the carcass or is determined to have been involved, circle anything that applies:

Predator	**Possible**	**Probable**	**Positive**
Bear (*Ursus* spp.)	* Old bear tracks discernible by shape or depressions in soil only. * Carcass may be in open (generally grizzly bear). * Carcass may be in forest cover (generally black bear). Note: bears may possibly scavenge	* Recent bear tracks that show track details. * Moist / wet bear scats near or on outer perimeter of bed sites. * Bed sites near carcass. * Bed sites contain bear hair. * Grizzly or black bear hair on trees or brush.	* Bear sign only. * Broken neck-rift on occipital condyle / cervical vertebrae. * Extensive bruising on back of hind quarters, ribs and / or shoulders. * Bite marks to spine behind shoulders. * Grizzly upper canine width 48-69 mm,

	carcasses (winter kill, cougar and wolf kills) during spring, so make sure no other carnivore sign is evident at the site. Bear predation may generally be directed at calves where most of the carcass is fully consumed	* Carcass buried with large amount of material including large sticks and dirt; area has churned (rototilled) appearance indicative of grizzly bear. * Carcass in tree cover or draw, but not cached, indicative of black bear. * Hide on carcass is inverted over head and down legs (“banana peel”) * Viscera consumed as food.	lower canine width 35-66 mm. * Black bear upper canine width 43-60 mm, lower canine width 37-55 mm. *Radiocollared bear located in the vicinity.
Wolf (*Canis lupus*)	* Old wolf tracks, discernible by shape and stride pattern only. * Carcass remains in open habitat with not much cover. * Feces in open and not covered; feces dry or chalky in appearance; or no feces present at all.	* Fresh wolf tracks discernible by detailed toe and pad arrangement. * Carcass remains scattered possibly >300 m from kill site. * No bed sites evident. * If bed sites, generally >2-4 oriented in spoke-wheel fashion around kill site; bed sites in open on grass or under canopy cover, but not necessarily at base of tree. * Bed sites contain wolf hair. * Radiocollared wolf at or near kill. * Moist, wet wolf feces	* Wolf sign only * Hemorrhage apparent on hide at back of metatarsus and femur areas. * If any hide or organs left to examine at throat: canine punctures to throat * Wolf upper canine width 40-53 mm, lower canine width 35-47 mm. * Radiocollared wolf located in the vicinity.
Coyote (*Canis latrans*)	* Old tracks. * Old scats	* Fresh tracks. * Remains scattered / moved some distance, especially downhill. * Fresh scats. * Remains buried with packed dirt. * Canine punctures to neck, throat, skull. * Extensive hemorrhaging of neck	* Coyote sign only. * Canine punctures 29-35 mm apart for upper canines and width 25-32 mm for lower canines. * Canine punctures 32-48 mm in diameter. * Radiocollared coyote located in vicinity
Cougar (*Puma concolor*)	* Old tracks. * Old scats, bed sites (check for hair). * Plucked/feathered hair * Breakage of large bones (i.e. skull, femurs)	* Fresh tracks. * Remains concealed near tree / low vegetation. * Remains covered / cached with light debris. * Scats, toilets, scrapes. * Rumen not consumed (covered / cached). * Chase, struggle, kill site evident. * Claw marks on shoulders, back, sides. * Canine punctures to neck, throat,	* Cougar sign only. * Canine punctures 45-50 mm apart for upper canines and width 30-40 mm for lower canines. * Canine punctures 64-79 mm in diameter. * Radiocollared cougar located in vicinity.

		skull. * Neck broken. * Extensive hemorrhaging of neck. * Drag marks to burial / cache site.	
***Lynx* spp. (*Lynx canadensis* or *Lynx rufus*)**	* Old tracks. * Old scats, bedsites (check for hair). * Plucked/feathered hair * Only small bones cracked / broken.	* Fresh tracks. * Remains concealed near tree / low vegetation. * Remains covered / cached with light debris. * Scats, toilets, scrapes. * Rumen not consumed (covered / cached). * Chase, struggle, kill site evident. * Claw marks on shoulders, back, sides. * Canine punctures to neck, throat, skull. * Neck broken. * Extensive hemorrhaging of neck. * Drag marks to burial / cache site.	* Lynx sign only. * Canine punctures 19-25 mm apart (bobcat). * Canine punctures 16-32 mm in diameter (bobcat)
Golden Eagle (*Aquila chrysaetos*)	* Old tracks. * Feces (“whitewash”). * Small downy feathers. * Carcass “hollowed out”. * Skin and large bones intact.	* Only upper portion of carcass fed upon. * Punctures in back near kidneys. * Backbone intact but devoid of ribs	* Eagle sign only. * Talon wounds on back, sides, neck. * Talon wounds 25-50 mm apart in a row or a shallow V. * Hallux wound 100-150 mm from toe wound.

This form was adapted from:

Barber-Meyer, S. M. 2006. Elk calf mortality following wolf restoration to Yellowstone National Park. Dissertation. University of Minnesota, Minneapolis, MN, USA.

Hatter, I. 1988. Effects of wolf predation on recruitment of black-tailed deer on northeastern Vancouver Island. Wildlife Branch, Ministry of Environment.

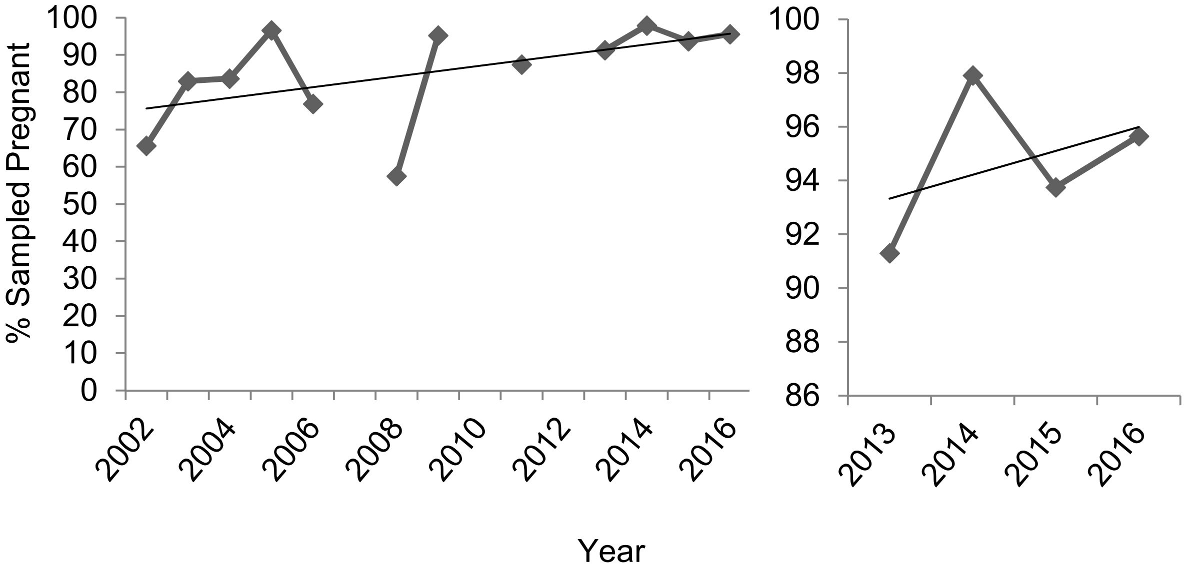


Figure B.3. In the left panel, pregnancy rates for the Ya Ha Tinda elk population, Alberta, Canada, in late winter (Feb – Mar) across all years 2002 – 2016, except 2007 and 2010. In the right panel, pregnancy rates during the years 2013 – 2016, determined by rectal palpation.

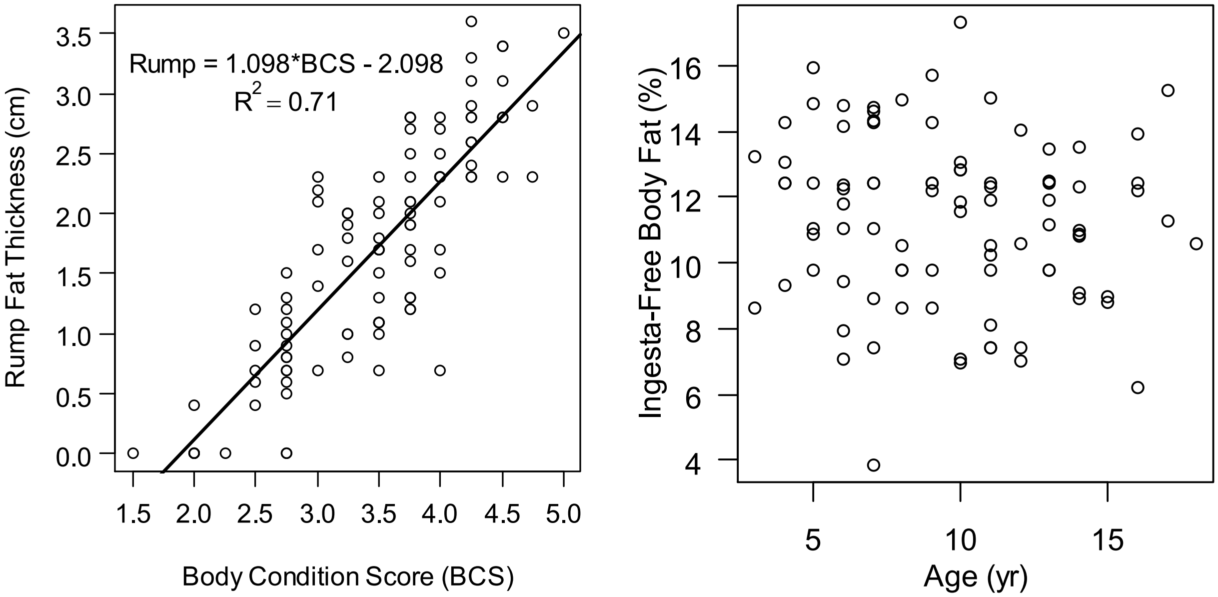


Figure B.4. In left panel, rump fat thickness (cm) regressed on body condition score (BCS) in adult females. In the right panel, Ingesta-Free Body Fat (IFBF, %) measured in late winter (Feb – Mar, 2014 – 2016) in relation to age (yr) of adult female elk in the Ya Ha Tinda elk population, Alberta, Canada.

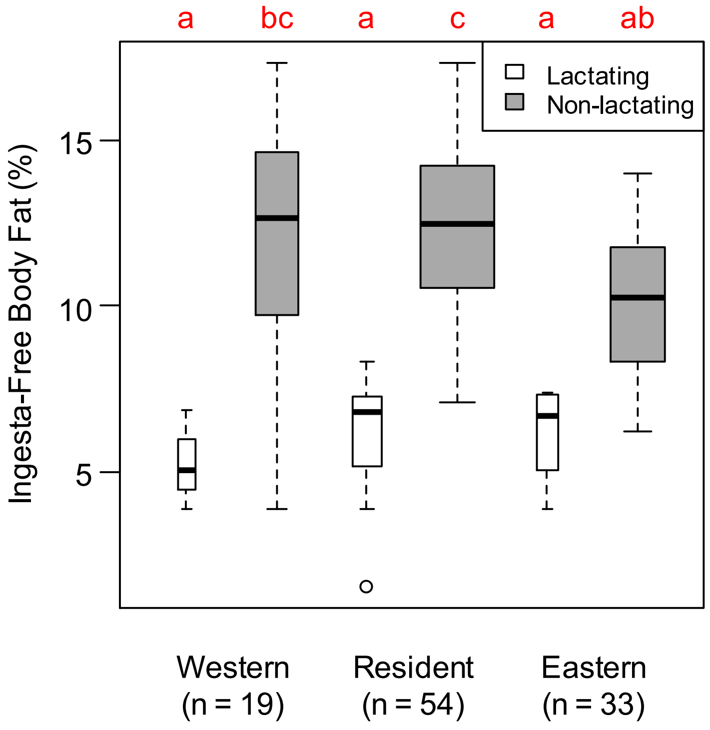


Figure B.5. Ingesta-Free Body Fat (%, IFBF) measured in late winter (Feb – Mar, 2014 – 2016) for adult female elk following 3 migratory tactics (eastern, resident, and western) in the Ya Ha Tinda elk population, Alberta, Canada.

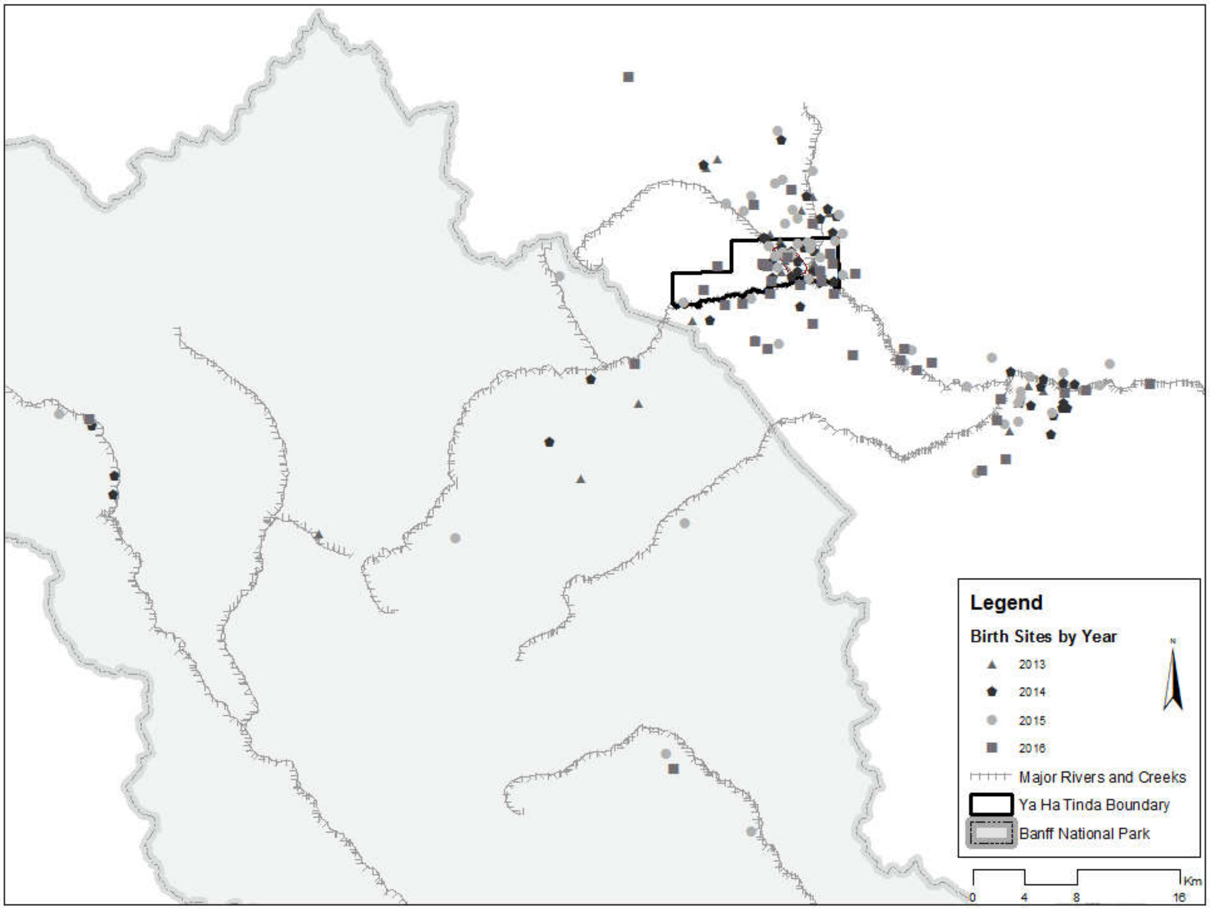


Figure B.6. Birth sites of elk calves located through use of vaginal implant transmitters (VITs) and/or neonatal elk calves in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. Based on known locations (*n* = 153), 12% of maternal elk gave birth in Banff National Park, 19% of elk gave birth to the north of the Ya Ha Tinda (YHT) ranch, mostly in the Bighorn Creek cut blocks and along Scalp Creek, 27% of elk gave birth to the east of YHT, 37% of elk gave birth in the vicinity of the ranch, and 4% gave birth to the south of the ranch.

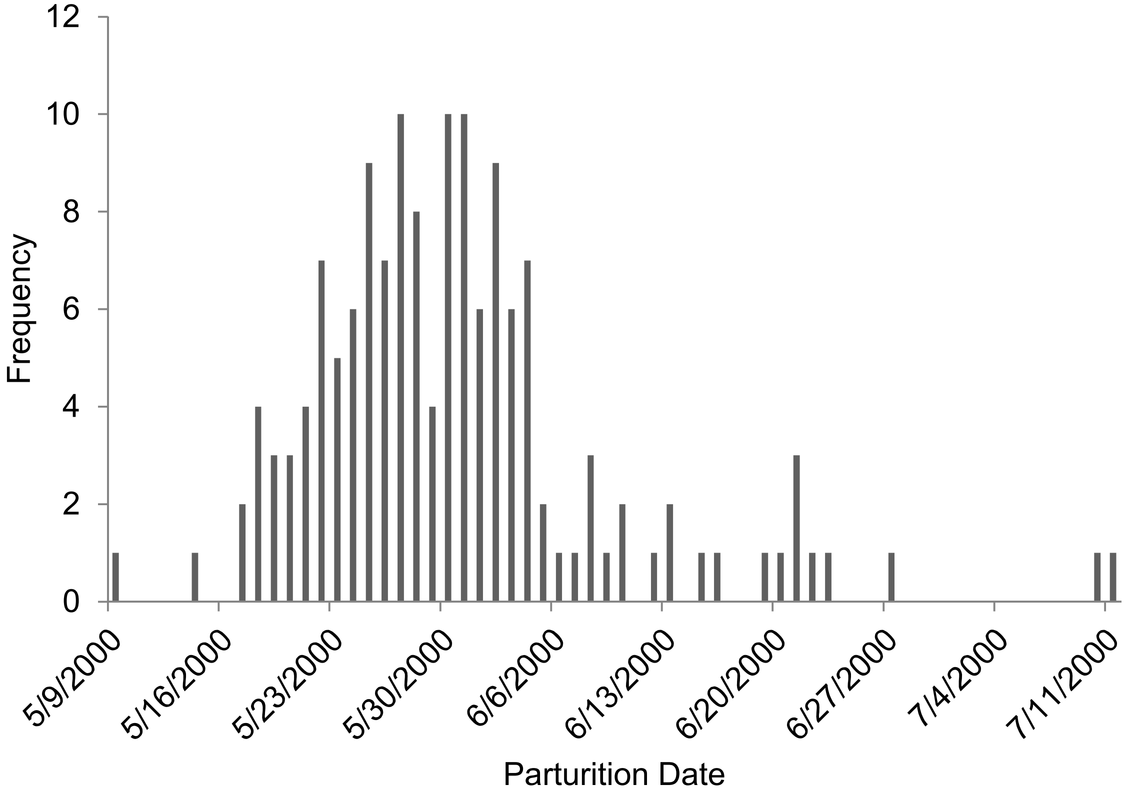


Figure B.7. Parturition dates (*n* = 147) determined through vaginal implant transmitters (VITs) or through age estimation of opportunistically caught calves in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. Known birth dates ranged from 9 May to 11 July.

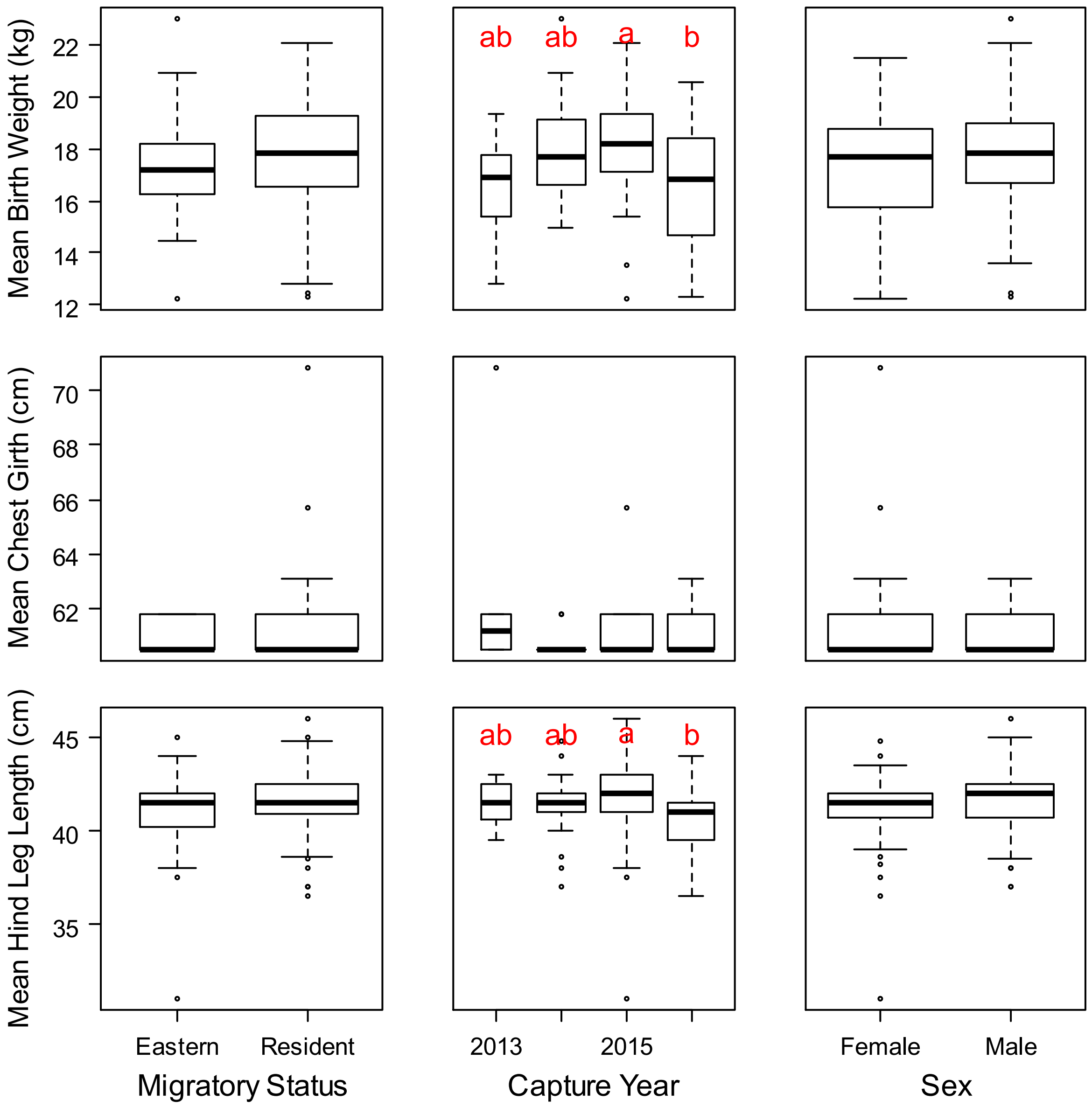


Figure B.8. Body measurements of calves (*n* = 94 used in Chapter 4 survival analysis) captured and marked in the years 2013 – 2016 for monitoring survival in the Ya Ha Tinda elk population, Alberta, Canada.

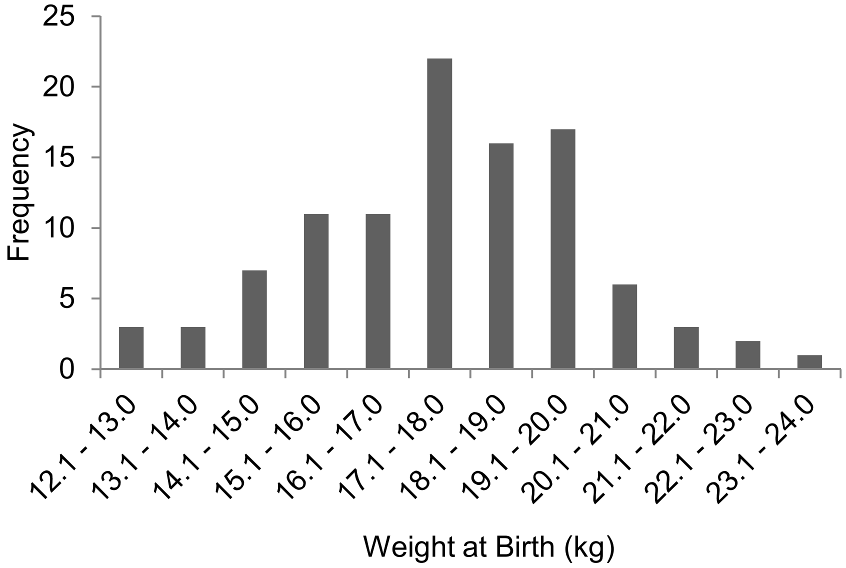


Figure B.9. Weights at birth (kg) for elk calves captured (*n* = 102) in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. We used the estimated daily growth rate of the calves to back-calculate weight at birth from weight at capture.

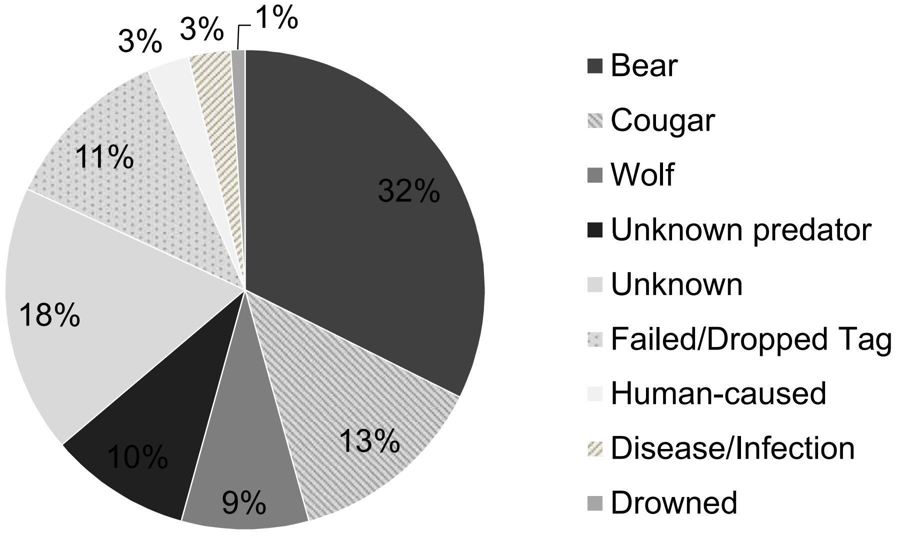


Figure B.10. Raw frequencies for causes of death of elk calves (*n* = 105) in the Ya Ha Tinda elk population, Alberta, Canada, 2013 - 2016. Note that the chart ignores differences in timing of the different causes of mortality (i.e., predation by bears tends to occur earlier in the neonatal period compared to that of other predators), and that the cumulative incidence functions reported in Chapter 4 are a more appropriate and accurate method for presenting percent mortality by cause.

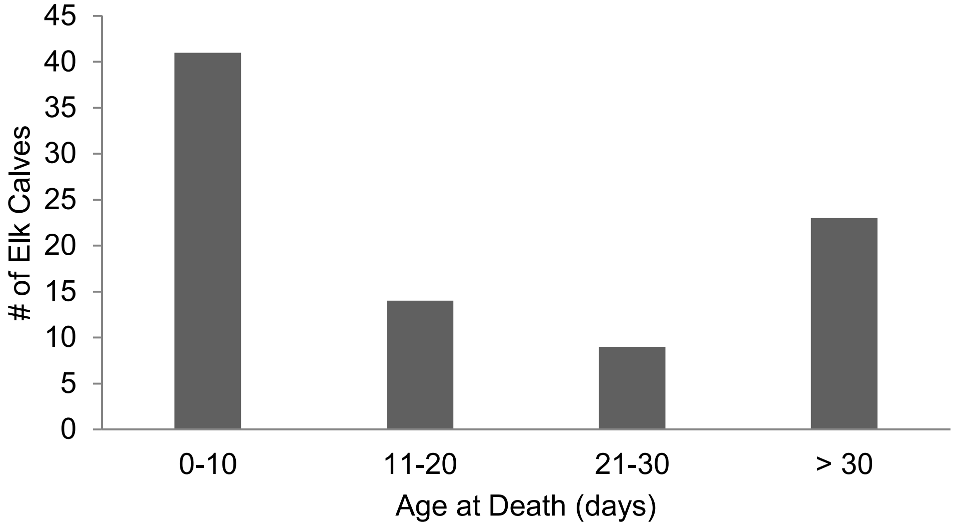


Figure B.11. Estimated age at death of elk calves (*n* = 105) in the Ya Ha Tinda elk population, Alberta, Canada, 2013 - 2016.

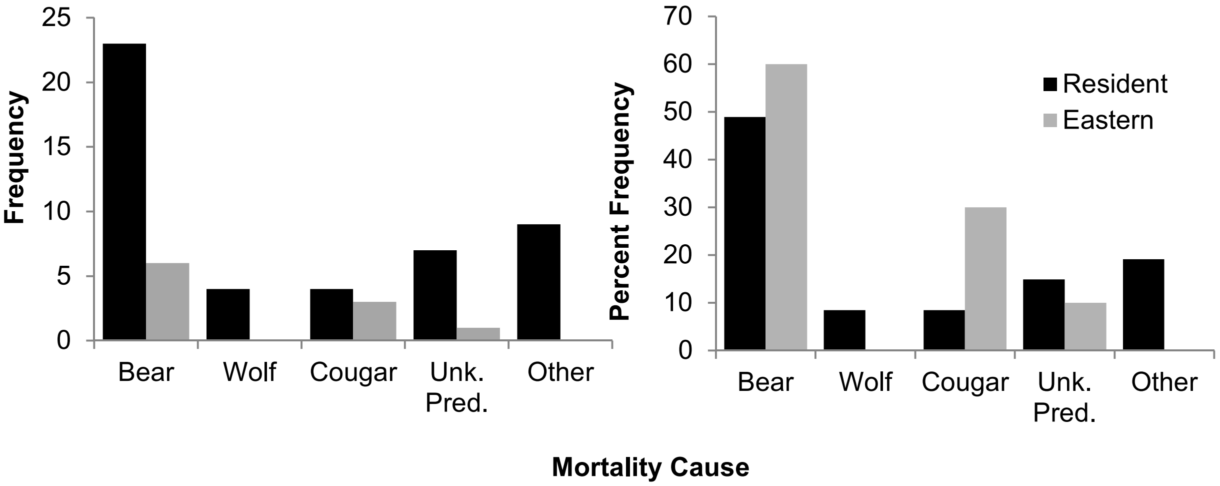


Figure B.12. In left panel, raw frequency, and in right panel, raw percent frequency, of mortality by cause in elk calves of elk following 2 migratory tactics (resident: *n* = 47, and eastern migrant: *n* = 10 used in Chapter 4 survival analysis) in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. Note that the cumulative incidence functions reported in Chapter 4 are a more appropriate and accurate method for presenting percent mortality by cause because of the timing of mortality by the different causes.

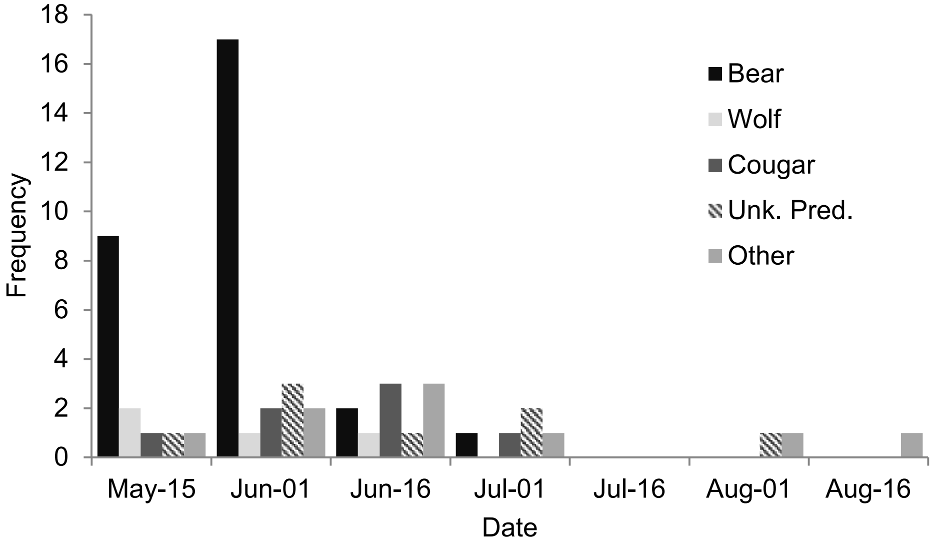


Figure B.13. Timing of mortality by cause in elk calves (*n* = 57 used in Chapter 4 survival analysis) in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016.

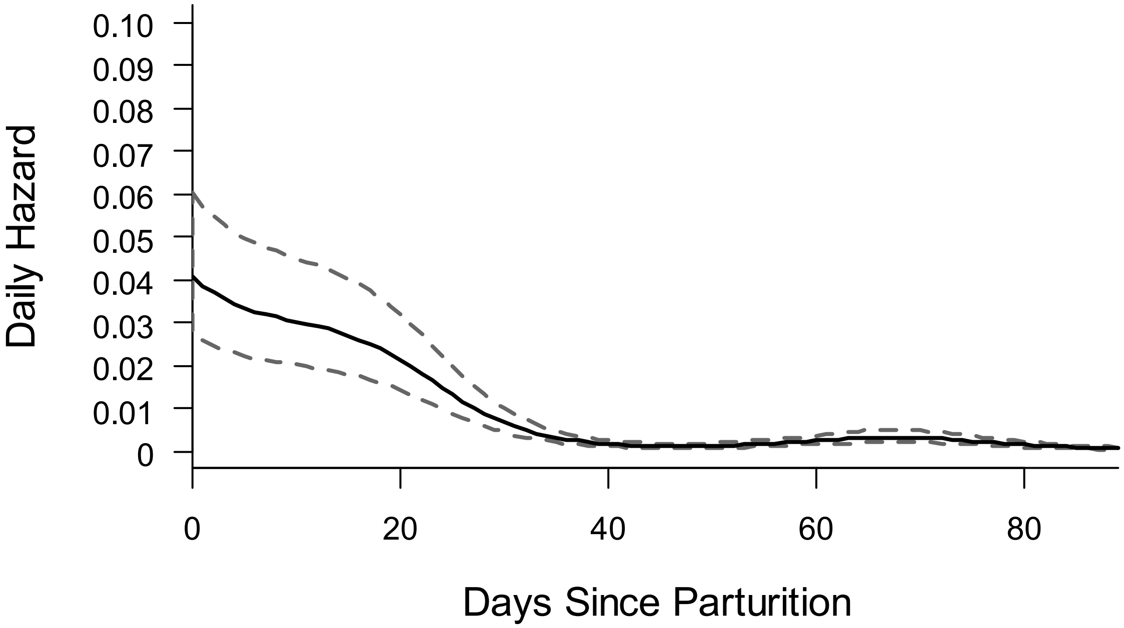


Figure B.14. Predicted daily hazard rates (solid line) of elk calves (*n* = 57 used in Chapter 4 survival analysis) in the Ya Ha Tinda population, Alberta, Canada, 2013 – 2016. Dashed lines represent the variation in hazard rate (based on the estimated sigma) and are the bounds of the 95% cumulative distribution. The overall cumulative hazard rate was 0.61.

APPENDIX C. R CODE FOR MODELING RISK OF MORTALITY

Design matrix Z for splines

```
numknots = 5                                                    # number of knots for spline
X = seq(0, 89)
knots = seq(from = 0, to = 89, length.out = numknots)
Z_K <- (abs(outer(X, knots, "-")))^3
OMEGA_all <- (abs(outer(knots, knots, "-")))^3
svd.OMEGA_all <- svd(OMEGA_all)
sqrt.OMEGA_all <- t(svd.OMEGA_all$v %*%
(t(svd.OMEGA_all$u)*sqrt(svd.OMEGA_all$d)))
Z <- t(solve(sqrt.OMEGA_all,t(Z_K)))
```

Null model without cause-specific mortality

```
model {

# Likelihood for mortality
for (t in 1:90) {                                               # t indexes time (e.g., day)
  spline[t] <- b[1]*Z[t,1] + b[2]*Z[t,2] + b[3]*Z[t,3] + b[4]*Z[t,4] + b[5]*Z[t,5]
  Err[t] ~ dnorm(0, inv.var_t)
}

for (i in 1:nAnimal) {
  for (t in enter[i]:exit[i]) {
     mu[i, t] <- spline[t] + Err[t]
     logit(p[i, t]) <- mu[i, t]
     death[i, t] ~ dbern(p[i, t])
}
}

# Priors
  # Prior distributions of the spline parameters
    for (s in 1:num.knots) {
      b[s] ~ dnorm(0, .346)  # use spline function
    }

  # Prior distributions for survival model parameters
          sigma_t ~ dunif(0, 10)
          inv.var_t <- 1/sigma_t^2
```

```
} # end model
```

Model with cause-specific mortality

```
model {

# Likelihood for cause-specific mortality
   for (t in 1:90) {
   for (k in 1:nState) {
     spline[t,k] <- b[1,k]*Z_C[t,1,k] + b[2,k]*Z_C[t,2,k] + b[3,k]*Z_C[t,3,k] + b[4,k]*Z_C[t,4,k] +
                              b[5,k]*Z_C[t,5,k]
     logit(p[t, k]) <- spline[t, k]
   }
   }

   for (i in 1:nAnimal) {
   for(t in enter[i]:exit[i] ){
       death[i,t,1:nState] ~ dmulti(p[t,1:nState],1)
   }
   }

# Priors
  # Prior distributions of the spline parameters
   for (s in 1:num.knots) {
   for (k in 1:nState) {
       b[s,k] ~ dnorm(0, .346)
   }
   }

} # end model
```

APPENDIX D. DETAILS OF RANDOM FOREST MODEL FOR PREDICTING DATES OF PARTURITION

OVERVIEW

Here we provide details of the Random Forest (RF) model used to predict dates of parturition for elk. Briefly, we used 60 known parturition events from 1 May to 15 July, 2013 – 2016, and the associated GPS data to build the model based on characteristics of elk movement.

METHODS

We followed the general approach of Hayes et al. (in prep.) and used a RF machine learning algorithm within program R (rfUtilities package; Evans et al. 2011, R Core Team 2017). Our approach in developing RF models followed Evans & Cushman (2009) and Murphy et al. (2010) by first identifying the most informative candidate variables among the movement statistics calculated for the 60 calving events (rf.modelSel function in the rfUtilities package). This process was bootstrapped 300 times to reduce reliance on the particular data used for covariate selection.

We used the Gini impurity index to quantify the importance of the variables in each model; the importance of a variable reflects the total decrease in node impurities (defined as how well the trees split the data) following a split on that variable, averaged over all trees in each RF (Liaw and Wiener 2002). We then averaged these values over the 1000 RF models to produce one value for each predictor variable. Importance of a combined set of variables (group) in a model was also calculated by weighting the importance of individual variables by the relative frequency of splits using that variable compared with the others in that group of variables, where a group of variables consisted of some of the descriptive statistics for each movement statistic and one time window (e.g., the mean, median, standard deviation, maximum, and total sum for step length and a time window of 216 hr comprised one set of variables).

We applied the model to 80 elk from 2002 – 2016 for which date of parturition was either known (n = 13) or unknown (n = 67).

Table D.1. Individuals in the Ya Ha Tinda elk population, Alberta, Canada, used for either model building or model prediction in a random forest analysis to identify date of parturition based on characteristics of movement data collected from 2002 - 2016. A subset of animals was used to examine selection of calving areas relative to selection for areas used in summer (Chapter 2).

Elk ID	Year	Known Preg.?	Date Known?	Date Pred.?	Birth Date	Loc. Known?	Easting	Northing	Mig. Tactic	Selection Analysis?	Comments
GR182	2002	Y	N	Y	6/6/2002	N	NA	NA	Resident	Y	
GP2	2003	Y	N	Y	5/28/2003	N	NA	NA	Western	Y	
YL15	2003	Y	N	Y	6/10/2003	N	NA	NA	Resident	Y	
YL25	2003	Y	N	Y	6/13/2003	N	NA	NA	Western	Y	
YL42	2003	Y	N	Y	6/6/2003	N	NA	NA	Western	Y	
YL5	2003	Y	N	Y	6/10/2003	N	NA	NA	Western	Y	Data removed first 2 wks of May
YL57	2003	N	N	Y	6/22/2003	N	NA	NA	Western	Y	
GR104	2004	Y	N	Y	6/13/2004	N	NA	NA	Western	Y	
YL58	2004	Y	N	Y	6/3/2004	N	NA	NA	Resident	Y	
YL59	2004	Y	N	Y	5/27/2004	N	NA	NA	Western	Y	
YL64	2004	Y	N	Y	6/3/2004	N	NA	NA	Resident	Y	
YL74	2004	Y	N	Y	6/5/2004	N	NA	NA	Western	Y	
YL78	2004	Y	N	Y	6/1/2004	N	NA	NA	Western	Y	
YL80	2004	Y	N	Y	6/25/2004	N	NA	NA	Resident	Y	
YL91	2004	Y	N	Y	5/28/2004	N	NA	NA	Resident	Y	
YL92	2004	Y	N	Y	5/19/2004	N	NA	NA	Western	Y	
YL93	2004	Y	N	Y	6/6/2004	N	NA	NA	Western	Y	
YL94	2004	Y	N	Y	5/30/2004	N	NA	NA	Resident	Y	
YL96	2004	Y	N	Y	6/8/2004	N	NA	NA	Western	Y	
GR100	2005	Y	N	Y	6/11/2005	N	NA	NA	Resident	Y	Data removed first 2 wks of May
GR154	2005	N	N	Y	6/13/2005	N	NA	NA	Resident	Y	Data removed first 2 wks of May
GR159	2005	Y	N	Y	6/1/2005	N	NA	NA	Resident	Y	Data removed first 2 wks of May
YL28	2005	Y	N	Y	6/20/2005	N	NA	NA	Resident	Y	Data removed first 2 wks of May
YL47	2005	Y	N	Y	6/1/2005	N	NA	NA	Resident	Y	Data removed first 2 wks of May
YL89	2005	Y	N	Y	6/23/2005	N	NA	NA	Western	Y	Data removed first 2 wks of May
GR122	2006	Y	N	Y	6/4/2006	N	NA	NA	Western	Y	

GR133	2006	Y	N	Y	6/4/2006	N	NA	NA	Western	Y	
GR154	2006	Y	N	Y	5/30/2006	N	NA	NA	Resident	Y	
GR169	2006	Y	N	Y	6/7/2006	N	NA	NA	Resident	Y	
GR172	2006	Y	N	Y	5/30/2006	N	NA	NA	Resident	Y	Data removed first wk of May
YL28	2006	Y	N	Y	6/16/2006	N	NA	NA	Resident	Y	
YL3	2006	Y	N	Y	6/7/2006	N	NA	NA	Western	Y	Data removed first wk of May
YL30	2006	Y	N	Y	5/24/2006	N	NA	NA	Western	Y	
YL4	2006	Y	N	Y	6/4/2006	N	NA	NA	Resident	Y	Data removed first wk of May
YL47	2006	N	N	Y	6/12/2006	N	NA	NA	Resident	Y	
GR169	2007	Y	N	Y	6/6/2007	N	NA	NA	Resident	N	Data removed first wk of May
YL47	2007	Y	N	Y	5/31/2007	N	NA	NA	Resident	N	
BL215	2009	Y	N	Y	5/28/2009	N	NA	NA	Resident	N	
BL222	2009	Y	N	Y	6/7/2009	N	NA	NA	Resident	N	
BL224	2009	Y	N	Y	5/29/2009	N	NA	NA	Resident	N	
BL252	2009	Y	N	Y	6/11/2009	N	NA	NA	Resident	N	
BL257	2009	Y	N	Y	6/5/2009	N	NA	NA	Resident	N	
BL259	2009	Y	N	Y	6/5/2009	N	NA	NA	Resident	N	
GR169	2009	Y	N	Y	5/23/2009	N	NA	NA	Resident	N	
BL201	2010	N	N	Y	6/6/2010	N	NA	NA	Resident	N	
BL234	2010	N	N	Y	6/7/2010	N	NA	NA	Resident	N	
BL245	2010	N	N	Y	7/5/2010	N	NA	NA	Resident	N	
BL250	2010	N	N	Y	6/5/2010	N	NA	NA	Resident	N	
BL269	2010	N	N	Y	6/18/2010	N	NA	NA	Resident	N	
OR54_BL260	2010	N	N	Y	6/16/2010	N	NA	NA	Resident	N	
OR9	2010	N	N	Y	6/7/2010	N	NA	NA	Eastern	N	
BL234	2011	N	N	Y	6/20/2011	N	NA	NA	Resident	N	
OR54_BL260	2011	N	N	Y	6/11/2011	N	NA	NA	Resident	N	
OR9	2011	N	N	Y	6/5/2011	N	NA	NA	Eastern	N	
OR41	2013	Y	N	Y	5/29/2013	Y	587697	5722393	Resident	Y	
OR77	2013	Y	Y	N	6/5/2013	Y	602473	5737241	Resident	Y	

OR78	2013	Y	N	Y	5/29/2013	Y	562904	5712358	Western	Y
OR79	2013	Y	Y	N	5/24/2013	Y	603552	5732450	Resident	Y
OR80	2013	Y	Y	N	6/2/2013	Y	597853	5735585	Resident	Y
OR81	2013	Y	N	Y	6/8/2013	Y	619082	5723446	Eastern	Y
OR82	2013	Y	Y	N	5/31/2013	Y	591802	5728800	Resident	Y
OR84	2013	Y	Y	N	5/19/2013	Y	601172	5738472	Resident	Y
OR85	2013	Y	N	Y	5/27/2013	Y	592930	5740667	Resident	Y
OR88	2013	Y	Y	N	6/8/2013	Y	598669	5735027	Resident	Y
OR89	2013	Y	Y	N	6/3/2013	Y	583227	5716632	Western	Y
OR90	2013	Y	N	Y	5/24/2013	Y	593765	5741419	Resident	Y
OR92	2013	Y	Y	N	6/19/2013	Y	617092	5722446	Eastern	Y
OR93	2013	Y	Y	N	5/28/2013	Y	600297	5737401	Resident	Y
OR94	2013	Y	Y	N	5/25/2013	Y	617866	5723815	Eastern	Y
YL116_OR83	2013	Y	Y	N	5/28/2013	Y	600699	5734631	Resident	Y
YL133_OR87	2013	Y	Y	N	5/27/2013	Y	598696	5732592	Resident	Y
OR23	2014	Y	Y	N	7/10/2014	Y	619628	5719993	Eastern	Y
OR39	2014	Y	Y	N	5/23/2014	Y	621468	5723849	Eastern	Y
OR40	2014	Y	N	Y	5/30/2014	Y	580797	5719396	Resident	Y
OR55_OR15	2014	Y	N	Y	5/29/2014	N	NA	NA	Western	Y
OR77	2014	Y	Y	N	6/4/2014	Y	602353	5737468	Resident	Y
OR78	2014	Y	N	Y	6/3/2014	Y	545350	5720688	Western	Y
OR90	2014	N	N	Y	6/3/2014	N	NA	NA	Resident	Y
OR98	2014	Y	Y	N	6/3/2014	Y	601034	5734566	Resident	Y
YL100	2014	Y	Y	N	5/26/2014	Y	598789	5734447	Resident	Y
YL101	2014	Y	Y	N	5/28/2014	Y	598101	5732139	Resident	Y
YL106	2014	Y	N	Y	5/25/2014	Y	547101	5716749	Western	Y
YL107	2014	Y	Y	N	5/22/2014	Y	597409	5735286	Resident	Y
YL109_OR35	2014	Y	Y	N	5/22/2014	Y	620538	5722037	Eastern	Y
YL111_OR6	2014	Y	Y	N	5/18/2014	Y	619017	5724287	Eastern	Y
YL114_BL274	2014	Y	Y	N	5/28/2014	Y	620939	5722004	Eastern	Y

YL115_OR34	2014	Y	N	Y	6/18/2014	Y	600652	5738437	Resident	Y
YL116_OR83	2014	N	N	Y	6/29/2014	N	NA	NA	Resident	Y
YL123_OR7	2014	Y	Y	N	5/27/2014	Y	617249	5722451	Eastern	Y
YL132_OR2	2014	Y	Y	N	6/3/2014	Y	602798	5731827	Resident	Y
YL133_OR87	2014	N	N	Y	5/8/2014	N	NA	NA	Resident	Y
YL136_BL284	2014	Y	Y	N	5/25/2014	Y	618828	5723730	Eastern	Y
YL138_BL295	2014	Y	Y	N	7/11/2014	Y	598771	5742856	Resident	Y
YL151_YL87	2014	Y	Y	N	5/14/2014	Y	601765	5736704	Resident	Y
GR513	2015	Y	Y	N	6/11/2015	Y	596363	5689234	Western	Y
OR54_BL260	2015	Y	Y	N	5/31/2015	Y	595791	5737283	Resident	Y
OR56_BL251	2015	Y	N	Y	6/11/2015	Y	589784	5695183	Western	Y
OR65_BL265	2015	Y	N	Y	6/5/2015	Y	598563	5726977	Western	Y
OR80	2015	Y	Y	N	6/19/2015	Y	599082	5736350	Resident	Y
OR89	2015	Y	N	Y	6/14/2015	N	NA	NA	Western	Y
OR90	2015	N	N	Y	6/21/2015	N	NA	NA	Resident	Y
OR92	2015	Y	Y	N	6/3/2015	Y	617069	5722437	Eastern	Y
OR99	2015	Y	Y	N	6/1/2015	Y	598879	5734094	Resident	Y
YL100	2015	Y	Y	N	5/30/2015	Y	601737	5733728	Resident	Y
YL107	2015	Y	Y	N	5/22/2015	Y	599999	5736695	Resident	Y
YL110_OR29	2015	Y	Y	N	6/4/2015	Y	596379	5730522	Resident	Y
YL112_OR38	2015	Y	Y	N	6/2/2015	Y	601744	5732683	Resident	Y
YL118_OR8	2015	Y	Y	N	5/25/2015	Y	613139	5723702	Eastern	Y
YL120_BL290	2015	Y	Y	N	6/1/2015	Y	594422	5737896	Resident	Y
YL124	2015	Y	Y	N	5/27/2015	Y	597806	5734578	Resident	Y
YL134_BL262	2015	Y	Y	N	6/2/2015	Y	613906	5716968	Eastern	Y
YL138_BL295	2015	Y	N	Y	6/15/2015	Y	598451	5743519	Resident	Y
YL139_BL220	2015	Y	Y	N	6/23/2015	Y	617308	5722831	Eastern	Y
OR100	2016	Y	Y	N	5/25/2016	Y	594371	5729964	Resident	Y
OR60_BL288	2016	Y	Y	N	6/1/2016	N	NA	NA	Western	Y
OR61	2016	Y	Y	N	6/20/2016	Y	601716	5732651	Resident	Y

OR66_BL293	2016	Y	Y	N	5/18/2016	Y	599199	5733716	Resident	Y
OR78	2016	Y	N	Y	5/24/2016	Y	545110	5721152	Western	Y
OR81	2016	Y	Y	N	5/26/2016	Y	620726	5723252	Eastern	Y
OR89	2016	Y	N	Y	6/16/2016	N	NA	NA	Western	Y
OR97	2016	Y	Y	N	5/20/2016	Y	602550	5733967	Resident	Y
OR99	2016	Y	Y	N	5/19/2016	Y	597877	5730843	Resident	Y
YL100	2016	Y	Y	N	5/30/2016	Y	592761	5731152	Resident	Y
YL112_OR38	2016	Y	N	Y	6/24/2016	Y	586918	5747659	Resident	Y
YL114_BL274	2016	Y	Y	N	5/25/2016	Y	627350	5723875	Eastern	Y
YL115_OR34	2016	Y	Y	N	6/9/2016	Y	595693	5730078	Resident	Y
YL118_OR8	2016	Y	Y	N	6/4/2016	Y	610410	5725560	Eastern	Y
YL120_BL290	2016	Y	Y	N	5/30/2016	Y	593777	5732975	Resident	Y
YL124	2016	Y	Y	N	5/21/2016	Y	597981	5731900	Resident	Y
YL133_OR87	2016	Y	Y	N	5/23/2016	Y	597704	5733051	Resident	Y
YL134_BL262	2016	Y	Y	N	6/2/2016	Y	614326	5717207	Eastern	Y
YL137_BE13	2016	Y	Y	N	6/1/2016	Y	601867	5731945	Resident	Y
YL151_YL87	2016	Y	Y	N	5/24/2016	Y	601188	5736340	Resident	Y
YL152_YL63	2016	Y	Y	N	5/30/2016	Y	601152	5728522	Western	Y
YL153	2016	Y	Y	N	6/13/2016	Y	597295	5733199	Western	Y
YL154	2016	Y	Y	N	6/4/2016	Y	607939	5725739	Eastern	Y
YL155_OR16	2016	Y	Y	N	5/22/2016	Y	615744	5722719	Eastern	Y
YL156	2016	Y	Y	N	6/12/2016	Y	600226	5731542	Resident	Y
YL158_OR21	2016	Y	N	Y	6/16/2016	N	NA	NA	Eastern	Y
YL159	2016	Y	Y	N	6/2/2016	Y	608268	5726653	Eastern	Y
YL161	2016	Y	Y	N	5/21/2016	Y	604427	5732448	Resident	Y
YL162_BC13	2016	Y	Y	N	5/23/2016	Y	602856	5730841	Resident	Y
YL163	2016	Y	Y	N	5/29/2016	Y	602740	5733258	Resident	Y
YL164_BL255	2016	Y	Y	N	6/3/2016	Y	596689	5727231	Resident	Y
YL166	2016	Y	Y	N	5/26/2016	Y	616090	5718017	Eastern	Y
YL167_OR10	2016	Y	N	Y	6/15/2016	N	NA	NA	Western	Y

YL169	2016	Y	Y	N	5/24/2016	Y	599497	5738969	Resident	Y
YL170	2016	Y	Y	N	5/27/2016	Y	609226	5724972	Eastern	Y
YL171	2016	Y	Y	N	5/27/2016	Y	622368	5723434	Eastern	Y
YL172	2016	Y	Y	N	5/22/2016	Y	615466	5721069	Eastern	Y

Table D.2. Sample sizes of parturition events used to build random forest models and for predictions of parturition dates for elk following 3 migratory tactics in the Ya Ha Tinda elk population, Alberta, Canada, from 2002 – 2016. Results from 2 time periods (early: 2002 – 2006 and late: 2013 – 2016) were further used to compare selection of calving areas relative to areas used during summer.

	Western Migs.		Residents		Eastern Migs.		Total	
Year	Build	Predict	Build	Predict	Build	Predict	Build	Predict
2002				1				1
2003		5		1				6
2004		7		5				12
2005		1		5				6
2006		4		6				10
2007				2				2
2008								
2009				7				7
2010				6		1		7
2011				2		1		3
2012								
2013		1	9	3	2	1	11	5
2014		3	8	5	7		15	8
2015		3	8	2	4		12	5
2016	1	5	11	2	10	1	22	8
Total	1	29	36	47	23	4	60	80

Table D.3. Average importance of predictor variables, calculated from 1,000 random forest models used to predict dates of parturition. Predictors included 5 descriptive statistics (mean, median, standard deviation, maximum, and total sum) for each of 6 movement statistics [step lengths (dist), relative turning angles, absolute turning angles, Euclidean displacement, and parallel (paraSd) and orthogonal variances] calculated over 6 moving-time windows (4, 24, 48, 96, 192, and 216 hr) from GPS data of elk in the Ya Ha Tinda population, Alberta, Canada, 2002 – 2016.

Metric	Average Importance
dist_sum_216	15.660
dist_mean_216	14.465
dist_mean_192	14.462
dist_sum_192	14.388
paraSd_sd_24	12.224
dist_median_96	11.988
dist_median_48	11.701
dist_sum_96	9.371
paraSd_sd_48	9.131
dist_sd_216	8.965
orthSd_sd_48	8.145
dist_median_24	7.725
dist_mean_96	7.646
dist_sd_192	7.122
paraSd_max_48	6.361
dist_median_192	6.009
orthSd_sd_24	5.912
orthSd_median_96	5.737
dist_median_216	5.562
orthSd_sd_192	5.399
paraSd_mean_192	5.334
paraSd_median_48	5.220
orthSd_max_48	5.157
paraSd_max_24	5.035
dist_max_216	5.020
paraSd_median_216	4.996
paraSd_sum_192	4.979
orthSd_sd_96	4.913
rel.angle_sd_192	4.752
paraSd_median_24	4.719
paraSd_median_192	4.690

rel.angle_sd_96	4.681
rel.angle_max_24	4.657
paraSd_mean_216	4.633
orthSd_median_216	4.523
orthSd_mean_192	4.520
rel.angle_sum_216	4.433
rel.angle_mean_216	4.411
dist_sd_96	4.403
orthSd_median_24	4.392
orthSd_mean_216	4.366
rel.angle_max_216	4.363
abs.angle_sd_48	4.358
rel.angle_max_48	4.355
paraSd_sum_216	4.318
orthSd_sd_216	4.268
orthSd_sum_192	4.223
rel.angle_max_192	4.199
paraSd_max_96	4.194
rel.angle_sd_216	4.179
abs.angle_max_96	4.158
paraSd_sd_192	4.083
orthSd_median_48	4.078
paraSd_median_96	3.994
paraSd_sd_216	3.986
orthSd_max_24	3.965
orthSd_sum_216	3.919
paraSd_mean_3	3.897
paraSd_sum_3	3.886
paraSd_max_3	3.875
paraSd_median_3	3.868
paraSd	3.865
abs.angle_sd_192	3.822
abs.angle_sd_216	3.809
paraSd_sd_96	3.806
abs.angle_sum_48	3.802
abs.angle_mean_48	3.775
dist_max_192	3.750
orthSd_max_96	3.697
rel.angle_sum_192	3.564
paraSd_sum_48	3.505
abs.angle_mean_216	3.427
abs.angle_sum_216	3.378

dist_mean_48	3.365
abs.angle_sum_192	3.346
abs.angle_max_48	3.312
abs.angle_mean_192	3.297
abs.angle_max_24	3.253
orthSd_mean_96	3.243
paraSd_mean_48	3.236
orthSd_median_192	3.223
orthSd_mean_24	3.221
orthSd	3.215
orthSd_median_3	3.215
orthSd_max_3	3.205
orthSd_sum_3	3.197
orthSd_mean_3	3.196
dist_sd_24	3.193
dist_sum_24	3.174
dist_sum_48	3.173
rel.angle_sd_48	3.156
paraSd_sum_96	3.134
orthSd_max_216	3.124
paraSd_mean_96	3.120
dist_mean_24	3.116
dist_max_96	3.077
abs.angle_max_192	2.998
paraSd_mean_24	2.990
orthSd_mean_48	2.968
rel.angle_max_96	2.950
orthSd_sum_48	2.920
orthSd_sum_24	2.901
orthSd_sum_96	2.899
dist_sum_3	2.828
dist_max_3	2.828
dist_mean_3	2.822
dist_median_3	2.815
dist	2.807
paraSd_max_216	2.784
dist_max_24	2.766
paraSd_sum_24	2.722
displacement_48	2.705
orthSd_max_192	2.705
dist_sd_48	2.693
displacement_24	2.671

paraSd_max_192	2.594
abs.angle_max_216	2.352
dist_max_48	2.127
abs.angle_sum_3	1.580
abs.angle_max_3	1.578
abs.angle_mean_3	1.570
abs.angle	1.568
abs.angle_median_3	1.566

Table D.4. Average importance of grouped predictor variables, calculated from 1,000 random forest models used to predict dates of parturition. Predictor variables [step lengths (Dist), relative turning angles, absolute turning angles, Euclidean displacement, and parallel (paraSd) and orthogonal variances (orthSd)] were grouped by their descriptive statistics (mean, median, standard deviation, maximum, and total sum) and moving-time window (4, 24, 48, 96, 196, or 216 hr). Statistics were calculated from GPS data of elk in the Ya Ha Tinda population, Alberta, Canada, 2002 – 2016.

Grouped Variable	Average Importance
Dist.216	10.570
Dist.192	10.148
Dist.96	8.340
paraSd.24	7.230
Dist.48	6.624
paraSd.48	6.052
orthSd.48	5.276
Dist.24	4.679
Rel.Angle.24	4.657
paraSd.192	4.547
orthSd.96	4.392
Rel.Angle.216	4.388
orthSd.24	4.363
paraSd.216	4.338
Rel.Angle.192	4.271
orthSd.192	4.206
Abs.Angle.96	4.158
orthSd.216	4.153
Rel.Angle.96	4.061
Abs.Angle.48	3.906
paraSd.4	3.894
Rel.Angle.48	3.839
paraSd.96	3.690
Abs.Angle.192	3.411
Abs.Angle.216	3.291
Abs.Angle.24	3.253
orthSd.4	3.213
Dist.4	2.830
Displacement	2.699
Abs.Angle.4	1.580
Rel.Angle.4	0.000

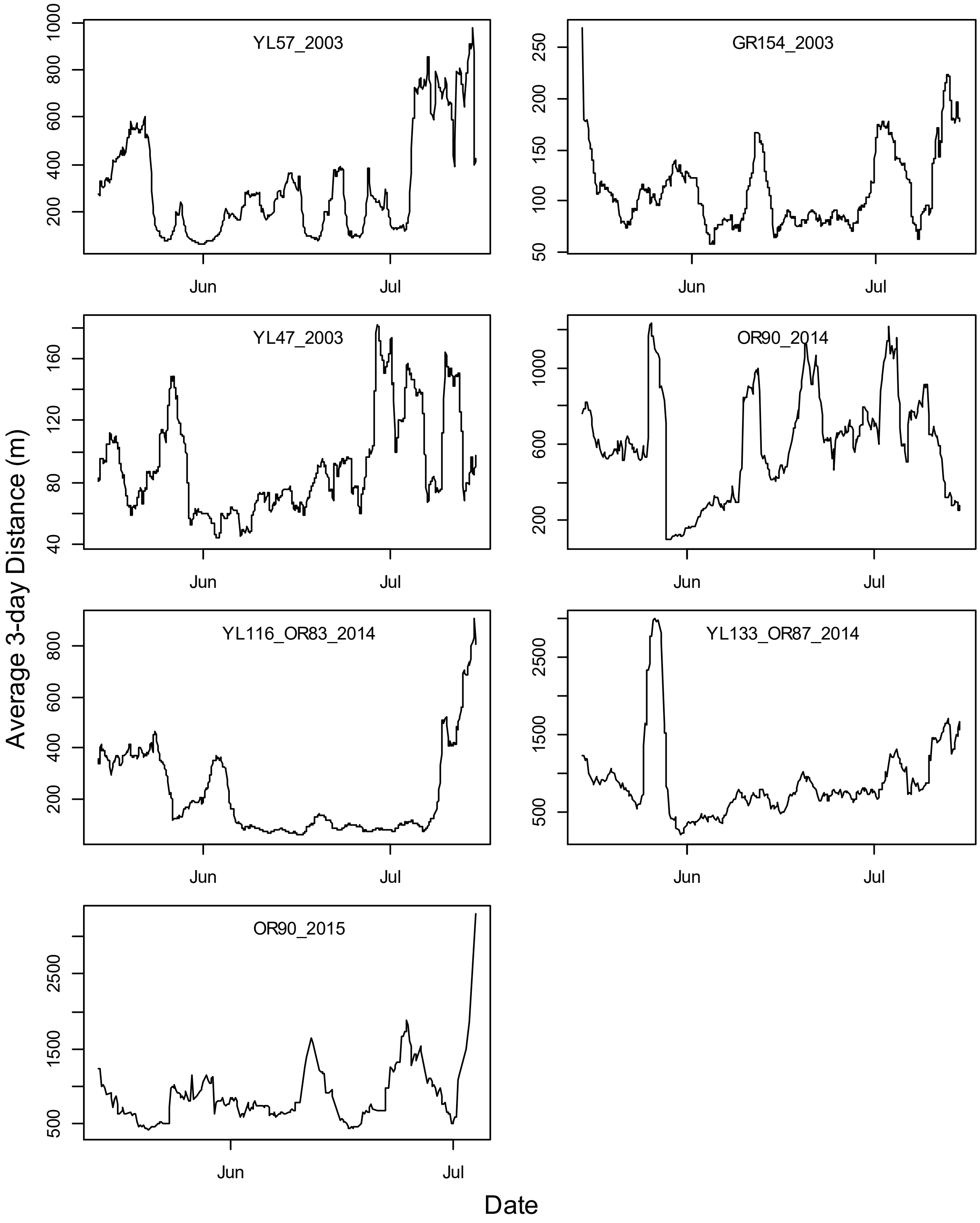


Figure D.1. Step lengths (m) averaged across 3-day moving windows in 7 animals assumed to be pregnant in the Ya Ha Tinda elk population, Alberta, Canada, 2002 – 2016. Depressed movement rates in late May or early June could be indicative of an elk calving event.

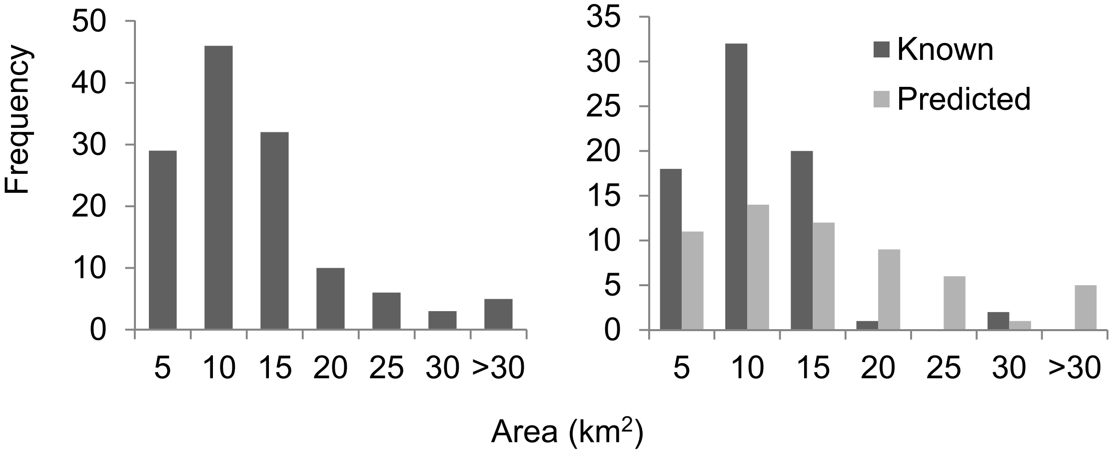


Figure D.2. Size (km^2) of 26-day calving areas (*n* = 131) used by maternal elk in the Ya Ha Tinda elk population, Alberta, Canada, 2002 – 2006 and 2013 – 2016.

APPENDIX E. LAND COVER AND ACCOUNTING FOR CLOSED CANOPY IN NDVI

OVERVIEW

The Normalized Difference Vegetation Index (NDVI) is a ratio [NDVI = (NIR – RED)/(NIR +RED)] of the amounts of near-infrared (NIR) and red (RED) light that are reflected by vegetation and captured by a satellite sensor. As such, NDVI is readily available at large spatiotemporal scales, and is often used as an index of the amount of high forage quality available to animals (Pettorelli et al. 2005, Hebblewhite et al. 2008), particularly when information on phenology and the amount or distribution of vegetation is limited or difficult to collect in the field.

However, the use of NDVI is not without problems. NDVI measurements can be affected by many factors including: topography; the height, composition, and architecture of plants; and canopy cover. Because NDVI is not typically reliable for predicting vegetation growth under closed canopies due to the high reflectance of near-infrared light by growing trees (Chen et al. 2004, Hebblewhite et al. 2008), researchers have approached analyses differently for open- and closed-canopy cover types by modeling closed-canopy forage growth with collected vegetation data (e.g., Hebblewhite et al. 2008) or by using land cover maps to create an open/closed-canopy mask for NDVI (e.g., Robinson et al. 2012). In many cases, however, the issue is simply ignored or explained away, which may not directly answer the question at hand and/or lead to confounding effects.

The true effects of collinear metrics (e.g., NDVI and the amount of closed canopy in an area) can be difficult to tease apart. Though opinions differ on which method is better, both regression, used to take the residuals of a particular habitat metric as an index of that metric, and path analysis, which allows for identification of the causal basis for collinearity as well as unbiased estimates of effects, have been used when there is collinearity (Koper et al. 2007, Ruffell et al. 2016). To account for the effects of closed canopy on measurements of NDVI in an analysis of elk calving site selection, we explored the relationship between the amount of closed canopy and NDVI using 2 approaches: 1) creating an open/closed canopy mask, and 2) regressing NDVI values on percent closed canopy to obtain the residuals as an index of NDVI.

METHODS

Calving Areas

To explore the relationship between NDVI and closed canopy, we used the calving areas of 131 maternal elk from 2 time periods: 2002 – 2006 and 2013 – 2016. We delineated each elk's calving area with piecewise regression using a broken-stick approach (Johnson et al. 2002) to determine the number of days that elk gradually increase their movements as calves become more mobile. For each elk, we created 95% utilization distributions around the GPS locations from known (*n* = 73 elk-years; 58 individual elk) or predicted (*n* = 60 elk-years; 52 individual elk) date of parturition through 26 days using fixed kernel analysis and the plug-in method for the smoothing factor using the ks package in program R (Duong 2018).

Open-Habitat Mask

We used a land cover map from Hebblewhite that was derived from LANDSAT-TM (Franklin et al. 2001). Land cover categories included: open, moderate, and closed conifer; deciduous forest; mixed forest; regenerating forest; herbaceous; shrub; water; rock/snow/shadow; cloud; burned forest, grassland, and shrub; and alpine herbaceous and alpine shrub (Table E.1). The land cover map was updated each year of our study with new burns and cutblocks, and old burns and cutblocks (>15 yr) were reclassified to moderate conifer. Data on burns and cutblocks were obtained from Banff National Park's fire database and Sundre Forest Products, Sundre, AB.

We created a land cover mask with only open habitats (regenerating forest; herbaceous; shrub; burned forest, grassland, and shrub; and alpine herbaceous and shrub; Table E.1) and excluded pixels with conifer, mixed, or deciduous forest, water, or rock/snow/shadow/cloud. For purposes of the analysis in this appendix, open conifer, deciduous forest, and mixed forest were included with open habitat; for all other analyses in the dissertation, they were included as closed habitat. NDVI values were extracted from only open habitat and averaged across each maternal female's calving area. We used NDVI values at the time of each maternal female's calving date, and at peak lactation, 3 weeks later.

Regression

We characterized the land cover of each 30x30-m pixel within each maternal female's calving area using the land cover map described above. We then calculated the percentage of each cover category by counting the number of pixels within each category then dividing by the calving area's total number of pixels. We summed moderate and closed conifer as a measure of the trees within closed canopy (%) that would be most likely to affect NDVI values.

We used a square power transformation for NDVI at calving and a cube power transformation for NDVI at peak lactation to minimize issues with normality. Pearson product-moment correlation coefficients were computed to assess the relationships between NDVI at calving and closed canopy, and between NDVI at peak lactation and closed canopy. We used the 'lm' function in the base package of R to fit 2 linear regression models, where NDVI during the 2 time periods (calving and peak of parturition) were the response variables as a function of the amount of closed canopy within used and available elk calving areas. We used the residuals of the 2 models as indices of NDVI at calving and NDVI at peak lactation respectively.

RESULTS

The daily area used by parturient mothers increased as calves became more mobile and then began to stabilize after 26.0 (± 2.03 SE) days (Figure E.1).

The indices of NDVI at calving and at peak lactation were correlated with closed canopy ($r_{(1472)} = 0.42$, $P < 0.0001$ and $r_{(1472)} = 0.29$, $P < 0.0001$, respectively, Figure E.2).

The percentage of moderate and closed conifer significantly predicted square-transformed NDVI at calving ($\beta = 0.002$, $t_{(1472)} = 17.96$, $P < 0.0001$) and cube-transformed NDVI at peak lactation ($\beta = 0.001$, $t_{(1472)} = 11.57$, $P < 0.0001$). The percentage of moderate and closed conifer also explained a significant proportion of variance in NDVI at calving ($R^2 = 0.18$, $F_{(1,\,1472)} = 322.5$, $P < 0.0001$) and in NDVI at peak lactation ($R^2 = 0.08$, $F_{(1,\,1472)} = 133.8$, $P < 0.0001$). Patterns of NDVI between migratory tactics and between time periods were similar whether using the open-habitat mask or the regression residuals as indices of NDVI (Figure E.3, Figure E.4).

Table E.1. Land cover categories in the Ya Ha Tinda study area, Alberta, Canada, including open (0) and closed (1) habitat classification and the average percent (%) and range of each category within 26-day elk calving areas (*n* = 131).

Land cover Type	Habitat Classification	Avg. %	Range
Open Conifer	1	8.79	0.00 – 46.12
Moderate Conifer	1	17.14	0.30 – 62.34
Closed Conifer	1	5.92	0.00 – 62.01
Deciduous	1	0.23	0.00 – 5.93
Mixed Forest	1	3.83	0.00 – 25.87
Regenerating Forest	0	3.22	0.00 – 30.55
Herbaceous	0	20.78	0.00 – 55.75
Shrubs	0	14.11	0.00 – 41.39
Water	N/A	0.32	0.00 – 3.37
Rock/Snow/Shadow	N/A	6.44	0.00 – 24.46
Cloud	N/A	0.01	0.00 – 0.32
Burned Forest	0	9.36	0.00 – 80.46
Burned Grassland	0	3.95	0.00 – 32.63
Burned Shrub	0	1.11	0.00 – 8.67
Alpine Herbaceous	0	3.64	0.00 – 38.18
Alpine Shrubs	0	1.15	0.00 – 26.67

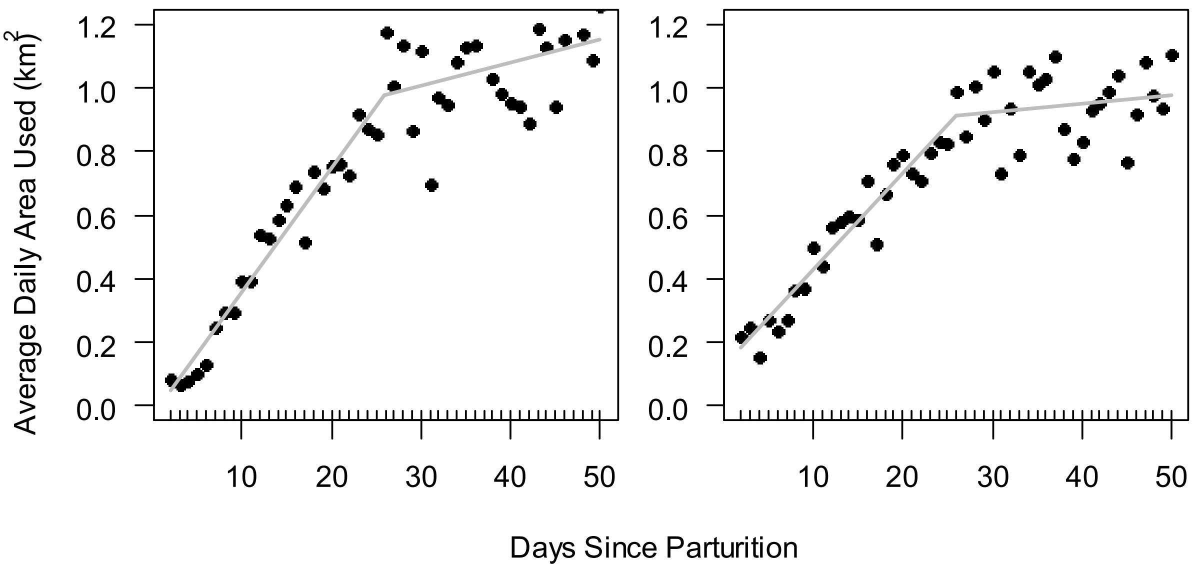


Figure E.1. Average area (km^2) used every 24 hr since day of parturition by maternal elk in the Ya Ha Tinda elk population, Alberta, Canada, 2002 – 2006 and 2013 – 2016. On left is the area used by elk since known (*n* = 73) days of parturition, and on right is the area used since both known and predicted (*n* = 131) days of parturition.

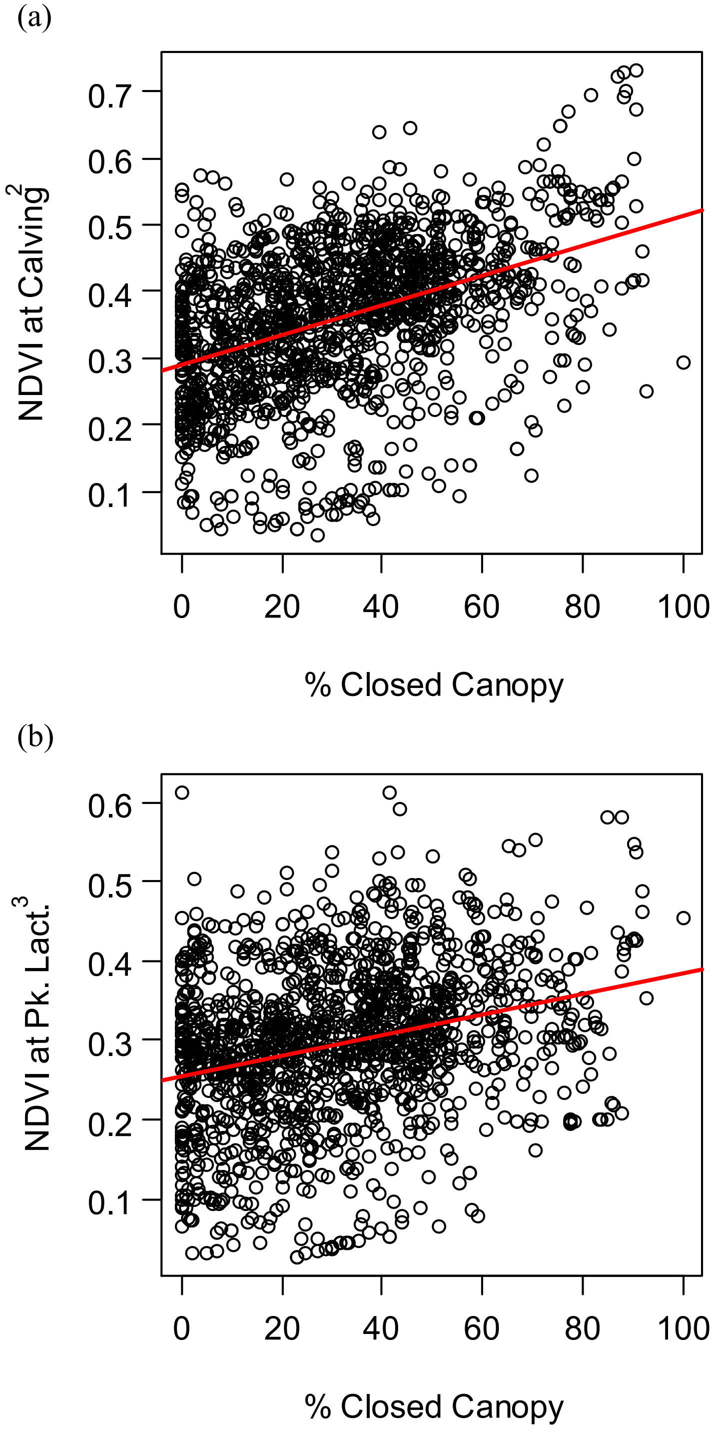


Figure E.2. Relationships between (a) the square transformation of NDVI at calving and the amount (%) of closed canopy, and (b) the cube transformation of NDVI at peak lactation and the amount (%) of closed canopy within 26-day elk calving areas in the Ya Ha Tinda population, Alberta, Canada, 2002-2006 and 2013-2016.

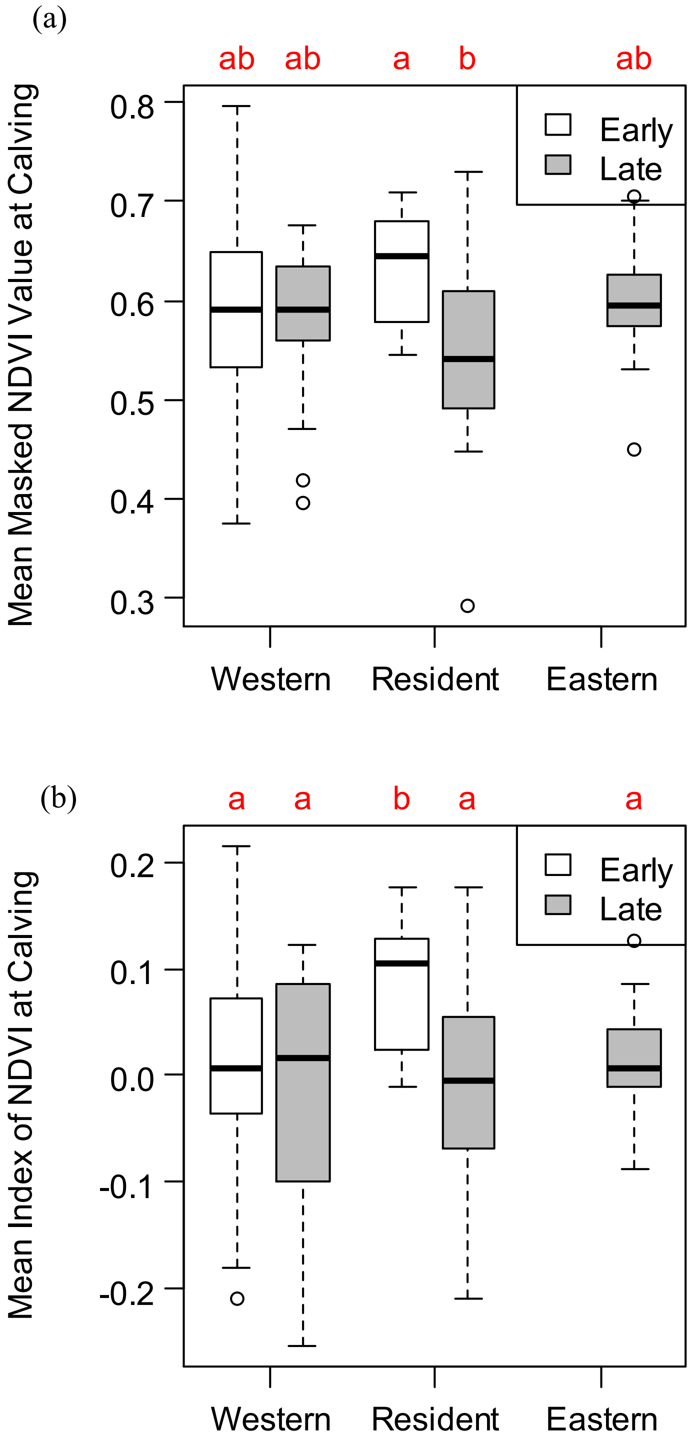


Figure E.3. NDVI at calving in open habitat (a), and (b) an index of NDVI after accounting for moderate and closed conifer (%) in calving sites (*n* = 131) of elk following 3 migratory tactics during 2 time periods (2002-2006 and 2013-2016) in the Ya Ha Tinda elk population, Alberta, Canada.

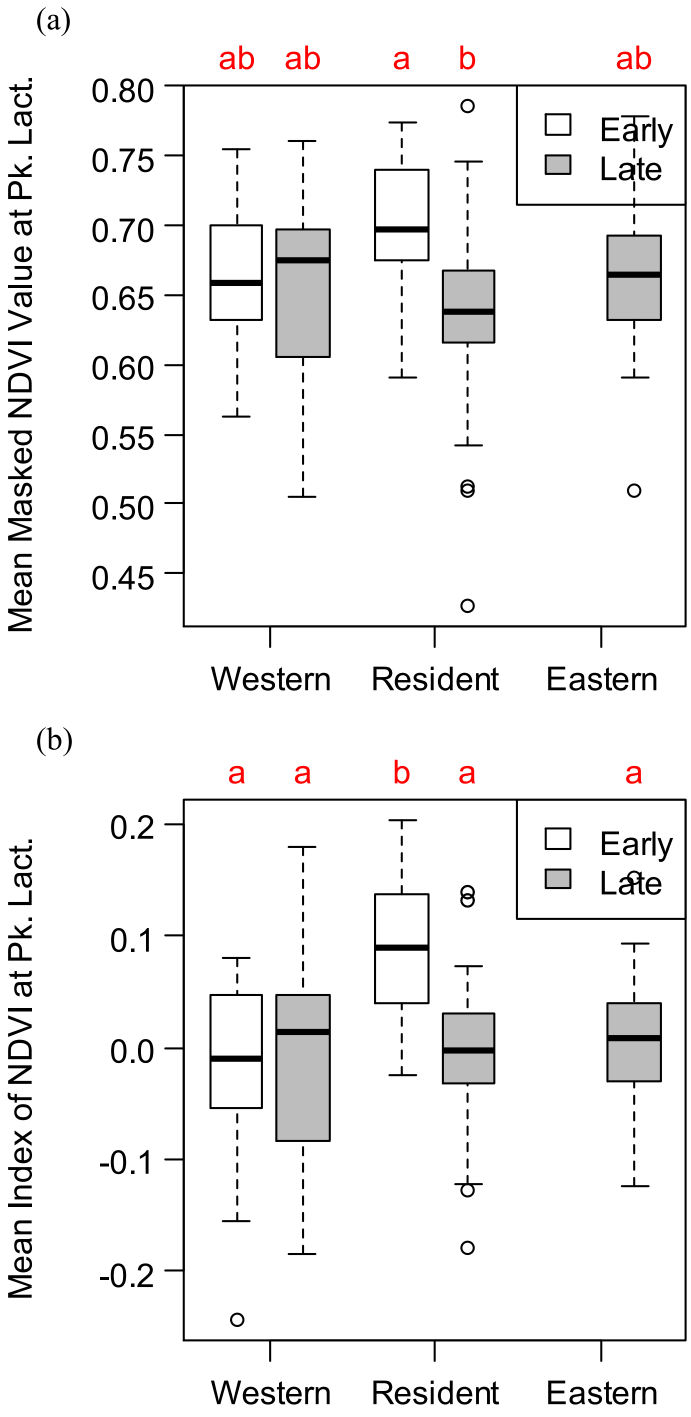


Figure E.4. NDVI at peak lactation in open habitat (a), and (b) an index of NDVI at peak lactation after accounting for moderate and closed conifer (%) in calving sites (*n* = 131) of elk following 3 migratory tactics during 2 time periods (2002-2006 and 2013-2016) in the Ya Ha Tinda elk population, Alberta, Canada.

APPENDIX F. FORAGE BIOMASS AT YA HA TINDA

OVERVIEW

For the years 2002 – 2004, annual peak (~1 Aug) forage biomass was estimated by Hebblewhite et al. (2008) using a general linear model to estimate herbaceous and shrub biomass at a 30-m^2 resolution as a function of year, land cover type, elevation (m), aspect and distance to the continental divide (km) based on field sampling along transects at 983 sites (Hebblewhite et al. 2008). For the years 2005 – 2016, we compared May – July precipitation to that which occurred in 2003 – 2004 because 2003 had low (167 mm) precipitation, and 2004 had high (319 mm) precipitation, and we used the peak biomass estimate from the year that was most similar because there was a year effect of May – July precipitation on total biomass (herbaceous + shrub). Precipitation data were obtained from the Alberta Climate Information Service (ACIS, http://www.agric.gov.ab.ca).

We adjusted for temporal changes in forage availability resulting from timber harvest or fire by modelling the changes in forage biomass up to 15 years, then assuming biomass reached pre-burn or pre-cut levels. For harvest, we used the models developed by Visscher et al. (2009: Table 1) that estimated herbaceous and shrub biomass separately them summed these to estimate total biomass. Visscher et al. (2009) sampled peak herbaceous and shrub biomass in 2001 – 2002 in stands aged 1 - 20 years in an area immediately north of the YHT following similar methods to Hebblewhite et al. (2009).

Herbaceous and shrub biomass in relation to time since fire was sampled on 187 plots in 2002 – 2004 and resampled in 2012 also following the methods of Hebblewhite et al. (2009). Maps of burned areas with date of burn origin were obtained from Banff National Park's fire database and Sundre Forest Products, Sundre, AB. Sampled sites were selected randomly within BNP and randomly within 1 km of road or accessible trail outside BNP. We developed separate quadratic relationships between time since burn and herb and shrub biomass for sites that were grasslands and sites that were forest/shrub prior to burning. We used quadratic models because they fit the data better than lognormal (herbaceous: ΔAIC = 533; shrub: ΔAIC = 387). After >15 growing seasons a forest/shrub site was considered moderate-canopy forest with total (herbaceous + shrub) biomass of 228.01 g/m^2 whereas grasslands were 216.86 g/m^2 (Hebblewhite 2006) starting in year 16 after a burn.

We adjusted forage biomass for plant growth within a season (1 July 2002 to 30 September 2016) based on remote sensing for open land cover types and field-based models derived by Hebblewhite et al. (2009) for closed-canopied types. In open habitats we adjusted peak biomasses to the nearest 16-day period based on normalized difference vegetation index (NDVI). NDVI-time series were smoothed for each 250-m^2 pixel using a temporal window of three intervals to reduce noise (Kawamura et al. 2005, Hebblewhite et al. 2006). Within each year, we used the ratio of the mean 16-day NDVI_i within the composite summer range of a migratory tactic to the maximum mean ($\mathrm{NDVI}_{\mathrm{max}}$) of a migratory tactic observed during the growing season of that year to adjust peak biomass in each 30m^2 pixel in all open land cover types (Hebblewhite et al. 2009). Forage growth in each 30-m pixel of closed-canopied, land cover types (Appendix E) was estimated following Hebblewhite et al. (2009) as:

$$Y_i = 37.7 + 1.9^*(\mathrm{JD}) - 0.0043^*(\mathrm{JD})^2 - 0.10^*(\mathrm{elevation})_i + 20.3^*(\mathrm{south})_i - 0.20^*(\mathrm{hillshade})_i\,,$$

where i = 16-day period within a growing season, JD is Julian day, elevation is in m, aspect is either north (0; 247.6° – 67.4°) or south (1; 67.5° – 247.4°) and hillshade (range 0 – 255; Hebblewhite 2006). The ratio of predicted biomass at time interval i to the maximum value observed (i.e., $\mathrm{Biomass}_{\mathrm{i}}/\mathrm{Biomass}_{\mathrm{max}}$) to the nearest 16-day period was then used to adjust peak biomass within all seasons.

APPENDIX G. PREDATION RISK BY WOLVES, BEARS, AND COUGARS FOR ELK AT YA HA TINDA

OVERVIEW

We modeled predation risk for elk by wolves in the eastern slopes of Banff National Park (BNP) based on the work of Hebblewhite (2006) and Hebblewhite & Merrill (2007). Briefly, Hebblewhite (2006) modeled the population-level resource selection function (RSF) for collared wolves during both day and night and weighted the RSF values by the spatial density of wolves adjusted by the kill rate/pack/day (Thurber et al. 1994) to create annual pack-level models of predation risk by wolves for elk. We used the RSF maps of Hebblewhite (2006) for 2002 – 2004 and extended these to the years 2005 – 2016 by incorporating changes in 2 covariates (land cover and distance to edge) in the population-level RSF model to derive updated annual RSF maps. Next, we modeled the spatial density of use by wolves using one kernel density estimate (KDE) for each pack across all years, and weighting these kernels by kill rate/pack/day calculated as a function of annual pack sizes. We combined the annual RSF maps and the annual spatial density of use to create annual layers of total predation risk by wolves for elk. For the analysis, we assumed wolf home ranges were relatively stable even if pack sizes varied in time and also that wolf selection did not change over time. We evaluated the latter assumption by comparing Hebblewhite's original day and night RSFs to a scat-based RSF developed in 2014 –2016 (Spilker 2018).

We also evaluated summer predation risk by grizzly bears for elk from 2002 – 2016 using RSF maps developed with data of GPS-collared grizzly bears and applied to annually changing landscape conditions. Based on available data from the study area (Whittington and Sawaya 2015, Alberta Environment and Parks 2016, Whittington et al. 2017), we incorporated differences in spatial density of grizzly bears into the RSFs.

Finally, we validated the total predation risk by comparing locations of wolf-killed and bear-killed elk during 2002 – 2016 with the predation risk measured at randomly-generated locations within the study area.

METHODS

Wolf Data

We developed predation risk maps for areas encompassed by the boundaries of 5 wolf packs that overlap the range of the Ya Ha Tinda (YHT) elk population in the eastern slopes of BNP: the Bow Valley (BV), Panther-Cascade (CA), Clearwater-Ranch (RA), Red Deer (RD), and Wildhorse-James (WH) packs. Wolves were captured and radiocollared (LOTEK, Ltd. LMRT-3 or GPS 3300sw) using foot-hold traps during summer, and with helicopter netgunning or aerial darting during winter (U. of Alberta animal care protocol # 353112). VHF-collared wolves (n = 14) were monitored from the air or ground 0.5 - 1x/week, and mean VHF location error was 218 m (n = 20 blind trials; Hebblewhite 2006). Data from GPS-collared wolves (n = 16) were resampled to a 2-hr fix rate, and location error was <113 m (Hebblewhite 2006). Wolves were monitored from 15 April to 14 October, 2002 – 2004, and all locations were assigned as day or night locations based on averaged monthly sunrise and sunset tables (from the Herzberg Institute of Astrophysics, NRC, http://www.hia-iha.nrc-cnrc.gc.ca/).

Even with radiotelemetry, monitoring and estimating abundance for wolves is extremely difficult (Fritts et al. 1997). Because of this, a combination of methods and data types are often used to construct time-series of wolf population numbers (Jędrzejewska et al. 1997, Hebblewhite 2006). Though imperfect, this approach may provide an index of the relative change in population over time, and has long been used in our study area in and around BNP (Cowan 1947, Green 1951, Mickle et al. 1986, Paquet 1993, Hebblewhite 2000, Callaghan 2002, Hebblewhite 2006) and by others elsewhere (e.g., Smith et al. 1999). Therefore, wolf distribution and abundance across our study area was estimated during 2002 – 2016 by summing late winter pack sizes using a census of the number and size of wolf packs occurring in the study area (Eggeman et al. 2016). Following similar approaches to earlier studies, for each pack, we estimated the maximum number of individuals observed each winter (February and March) from a combination of direct observations and telemetry for radiocollared animals (Paquet 1993, Hebblewhite 2006), annual snow-tracking surveys (Hebblewhite 2006), and a network of over 50 remote cameras (Table G.1; Steenweg et al. 2015). Missing data on wolf pack sizes from some years (n = 18 pack size-years) were substituted with the mean size (6.4 ± 1.4) of all wolf packs from the entire period 2002 – 2016. One home range boundary for each pack was derived from

GPS data collected from collared wolves in 2002 – 2016; we assumed home ranges remained relatively stable over time, based on the boundaries for the 2 packs for which we had GPS data over time (Table G.2; Figure G.1).

Bear Data

RSF maps for bears were developed from 5,101 GPS locations collected between 1999 and 2006 from 11 collared female grizzly bears from the Clearwater grizzly bear population unit (Nielsen 2007).

Based on the Alberta Grizzly Bear Recovery Plan (2016), our study area lies within Bear Management Area (BMA) 4 which had a density of 5.25 bears/1000 km^2 in 2005, though this estimation covered only the eastern half of our study area and included only a small portion of eastern BNP (Alberta Environment and Parks 2016). Later studies from 2006 – 2008 and 2012 – 2014 estimated the density to be 12.4-15.1 bears/1000 km^2, but these studies covered BNP and areas farther west, excluding the eastern half of our study area (i.e., the area east of BNP; Whittington and Sawaya 2015, Whittington et al. 2017). Because the grizzly bear population has remained relatively stable over the course of this study (Whittington et al. 2017) we opted to keep bear numbers constant through time rather than adjust the RSFs by annually changing numbers as we did for wolves. However, we did adjust the annual grizzly RSFs spatially by the density of grizzly bears inside versus outside of BNP (described below).

Resource Selection Component of Predation Risk by Wolves

GPS data from collared wolves during the summers (15 Apr - 14 Oct) of 2002 – 2004 were used to develop resource selection functions for the diurnal and nocturnal periods (described above) in a used-available framework with fixed-effects logistic regression (Hebblewhite 2006):

Day:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_k x_k)$$

Night:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_k x_k)$$

where $w(x)$ is the probability of selection as a function of the coefficients, β_i, estimated using an exponential model and the environmental predictors x_i: landcover, elevation (m), slope (%), aspect class (north, south, flat), distance to hard habitat edges (km), and distance to human activity along linear features (km). Because human activity on linear features influences wolf movement in BNP (Paquet et al. 1996, Hebblewhite 2006), Hebblewhite (Hebblewhite 2006) added random intercepts for wolves and pack and a random coefficient for proximity to high human activity in a mixed-effects generalized linear mixed model (GLMM) with the logit link (Skrondal and Rabe-Hesketh 2004) to allow for pack and individual-level variation in wolves' response to human activity.

The landcover map used by Hebblewhite (2006) was derived from LANDSAT-TM (Franklin et al. 2001). Landcover types were collapsed into 9 categories: forested (including closed and moderate conifers, mixed, and deciduous), open conifer, herbaceous, shrubs, rock/ice/snow, alpine herbaceous and alpine shrub, prescribed and natural fire, and cutblocks. For the years >2004, the landcover map was updated with new burns and cutblocks each year, and old burns and cutblocks (>15 yr) were reclassified to moderate canopied-cover conifer. As a result, distances to edge between open and closed-canopied habitats or edge created by a river or stream changed from year to year. Data on burns and cutblocks were obtained from Banff National Park's fire database and Sundre Forest Products, Sundre, AB. Proximity to high human activity (>100 human-use events/month) along linear features was quantified from the Human Use Digital Atlas of the Central Rockies Ecosystem (Jevons 2001, Hebblewhite 2006). Night and day were delineated from averaged monthly sunrise and sunset tables (from the Herzberg Institute of Astrophysics, NRC, http://www.hia-iha.nrc-cnrc.gc.ca/).

Spatial Density Component of Predation Risk by Wolves

We assumed predation risk was a function of not only wolf occurrence but also spatial density of use and number of wolves in the area. Therefore, we weighted the RSFs by a spatial density component that combined kernel density estimates (KDEs) of pack boundaries and a nonlinear effect of pack size based on kill rate/pack/day (Thurber et al. 1994, Hebblewhite 2006):

$$Y = 0.385 \times (1.000 - 0.726^{X})$$

We first calculated one 95% KDE for each pack across all years following Kie (2013) and using a rule-based ad hoc method for selecting bandwidth (Figure G.2). The KDEs were then multiplied by the annual kill rates and scaled from 0 – 1 (Figure G.3) to derive annual probability density functions (PDFs). In areas where wolf pack boundaries overlapped, we summed the pack sizes and PDFs and rescaled back to 0 – 1, and in areas outside of wolf pack boundaries, we used the average pack size across years (6.4) and the average KDE across packs (0.2) to create an average PDF (Figure G.3). Finally, the resulting PDFs were then multiplied by the day and night RSFs to create the population-level predation risk models for 2002 – 2016 (Figure G.4).

Resource Selection and Spatial Density Components of Predation Risk by Bears

GPS data from collared bears (1999 – 2006) were employed in a used-available framework (as described above) to develop population-level resource selection functions for 3 seasons: 1 May – 15 June (hypophagia), 16 June – 31 July (early hyperphagia), and 1 August to 15 October (late hyperphagia; Nielsen 2007).

Environmental predictors for resource selection by bears included forest canopy [crown closure (0 – 100) in treed or regenerating sites, species composition in upland treed sites, and distance to edge (500-m exponential scale)], terrain [soil wetness (average within 150-m radius) and distance to stream (500-m exponential scale)], land cover type (wet-tree, regenerating forests, shrub, wet-herb, upland-herb, non-vegetated), and human use (Nielsen 2007). Forest canopy and land cover type were dynamic layers that were updated each year, while terrain and human use were static layers and not updated. Roads and trails were not included in the resource selection models because they are often correlated with other habitat characteristics and likely do not limit bear use within home range (as opposed to broader scales such as home range placement within the landscape; Nielsen 2007).

The output RSF map was scaled from 0 – 10. Though the habitat model predicts outside the minimum convex polygon (MCP) of sampled animals, a female bear range scalar was used to reduce overall habitat values and prevent overextrapolation in areas outside of the population unit. A non-habitat mask was applied, and the final RSF map was reclassified into 10 classes. Class break points followed a quantile-based approach. Predictive accuracy of the final grizzly RSF maps was validated with withheld GPS points (10%; Nielsen 2007).

To express considerable spatial differences in density of grizzly bears inside versus outside of BNP, we created a PDF for grizzly bears that weighted the area inside BNP by a factor of 2.62, which represented the average difference between the reported grizzly bear densities of the 2 areas (Figure G.5). Because animals do not adhere to human-designed political boundaries, we smoothed the RSF values along the park border using a 13x13-km moving window, the size of a female grizzly's average home range (520 km^2 ≈ 12.9-km radius; Stevens 2002) to more gradually decrease the density from within to outside the park boundary. Finally, we multiplied the annual RSFs for the hypophagia and early hyperphagia seasons by the PDF (Figure G.6).

Validation of the Wolf and Grizzly Predation Risk Models

We validated the total predation risk by 1) testing for correlation between the telemetry-based wolf and bear RSFs described here and RSFs developed from wolf and bear scat located in 2014 – 2015 (Spilker 2018), and 2) using a t-test to compare the telemetry-based predation risk values at 740 locations of wolf scat and 373 locations of grizzly bear scat with the predation risk measured at 1000 randomly-generated locations. We considered a significant difference ($P \leq 0.05$) between predation risk at scat sites and predation risk at random locations as indication of the high predictive accuracy of the predation risk models.

Table G.1. Maximum number of wolves in each pack estimated from radiotelemetry, direct observations, snow tracking, and remote cameras during February and March 2002 - 2016 in the eastern slopes of Banff National Park, Alberta, Canada.

Pack	2002-03	2003-04	2004-05	2005-06	2006-07	2007-08	2008-09	2009-10	2010-11	2011-12	2012-13	2013-14	2014-15	2015-16	2016-17	Avg.
Bow Valley	2	2	3	4	6	8	4	4.4[a]	4	6	4	8	3	5	3	4.4
Panther-Cascade	9	7	4	4	6	7	6	7	6	4	5.4[a]	2	5	5	4	5.4
Red Deer	12	14	7	3	2	4	4	7	4	6	6	11	8	5	4	6.5
Wildhorse-James	5	6	7	7	6.4[a]	6.4[a]	6.4[a]	6.4[a]	6.4[a]	6.4[a]	7	6.4[a]	6.4[a]	6.4[a]	6.4[a]	6.4
Ranch	15	26	1	2	8.1[a]	8	4	8.1[a]	7	3	7	8.1[a]	8.1[a]	8.1[a]	8.1[a]	8.1
Total	43	55	22	20	28.5	33.4	24.4	14	27.4	25.4	29.4	35.5	30.5	29.5	25.5	30.8

[a] The average pack size was used when data was missing.

Table G.2. Number of GPS locations from collared wolves in the eastern slopes of Banff National Park, Alberta, Canada, 2002 - 2016.

Pack	2002-03	2003-04	2004-05	2005-06	2006-07	2007-08	2008-09	2009-10	2010-11	2011-12	2012-13	2013-14	2014-15	2015-16	2016-17	Avg.
Bow Valley			3917	115				104	415	69	290			200	248	669.8
Panther-Casc.	1072	3588	5622											233	263	2155.6
Red Deer	841	949	7926								297					2503.3
Wild.-James		5059	3774													4416.5
Ranch		7811	10581													9196.0
Total	1913	17407	31820	115				104	415	69	587			433	511	18941.1

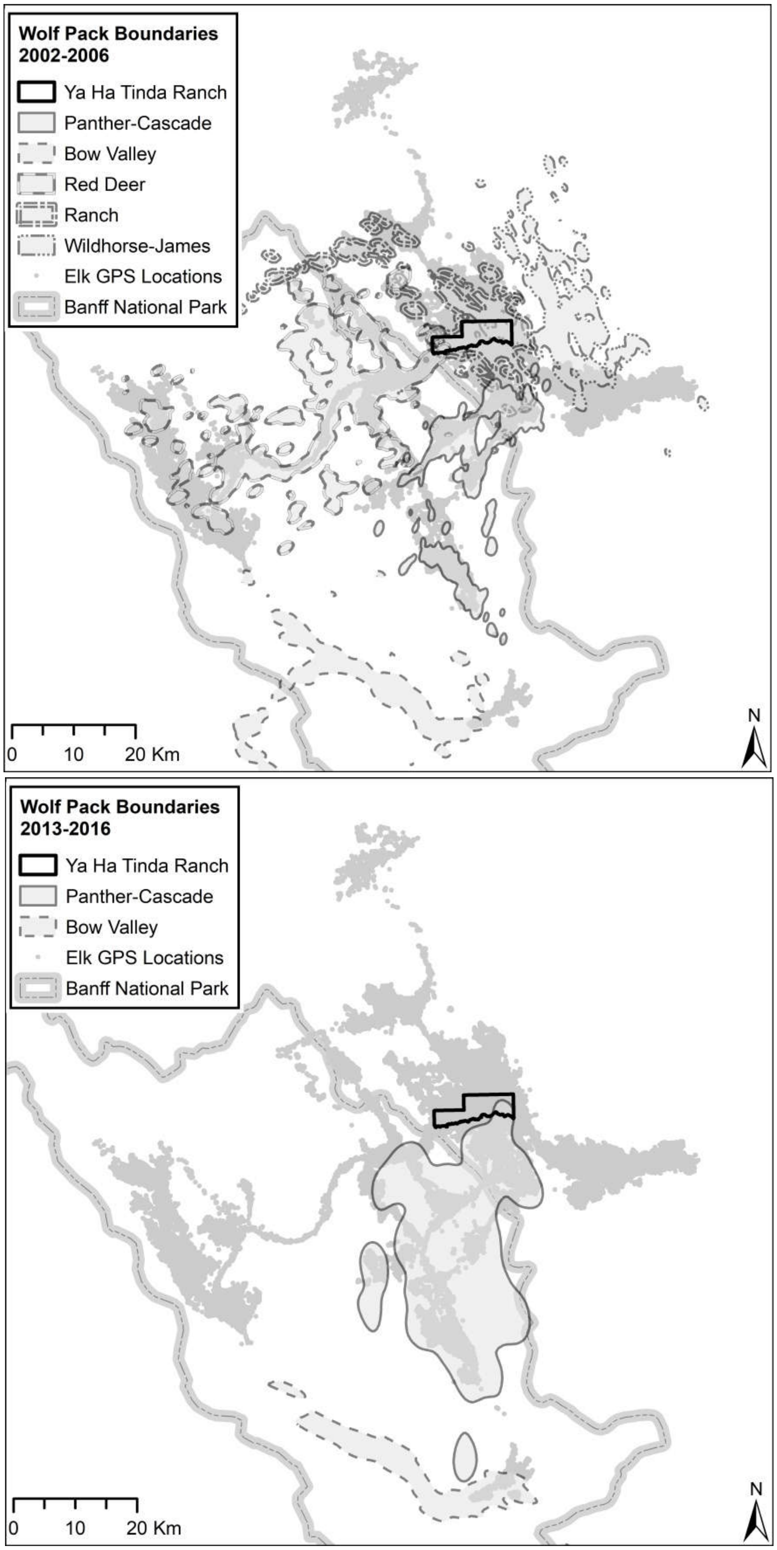


Figure G.1. 95% home range estimates for GPS-collared wolves during 2002 – 2006 (Panther-Cascade, Bow Valley, Red Deer, Ranch, and Wildhorse-James packs) and during 2013 – 2016 (Panther-Cascade and Bow Valley packs) on the eastern slopes of Banff National Park, Alberta, Canada.

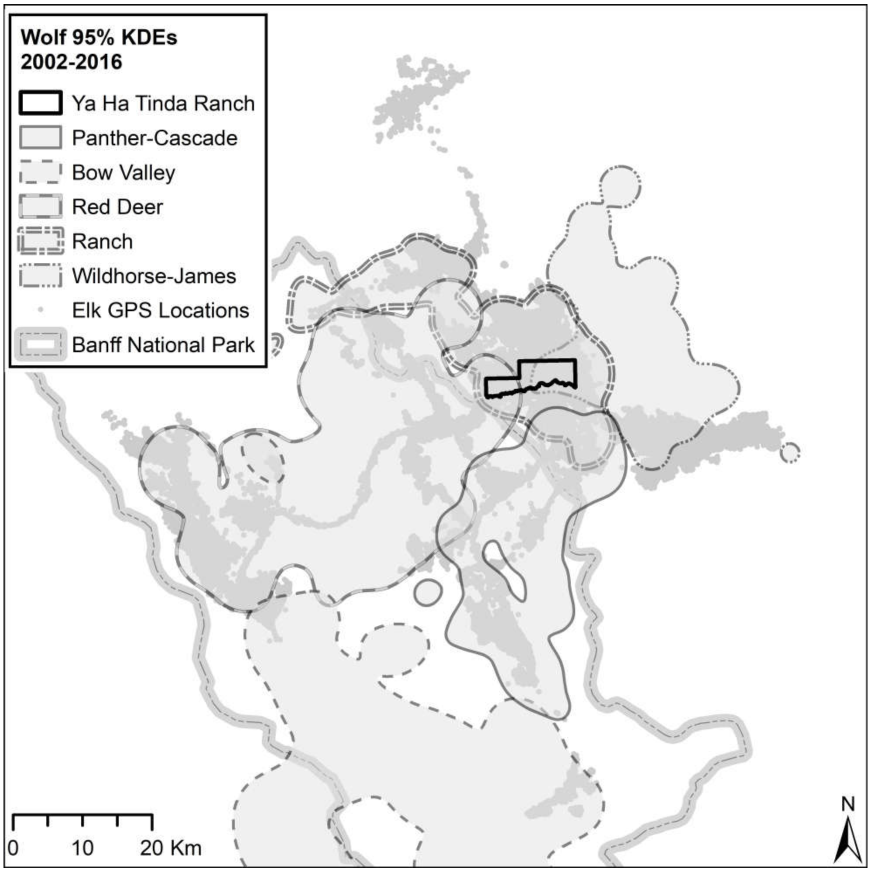


Figure G.2. Home ranges (95% Kernel Density Estimates) of 5 wolf packs in the eastern slopes of Banff National Park, Alberta, 2002 – 2016.

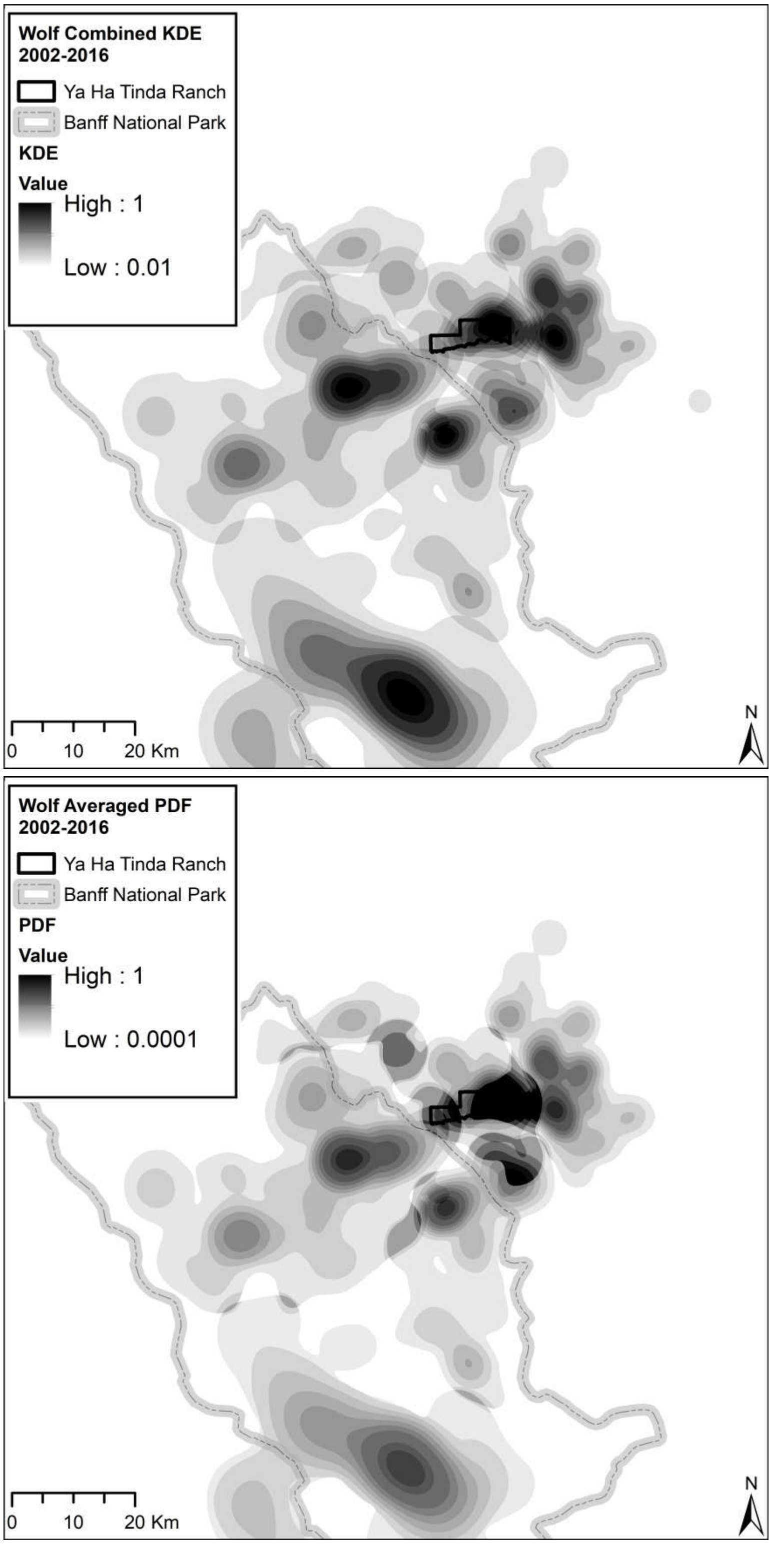
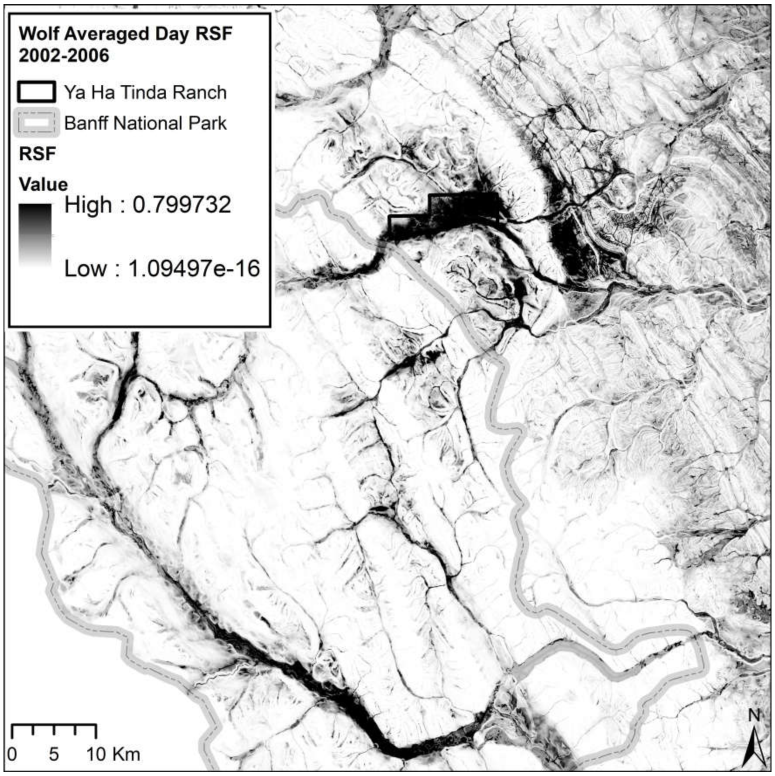


Figure G.3. Kernel Density Estimate of 5 wolf packs combined (top) and averaged Probability Density Function (PDF; bottom) from the eastern slopes of Banff National Park, Alberta, Canada, 2002 – 2016. Density functions were calculated separately for each wolf pack, then combined and weighted by the average size of each pack to create the PDF.



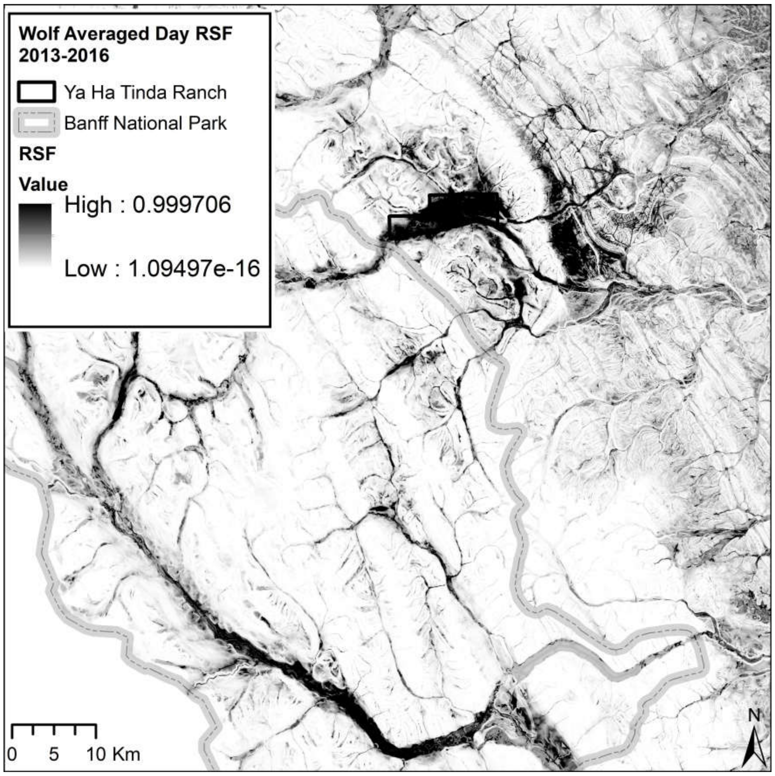


Figure G.4. Maps of predation risk by wolves for elk during the day in 2002 – 2006 (top) and 2013 – 2016 (bottom) created by combining pack size, spatial density of use, and pack-level resource selection in the eastern slopes of Banff National Park, Alberta, Canada.

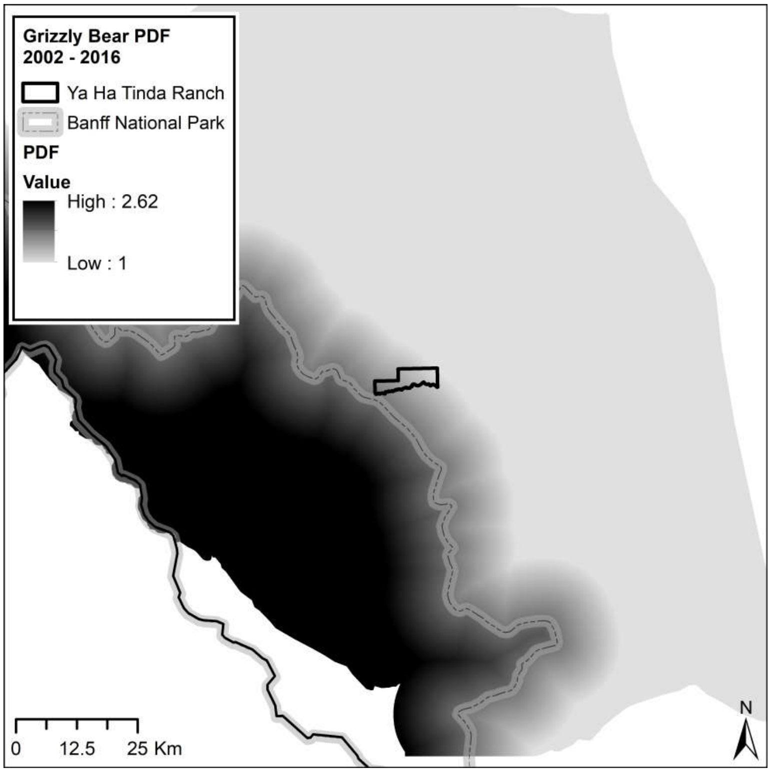


Figure G.5. Grizzly bear Probability Density Function (PDF) used to create maps of resource selection and predation risk in the eastern slopes of Banff National Park, Alberta, Canada, 2002 – 2016.

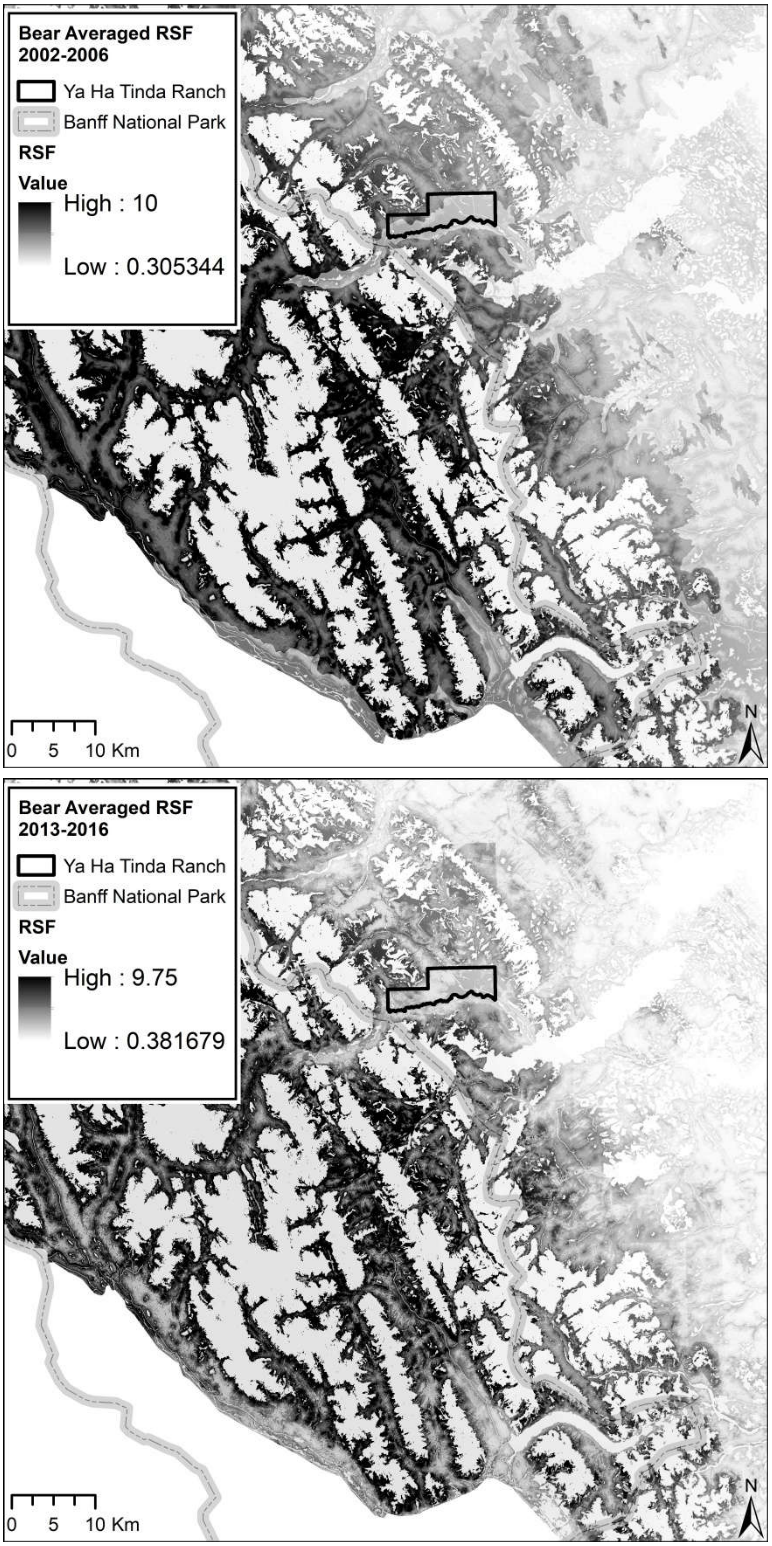


Figure G.6. Maps of predation risk by bears for elk in 2002 – 2006 (top) and 2013 – 2016 (bottom) created by combining spatial density of use and resource selection in the eastern slopes of Banff National Park, Alberta, Canada.

APPENDIX H. POTENTIAL FOR TRADE-OFFS BETWEEN FORAGE AND PREDATION RISK BY ELK AT YA HA TINDA

METHODS

To explore the potential for trade-offs between forage greenness, forage biomass, open habitat, and predation risk made by maternal elk following each migratory tactic (early [2002 – 2006] and late [2013 – 2016] western migrants, early and late residents, and eastern migrants [late only]), we used Pearson's product moment correlation tests. Points (*n* = 500) were distributed randomly throughout each migratory tactic's 95% utilization distribution, created with fixed-kernel analysis and the plug-in method for the smoothing factor in the ks package of program R (Duong 2018). The points were then buffered by a radius of 1,860 m to create circular polygons of the same-sized area as the average calving area (10.87 km^2). Normalized Difference Vegetation Index (NDVI) and forage biomass (g/m^2) in open areas at the time of calving, the percentage of open habitat, and the resource selection function (RSF) values for bears and wolves (both day and night) were extracted from GIS layers for each year and averaged across each polygon. We examined the correlation between NDVI, forage biomass, and the RSF values for each migratory tactic by year, and also averaged the values across years within each migratory tactic to examine correlation by time period.

RESULTS

Overall, positive correlations between forage biomass and RSF values for wolves, and NDVI and RSF values for wolves, indicated there is the potential for western migrants and residents to make trade-offs between forage biomass and forage greenness and predation risk by wolves (Table H.1 – G.4). This did not hold true for forage greenness for residents in 2015, when the relationship between NDVI and RSF values for wolves was negative, or for eastern migrants (Table H.5). Positive correlation between forage biomass and RSF values for bears, and NDVI and RSF values for bears, indicated the potential for trade-offs to be made by eastern migrants during the late period (Table H.5).

Table H.1. Results from Pearson correlation analyses between predation and habitat characteristics of calving areas of western migrant elk by year and averaged across 2002 – 2006, in the Ya Ha Tinda study area, Alberta, Canada. The correlation coefficient, *r*, is displayed; bold marks significant correlation at least at the 0.05 level while values in red indicate a switch in the sign of the relationship from year to year.

2002	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.836**	---				
% Herb-Shrub	**0.512**	**0.523**	---			
% Forest	**0.466**	**0.574**	**0.182**	---		
Wolf	**0.372**	**0.440**	**0.576**	**0.184**	---	
Bear	**-0.103**	0.010	**-0.105**	**0.261**	-0.019	---

2003	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.800**	---				
% Herb-Shrub	**0.503**	**0.481**	---			
% Forest	**0.547**	**0.608**	**0.182**	---		
Wolf	**0.368**	**0.451**	**0.571**	**0.200**	---	
Bear	0.014	**0.103**	**-0.105**	**0.254**	-0.002	---

2004	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.824**	---				
% Herb-Shrub	**0.513**	**0.587**	---			
% Forest	**0.555**	**0.620**	**0.185**	---		
Wolf	**0.338**	**0.462**	**0.554**	**0.167**	---	
Bear	-0.001	0.017	**-0.105**	**0.252**	0.020	---

2005	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.727**	---				
% Herb-Shrub	**0.354**	**0.520**	---			
% Forest	**0.389**	**0.577**	**0.182**	---		
Wolf	**0.233**	**0.439**	**0.594**	**0.159**	---	
Bear	-0.014	0.054	**-0.093**	**0.265**	-0.027	---

2006	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.663**	---				
% Herb-Shrub	**0.311**	**0.387**	---			
% Forest	**0.344**	**0.534**	**0.191**	---		
Wolf	**0.219**	**0.389**	**0.576**	**0.186**	---	
Bear	0.067	**0.230**	-0.017	**0.356**	-0.001	---

2002 - 2006	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.792**	---				
% Herb-Shrub	**0.482**	**0.517**	---			
% Forest	**0.506**	**0.600**	**0.181**	---		
Wolf	**0.340**	**0.457**	**0.579**	**0.182**	---	
Bear	-0.004	0.087	-0.085	**0.282**	-0.006	---

Table H.2. Results from Pearson correlation analyses between predation and habitat characteristics of calving areas of western migrant elk by year and averaged across 2013 – 2016, in the Ya Ha Tinda study area, Alberta, Canada. The correlation coefficient, *r*, is displayed; bold marks significant correlation at least at the 0.05 level while values in red indicate a switch in the sign of the relationship from year to year.

2013	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.631**	---				
% Herb-Shrub	**0.253**	**0.537**	---			
% Forest	**0.222**	**0.411**	**-0.098**	---		
Wolf	**0.215**	**0.424**	**0.530**	**-0.105**	---	
Bear	-0.014	**-0.130**	**-0.319**	**0.314**	**-0.274**	---

2014	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.720**	---				
% Herb-Shrub	**0.272**	**0.528**	---			
% Forest	**0.246**	**0.387**	**-0.098**	---		
Wolf	**0.358**	**0.499**	**0.513**	-0.077	---	
Bear	**-0.097**	**-0.239**	**-0.218**	**0.118**	**-0.224**	---

2015	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.527**	---				
% Herb-Shrub	0.078	**0.291**	---			
% Forest	**0.278**	**0.458**	**-0.097**	---		
Wolf	**0.103**	**0.321**	**0.525**	**-0.106**	---	
Bear	0.051	**-0.153**	**-0.210**	**0.114**	**-0.235**	---

2016	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.485**	---				
% Herb-Shrub	**0.11**	**0.459**	---			
% Forest	**0.268**	**0.416**	**-0.097**	---		
Wolf	**0.281**	**0.421**	**0.508**	-0.076	---	
Bear	-0.023	**-0.220**	**-0.210**	**0.114**	**-0.230**	---

2013 - 2016	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.577**	---				
% Herb-Shrub	**0.206**	**0.473**	---			
% Forest	**0.276**	**0.432**	**-0.098**	---		
Wolf	**0.268**	**0.436**	**0.519**	**-0.091**	---	
Bear	-0.018	**-0.193**	**-0.251**	**0.176**	**-0.249**	---

Table H.3. Results from Pearson correlation analyses between predation and habitat characteristics of calving areas of resident elk by year and averaged across 2002 – 2006, in the Ya Ha Tinda study area, Alberta, Canada. The correlation coefficient, *r*, is displayed; bold marks significant correlation at least at the 0.05 level while values in red indicate a switch in the sign of the relationship from year to year.

2002	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.904**	---				
% Herb-Shrub	**0.310**	**0.493**	---			
% Forest	**0.462**	**0.358**	**-0.337**	---		
Wolf	**0.451**	**0.527**	**0.636**	-0.055	---	
Bear	**-0.251**	**-0.258**	**-0.307**	**0.101**	**-0.259**	---

2003	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.846**	---				
% Herb-Shrub	**0.380**	**0.523**	---			
% Forest	**0.564**	**0.343**	**-0.337**	---		
Wolf	**0.466**	**0.515**	**0.646**	-0.067	---	
Bear	**-0.182**	**-0.243**	**-0.307**	**0.101**	**-0.256**	---

2004	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.869**	---				
% Herb-Shrub	**0.424**	**0.650**	---			
% Forest	**0.543**	**0.310**	**-0.330**	---		
Wolf	**0.430**	**0.549**	**0.666**	**-0.107**	---	
Bear	**-0.188**	**-0.294**	**-0.307**	**0.092**	**-0.266**	---

2005	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.670**	---				
% Herb-Shrub	**0.228**	**0.639**	---			
% Forest	**0.616**	**0.269**	**-0.335**	---		
Wolf	**0.256**	**0.537**	**0.683**	**-0.111**	---	
Bear	-0.058	**-0.289**	**-0.310**	**0.100**	**-0.273**	---

2006	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.623**	---				
% Herb-Shrub	0.032	**0.426**	---			
% Forest	**0.539**	**0.279**	**-0.321**	---		
Wolf	**0.099**	**0.400**	**0.648**	-0.044	---	
Bear	-0.041	**-0.214**	**-0.323**	-0.041	**-0.262**	---

2002 - 2006	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.863**	---				
% Herb-Shrub	**0.353**	**0.572**	---			
% Forest	**0.572**	**0.318**	**-0.332**	---		
Wolf	**0.437**	**0.526**	**0.658**	-0.077	---	
Bear	**-0.208**	**-0.287**	**-0.323**	0.073	**-0.274**	---

Table H.4. Results from Pearson correlation analyses between predation and habitat characteristics of calving areas of resident elk by year and averaged across 2013 – 2016, in the Ya Ha Tinda study area, Alberta, Canada. The correlation coefficient, *r*, is displayed; bold marks significant correlation at least at the 0.05 level while values in red indicate a switch in the sign of the relationship from year to year.

2013	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.695**	---				
% Herb-Shrub	0.045	**0.588**	---			
% Forest	**0.654**	**0.325**	**-0.145**	---		
Wolf	0.068	**0.372**	**0.348**	**-0.327**	---	
Bear	-0.053	**-0.345**	**-0.386**	0.061	**-0.318**	---

2014	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.925**	---				
% Herb-Shrub	**0.291**	**0.567**	---			
% Forest	**0.290**	**0.209**	**-0.145**	---		
Wolf	**0.438**	**0.468**	**0.351**	**-0.337**	---	
Bear	**-0.366**	**-0.359**	**-0.154**	0.074	**-0.267**	---

2015	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.134**	---				
% Herb-Shrub	**-0.298**	**0.373**	---			
% Forest	**0.430**	**0.133**	**-0.145**	---		
Wolf	**-0.297**	**0.432**	**0.352**	**-0.335**	---	
Bear	0.109	**-0.276**	**-0.141**	0.054	**-0.257**	---

2016	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.374**	---				
% Herb-Shrub	**-0.243**	**0.594**	---			
% Forest	**0.158**	**0.204**	**-0.145**	---		
Wolf	**0.192**	**0.452**	**0.337**	**-0.320**	---	
Bear	**-0.156**	**-0.294**	**-0.141**	0.054	**-0.253**	---

2013 - 2016	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.783**	---				
% Herb-Shrub	0.076	**0.555**	---			
% Forest	**0.453**	**0.225**	**-0.145**	---		
Wolf	0.293	**0.449**	**0.348**	**-0.330**	---	
Bear	**-0.273**	**-0.351**	**-0.218**	0.065	**-0.293**	---

Table H.5. Results from Pearson correlation analyses between predation and habitat characteristics of calving areas of eastern migrant elk by year and averaged across 2013 – 2016, in the Ya Ha Tinda study area, Alberta, Canada. The correlation coefficient, *r*, is displayed; bold marks significant correlation at least at the 0.05 level while values in red indicate a switch in the sign of the relationship from year to year.

2013	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.584**	---				
% Herb-Shrub	**0.404**	**0.798**	---			
% Forest	**0.523**	**0.614**	**0.350**	---		
Wolf	**-0.116**	**-0.154**	**-0.113**	**-0.291**	---	
Bear	0.029	**0.212**	**0.225**	**0.408**	**-0.161**	---

2014	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Biomass	**0.710**	---				
% Herb-Shrub	**0.560**	**0.804**	---			
% Forest	**0.671**	**0.672**	**0.351**	---		
Wolf	**-0.145**	**-0.175**	**-0.126**	**-0.298**	---	
Bear	0.133	**0.113**	**0.141**	**0.267**	-0.067	---

2015	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.543**	---				
% Herb-Shrub	**0.395**	**0.772**	---			
% Forest	**0.309**	**0.682**	**0.351**	---		
Wolf	0.020	**-0.216**	**-0.136**	**-0.333**	---	
Bear	0.013	**0.128**	**0.131**	**0.275**	-0.079	---

2016	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Biomass	**0.595**	---				
% Herb-Shrub	**0.447**	**0.785**	---			
% Forest	**0.354**	**0.694**	**0.351**	---		
Wolf	0.017	**-0.183**	**-0.123**	**-0.296**	---	
Bear	0.026	**0.129**	**0.131**	**0.275**	-0.066	---

2013 - 2016	NDVI	Forage	% Hrb/Shr	% Forest	Wolf	Bear
NDVI	---					
Forage	**0.657**	---				
% Herb-Shrub	**0.493**	**0.795**	---			
% Forest	**0.526**	**0.670**	**0.351**	---		
Wolf	-0.072	**-0.183**	**-0.126**	**-0.306**	---	
Bear	0.050	**0.160**	**0.173**	**0.335**	**-0.108**	---

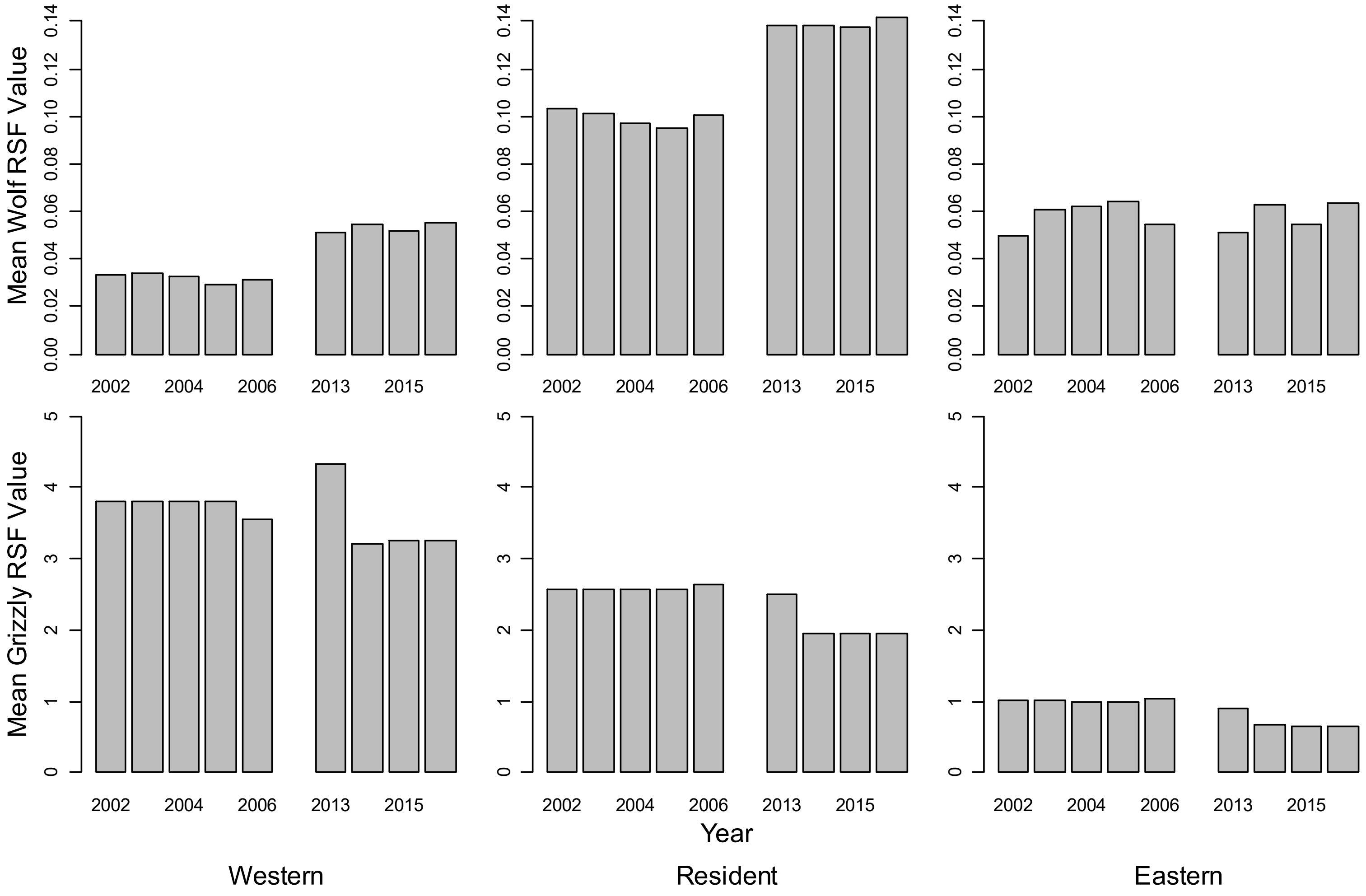


Figure H.1. Predation characteristics of calving areas of elk with 3 different migratory tactics and 2 time periods (early: 2002 – 2006 and late: 2013 – 2016) in the Ya Ha Tinda elk population, Alberta, Canada.

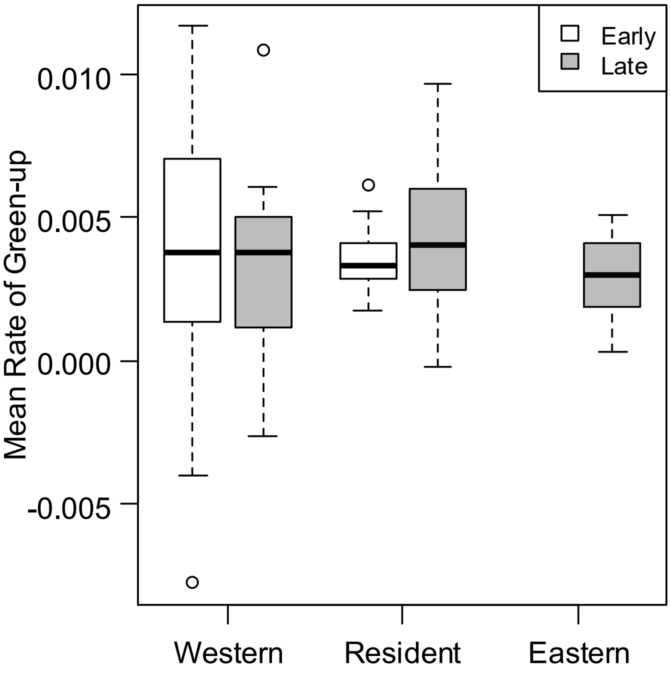


Figure H.2. Mean rate of forage green-up on 26-day calving areas (*n* = 131) of elk with 3 different migratory tactics and during 2 time periods (early: 2002 – 2006 and late: 2013 – 2016) in the Ya Ha Tinda elk population herd, Alberta, Canada.

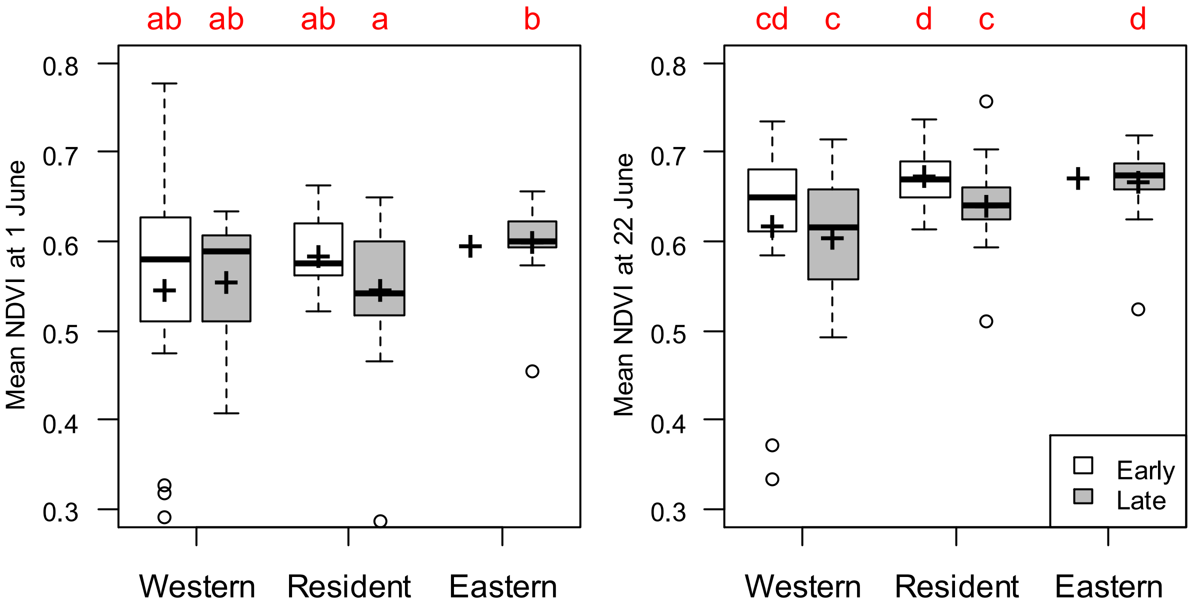


Figure H.3. Differences in forage greenness (NDVI) on 1 June (median date of calving) and 22 June (peak lactation) averaged across calving areas of elk with 3 different migratory tactics and 2 time periods (early: 2002 – 2006 and late: 2013 – 2016) in the Ya Ha Tinda elk population, Alberta, Canada. The mean for each migratory tactic-year is shown by the + symbol; there were very few eastern migrants during the early years, so we used the calving areas of eastern migrants from the later years to show what NDVI would've been in those same areas.

APPENDIX I. SELECTION BY ELK FOR CALF-REARING AREAS AT YA HA TINDA

Table I.1. Results of fitting univariable conditional logistic regression models for selection of predation and habitat characteristics within calving areas relative to areas used during summer for migrant and resident elk in the Ya Ha Tinda population, Alberta, Canada. The metrics considered for predation included wolf (Wolf) and bear (Bear) resource selection function values, and habitat characteristics included % herbaceous or shrub (Hrb/Shr), % forest (Forest), % edge (Edge), % burned (Burn), % cut (Cut), forage greenness measured by Normalized Vegetation Difference Index (NDVI), and forage biomass available (g/m^2; Forage). Shown are the parameter estimates (β), standard error (SE), selection strength (SS), 95% confidence interval (CI) for the SS, and the likelihood ratio test statistic (*G*) and *P* value (*P*).

Time Period	Mig. Tactic	Model Term	Parameter Est.	SE	SS	SS 95% LCI	SS 95% UCI	*G*	*P*
2002 - 2006	Western	Wolf	0.62	0.45	1.86	0.76	4.51	1.66	0.20
		Bear	0.92	0.40	2.52	1.14	5.55	6.16	0.01
		NDVI	0.73	0.29	2.08	1.17	3.71	7.35	0.01
		Forage	0.27	0.28	1.31	0.76	2.24	0.93	0.34
		% Herb-Shrub	1.34	0.45	3.81	1.56	9.28	10.70	0.00
		% Edge	-0.08	0.34	0.92	0.48	1.79	0.05	0.82
		% Burn	0.13	0.69	1.13	0.30	4.36	0.03	0.86
		% Cut	--	--	--	--	--	--	--
	Resident	Wolf	1.88	0.45	6.56	2.74	15.72	25.80	0.00
		Bear	-0.53	0.66	0.59	0.16	2.14	0.68	0.41
		NDVI	2.46	0.74	11.73	2.74	50.18	13.20	0.00
		Forage	1.27	0.48	3.57	1.39	9.14	8.67	0.00
		% Herb-Shrub	2.29	0.52	9.86	3.56	27.32	33.90	0.00
		% Edge	-2.86	0.82	0.06	0.01	0.29	24.80	0.00
		% Burn	0.94	0.85	2.56	0.48	13.50	1.16	0.28
		% Cut	-3.27	4.15	0.04	0.00	128.86	1.40	0.24
2013 - 2016	Western	Wolf	-0.35	0.46	0.70	0.28	1.74	0.64	0.42
		Bear	1.28	0.47	3.59	1.43	9.02	10.00	0.00
		NDVI	0.88	0.35	2.41	1.21	4.79	7.42	0.01
		Forage	0.15	0.32	1.16	0.62	2.18	0.21	0.65
		% Herb-Shrub	0.38	0.35	1.46	0.74	2.88	1.18	0.28
		% Edge	0.15	0.25	1.17	0.72	1.89	0.36	0.55
		% Burn	0.28	0.31	1.32	0.72	2.40	0.77	0.38
		% Cut	--	--	--	--	--	--	--
	Resident	Wolf	0.86	0.18	2.36	1.64	3.39	27.20	0.00
		Bear	-1.32	0.55	0.27	0.09	0.79	6.24	0.01
		NDVI	1.52	0.31	4.56	2.47	8.40	27.40	0.00

	Forage	1.28	0.29	3.58	2.03	6.33	25.10	0.00
	% Herb-Shrub	0.92	0.19	2.50	1.74	3.59	29.70	0.00
	% Edge	-0.98	0.25	0.37	0.23	0.61	20.20	0.00
	% Burn	-0.01	0.17	0.99	0.71	1.39	0.00	0.96
	% Cut	2.85	2.23	17.29	0.22	1358.72	1.47	0.23
Eastern	Wolf	-1.39	1.15	0.25	0.03	2.36	1.88	0.17
	Bear	2.26	1.15	9.63	1.02	90.99	4.11	0.04
	NDVI	0.79	0.48	2.21	0.85	5.71	2.98	0.08
	Forage	0.52	0.20	1.68	1.13	2.50	6.54	0.01
	% Herb-Shrub	1.03	0.31	2.80	1.51	5.17	10.20	0.00
	% Edge	0.21	0.19	1.24	0.85	1.80	1.28	0.26
	% Burn	-0.50	0.22	0.60	0.39	0.94	6.52	0.01
	% Cut	0.27	0.13	1.31	1.02	1.68	4.51	0.03

Table I.2. Results of top models for selection of predation and habitat characteristics within calving areas relative to areas used during summer for migrant and resident elk in the Ya Ha Tinda population, Alberta, Canada. The metrics considered for predation included wolf (Wolf) and bear (Bear) resource selection function values, and habitat characteristics included % herbaceous or shrub (Hrb/Shr), % forest (Forest), % edge (Edge), % burned (Burn), % cut (Cut), forage greenness measured by Normalized Vegetation Difference Index (NDVI), and forage biomass available (g/m^2; Forage). Shown are the number of parameters (k), deviance, log likelihood (LL), Akaike's Information Criterion adjusted for small sample size (AICc), and model weights.

Time Period	Mig. Tactic	Model	k	Dev.	LL	AICc	ΔAICc	Wt
2002 - 2006	Western	Hrb/Shr*NDVI + Bear	4	38.32	-19.16	46.33	0.00	0.80
		Bear*Hrb/Shr + NDVI	4	43.00	-21.50	50.99	4.66	0.08
		Bear*NDVI + Hrb/Shr	4	44.62	-22.31	52.62	6.29	0.03
		Bear + Hrb/Shr + NDVI	3	47.18	-23.59	53.17	6.84	0.02
		Bear + Hrb/Shr + NDVI + Burn	4	45.86	-22.93	53.85	7.52	0.02
		Bear + Hrb/Shr + NDVI + Forest	4	46.42	-23.21	54.43	8.10	0.02
		Bear + Hrb/Shr + NDVI + Edge	4	46.58	-23.29	54.57	8.24	0.02
		Wolf + Bear + Hrb/Shr + NDVI	4	46.96	-23.48	54.95	8.62	0.01
		Bear + Hrb/Shr + NDVI + Cut	4	47.22	-23.61	55.22	8.89	0.01
	Resident	NDVI + Forest	2	40.46	-20.23	44.47	0.00	0.34
		Wolf + NDVI + Forest + Cut	4	37.40	-18.70	45.41	0.94	0.21
		NDVI*Forest	3	39.50	-19.75	45.50	1.03	0.20
		NDVI + Forest + Bear	3	40.42	-20.21	46.43	1.96	0.13
		NDVI + Forest + Burn	3	40.50	-20.25	46.50	2.03	0.12
2013 - 2016	Western	Bear*Forest + NDVI	4	48.60	-24.30	56.60	0.00	0.30
		Bear + NDVI + Forest	3	51.72	-25.86	57.72	1.12	0.17
		Bear + NDVI + Edge	3	52.60	-26.30	58.59	1.99	0.11
		Bear + NDVI + Hrb/Shr	3	53.04	-26.52	59.05	2.45	0.09
		Bear + NDVI	2	55.18	-27.59	59.19	2.59	0.08
		NDVI*Forest + Bear	4	51.46	-25.73	59.47	2.87	0.07
		Bear*NDVI + Forest	4	51.80	-25.90	59.80	3.20	0.06
		Bear + NDVI + Burn	3	54.68	-27.34	60.69	4.09	0.04

	Bear + NDVI + Forage	3	54.92	-27.46	60.92	4.32	0.04
	Bear + NDVI + Wolf	3	54.98	-27.49	60.98	4.38	0.03
Resident	Forage*Hrb/Shr + NDVI*Forage + Forest	6	142.78	-71.39	154.79	0.00	0.88
	Forage*Hrb/Shr + NDVI + Forest	5	149.32	-74.66	159.31	4.52	0.09
	Forage*Hrb/Shr + Forage*Forest + NDVI	6	149.18	-74.59	161.19	6.40	0.04
	Forage*Forest + NDVI + Hrb/Shr	5	163.62	-81.81	173.62	18.83	0.00
	NDVI*Forage + Forest + Hrb/Shr	5	171.78	-85.89	181.79	27.00	0.00
	NDVI*Forest + Forage + Hrb/Shr	5	173.64	-86.82	183.64	28.85	0.00
	Wolf + Bear + NDVI + Forage + Forest + Hrb/Shr + Cut	7	169.90	-84.95	183.91	29.12	0.00
	NDVI + Forage + Forest + Hrb/Shr	4	176.28	-88.14	184.28	29.49	0.00
	NDVI*Hrb/Shr + Forage + Forest	5	175.62	-87.81	185.63	30.84	0.00
	NDVI + Forage + Forest + Hrb/Shr + Burn	5	175.84	-87.92	185.84	31.05	0.00
	Forest*Hrb/Shr + NDVI + Forage	5	176.32	-88.16	186.32	31.53	0.00
Eastern	Burn*Cut + Wolf + NDVI + Hrb/Shr	6	81.90	-40.95	93.89	0.00	0.49
	Burn*Cut + Wolf*Cut + NDVI + Hrb/Shr	7	81.72	-40.86	95.72	1.83	0.19
	Wolf*Cut + NDVI + Hrb/Shr + Burn	6	85.24	-42.62	97.25	3.36	0.09
	Wolf + NDVI + Hrb/Shr + Burn + Cut	5	89.14	-44.57	99.14	5.25	0.03
	Hrb/Shr*Burn + Wolf + NDVI + Cut	6	87.38	-43.69	99.37	5.48	0.03
	Hrb/Shr*Cut + Wolf + NDVI + Burn	6	87.50	-43.75	99.50	5.61	0.03
	Wolf + Bear + NDVI + Hrb/Shr + Burn + Cut	6	87.68	-43.84	99.69	5.80	0.03
	Wolf*Hrb/Shr + NDVI + Burn + Cut	6	88.24	-44.12	100.24	6.35	0.02
	Wolf*NDVI + Hrb/Shr + Burn + Cut	6	88.68	-44.34	100.69	6.80	0.01
	Wolf*Burn + NDVI + Hrb/Shr + Cut	6	89.04	-44.52	101.03	7.14	0.01
	NDVI*Burn + Wolf + Hrb/Shr + Cut	6	89.12	-44.56	101.12	7.23	0.01
	Wolf + NDVI + Hrb/Shr + Burn + Cut + Forest	6	89.18	-44.59	101.18	7.29	0.01
	NDVI*Hrb/Shr + Wolf + Burn + Cut	6	89.20	-44.60	101.21	7.32	0.01
	NDVI*Cut + Wolf + Hrb/Shr + Burn	6	89.24	-44.62	101.23	7.34	0.01

* denotes an interaction between 2 variables, the main effects of which were also included in the model

Table I.3. Summary statistics for factors related to predation risk and habitat characteristics in calving areas of elk following 3 different migratory tactics and during 2 time periods (early: 2002 – 2006 and late: 2013 – 2016) in the Ya Ha Tinda elk population, Alberta, Canada. Kruskal-Wallis indicates the differences between the combined migratory tactic-time periods.

	Western Migrants				Residents				Eastern Migrants		Univariate K-W	
	Early		Late		Early		Late		Late			
	$\bar{X}$	*SE*	$\bar{X}$	*SE*	$\bar{X}$	*SE*	$\bar{X}$	*SE*	$\bar{X}$	*SE*	χ^2_4	P
Wolf	0.06	0.02	0.06	0.02	0.23	0.02	0.29	0.01	0.05	0.00	81.36	<0.0001
Bear	4.73	0.43	4.45	0.36	2.47	0.17	1.92	0.08	1.01	0.14	84.21	<0.0001
% Herb-Shrub	32.25	3.53	26.50	5.40	54.40	2.65	51.65	1.56	16.78	2.47	68.89	<0.0001
% Edge	10.33	0.92	10.90	1.91	8.02	0.63	5.43	0.62	14.73	1.15	45.60	<0.0001
% Burned	6.58	2.63	21.61	7.14	4.86	2.11	18.16	1.79	14.09	5.28	25.08	<0.0001
% Cut	0.03	0.02	0.00	0.00	0.12	0.05	0.15	0.06	15.78	1.89	82.46	<0.0001
Forage Biomass	267.96	26.49	267.63	27.34	356.05	16.43	340.56	8.86	267.34	20.55	21.59	0.0002
NDVI	0.61	0.03	0.58	0.02	0.65	0.01	0.59	0.01	0.62	0.01	17.14	0.002

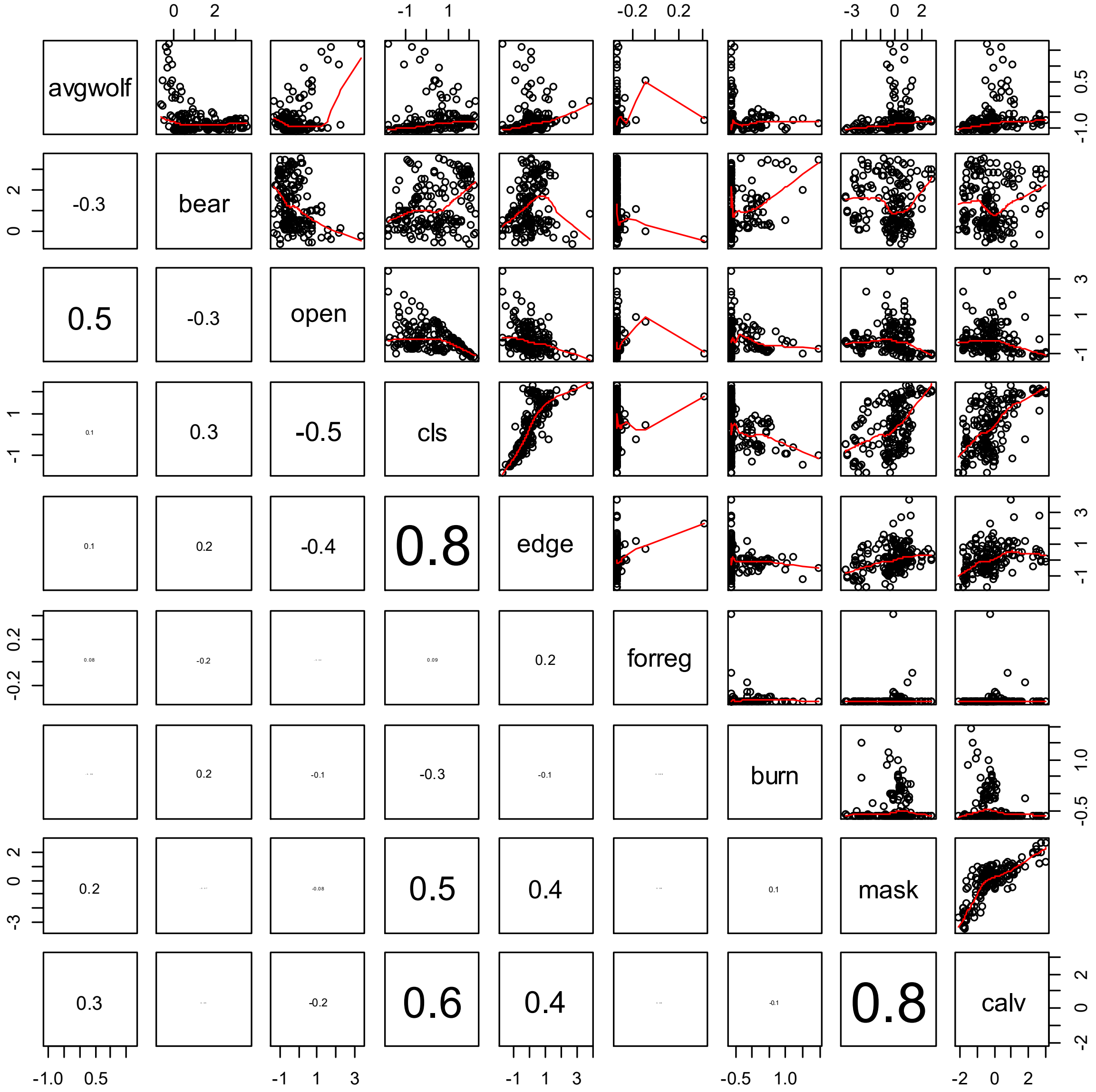


Figure I.1. Pairwise plot for early (2002 – 2006) western migrants in the Ya Ha Tinda elk population, Alberta, Canada.

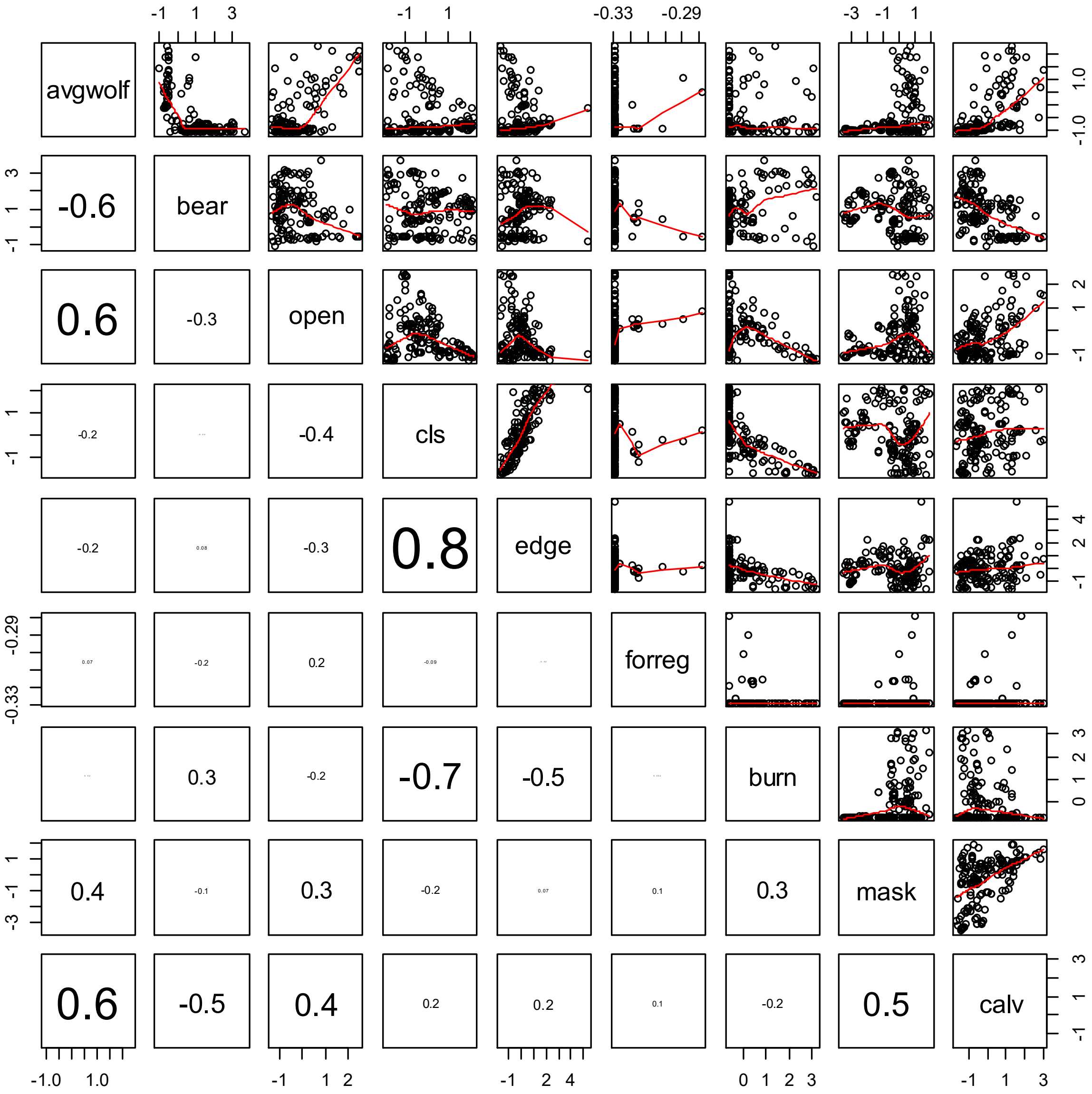


Figure I.2. Pairwise plot for late (2013 – 2016) western migrants in the Ya Ha Tinda elk population, Alberta, Canada.

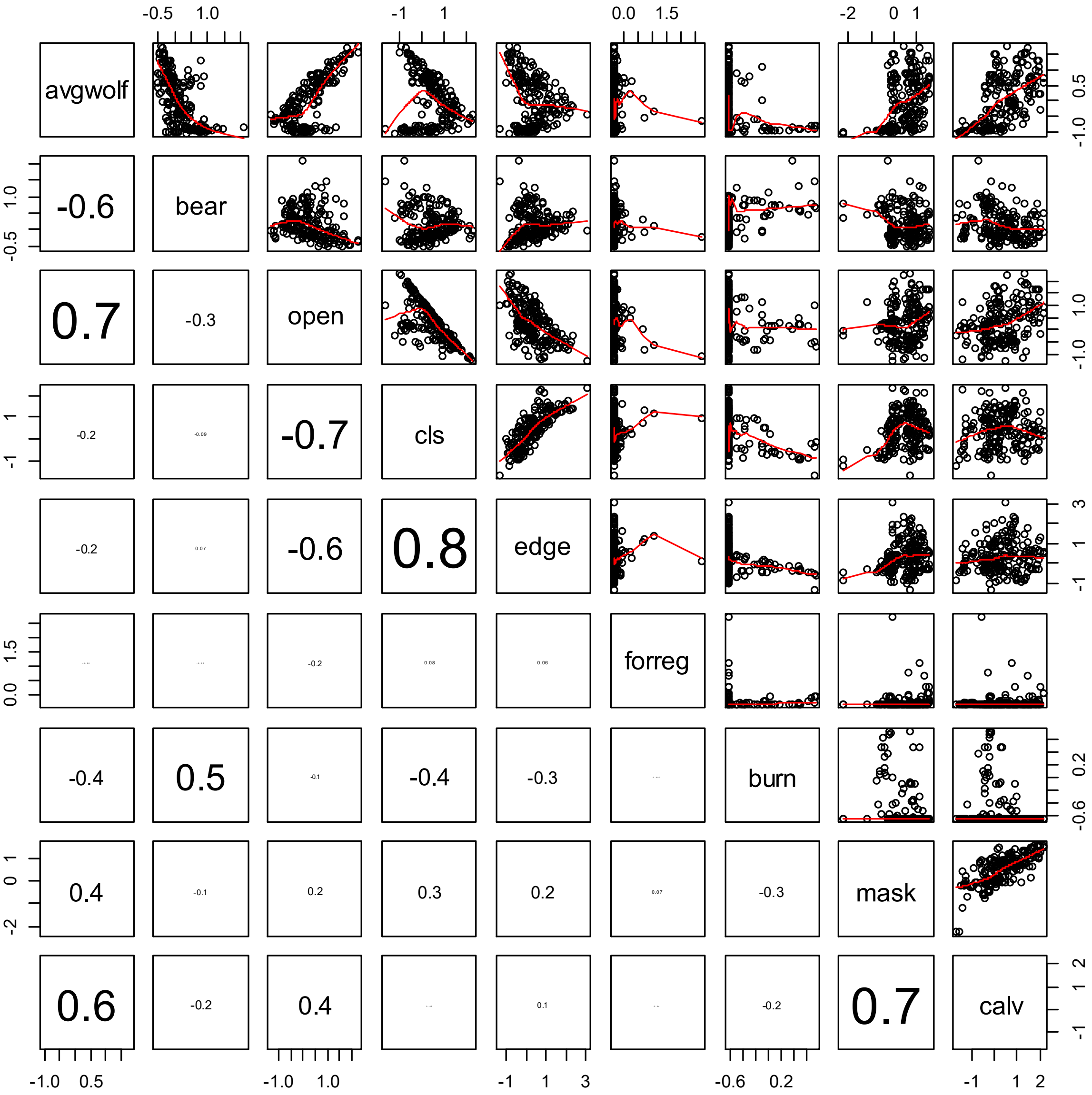


Figure I.3. Pairwise plot for early (2002 – 2006) residents in the Ya Ha Tinda elk population, Alberta, Canada.

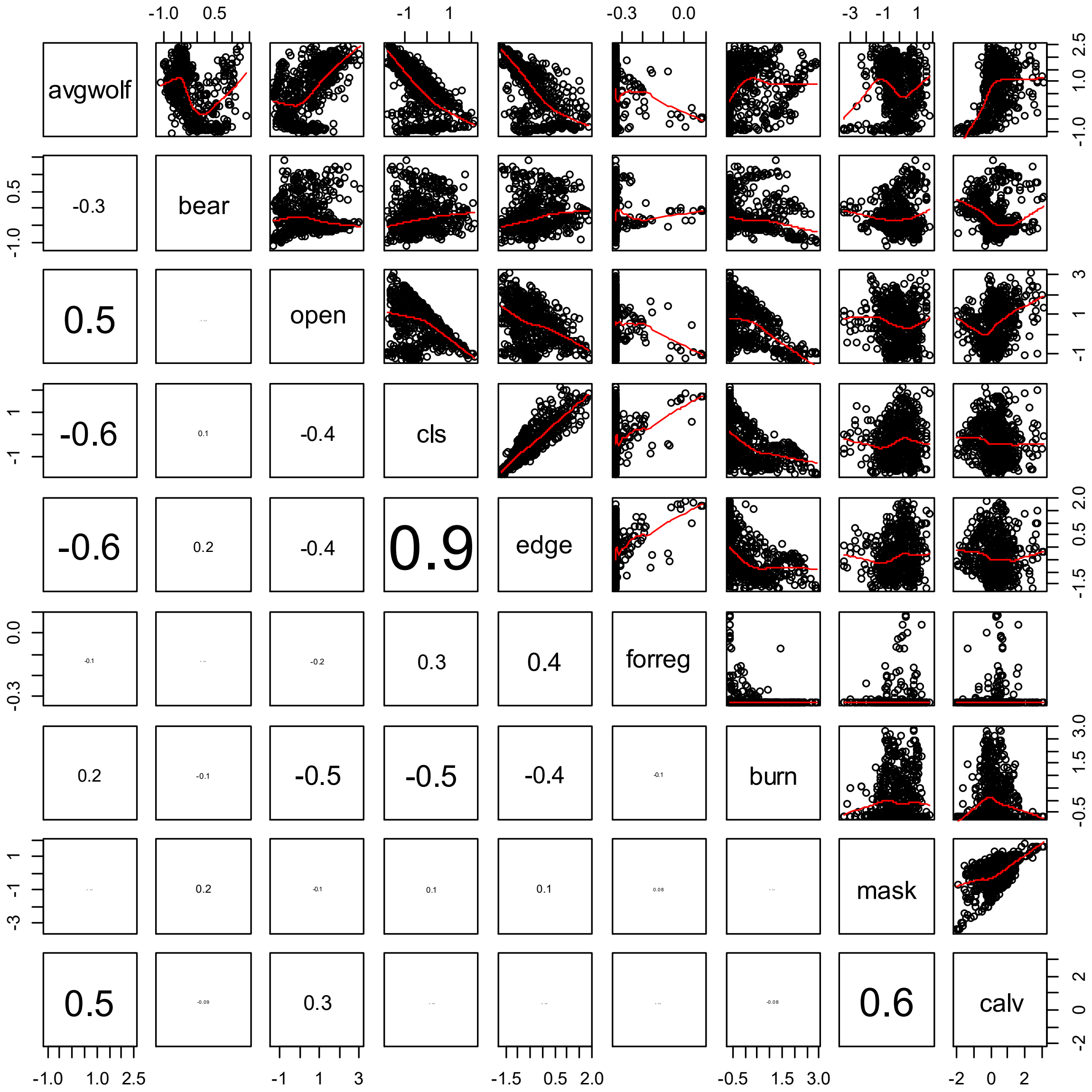


Figure I.4. Pairwise plot for late (2013 – 2016) residents in the Ya Ha Tinda elk population, Alberta, Canada.

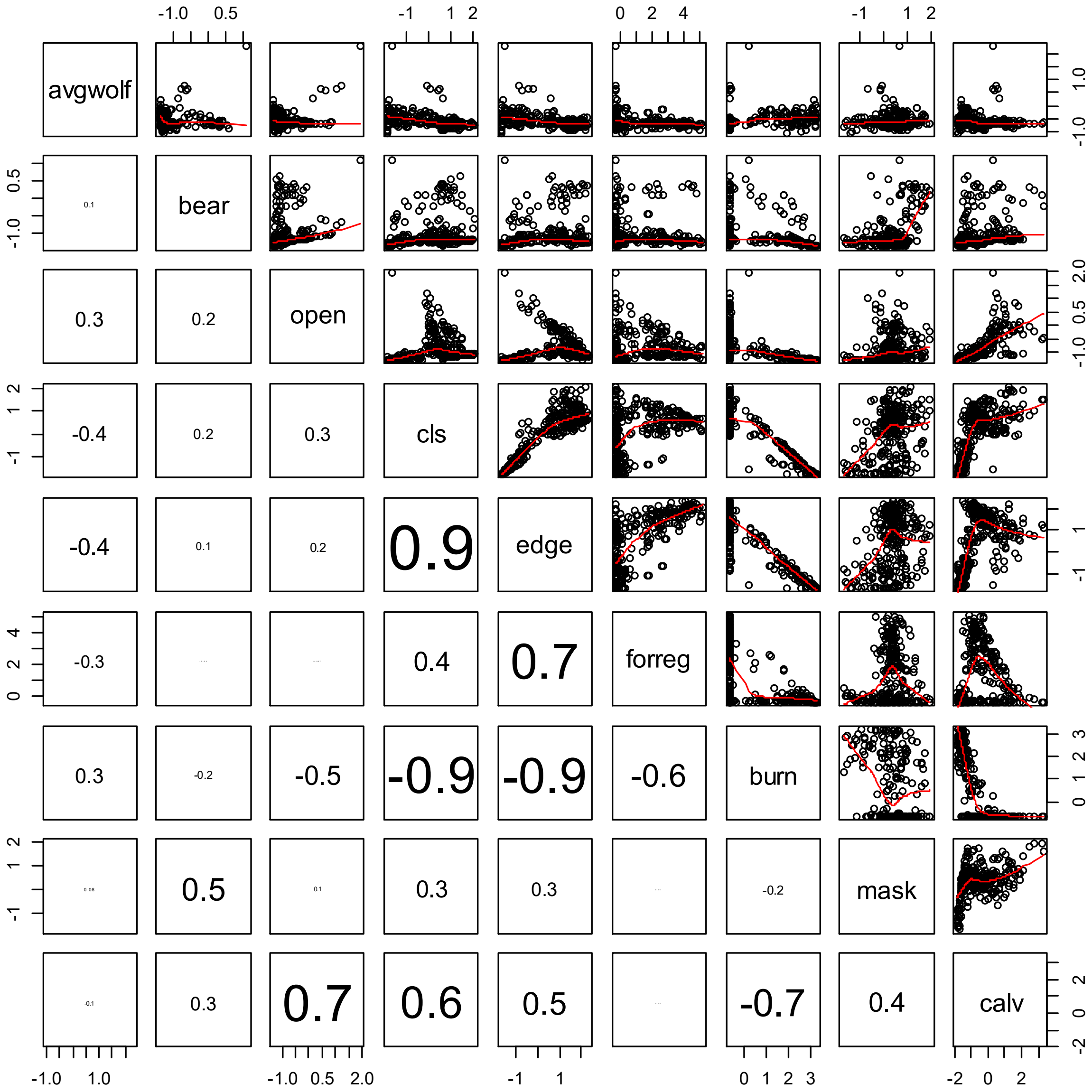


Figure I.5. Pairwise plot for eastern migrants (2013 – 2016) in the Ya Ha Tinda elk population, Alberta, Canada.

APPENDIX J. FINE-SCALE HABITAT EXPOSURE FOR ELK COW-CALF PAIRS

METHODS

Location of Plots

Plots were located at birth sites, nearby capture (i.e., hiding) sites, or subsequent relocations of elk cow-calf pairs. To relocate elk cow-calf pairs in the weeks following capture, we randomly selected without replacement at least one tagged calf each day. If we were able to obtain a visual of the calf, we recorded the GPS coordinates, bearing, and distance (m) using a rangefinder. If a visual could not be obtained and the habitat was homogeneous (i.e., a 'stand' of trees or shrubs, or open grassland), we estimated the location by walking around the elk group and taking multiple telemetry bearings of both the calf and the maternal female. If a visual could not be obtained and the habitat was very heterogeneous, the location was deemed not representative of the habitat used and the effort was abandoned. When possible, adult female locations were determined through downloading GPS data soon after the calf location. If the data was not downloadable, females were located with telemetry similar to the calves.

Sampling

One plot was sampled for the calf location, one for the maternal female location, and one plot was sampled for a "random" location (Figure J.1), placed equidistant from both the elk cow/calf plots, at the same distance as that between the elk cow and calf plots (e.g., if the elk cow/calf plots were 50 m from each other, the random plot was placed 50 m from the elk cow plot and 50 m from the calf plot). A coin was flipped to determine the side of the "triangle" that the random plot was placed (e.g., in the example below, whether the plot would be to the north or south of the cow/calf plots). If the cow and calf were found to be within 50 m of each other, only 1 plot was completed for both cow and calf and a random plot was placed 50 m away. When there was a visual only on the group but not the targeted animals, a random location for the cow/calf plot was chosen within the known group location. In this case, the random plot was placed 200 m away in a random direction to make sure it was outside the area of the elk group. So as not to disturb cow-calf pairs, we returned to the locations the next day or as soon as possible afterwards (within 2 weeks) to take measurements.

We extended 2 measuring tapes across plot center to create line transects of 15 m (from plot center) to each of the 4 cardinal directions. At plot center, we noted habitat type (grassland: >60% covered by grass/forbs; shrubland: >60% covered by shrubs; coniferous forest: >60% pine or spruce canopy cover; deciduous forest: >60% aspen; mixed: >60% not composed of any one type) and whether the site had been burnt or cut. We measured slope (%) with a clinometer, aspect (^{0}) with a compass, and recorded elevation (m) from a GPS unit. We estimated mean canopy cover (%) using an ocular sighting tube (i.e., toilet paper roll) at plot center, and at 10, 20, and 30 m to plot center from each of the 4 cardinal directions. We estimated distance (m) to the nearest edge (e.g., forest to clear cut, road, river) using a measuring tape or with GIS when the distance was too great to estimate in the field. To estimate mean hiding cover (%), from each of the 4 cardinal directions at 10, 20, and 30 m to plot center, we recorded the number of squares of a cover board ≥50% visible from 2 heights (i.e., kneeling and standing) to approximate the average eye height of a large predator on 4 legs or a bear standing upright (i.e., 0.5 – 1 m and 2 – 2.5 m; Panzacchi et al. 2010). Finally, we measured distance to cover as the distance (m) to the nearest grass clump, shrub, rock, etc., big enough to hide a calf lying prone.

Shrubby vegetation and down/dead cover. — Walking along the right hand side of the line transect created by the measuring tapes, we identified plants intercepted by the tape, and recorded intercept distance (i.e., starting and ending points of continuous plant cover). Cover (%) was calculated by adding all intercept distances and expressing the total as a proportion of tape length (Caratti 2006).

We recorded shrubby vegetation <1 m in height by species by noting the starting and ending points of continuous cover, ignoring gaps of <5 cm and plants <3 cm in height. Trees <1 m in height were treated as shrubs. Shrubs of specific species <1 m in height were not counted in the line intercept method, but included in the biomass plots instead. This included willow (*Salix* spp.) and kinnikinnick (*Arctostaphylos uva-ursi)* <15 cm in height. Rosa spp. were counted in the line intercept. We measured shrubby vegetation >1 m and <2 m in height by species by noting the starting and ending points of continuous cover, ignoring gaps of <5 cm and treating trees <1 m in height as shrubs.

We recorded the starting/ending points of continuous cover of down and dead logs/trees that intercepted the tape, ignoring gaps of <5 cm, and individual, small, down branches <2 cm in width, unless they were in a group of branches big enough to hide a calf; if so, the group of branches was counted as continuous cover. Down and dead trees that were >1 m in height were recorded in the 'Shrubs >1 m and <2 m in Height' category.

Biomass. — In 4 0.25-m^2 plots, located 5 and 15 m on each side of the center point, **we** estimated % forb, % grass/sedge, and % shrub (for small shrubs <15 cm in height and not included in the line intercept). For forbs and grasses, we also estimated the % green and the % standing dead of each. We clipped and bagged biomass by forbs, grass, and shrubs. Biomass was dried in the oven for 24 hr at 100°C.

Elk pellet collection. — We *c*ollected 2 samples of elk pellets at each calf, cow, or random plot and dried them in sun or in the drying oven at <50°C.

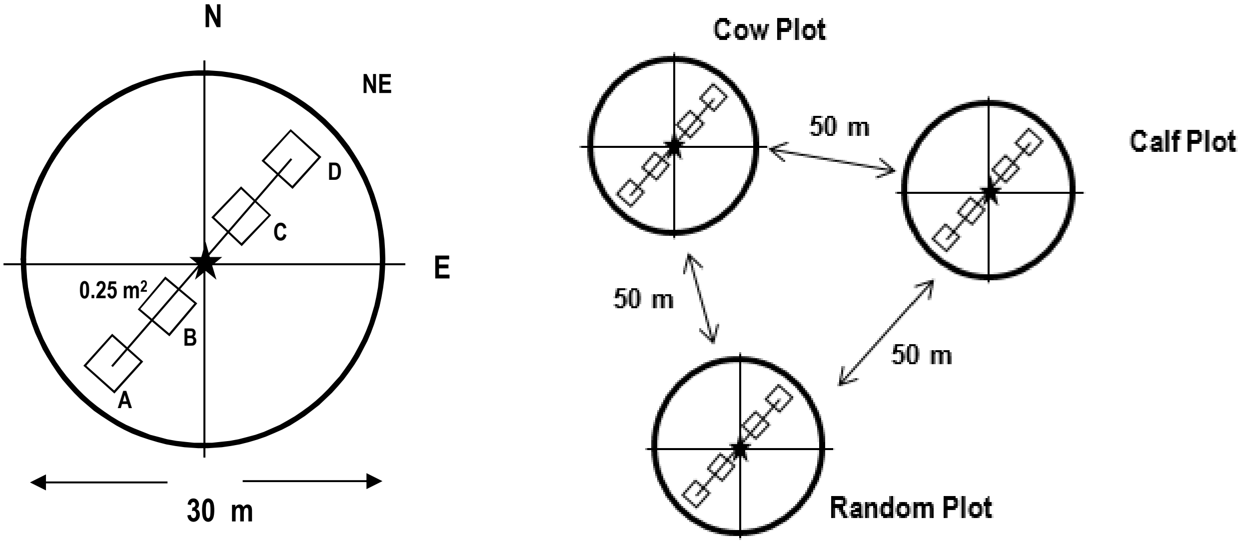


Figure J.1. Schematic diagram of sampling design for fine-scale habitat used by elk cow-calf pairs in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016.

APPENDIX K. SELECTION BY ADULT FEMALE ELK WITH AND WITHOUT CALVES

OVERVIEW

Here we report results for an analysis on a subset of animals from Chapter 3 for which calf survival was known to understand whether a calf survives or not affects selection during the 26-day calving period. We tested the assumption that selection patterns during calving relative to summer do not change given a calf dies in several ways: (1) we determined the sizes of calving areas for a subset of animals (*n* = 31) with calf mortalities known to have occurred within 26 days of parturition; (2) we examined the distribution of mortality times to understand whether most mortalities occurred immediately after parturition or were spread throughout the 26 days, which would lead to an expectation of a quick change versus constant selection patterns; (3) we tested whether including a categorical variable for calf survival in the top models of selection improved model fit; and (4) we checked for differences in use between elk with calves that survived and elk with calves that died using t-tests and the variables found in the top models of selection

RESULTS AND DISCUSSION

Of the GPS-collared animals included in the Chapter 3 analysis for which survival was known, 16 were eastern migrants (*n* = 11 calves survived, *n* = 5 died), and 36 (*n* = 10 calves survived, *n* = 26 died) were residents (Table K.1).

In Chapter 3, we identified a 26-day (± 2.03 *SE*) period during which movements of elk with known and predicted dates of parturition increased more dramatically after birth before reaching an asymptote (piecewise regression $R^2 = 0.91$, *n* = 131). The threshold for elk with calves that died within 26 days of parturition was virtually the same, estimated at 25.0 (± 1.92 *SE*) days (Figure K.1). The similar threshold indicates that maternal elk that lose their calves do not immediately expand their movements to use the same amount of area that they use outside the calving period.

Visual inspection of the mortality times of the calves that died within 26 days of parturition showed that after an initial pulse of mortalities by less than one-third of the calves within 3 days post-parturition, the distribution of mortality times up to 26 days is fairly uniform Figure K.2). This uniform distribution suggests that the results of the Chapter 3 selection analysis should be valid and fairly representative across the individuals following a particular migratory tactic, regardless of whether the individual lost its calf or not. In other words, selection should not change drastically because the majority of calves did not die right away.

Including a categorical variable for calf survival did not improve the models of selection during calving based on AIC_c (Table K.2). There were no differences in use of forage biomass available ($t_{(11)} = -0.10$, $P = 0.92$), NDVI ($t_{(34)} = -1.00$, $P = 0.33$), herbaceous/shrub habitat ($t_{(10)} = 0.61$, $P = 0.56$), or forested habitat ($t_{(10)} = -2.09$, $P = 0.06$) between residents with calves that survived and residents with calves that did not survive. There were also no difference in use of predation risk by wolves ($t_{(5)} = -0.22$, $P = 0.83$), NDVI ($t_{(14)} = -0.81$, $P = 0.43$), herbaceous/shrub habitat ($t_{(14)} = -1.26$, $P = 0.23$), burned habitat ($t_{(4)} = 1.99$, $P = 0.12$), or cut habitat ($t_{(14)} = -1.37$, $P = 0.19$) between eastern migrants with calves that survived and eastern migrants with calves that did not survive

Table K.1. Animals used to assess whether selection during calving differs between elk with calves that survived and elk with calves that died in the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016.

Adult Female Elk ID	Year	Migratory Tactic	Birth Date	Est. Age at Death (days)	Survived?
OR54_BL260_2015	2015	Resident	5/31/2015	16	0
OR61_2016	2016	Resident	6/20/2016	NA	1
OR77_2013	2013	Resident	6/5/2013	9	0
OR77_2014	2014	Resident	6/4/2014	NA	1
OR79_2013	2013	Resident	5/24/2013	NA	1
OR80_2013	2013	Resident	6/2/2013	21	0
OR80_2015	2015	Resident	6/19/2015	NA	1
OR81_2016	2016	East	5/26/2016	NA	1
OR84_2013	2013	Resident	5/19/2013	9	0
OR88_2013	2013	Resident	6/8/2013	15	0
OR92_2015	2015	East	6/3/2015	NA	1
OR94_2013	2013	East	5/25/2013	NA	1
OR97_2016	2016	Resident	5/20/2016	0	0
OR98_2014	2014	Resident	6/3/2014	4	0
OR99_2015	2015	Resident	6/1/2015	13	0
OR99_2016	2016	Resident	5/19/2016	5	0
YL100_2014	2014	Resident	5/26/2014	3	0
YL100_2015	2015	Resident	5/30/2015	NA	1
YL100_2016	2016	Resident	5/30/2016	21	0
YL101_2014	2014	Resident	5/28/2014	6	0
YL107_2015	2015	Resident	5/22/2015	2	0
YL109_OR35_2014	2014	East	5/22/2014	NA	1
YL110_OR29_2015	2015	Resident	6/4/2015	NA	1
YL111_OR6_2014	2014	East	5/18/2014	NA	1
YL112_OR38_2015	2015	Resident	6/2/2015	3	0
YL114_BL274_2014	2014	East	5/28/2014	NA	1
YL114_BL274_2016	2016	East	5/25/2016	7	0
YL115_OR34_2016	2016	Resident	6/9/2016	NA	1
YL116_OR83_2013	2013	Resident	5/28/2013	10	0
YL118_OR8_2015	2015	East	5/25/2015	NA	1
YL118_OR8_2016	2016	East	6/4/2016	8	0
YL120_BL290_2015	2015	Resident	6/1/2015	13	0
YL120_BL290_2016	2016	Resident	5/30/2016	14	0
YL123_OR7_2014	2014	East	5/27/2014	NA	1
YL124_2015	2015	Resident	5/27/2015	23	0
YL124_2016	2016	Resident	5/21/2016	2	0
YL132_OR2_2014	2014	Resident	6/3/2014	22	0
YL133_OR87_2013	2013	Resident	5/27/2013	17	0
YL133_OR87_2016	2016	Resident	5/23/2016	NA	1

YL134_BL262_2016	2016	East	6/2/2016	NA	1
YL136_BL284_2014	2014	East	5/25/2014	22	0
YL137_BE13_2016	2016	Resident	6/1/2016	1	0
YL151_YL87_2014	2014	Resident	5/14/2014	NA	1
YL151_YL87_2016	2016	Resident	5/24/2016	2	0
YL155_OR16_2016	2016	East	5/22/2016	1	0
YL156_2016	2016	Resident	6/12/2016	21	0
YL159_2016	2016	East	6/2/2016	25	0
YL161_2016	2016	Resident	5/21/2016	3	0
YL163_2016	2016	Resident	5/29/2016	NA	1
YL169_2016	2016	Resident	5/24/2016	6	0
YL171_2016	2016	East	5/27/2016	NA	1
YL172_2016	2016	East	5/22/2016	NA	1

Table K.2. Results of models, with and without a categorical variable for calf survival, for selection of predation and habitat characteristics within calving areas for migrant and resident elk in the Ya Ha Tinda population, Alberta, Canada. Shown are the number of parameters (k), deviance, log likelihood (LL), Akaike's Information Criterion adjusted for small sample size (AICc), and model weights.

Migratory Tactic	Model	k	Dev.	LL	AIC$_c$	ΔAICc	Wt.
Resident	Model[a] without survival	6	187.66	-93.83	199.66	0.00	0.52
	Model with survival	7	185.84	-92.92	199.85	0.19	0.48
Eastern	Model[b] without survival	8	79.46	-39.73	95.47	0.00	0.62
	Model with survival	9	78.50	-39.25	96.50	1.03	0.37

[a] NDVI + Herb-Shrub + Edge + Cut

[b] Wolf + NDVI + Herb-Shrub + Burn + Cut + Wolf*Cut

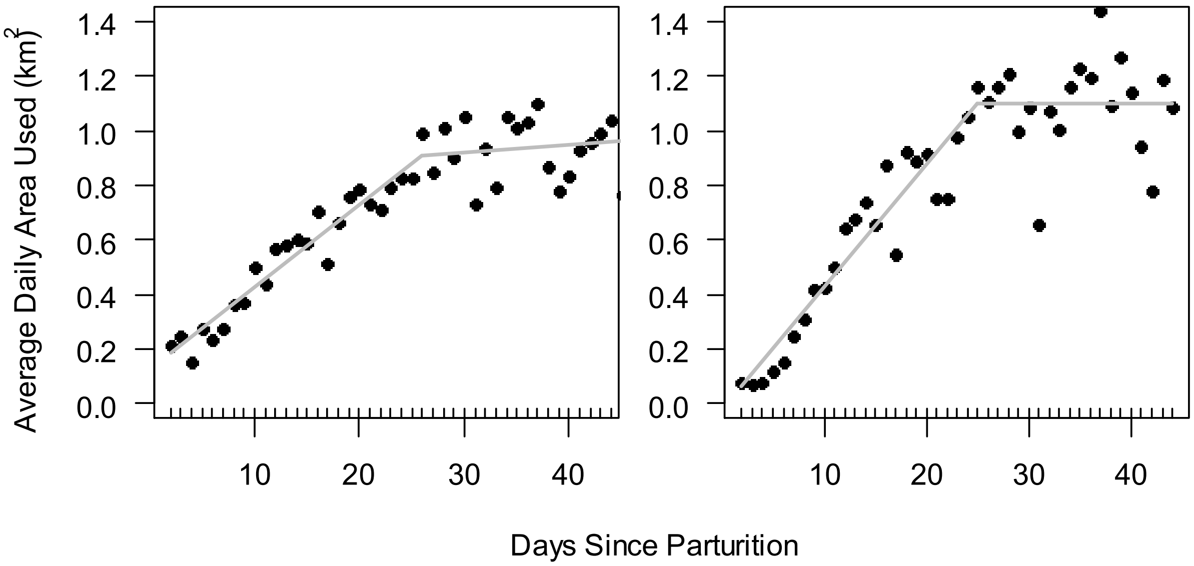


Figure K.1. Average area (km^2) used every 24 hr since day of parturition by maternal females in the Ya Ha Tinda elk population, Alberta, Canada, 2002 – 2006 and 2013 – 2016. On left is the area used by maternal females with known and predicted (*n* = 131) dates of parturition, and on right is the area used by females (*n* = 31) whose calves died within 26 days of parturition. The figure on left shows a breakpoint at 26.0 (SE: 2.03) days, and the figure on right shows a breakpoint at 25.0 (*SE*: 1.92) days. Lines represent a fitted segmented or piecewise regression model ($R^2 = 0.88$ and 0.86, respectively).

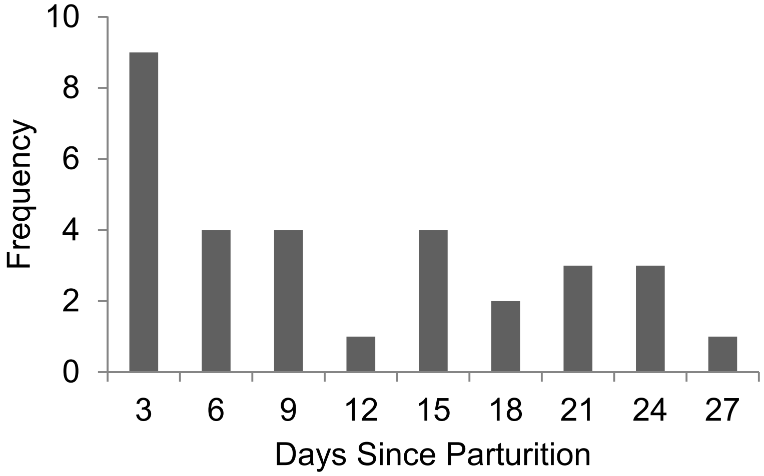


Figure K.2. Distribution of mortality times for calves (*n* = 31) from the Ya Ha Tinda elk population, Alberta, Canada, 2013 – 2016. Five calves were offspring of elk with an eastern migratory tactic, and 26 calves were offspring of elk with a resident tactic.

APPENDIX L. ESTIMATING AGE IN NEONATAL ELK: WHAT TO MEASURE?

(DRAFT IN PROGRESS)

INTRODUCTION

A juvenile ungulate's date of birth, in relation to body weight and early development, and interacting with density dependence, influences its recruitment (Clutton-Brock et al. 1987) and even its lifetime fitness (Albon et al. 1987, Plard et al. 2015). The annual variation in population trajectories of large ungulates is largely determined by the highly variable survival of juveniles (Gaillard et al. 1998, 2000, Raithel et al. 2007, Griffin et al. 2011) that are most vulnerable to mortality in their first weeks of life (Linnell et al. 1995). Thus, collecting data on neonates, particularly date of birth or age at capture, for use in age-based, staggered-entry survival models is often a goal in ungulate studies.

A common approach is to estimate date of birth from morphological metrics taken in the field during capture and shortly after birth. Body mass, chest girth, new hoof growth, and length of hind foot, tail, head, or body have been used to predict neonatal age. In neonatal deer, a number of neonatal age models have been developed (Haugen and Speake 1958, Robinette et al. 1973), with new hoof growth being the most commonly-used metric (Whittaker and Lindzey 1999, Brinkman et al. 2004). In contrast, neonatal age models for elk have not been published, and most elk calving studies continue to rely on Johnson (1951).

There is little concern towards overall accuracy or effect of sampling error on outcomes of studies employing neonatal age models (Conn and Diefenbach 2007), and few neonatal age models have been rigorously validated. The sources of accuracy in the existing models arise from 3 main problems: (1) complexity, (2) subjectivity/lack of repeatability, consistency, or applicability, and (3) sensitivity to measurement error. It may not be possible to develop a simple model that is applicable across individuals and study areas. But from an animal care perspective, we can eliminate the need to take multiple body measurements and limit handling time by determining which morphological measurements are the most important for elk calves.

Most elk researchers continue to rely on Johnson (1951) to determine age at capture. However, the Johnson method is categorical and subjective, and was developed without knowing the actual ages of calves. If actual ages are unknown, biased age estimates can arise from age misclassification, and give a false sense of security against early-survivor bias. Furthermore, key details are missing in the Johnson paper, such as whether the incisor measurement was taken at the middle of the incisor or on the outer edge. The only other neonatal elk model is not readily available because it has not been published in peer-reviewed literature (Montgomery 2005, Zager et al. 2008). In addition, this model is not recommended for wild-caught elk calves because it was developed from measurements on captive elk calves and therefore overestimates age in wild populations, likely due to differences in daily weight gain (Montgomery 2005).

Factors such as habitat, sex, multiparity, and maternal age or body condition can influence both date of birth and neonatal development (Robinette et al. 1973, Sams et al. 1996), and therefore can affect the variation in measurements meant to capture development and physiology across individuals and across study sites. Just slight changes in body mass or new hoof growth can mean big changes in age estimation (e.g., new hoof growth of just 1 mm can mean a 3-day difference in age; Brinkman et al. 2004). This is compounded by the fact that most studies do not describe methods and measurements well enough to determine if all researchers are recording specific measurements the same way; for example, hoof growth measurements are likely being measured at different spots on the hoof leading to variation.

Our objectives were to compare the outcomes of several models for aging neonatal elk to for consistency in terms of simplicity, repeatability, and sensitivity.

STUDY AREAS

We collected calf measurement data from 5 study areas across the western United States and Canada: Ya Ha Tinda (YHT) in Alberta, Canada, Sled Springs and Wenaha in Oregon, USA, and Humboldt/Del Norte (HDN) and Siskiyou/Modoc/Shasta (SMS) in northern California, USA.

During 2013-2016, we collected data from 121 calves in YHT.

During 2002 – 2007 in Oregon, USA, calves (n = 343; n = 289 complete cases) were caught in 2 adjacent areas: Sled Springs and Wenaha wildlife management units. These areas are characterized by ponderosa pine (*Pinus ponderosa*) at lower elevations with mixed stands of ponderosa pine, lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*) and Engleman spruce (*Picea engelmannii*) occurring at intermediate elevations. At the highest elevations, subalpine fir (*Abies lasiocarpa*) is the dominate species. Sled springs and Wenaha vary in elevation from about 700-1600m and both summer and winter elk ranges are found at each site. The climate is characterized by warm, dry summers and cold, snowy winters. The area is comprised of mostly public lands, managed by the U.S. Forest Service and the Oregon Department of Fish and Wildlife (ODFW).

From 2016 – 2018, calves (*n* = X; *n* = X complete cases) were caught in 2 areas: HDN along the northwestern coast of California and eastward in SMS to the vicinity of Mount Shasta. Most elk found in coastal HDN exist in coastal coniferous rainforests, mainly comprised of coast redwoods (*Sequoia sempervirens*), Douglas-fir (*Pseudotsuga menziesii*), and Sitka spruce (*Picea sitchensis)*, or open grassland and oak woodlands (Weckerly and Ricca 2000, Barbour et al. 2007). The climate is characterized by mild, dry summers and cool, but extremely wet winters (Harper et al. 1997, Weckerly and Ricca 2000). Snow is not common with winter temperatures rarely dropping below freezing, but does occur in some parts of HDN with higher elevations. The HDN study area is comprised of private, public, and tribal land, with large dairy and timber operation throughout most of the area. The SMS study area consists of……

METHODS

Calf Capture

During winters prior to calving season, Vaginal Implant Transmitters (VITs) with Precise Event Timing (PET) mechanisms (Advanced Telemetry Systems Model No. XXXX and Lotek Wireless, Inc., Iridiumtrack) were placed in pregnant, radiocollared females in the YHT, HDN, and SMS elk populations. The VITs were expelled with the calves when the elk gave birth in May through June; upon expulsion, the VITs emitted a signal that allowed birth sites to be precisely located and the time of birth to be determined to the nearest half hour. Field crews captured calves opportunistically, or by using VITs to locate calves at or near the birth sites. Once calves were captured, blindfolded, and hobbled, measurements were taken and calves were released after no more than 10 minutes of handling time.

Calf Measurements

At YHT, HDN, and SMS the following calf measurements were taken:

Tooth eruption. — In 2013-2014, we measured the inside edge and middle of both right and left incisors to the nearest 0.1 mm using Vernier calipers. In 2015-2018, we measured the inside edge, middle, and outer edge on only one incisor.

Umbilicus. — We measured the diameter of the navel umbilicus with calipers, and recorded the degree of healing within 3 categories: bloody, moist, not scabbed; little blood, lightly scabbed; or dry scab. We also noted whether part of the umbilical cord was still present and moist or dry, or absent.

Hoof growth. — Hoof growth was measured as the distance from the hairline to the growth line on the outside edge of the hoof (Brinkman et al. 2004). Hardening of the hooves (whether the walking surface was ragged or smooth, and whether the hooves themselves were entirely soft; less than half hardened; or all hardened) and the dew claws (entirely soft; upper ¼" hardened; tips soft and white; or entirely hard and dark) was also noted.

Stature and stability. — If the calf stood, we noted the calf's stature as: unable to stand; insecure, wobbly, with legs spread; somewhat sturdy; or very sturdy. We also noted whether the calf tried to run and if it was standing humped; somewhat erect; or very erect.

Weight. — Weight of the calf was taken to the nearest 0.5 lb through use of a hanging spring scale and canvas weigh bag. The weight was converted to kg, and the weight of the blindfold, hobbles, and weigh bag were subtracted from the total weight to obtain the final weight of the calf at capture.

Chest girth. — Girth of the calf was measured to the nearest 0.5 cm using a flexible cloth measuring tape, placing the tape behind the shoulders and elbows and just posterior to the crest of the withers, and pulling the tape snugly (Cook et al. 2003).

Hind leg length. — We measured the hind leg by straightening the leg, and measuring to the nearest 0.5 cm from the tip of the calcareal tuber or tarsal (ankle) to the tip of the hoof.

Sex. — Sex of the calf was determined as either male or female.

At the OR study sites, calf measurements included: sex, outside edge and middle of incisor (mm), front hoof growth (mm), and weight at capture (kg).

Incisor Estimates

To ensure that all study areas had measurements for the inside edge, middle, and outer edge of incisors, we used simple linear regression to predict the outer edge of the incisor for years in which this measurement was not taken at YHT (n = 67), and also to predict the inside edge of the incisor at the OR study site. We first fit the models separately for each study site. We then combined the YHT and OR data and included study site as a covariate.

- first determined whether inside edge or middle of incisor was best predictor for outer edge using data from YHT and CA
- whether middle or outer edge was better for inside edge
- then combined data from YHT, CA, and OR to come up with regression equation for outer edge as a function of middle at YHT, and predicted inside edge for OR

Neonatal Age Model

We used measurements from XX calves in YHT and XX calves in CA to build a model for predicting age at capture. We used a random forest (RF) with program R (rfUtilities package; Evans et al. 2011, R Core Team 2017) to model neonatal elk ages. We included …variables in the RF as possible covariates.

We first performed a variable selection bootstrap (999 times) process with the rf.modelSel function within the rfUtilities package. We then produced the final predictive model from 999 bootstrapped RF models that contained the covariates retained from the variable selection process.

We applied the RF model to XX calves with unknown ages.

RESULTS

Descriptive Statistics

Incisor Estimates

The middle of the incisor was a better predictor for the outer edge of the incisor than was inside edge, based on AIC_c (158.2 vs. 201.0 respectively). The model Outer = 0.692*Middle + 1.705 explained 81% of the variance in outer edge of incisor at YHT ($R^2 = 0.81$, $F_{1, 65} = 285.7$, $p < 0.0001$; Fig. 1). The regression equation for outer edge of incisor as a function of middle of incisor was similar at OR: Outer = 0.721*Middle + 1.586, and explained 82% of the variance ($R^2 = 0.82$, $F_{1, 328} = 1501$, $p < 0.0001$; Fig. 1). When the data for YHT and OR was combined, the regression equation was Outer = 0.718*Middle + 1.602, and explained 82% of the variance ($R^2 = 0.82$, $F_{1, 395} = 1840$, $p < 0.0001$; Fig. 2). Adding study area as a covariate did not improve the model, suggesting the equation may be useful and generalizable across study areas.

The middle of the incisor was also the better predictor for the inside edge of the incisor at YHT. The model Inside = 0.721*Middle -1.246 explained 68% of the variance in the inside edge of incisor ($R^2 = 0.68$, $F_{1, 65} = 138.3$, $p < 0.0001$; Fig. 3). Because the relationship between middle and outside edge of the incisor was similar for YHT and OR, we felt it reasonable to use the equation for the inside edge of incisor at YHT to predict the inside edge of incisor at OR.

Neonatal Age Model

- In a random forest framework, model with both categorical and continuous predictors performed best.
- But the model with only categorical predictors was close → quicker and easier to use categorical predictors in the field and take only 1-2 measurements

Table L.1. Mean measurements (range) taken on elk calves captured in the Ya Ha Tinda population, Alberta, Canada, 2013 - 2016.

			Standard Measurements								
			millimeters							centimeters	
	Age Class	# of Calves	Navel Diam.	Left Incisor Inside	Left Incisor Middle	Right Incisor Inside	Right Incisor Middle	Incisor Outer	Hoof Growth Line to Hair Line	Chest Girth	Right Hind Leg
A	Newborn	88	13.0	0.7	3.1	1.1	3.5	3.6	10.6	60.7	41.3
	- 1 day		(6.0 - 27.0)	(0.0 - 4.6)	(0.0 - 8.6)	(0.0 - 5.0)	(0.0 - 8.7)	(1.0 - 6.1)	(4.2 - 19.0)	(41.0 - 76.0)	(31.0 - 46.0)
B	2-4 days	14	11.3	2.4	4.4	2.6	4.4	4.5	11.4	62.2	40.7
			(4.2 - 19.1)	(0.0 - 4.5)	(2.2 - 6.5)	(0.0 - 3.9)	(1.4 - 6.5)	(3.2 - 5.6)	(4.5 - 14.7)	(47.5 - 73.0)	(31.5 - 44.5)
C	5-7 days	3	7.0	3.2	4.8	4.6	6.5	2.5	10.1	64.6	41.0
			(5.0 - 8.5)	(1.5 - 4.8)	(2.0 - 8.2)	(4.5 - 4.7)	--	--	(7.1 - 13.0)	(53.0 - 70.8)	(37.0 - 44.0)
D	8+ days	1	12.6	6.2	8	6.3	8.7	--	9.5	68	43