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Strategy-specific Differentiation in Response to Resources and Drivers of Spring Migration Phenology in Rocky Mountain Elk

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STRATEGY-SPECIFIC DIFFERENTIATION IN RESPONSE TO RESOURCES AND DRIVERS OF SPRING MIGRATION PHENOLOGY IN ROCKY MOUNTAIN ELK

by

Storm A. Crews

B.S., Appalachian State University, 2017

A Thesis
Submitted in Partial Fulfillment of the Requirements for the
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Master of Science

In the field of Zoology

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AN ABSTRACT OF THE THESIS OF

Storm A. Crews, for the Master of Science degree in Zoology, presented on April 26, 2023, at Southern Illinois University Carbondale.

TITLE: STRATEGY-SPECIFIC DIFFERENTIATION IN RESOURCE RESPONSES AND DRIVERS OF SPRING MIGRATION PHENOLOGY IN ROCKY MOUNTAIN ELK

MAJOR ADVISORS: Dr. Guillaume Bastille-Rousseau, Dr. Nathaniel Rayl

Elk (*Cervus canadensis*) are known to exhibit high movement strategy diversity compared to other ungulate species. Most elk populations are migratory or partially migratory, presenting unique conservation and management challenges. For example, successful maintenance of multiple seasonal ranges and connectivity between them is necessary to conserve populations with migratory behaviors. Further study of the structure and maintenance of movement strategy diversity within partially migratory populations is needed to assist management and refine fundamental ecological theory. Improved understanding of the determinants of elk migratory timing is also important, with the dynamics of significant drivers likely to shift under future climate change and anthropogenic expansion.

I investigated strategy-specific environmental responses in multiple Rocky Mountain elk populations and found evidence for a differentiation in resource use and selection among sympatric individuals using differing strategies. This result suggests a potential mechanism for the reduction of intraspecific competition and heightened population densities in partially migratory herds. However, the nature and strength of differentiation was found to be context dependent. I found that elk avoid human development and seasonally select for forage quantity over quality at relatively fine scales, highlighting some consistent selection responses as well. Overall, this analysis demonstrated intrapopulation response heterogeneity in partially migratory elk populations and characterized strategy-specific patterns of resource use and selection.

I investigated how spring migratory timing and duration relate to spatiotemporal forage dynamics, finding that departure dates are affected by vegetative green-up along migratory corridors, while the duration of migration is influenced by the timing of green-up at the summer range. These results highlight a form of migratory plasticity, wherein migrants modulate both their departure date and the duration of their migration as a function of vegetative phenology. Additionally, I present a framework to quantify optimality of migratory movements in relation to peak forage conditions. On average, elk were found to exhibit high optimality, with interindividual variability along a gradient. My findings suggest a variety of responses to green-wave phenology, with optimality of movements differing as a function of individual and study area. This work contributes to the growing understanding of migratory plasticity as multidimensional and highlights the variability of migratory behavior within and among populations.

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PREFACE

Elk (*Cervus canadensis*) are an economically and ecologically significant ungulate species with a current geographical range spanning many pockets of the continental United States and Canada, concentrated primarily in western North America and eastern Asia (Brook et al. 2018). Elk are of primary conservation interest in the United States due to the sizeable role they play in recreational hunting and tourism economies (Pickton 2004, Koontz & Loomis 2005, Chapagain et al. 2020) and livestock and wildlife disease dynamics (Rayl et al. 2021). These and other cultural and ecological processes dependent upon elk have made the species a target of extensive management efforts, rendering improved understanding of their spatial ecology a highly desirable aim.

Human encroachment on ungulate habitat has been hypothesized to negatively impact population sizes and individual fitness (Polfus & Krausman 2012, Kitina Nyamasyo & Odiara Kihima 2014, Johnson et al. 2017). Dwindling habitat and reduction of habitat connectivity are trends seen globally in the Anthropocene, with the dual pressures of a growing human population and a changing climate driving negative outcomes for affected species (Tucker et al. 2018, Segan et al. 2016). Colorado harbors the highest state-wide population of elk in the country, with 2020 estimates projected at over 290,000 individuals (Colorado Parks & Wildlife 2020). However, increasing anthropogenic encroachment upon elk habitat by way of expanding residential, recreational, and infrastructural development may impact Colorado’s elk herds. Colorado is among the fastest growing states, with a human population projected to grow to 7.8 million people by 2040 - an increase of roughly 34% beyond 2020 estimates (World Population Review 2021). The decline in landscape connectivity associated with expanding development puts migratory species with large space use requirements at particular risk, potentially imperiling access to seasonal ranges for migratory elk (Sawyer et al. 2013). In some systems, increases in agricultural land use have been linked to lower prevalence of migratory behaviors in elk due to the nutritional benefits of irrigated agriculture, altering herd-level movement strategy composition (Barker et al. 2019). Climate change has the potential to have further negative impacts upon elk population productivity due to future declines in habitat quality and land use change (Middleton et al. 2013).

The movement ecology of elk herds in the Southern Rockies ecoregion of Colorado is diverse. Herds of elk in this system tend to display partially migratory behavior, wherein a fraction of the herd migrates between distinct seasonal ranges while other individuals remain in the same range year-round as residents. Management techniques aimed at the conservation of partially migratory ungulate populations differ from those of fully migratory or fully residential populations (Berg et al. 2019). Given the diversity of movement strategies within herds, and differential proportions of movement strategies among herds, assessment of relative abundances of strategies at the herd level is necessary. Successful conservation and management necessitate an understanding of spatial requirements, habitat selection, and resource use. A detailed exploration of differential resource use among conspecifics exhibiting differing movement strategies opens the door to more effective management strategies, allowing for preferential management of specific resources in light of known proportions of movement strategies within a given herd. It would also contribute to current theory on the evolutionary benefits of partial migration in ungulate populations.

The preservation of migratory behavior presents unique challenges, requiring an intimate understanding of both the spatial and temporal components of the process (Bolger et al. 2008). It is necessary not only to measure the physical parameters of migratory events – e.g. the locations, extents, and characteristics of seasonal ranges, the distances between ranges, and corridor connectivity - but also their phenological parameters, such as migration timing and duration. Determination of these temporal parameters can better inform management strategies, so estimating them can be of practical value. An exploration into migratory phenology also benefits our understanding of the theoretical foundations of a species' ecology (Rickbeil et al. 2019). Identification of the environmental determinants of migration timing can elucidate significant drivers of animal movement and behavior.

This thesis contains two chapters, investigating differing aspects of elk spatial ecology. In the first chapter, I constructed models to explore differentiation in resource use and selection between movement strategies within partially migratory elk populations and relate landscape-level forage predictability to movement strategy frequencies. In the second chapter, I model the relationship between migratory phenology and spatiotemporal forage dynamics and quantify heterogeneity in migratory movement optimality.

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CHAPTER 1

DIFFERENCES IN RESOURCE USE AND SELECTION BETWEEN MOVEMENT STRATEGIES IN ROCKY MOUNTAIN ELK

INTRODUCTION

Movement strategies are broad-scale movement behaviors exhibited by mobile animals aimed at maximizing fitness benefits and minimizing costs in the context of the surrounding environment (Nathan et al. 2008, Bastille-Rousseau et al. 2015, Shaw 2020). Movement strategies employed by animals include residency, wherein animals remain within a defined home range throughout the year, migration, which entails seasonal travel between distinct and generally discontinuous ranges, and alternative strategies such as nomadism, dispersal, and mixed-migration (Chapman et al. 2011). Identifying the factors and conditions associated with the prevalence of differing movement strategies and strategy-specific responses to resources are important tasks with both theoretical and practical applications (Singh & Leonardsson 2014, Barker 2018). This is of particular concern in animals exhibiting a mixture of movement strategies, such as ungulate or avian species, due to the potential for populations to respond effectively to changing environments as a function of their movement strategy composition. For example, populations with high proportions of migrants may be more severely impacted by reductions in habitat connectivity, but more capable of coping with density-dependent processes such as disease outbreaks (Bolger et al. 2008, Rayl et al. 2021).

The environmental conditions influencing frequency of one movement strategy over another are often described as a function of spatiotemporal resource patterns (Mueller et al. 2011, Singh 2012, Riotte-Lambert & Matthiopoulos 2020). Landscapes exhibiting high spatiotemporal predictability should be expected to harbor analogously predictable movement strategies (i.e. residency or migration) in a manner dependent upon the spatial layout of relevant habitat and resources (Van Moorter et al. 2013). Residency is to be expected in landscapes exhibiting high resource predictability at localized spatial scales, while migration is expected when such resources vary but are predictable over larger spatial and seasonal scales (Borowik et al. 2020, Riotte-Lambert & Matthiopoulos 2020). Alternative strategies such as nomadism are to be expected in landscapes with more stochastic and unreliable resource distributions, rewarding erratic movement behaviors (Mueller et al. 2011). Relating strategy frequency to the predictability and seasonality of important spatiotemporally variable resources, such as forage, may inform predictions on how population-level strategy prevalence could shift in response to landscape changes induced by climate change and anthropogenic influence, rendering investigation of this association desirable.

While landscape-level properties may provide insights into the frequency of strategies on a landscape, they do not shed light on the distinct responses to resources that different strategies might exhibit in their environment. Resource selection, the disproportionate use of a resource relative to its availability, is a concept of central significance in spatial ecology (McLoughlin et al. 2010). Studying trends in resource use and selection contribute significantly to our theoretical understanding of a species' spatial ecology and may inform pragmatic applications aimed at management and conservation. Of particular interest is the question of whether individuals engaging in differing movement strategies respond to the environment in unique ways (i.e. whether they reliably vary in patterns of resource use and selection). Differential response to resource availability as a function of movement behavior could indicate that differing strategies engage in an evolutionary tradeoff, with unique resource interactions conferring differing fitness costs and benefits in a given environmental context.

Partially migratory populations (populations with stable maintenance of both migratory and non-migratory strategies) offer uniquely valuable study systems to explore these questions at multiple scales, as they allow for consideration of not only which broad environmental characteristics are associated with frequencies of movement strategies, but how landscapes hosting differing movement strategies are used by each (Merrill et al. 2020). Differences and similarities in patterns of resource selection between residents, migrants, or intermediate movement strategies may reveal theoretical insights into how environments can successfully support alternate strategies simultaneously (Berg et al. 2019). Relevant population-level metrics such as fitness and mortality can be influenced as a result of the presence of multiple strategies within a herd (Hebblewhite et al. 2011, Berg et al. 2019). Identifying resource selection between differing movement strategies may also aid management of partially migratory populations, by facilitating approaches that account for intrapopulation diversity in resource requirements if such diversity is significant. Like many large ungulates in temperate climates, some elk populations exhibit partial migration. Elk herds in the Rocky Mountains of Alberta, for example, are seen to stably maintain partial migration within their populations (Merrill et al. 2020). Thus, elk are a desirable study system to investigate strategy-specific resource selection.

In this chapter, I used tracking data from four elk herds located in the Southern Rockies, Wyoming Basin, and Colorado Plateau ecoregions, mostly confined to the U.S. state of Colorado. First, I classified movement strategies of each individual as either migratory or non-migratory and assessed herd-level composition of these strategies. Then, I related strategy frequency to landscape-level predictability and seasonality of forage quality. I predicted that landscapes with greater predictability and greater seasonality would be associated with higher proportions of migrants. Second, I evaluated strategy-specific resource use in seasonal ranges. I predicted that anthropogenic, habitat, productivity and snow characteristics would be significant drivers of differential seasonal resource use between strategies, with likely herd-specific variation. Specifically, I predicted that migrants would associate with areas of lower human development, greater forage availability, and of differing habitat composition compared to non-migrants during the summer period, with fewer differences between strategies during the winter period due to range sympatry. Lastly, I modeled fine-scale seasonal resource selection of individuals to compare strategy-specific resource selection. I predicted that resource selection would differ between movement strategies, with measurable influences of anthropogenic, habitat, productivity, and snow resources. Specifically, I predicted that migrants would show greater aversion to anthropogenic development, higher selection for quality forage, differing preferences for habitat types, and greater tolerance for snow cover relative to non-migrants, with trends varying across seasons.

METHODS

Study Area

I studied elk from the Avalanche Creek (Colorado Parks and Wildlife Data Analysis Unit [DAU] E-15), Bear’s Ears (DAU E-2), Trinchera (DAU E-33), and Uncompahgre Plateau (DAU E-20) elk herds that wintered in Colorado, USA (Figure 1.1). Elk from the Bear’s Ears herd occasionally crossed into Wyoming and elk from the Trinchera herd often crossed into New Mexico. All four herds occupy the Southern Rockies ecoregion, with some herds additionally occupying other ecoregions; namely, the Colorado Plateau in Uncompahgre Plateau, and both the Colorado Plateau and Wyoming Basin in Bear’s Ears (Environmental Protection Agency 2021).

Elevation varies greatly throughout the herd ranges, from around 1,500 meters in low-lying valleys and river confluences to over 4,000 meters at mountain peak tops (Banulis 2006, Vitt 2007, Finley and Grigg 2008, Mao 2013). Climate in the herd ranges varies largely as a function of elevation, with higher altitudes receiving more precipitation on average than low-lying areas, and temperatures decreasing as elevation increases; snow fall is more substantial and more easily retained at higher altitudes. Taken together, this results in harsher, longer, and colder winters at high elevations with shorter, milder summers. The reverse seasonal trend is true in low regions, with milder winters and hotter summers. Like many temperate migratory ungulates, migratory elk in this region tend to travel from low elevation winter ranges to high elevation summer ranges.

Vegetation communities in the herd ranges also shift with elevation. Though trends differ among areas, dominant communities include alpine systems or the absence of vegetation above 3,500 meters; Spruce (*Picea engelmannii*) and Fir (*Abies lasiocarpa; Pseudotsuga menziesii*) from 2,500 to 3,500 meters; Aspen (*Populus tremuloides*) and mixed Aspen/conifer from 2,000 to 2,500 meters; montane shrubs, Oak (*Quercus gambelii*), and sagebrush (*Artemisia* sp.) around 2,000 meters; and Pinyon-Juniper systems (*Pinus* and *Juniperus* sp.), plains grasslands, or sagebrush steppe in foothills, high desert, or desert basins below 2,000 meters (Banulis 2006, Vitt 2007, Finley and Grigg 2008, Mao 2013). Significant ecological wetlands and riparian buffer zones at the base of river valleys are dominated by narrowleaf cottonwood (*Populus angustifolia*) and willow (*Salix* sp.) species (Mao 2013).

Animal capture and monitoring

Between 2017 and 2021, 513 yearling and adult female elk (*Cervus canadensis*) were captured and fitted with GPS collars from the Avalanche Creek (n = 104; tracked from 2019-2021), Bear's Ears (n = 138; tracked from 2019-2021), Trinchera (n = 113; tracked from 2017-2021), and Uncompahgre Plateau (n = 158; tracked from 2017-2021) herds. Estimated total population sizes vary by herd, with ~4,500 in Avalanche Creek (Mao 2013), ~15,900 in Bear's Ears (Finley and Grigg 2008), ~18,100 in Trinchera (Vitt 2007), and ~9,700 in Uncompahgre Plateau (Banulis 2006).

Elk from the Bear's Ears herd were captured on two distinct winter ranges. Although these elk occupy the same DAU, I considered them separate herds due to their generally distinct winter ranges (hereafter, "Bear's Ears herd" for the portion of the herd wintering in the western part of DAU E-2, and "Steamboat herd" for the portion of the herd wintering in the eastern part of DAU E-2). All procedures were approved by the Colorado Parks and Wildlife Animal Care and Use Committee (protocol IDs: 01-2020, 03-2020).

Elk captures were carried out on the winter ranges of each herd, primarily occurring from late February to mid-March before the onset of spring migration, with Steamboat captures taking place in mid-to-late January. Elk were captured via helicopter net-gunning or chemical immobilization and fitted with ATS GPS collars. The resulting tracking data consists of logged elk locations generally two to four hours apart, and up to one year or more of locations per individual, though both fix rate and tracking duration varied by herd. Given that an individual's fix rates were occasionally variable over the year, individual trajectories were resampled at the lowest available temporal resolution to avoid biasing sampling among seasons (e.g. if an individual had a fix schedule that changed from 2-hour intervals in part of the year to 4-hour intervals in another part of the year, its trajectory was resampled from 12 points per day to 6 points per day).

Overview of Analyses

I followed a series of steps to conduct resource use and selection analyses. First, I classified elk as either migrant or non-migrant at the individual level. Second, I estimated migratory phenological parameters (i.e. dates of range departure and range arrival) and used these to delineate ranges and seasonal space use of individuals. I then extracted a variety of covariates from ranges and locations to generate seasonal, herd-level, strategy-specific resource use and resource selection models.

Movement Strategy Classification

To classify broad-scale movement strategies of individual elk, I used trends in Net-Squared Displacement (NSD) and elevation shifts over time (Bunnefeld et al. 2011). I classified elk as either migrants or non-migrants, with migrants generally displaying a clear delineation of discontiguous seasonal space use (Figure 1.2). I considered individuals with continued displacement away from their initial capture range throughout the year dispersers, and individuals with consistent intermediate space use between two ranges (either by NSD or elevation) commuters, and classified both as non-migratory. I resampled trajectories to daily locations before classification, and considered individual elk-years as the unit of analysis (Bunnefeld et al. 2011). Individuals with insufficient data to determine movement strategy were excluded (i.e. individuals with less than or equal to a few months of data and ambiguous movement trends; n = 126).

I used automated model fits from the R package MigrateR (Spitz et al. 2017) to classify movement strategies at the individual level, then visually inspected the locations of each elk-year to confirm classifications. Some individuals exhibited seasonally distinct space use that nevertheless had some level of spatial overlap, resulting in complex cases. A threshold of 5% spatial overlap of 95% KDEs of seasonal space use was selected to aid with these complex cases, with individuals exceeding this degree of overlap considered non-migrants.

Range and Season Delineation

My goal was to delineate seasonal space use of each individual using the timing estimates of migratory movements. This required estimating departure and arrival dates from seasonal ranges of migrants. Initial parameter estimates were produced by fitting a movement model using MigrateR at the individual level. This provides automated model fits and parameters allowing for the calculation of estimated departure and arrival dates for migratory events. Though these estimates can be quite accurate, complex movement patterns may produce poorly fit models, e.g., in the case of mixed-migrants (Cagnacci et al. 2016). In these cases, I visually assessed model fits and manually corrected any misclassifications or poor parameter estimates, considering both displacement and elevation patterns.

I systematically further corrected departure date estimates by first generating a kernel density estimate (KDE) of space use using the temporal period immediately prior to the estimated departure date. I set this period to two weeks, but altered when necessary (e.g., when excursions or similar movements occurred close to the migration date, introducing uncharacteristic spatial bias). Locations during this period were cropped by the boundary of the 95% KDE and the latest point within the KDE was assigned as the new departure date estimate. Arrival date estimates were corrected via an analogous process but using the temporal period following the initial arrival date, and identifying the first point in time of remaining locations. I used a three-range approach (winter, summer, winter 2) to delineate ranges. Seasonal ranges were differentiated from excursion events by setting a 30-day threshold, i.e., if an individual departed and returned to their current seasonal range within 30 days this was considered an excursion, not a migration (Cagnacci et al. 2016). To designate seasonal space use for non-migrants, I took the median date for each migration per herd, and subset seasonal periods for non-migrants accordingly within that herd. I generated 95% seasonal range KDE's at the individual level, to delineate seasonal space use.

Geospatial and Spatiotemporal Covariates

I selected suites of variables I hypothesized might reveal differences in resource use and selection between differing movement strategies. I grouped these variables into blocks of variables associated with specific hypotheses (See Table 1.2 and 1.3). Highly correlated variables ($p > 0.7$) were excluded from analyses.

Normalized Difference Vegetation Index (NDVI) and snow metrics were derived from the MOD09Q1 Version 6 Moderate Resolution Imaging Spectroradiometer/Terra Reflectance product (MODIS; 250 meter spatial resolution, 8 day temporal resolution, Vermote 2015). Normalized Difference Vegetation Index is a commonly used measure of vegetative productivity frequently used in ungulate movement analyses (Pettorelli et al. 2011). Raw MODIS imagery was downloaded from 2007 to mid-2022, reprojected to a local coordinate reference system, and resampled. I followed the methodology of Bischof et al. (2012) and Merkle et al. (2016) to process imagery and fit a double-logistic curve to a time series of 8-day NDVI values on a per-pixel basis to interpolate daily NDVI estimates for each pixel. This allowed me to calculate the Instantaneous Rate of Green-up (IRG), a measure related to the rate of change in productivity, and by extension, vegetation quality, and hypothesized to be a significant predictor associated with migratory movements in ungulates (Merkle et al. 2016). Measures of snow coverage were extracted from the same remote sensing product (250 meter spatial resolution, 8 day temporal resolution).

I developed covariates to measure the seasonality (intra-annual variation) and predictability (inter-annual variation) of NDVI and snow cover. For NDVI, I calculated seasonality covariates on a per-pixel basis by annually calculating the standard deviation of the variable in question using daily interpolated values for each year from 2007-2021 and taking the mean of these annual values. I calculated predictability covariates by extracting values on constant ordinal days across years and taking the standard deviation of these values per pixel (Bastille-Rousseau et al. 2017). Given that measures of snow cover were not interpolated at the daily level, the same process was performed at the lower temporal resolution of 8-days for similar metrics with respect to snow cover. For ease of interpretability, I transformed predictability covariates by subtracting values from 1 before modeling.

I derived hydrological covariates (hydrological feature length per unit area, and distance to hydrological feature) from the National Hydrography Dataset (USGS 2020). I derived topography from the Shuttle Radar Topography Mission (SRTM, 30 meter resolution) dataset (NASA 2013). I extracted land cover covariates from the 2019 NLCD dataset (National Land Cover Database, 30 meter resolution; USGS 2021), and separated them into five categories: residential development, crop cover, forest, open habitat, and other. I combined both the Shrub/Scrub and Grassland/Herbaceous categories in the NLCD dataset to create the open habitat category. I derived road-related covariates from the TIGER county roads dataset, retaining primary, secondary, and local roads, paved areas, service roads, highway ramps, and rural 4WD vehicular trails (Feature classes S1100, S1200, S1400, S1500, S1630, S1730, S1780 in dataset; US Census Bureau 2021).

During captures, researchers measured a rump body-condition score and the depth of maximum rump fat via ultrasonography (Cook et al. 2010). I estimated the percent of ingesta-free body fat (IFBF) using the newLIVINDEX for elk, which combines the rump body condition score and maximum rump fat thickness (Cook et al. 2010).

Objective 1: Quantifying Landscape-level Spatiotemporal Trends in Forage and Investigating Herd and Strategy-Specific Body Condition Estimates

I generated measures of spatiotemporal trends in forage for each study area, assessing both averages and variability in NDVI predictability and NDVI seasonality at the landscape scale. I also did so for elevation, given the a priori assumption that topographic heterogeneity likely impacts these covariates at this scale. I generated 100% MCP's (Minimum Convex Polygons) for all available location data per herd and extracted these three covariates within the MCPs. I then summarized them by taking the mean and standard deviation respectively.

I used statistical tests to investigate differences in IFBF distributions 1) among herds, 2) among strategies, and 3) between strategies in the same herd. A one-way analysis of variance (ANOVA) with IFBF estimates as a response variable and herd as a categorical independent variable was used to test for differences among herds; a one-way ANOVA with IFBF estimates as a response variable and movement strategy as a categorical independent variable was used to test for differences among strategies; a Welsh two sample t-test was used to test for differences among strategies within herds.

Objective 2: Assessing Seasonal Resource Use of Differing Movement Strategies

I generated individual-level 95% KDEs for every available seasonal period (i.e. winter, summer, winter 2) to summarize seasonal range characteristics and examine differences in resource use between strategies (Bastille-Rousseau et al.. 2020). Table 1.2 displays the covariates extracted and summarized at the seasonal range scale per individual.

I used mixed-effects logistic regression with movement strategy as a binomial response variable (migrant =1, resident =0) and elk ID-season as a random factor. I generated separate models for each herd-season combination, including winter and winter 2 ranges within the same model. This resulted in summer and winter models for herds, with final models selected using Akaike Information Criterion for small sample sizes (AICc; Burnham & Anderson, 2002). All variables with a Variance Inflation Factor (VIF) of greater than or equal to five were removed from models. In cases where delta AICc was within two of the highest ranking model, I chose the model with the greatest complexity to include every potentially relevant variable. No model was generated for Bear's Ears for this objective due to the absence of non-migrants. Models were fitted using glmmTMB in R (Brooks et al. 2017).

Objective 3: Investigating Differences in Third-order Resource Selection between Movement Strategies

I estimated resource selection functions (RSFs) for each strategy-herd-season combination using mixed-effects exponential regression (Johnson et al. 2006). Using KDEs of seasonal ranges to define availability, I extracted all covariates (see Table 1.3) from used locations and 10,000 randomly generated available locations per ID-season-year, associating random dates with random locations (Bastille-Rousseau et al. 2015). Random locations were generated using the spsample function and random dates generated using the sample function (i.e. discrete uniform distributions) from dates in the relevant seasonal period in R. This framework allowed me to explore elk selection within seasonal ranges as a function of movement strategy. Resource selection functions were generated with the R package glmmTMB using a binomial distribution, logit link, ID-Season-Year random intercepts, and random slopes for each variable when possible (Muff et al. 2020). In the event of convergence issues, random slopes were iteratively removed from one covariate at a time until convergence was achieved. All variables with a VIF greater than or equal to five were removed from models. I natural log transformed distance variables and added 1 before inclusion in the model to account for 0's.

RESULTS

Movement Strategy Frequencies

Three hundred and eighty-seven elk-years were used in the final analyses (n = 387 elk), with an average tracking duration of 324 days (SD = 64) per individual. On average, 3349 GPS locations were used per individual (SD = 1556), with a total of 1,296,309 GPS locations. Movement strategy frequency varied by study area, with a total of 224 elk classified as migrants and 163 classified as non-migrants (Figure 1.3). Movement strategies and migrations varied by study area, with migrations of differing distances and elevation gradients present, as well as residency and elevational commuting, wherein individuals engaged in semi-regular space use of areas between two ranges along some elevation gradient. Avalanche Creek exhibited moderate-distance high-elevation migrations and residency; Bear's Ears exhibited long-distance migrations; Steamboat exhibited moderate and long-distance migrations alongside residency and elevational commuting; Trinchera exhibited short and moderate-distance elevational migrations alongside residency; Uncompahgre Plateau exhibited moderate and long-distance elevational migrations alongside residency and elevational commuting.

Landscape-level Trends in Forage Quantity Predictability and Seasonality, and Elevation

Summarized landscape-level measures of predictability and seasonality of NDVI varied by study area (Figure 1.4). No clear trends were present when plotting averages against estimated percentage of migratory individuals within herds (mean predictability $R^2 = 0.03$; mean seasonality $R^2 = 0.087$), but a minor positive relationship can be seen between variation in both NDVI metrics and population-level migrant percentages (SD predictability $R^2 = 0.55$, SD Seasonality $R^2 = 0.58$). There was no clear trend between elevation metrics and migrant percentages (mean elevation $R^2 = 0.12$; SD elevation $R^2 = 0.15$).

Ingesta-Free Body Fat Analysis

Estimates for IFBF values were calculated for 277 individuals, with varying sample sizes per herd (Table 1.4). Body condition data was not collected from Steamboat elk, so estimates for the E2 DAU only included western migratory Bear’s Ears individuals. Average IFBF across herds was 7.6 +/- 1.76. A one-way ANOVA showed a significant difference in IFBF distributions among herds ($F(3,273) = 6.284$; $p < 0.001$; Figure 1.5). Average IFBF of migrants was 7.37 +/- 1.38, while for non-migrants it was 8.03 +/- 2.26 across herds. A one-way ANOVA showed a significant difference in IFBF distributions among strategies ($F(1, 275) = 8.902$, $p < 0.01$; Figure 1.6).

A Welch two sample t test was performed to compare differences in the average IFBF estimate between strategies within each herd. Difference in strategy-specific IFBF was non-significant in Avalanche Creek ($t(60.573) = -1.24$, $p = 0.218$), significant in Trinchera ($t(10.396) = -2.49$, $p = 0.03$), and non-significant in Uncompahgre Plateau ($t(17.672) = 0.5$, $p = 0.623$). Herd-specific strategy-specific IFBF distributions are displayed in Figure 1.7.

Characterization of Seasonal Resource Use

Trends and variables in summer models varied by study area, with differing suites of variable block combinations selected among populations. Collectively, they indicate that migrant summer use differs minimally from non-migrant summer use (Table 1.5). Three covariates suggested significant herd-specific responses with two being in the same herd; migrant use in the Uncompahgre Plateau herd (UP) was positively associated with predictability of NDVI and mean snow cover compared to non-migrants, while percentage of forest cover was positively associated with non-migrants in the Steamboat herd (SB). Moreover, a few other associations were qualitatively of interest. Predictability of NDVI (UP), average snow cover (AC, TR), percentage of cropland (UP), and road density (TR, UP) were all positively associated with migratory summer use in models that included them. Percentage of forest cover (SB), percentage of development (UP), percentage of open habitat (SB), availability of hydrology (SB), average NDVI (UP), and average IRG (UP) were positively associated with non-migrant summer use. Predictability of snow cover was positively associated with migratory summer ranges in two herds (AC, TR), but negatively associated in Uncompahgre Plateau.

Trends and variables in winter models also varied by study area, with differing suites of variable block combinations selected among populations. Overall responses indicated a stronger trend of strategy-specific use during this time compared to summer (Table 1.6). Nine covariates showed significant trends, with percentage of development, crop cover percentage, hydrological availability, forest percentage, open habitat percentage, and snow seasonality positively associated with migrant use in at least one study area each. Forest edge, open habitat percentage, mean elevation, and mean snow cover were positively associated with non-migrant use in at least one study area each. Significant conflicting (i.e. opposite) trends existed amongst study areas for two covariates – crop cover percentage and open habitat percentage. Percentage of development (AC), percentage of forest cover (AC, SB, UP), predictability of NDVI (AC), and snow seasonality (SB) were positively associated with migrant winter ranges. Average elevation (UP) and NDVI seasonality (AC) were positively associated with non-migrant space use during this period. The directionality of parameter estimates for availability of hydrology, percentage of crop cover, percentage of forest edge, percentage of open habitat, average snow cover, and predictability of snow cover was inconsistent between study area models that included these covariates, indicating a system-specific response in use of these features among differing movement strategies.

Summer RSFs:

The full model incorporating all variable blocks was the top model for all herds, except in Trinchera and Uncompahgre Plateau. However, in some models specific variables within variable blocks were not included due to collinearity (e.g., no elevation in either Avalanche Creek strategy model, and no current IRG or snow cover in the Steamboat migrant model). The non-migrant models in both Trinchera and Uncompahgre Plateau lacked snow covariates, while the migrant model in Uncompahgre Plateau lacked productivity covariates (Table 1.7). Five responses showed high consistency among all strategies and herds with common covariates in their top models during the summer period. In almost all cases, elk avoided roads and development, selected for current NDVI, and selected against snow cover and predictability of NDVI. Crop use varied widely, with opposing trends between strategies in one herd (SB), and much stronger selection in migrants compared to non-migrants in another (AC). Differences in habitat selection between strategies were prevalent, with opposing trends in selection for open habitat (AC, SB), distance to hydrology (AC, TR), and elevation (SB, TR) each in two herds, while opposing selection of ‘other’ habitat was present in one herd (AC). Selection of productivity metrics differed among strategies in relation to IRG with weak but consistent opposing selection in two herds (AC, TR). Lastly, selection of snow metrics differed among strategies in relation to predictability of snow cover in one herd (AC).

Winter RSFs:

The full model incorporating all variable blocks was the top model for all herds except Trinchera, wherein the migrant model did not incorporate snow covariates. Again, some covariates within variable blocks were not included due to collinearity (Table 1.8). Four responses showed high consistency among all strategies and herds with common covariates in their top models during the winter period. In almost all cases, elk avoided roads and development, and selected for open habitat and distance to hydrology (with a few non-response exceptions for roads, development, and open habitat). Response to crops was system-specific, with strategy-agnostic selection in one herd (AC), and uni-strategy responses in two (i.e. one strategy showed positive selection, while the other showed no response; TR, UP). Crops were otherwise selected against in two herds (SB, BE), wherein strategy-specific comparison was not possible. Selection for habitat covariates was variable, with all strategies in all herds selecting against ‘other’ habitat apart from Trinchera, wherein the effect was positive for both strategies. Two herds selected for higher elevation regardless of strategy (UP; BE migrants did as well), two herds selected for lower elevation regardless of strategy (AC, TR), and one herd exhibited opposing trends in elevation between strategies (SB). Elk selected against current NDVI in all herds, with the exception of non-migrants in Steamboat and migrants in Avalanche Creek. Predictability of NDVI was selected less than expected in three herds regardless of strategy (AC, TR, BE), selected for by both strategies in one herd (SB), and exhibited opposing trends in one herd (UP). Selection for IRG was positive in three herds (TR, UP, BE), negative in one (AC), and exhibited opposing trends in one (SB). Snow cover was selected for by two herds (UP, BE), exhibited opposing trends in two herds (AC, SB), and was selected against by non-migrants in Trinchera. Lastly, three herds selected positively for predictability of snow cover (AC, SB, UP), while non-migrants in Trinchera and migrants in Bear's Ears displayed negative selection.

DISCUSSION

This analysis estimated movement strategy frequencies in four Rocky Mountain elk herds in differing environmental contexts, revealing strategy diversity among herds. I found a potential weak association between variation in forage predictability and seasonality and population-level movement strategy composition. I also investigated strategy-specific seasonal resource use and selection in each herd and found some evidence for differentiation among strategies. This differentiation was found to be system-specific with largely inconsistent trends across study areas, implying that strategy-specific selection is complex and may be environmentally contextual. Differences in use and selection among strategies may play an important role in contributing to the maintenance of partial migration in populations (Berg et al. 2019). This should be particularly consequential in the winter period, where differentiation of response during range sympatry may facilitate greater population densities (Svanback & Bolnick 2007). Despite multiple herd-specific differences, I also found some consistent similarities in selection as well. Elk consistently responded negatively to human development and roads at fine-scales, revealing a strategy-agnostic directional aversion to these features. Interestingly, I also found potential evidence that the strength of feature avoidance may vary by strategy. Though differences in response were statistically non-significant between strategies, migrants consistently demonstrated stronger aversion to roads compared to non-migrants in the same herd.

Alternatively, non-migrants consistently showed stronger aversion to development compared to migrants. This highly uniform result across herds provides qualitative evidence that elk exhibiting differing strategies may have specific levels of avoidance or relative tolerance of particular anthropogenic features. Overall, my work found strategy-specific response heterogeneity to available resources and demonstrated divergence in resource use and selection.

Movement Strategy Frequencies and Landscape Analysis

Estimates of migratory frequency in these four herds suggest that population-level strategy composition varies in Rocky Mountain elk. This variance indicates that there are multiple viable movement strategies, but that this viability varies by system, impacting frequency. This could relate to an environment’s ability to support differentiation of use and selection among sympatric strategies, allowing differing strategies to equalize their fitness and coexist (Fretwell & Lucas 1970). For simplicity my classification framework condensed strategy diversity into a binary of migratory vs non-migratory, but movement strategies are increasingly acknowledged as lying on a continuum from residency to migration (Cagnacci et al. 2011, Berg et al. 2019, van de Kerk et al. 2021). Future work should incorporate this heterogeneity to better understand intermediate strategy frequencies.

Two variables appeared explanatory in my landscape analysis: variation in forage predictability and variation in forage seasonality over the landscape. These were positively associated with the frequency of migrants observed in a system. The other variables investigated did not appear to be linked to movement strategy frequencies (mean forage predictability and seasonality, mean elevation and elevation variability across the landscape). This result is counter to expectation, as theory suggests that landscapes with more ‘stability’, i.e. less variation in forage expectation, would be more likely to have higher migrant frequencies (Riotte-Lambert &

Matthiopoulos 2020, Abrahms et al. 2021). A comparative multi-species study focused on ungulates found that landscapes with high resource predictability harbored migratory movements, while landscapes with low predictability were more closely associated with alternative behaviors, like nomadism (Mueller et al. 2011). Studies in Galapagos Tortoise species suggest a strong link between population strategy composition and landscape-level predictability in a partially migratory system (Bastille-Rousseau et al. 2017). My results indicate that this relationship is potentially more complex in elk than it is in other systems. The drivers of migratory propensity in elk may be complex, as evidenced by their high degree of strategy plasticity relative to other ungulates (Eggeman et al. 2016, Xu et al. 2021). My results imply that landscape predictability alone doesn't determine migrant frequency, with additional factors such as density-dependent processes likely influencing strategy composition in elk (Eggeman et al. 2016, Berg et al. 2019).

Body Condition Analysis

Results qualitatively suggest that the highest average body condition (IFBF) is in Avalanche Creek and the lowest is in Bear's Ears. Both Trinchera and Uncompahgre Plateau's averages were intermediate between the two. Additionally, body condition varied by movement strategy, with non-migrants overall having a higher body condition compared to migrants. Given that IFBF values were estimated from data taken on the winter range prior to migration, it's possible that a heightened winter body condition discourages migratory behavior, which could describe Barker et al's findings that supplemental feeding is associated with lower rates of migration in some systems (Barker et al. 2019). This is somewhat surprising, noting that migration itself is energetically costly, but perhaps implies that the energetic benefits of migration (e.g. green-up along migration and/or at an alternate summer range) outweigh these costs and influence strategy at the individual level. Alternatively, it could indicate that there is a tradeoff between strategy and body condition, at least during the winter period, with other potential benefits gathered in lieu of increased body condition (e.g. disease avoidance or altered risk exposure).

However, Uncompahgre Plateau exhibited the reverse of the overall trend, with heightened body condition in migrants compared to non-migrants, though the disparity among strategies was smaller than in other herds, possibly indicating that differing strategies compensate more successfully in this herd. Despite the finding that non-migrants are on average of higher body condition, these differences should be considered carefully, as these strategy-specific differences in body condition were only statistically significant in Trinchera, and it should be noted that representative sample sizes among strategies in both Trinchera and Uncompahgre Plateau were highly imbalanced. Additionally, Avalanche Creek's heightened mean for non-migrants may be due to the presence of a few substantial high outliers, though the fact that these only occur in that herd underscores their relatively higher fitness compared to the other herds. That migrants overall have lower body condition compared to non-migrants is further supported by the fact that Bear's Ears has both the lowest average IFBF values and the least variation, with a fully migratory herd. All of this taken together suggests that the strategy individuals exhibit is likely to impact fitness, though without measures of body condition throughout the year (before spring migration, before fall return migration, upon return at winter range), it is difficult to measure the degree and extent to which this is the case. It is likely that more migratory herds are at greater risk of adverse population responses to stochastic weather events on the winter range, given their comparatively diminished body condition.

Anthropogenic Covariates

Elk avoided roads and human development, indicating that elk are averse to human modification at fine scales (Table 1.7 and 1.8). However, avoidance of roads was stronger in migrants, while avoidance of development was stronger in non-migrants. This difference in selection strength suggests a strategy-specific response to differing anthropogenic features. Seasonal use models showed some evidence for differentiation in use of development, but this was limited to only one study area (Table 1.6). My findings reinforce prior work demonstrating aversion to roads in elk and other ungulates (Montgomery et al. 2013, Passoni et al. 2021), and elk preference for areas with less human development (Webb et al. 2011, Gigliotti et al. 2023). Many studies illustrate that elk display increased aversion behaviors in disturbed areas, consistent with my results (Morrison et al. 1995, Harju et al. 2011, Buchanan et al. 2014, Gigliotti et al. 2023). However, my findings posit that there may be a strategy-specific differentiation in response to disturbance. This difference may relate to behavioral tendencies such as flight distance, and could contribute to differences in habitat use on sympatric ranges (Stankowich 2008, Berg et al. 2019). The consistency of this pattern in other systems should be investigated in future work.

Responses to crop cover were inconsistent, in both use and selection models (Table 1.5, 1.6, 1.7, 1.8). Prior work has shown that crop cover likely plays an important but complex role in population movement strategy composition and migratory behavior (Jones et al. 2014, Barker 2018, Barker et al. 2019). It has been shown that availability of irrigated agriculture on overwinter ranges of elk populations disincentivizes migration via supplementation of forage, increasing frequencies of resident individuals, and delays migratory departure (Jones et al. 2014, Barker 2018). This result is diminished in areas with sufficient availability of high quality native forage (Barker et al. 2019). It is likely that response to crop cover is highly context specific. My results reflect this, as strategy-specific response to crop cover differs in every model in which a response was estimated. The diversity of response may relate to differences in native forage availability among study areas, differences in crop cover abundance, the type of agriculture, the irrigation regime, or other related factors. There is some evidence for differentiation in use of crop cover among strategies during the winter period, but trends oppose in differing study areas, reinforcing the contextual nature of response to this resource.

Productivity

Elk selected strongly for NDVI in summer, with similar responses among strategies (Table 1.7). This supports literature showing the importance of forage quantity in influencing ungulate movement in summer and suggests that responses are consistent among strategies (Mueller et al. 2011, Lendrum et al. 2014). Elk's lack of response to NDVI in winter models (Table 1.8) likely relates to low vegetative productivity during this period and indicates that forage quantity is not a strong driver of selection on overwinter ranges (at least, as measured by NDVI). Use models provided minor evidence (n = 2 models) that seasonal use of NDVI does not reliably differ among strategies, suggesting that strategies have access to similar quantities of seasonal forage.

Elk showed negative or no response to NDVI predictability in summer (Table 1.7). Spatiotemporal predictability of resources are known drivers of animal movement at broader scales (Riotte-Lambert & Matthiopoulos 2020, Abraham et al. 2022), but my results suggest a weaker influence at finer scales. Summer use models provided minor evidence of higher NDVI predictability in migrant ranges (Table 1.5), supporting theoretical expectations and implying that migrants seek ranges with higher forage predictability, despite failing to select for it at finer scales (Bischof et al. 2012). Lack of selection for predictability implies a localized selection response, with current forage quantity a stronger driver of selection than long-term trends (Table 1.7 and Table 1.8). This result is sensible given the immediate fine-scale forage needs of individuals. Winter use models weakly suggest no difference in use among strategies in this period, while winter selection models showed greater inter-population variation in response than summer models (consistent negative response in Steamboat and consistent positive response in Trinchera; Table 1.6, 1.7, and 1.8). My results suggest that responses in selection to forage predictability do not vary by strategy within populations, but can vary by study area.

My results indicate that IRG does not greatly impact selection during either seasonal period in these systems, and that when strategy-specific responses exist, they are minor (Table 1.7 and Table 1.8). Migrants have shown selection for IRG along migratory corridors in some systems (Merkle et al. 2016, Aikens et al. 2017), but my results suggest that this is not the case on seasonal home ranges. Taken together, my findings suggest that during the summer period elk select for forage quantity over quality at relatively fine scales, potentially sacrificing nutritional quality (Hebblewhite et al. 2008, Bishof 2012). Prior work has shown that tradeoffs among selection for quality forage and other necessities can be ecologically complex (Hebblewhite & Merrill 2009). My results could be due to tradeoffs in risk or density-dependent processes such as intraspecific competition, reducing access to quality forage. It may also be that little difference among local forage quality exists at any given moment in time, with quantity valued over intrinsic quality. Lastly, it may be that high forage quantity is associated with dense foliage offering non-nutritional benefits such as predator avoidance. It should be noted that the resolution of productivity covariates in this analysis was 250 meters, which is larger than other covariates and represents a slightly broader spatial scale. Thus, it is possible that the spatial resolution of productivity metrics hinders the ability to detect preferences of quality vs. quantity at scales finer than 250 meters.

Habitat and Snow Covariates

I found evidence for strategy-specific responses to habitat features, with differences in selection more pronounced during the summer (Table 1.7), while strong differences in use were seen in the winter period (Table 1.6). Most trends were not consistent across study areas, indicating a strong effect of environmental context. This result is expected given the differing habitat compositions of these areas, however a few trends were largely consistent. Namely, non-migrants were more likely to select for lower elevations in all but one system (Table 1.7 and Table 1.8), while water availability and percent forest cover were primarily associated with migrant use in winter models (Table 1.6). My finding that strategy-specific differences in habitat use exist during the winter period is noteworthy, as this is the period during which range sympatry should be greatest. If differing movement strategies show unequal preference for similar kinds of habitat, this may contribute to differentiations in overall space use, which could act to reduce intraspecific competition (Svanback & Bolnick 2005, Svanback & Bolnick 2007). Previous research has demonstrated that within a population, there can be variation in responses to similar levels of resource availability, resulting in differing consequences of risk and reward for individuals (Losier et al. 2015). My results support this finding of intrapopulation response heterogeneity, which thus may have similar individual-specific consequences.

Theoretical Implications

My results highlight strategy-specific responses to available resources in a variety of study areas and environmental contexts. These findings should have implications for the maintenance of partial migration in these and other systems (Berg et al. 2019). Partial migration has been linked to density-dependent mechanisms, with seasonal reductions in density impacting per capita access to forage during the productive season (Alerstam 2003, Mysterud et al. 2011, Mysterud et al. 2012). In sympatric periods, differentiation in selection and use should lead to a reduction in intraspecific competition for similar resources and increase the effective carrying capacity of an environment during the period of greatest simultaneous use (Svanback & Bolnick 2005). This differentiation is perhaps a major facilitative mechanism for the existence of partial migration within a population. Previous work has shown that differentiation in selection among individuals is likely to be high during resource-limited periods in a non-migratory system (Bastille-Rousseau and Wittemyer 2019), and my results suggest that this may be true in partially migratory systems as well. Future studies directly linking the strength of differentiation and population densities in partially migratory populations should explore this relationship.

I found three varieties of strategy-specific selection response: full differentiation (directionally opposing responses of selection), uni-strategy response (selection in one strategy and lack of response in the other), and unequal response (directionally consistent response, but unequal in magnitude). The individual causes of these may be unique and warrant further study, but overall could be due to differing intensities in intraspecific competition. If so, differentiation in use ultimately may emerge as a function of density-dependent population-level factors driving the strength of competition (Svanback & Bolnick 2007). As noted in previous literature, fluctuations in population density may impact regulation of movement strategy composition over time partially as a function of changes in competition pressure (Eggeman et al. 2016, Berg et al. 2019). Future studies looking at changes in selection as a function of changes in population density should strengthen understanding of this relationship.

Management Implications

Estimation of population migration frequencies has important implications for management and conservation of Rocky Mountain Elk and other partially migratory ungulates. Conservation needs of populations will differ as a function of strategy composition (Bolger et al. 2008, Kauffman et al. 2021). Maintenance of connectivity between ranges should be a heightened priority in more migratory herds, and management or protection of both the winter and summer range is necessary (Sawyer et al. 2009, Kauffman et al. 2021). If strategies differ in resource selection and use, management of relevant resources should take this into account in accordance with the frequency composition of each strategy. As such, I suggest that estimating the frequency of monitored herds provides valuable information for effective management in partially migratory ungulate populations.

A consistent negative response to anthropogenic disturbance implies that continued development will negatively impact elk movement regardless of strategy. However, the finding that the strength of response may be feature-specific indicates that the specific nature of the development could be meaningful. For example, if migratory individuals show stronger relative aversion to roads, while non-migrants show stronger aversion to development overall, populations with differing strategy frequencies may respond unequally to differing forms of human disturbance – e.g. road expansions may disproportionately deter selection in more migratory herds, while more sedentary herds may suffer more greatly from residential or recreational development. This knowledge alongside estimates of strategy prevalence and space use can guide management decisions in consulting on human expansion in sensitive areas.

One interesting system to highlight is Avalanche Creek. This herd is knowingly threatened by continued recreational and residential expansion nearby (Mao 2013). Use models showed much greater relative migrant use of developed areas in this study area during the sympatric period compared to non-migrants. This indicates that migrants are likely disproportionately exposed to human development, and that continued development in the area should take special care to prevent reduction of elk habitat and corridor connectivity. Future management policy should consider the potential for strategies to be subjected to unequal risk on sympatric ranges and should measure differences in response to better maintain optimal strategy diversity. Evidence for inconsistent strategy and system-specific response to crop cover implies that this resource likely plays a complex role in elk selection and use. Related management implications should thus be considered on a case-by-case basis for this resource, with differing intensities of agricultural land use and variety of crop cover potentially influencing these discrepancies.

My results indicate a potential mechanism for maintenance of partial migration and heightened population density in elk. If strategy diversity facilitates increased population densities, the reduction of migratory behavior could lead to overall population declines. A reduction in elk numbers and density due to the decline of migratory behaviors could have numerous ecological consequences such as shifts in prey availability for predators, (Nelson et al. 2012, Eisenberg et al. 2013), alteration of disease dynamics (Cotterill et al. 2018), changes in vegetation and forest structure (Eisenberg et al. 2013, Seager et al. 2013), and negative impacts on biogeochemical cycling (Cline et al. 2017). Declines would also incur economic cost. Elk hunting opportunities are highly valued by the public and underlie a substantial industry (Koontz and Loomis 2005, Chapagain 2020). Additionally, hunting provides a significant proportion of the funding necessary for conservation (Heffelfinger et al. 2013). Loss or reduction of migration in partially migratory herds could lead to a decline in hunting opportunities due to diminished population sizes and hunter access. It is thus important to effectively manage resources for maintaining strategy diversity within populations, and better understanding of strategy-specific responses should serve to inform the management of partially migratory herds.

CHAPTER 2

DRIVERS OF SPRING MIGRATION PHENOLOGY IN ROCKY MOUNTAIN ELK

INTRODUCTION

The timing and duration of migration events vary broadly as a function of species, geographic location, and environmental drivers. Proposed determinants of migratory timing in taxa as varied as mammalian, avian, reptilian, and invertebrate species often relate to cyclical phenomena (De Robertis 2002, Robson and Barriocanal 2011, Bastille-Rousseau et al. 2017, Rickbeil et al. 2019). Avoidance of predation (Hebblewhite and Merrill 2007), access to forage quality (Avgar et al. 2014), access to water (Cain et al. 2016), and alleviation of extreme seasonal conditions are all presumed drivers of migratory behavior, with the temporal nature of these and other factors seen to influence migratory timing (Mysterud 2013, Rivrud et al. 2019). However, the magnitude and direction in which these factors influence migratory parameters is often species- or system-specific (Merkle et al. 2016). Movement ecology studies that incorporate multiple disparate populations of a single species can be fruitful in this regard, as studying migratory behavior in differing environmental contexts could help tease apart the mechanisms of migration.

The Forage Maturation Hypothesis (FMH) relates ungulate movement to the spatiotemporal onset and distribution of high quality forage, where energy intake is maximized at an intermediate stage of growth that balances quality and quantity (Fryxell 1991). Under this framework, individuals alter their movement to maximize access to high quality forage, i.e. when forage is young and exhibiting high growth rates. The idea has spawned a popular mechanistic explanation for ungulate migration phenology, called the Green-wave Hypothesis (GWH), which asserts that migratory individuals are driven by dynamic wave-like gradients of vegetative productivity, moving to maximize access to optimal forage along the migratory corridor (Drent et al. 1978, Van der Graaf et al. 2006, Bischof et al. 2012). This movement along the gradient is often colloquially referred to as 'surfing' the green-wave and has shown success in explaining migratory behavior and phenology in many systems (Lendrum et al. 2014, Aikens et al. 2017, Rickbeil et al. 2019). The FMH and resultant GWH are important hypotheses for the investigation of migratory timing because they directly relate migratory movements and their motivation to temporally dynamic and measurable environmental phenomena.

Surfing is not the only response to vegetation observed in migratory ungulates. One study noted that Norwegian red deer opt to 'jump' the green-wave, prioritizing peak green-up upon arrival at their summer range instead of along the migratory corridor (Bischof et al. 2012). A comparative analysis of five ungulate species failed to find evidence of surfing in Greater Yellowstone Ecosystem elk populations or Utah bison and illustrated a diversity of ungulate responses to the green-wave (Merkle et al. 2016). Under the FMH, migratory timing should play a primary role in determining migrant access to optimal forage. Animals thus may be prioritizing differing aspects of migration as a function of their biology, implying a continuum of how individuals trade-off access to vegetation quality. For example, optimization could occur prior to departure, along the corridor (surfing), post-arrival, or through some combination of all of these. These responses result from the temporal parameters of migratory movements (e.g. departure date and duration) and are thus closely tied to their mechanistic determinants. Understanding the trade-offs made could enhance theory underlying migratory timing and the sources of its variability among populations and systems.

Overall responses to forage phenology may vary among species and populations, but even within a population interindividual migratory behavior is not homogenous. Variation in factors such as departure dates, migration duration, distance traveled between seasonal ranges, number of stopover sites, and speed of travel have led to the concept of diverse intrapopulation ‘migratory portfolios’ (Lowrey 2020 et al., Xu et al. 2021). Ultimately, this variation should result in differential access to peak forage quality among individuals within a population, with differences in access likely conferring differences in fitness over time, though interannual variability in factors such as climate and stochastic events may alter the benefits of a particular approach (Middleton et al. 2018). Thus, a formal measure of ‘optimality’ – difference in forage quality between an individual’s contemporaneous use of a location and the maximum quality of forage available at that location throughout the year – can be estimated to investigate interindividual differences in access to peak forage. When this optimality is highest (prior to departure, during the migration, or upon arrival at the opposite range) can also provide insight into where an individual might fit in the continuum of the GWH (e.g. ‘surfing’, ‘jumping’, intermediate behaviors). Doing so might therefore reveal the prevalence of these mechanisms among individuals, and provide a quantification of interindividual differences. Similar attempts to specifically quantify interindividual variation in surfing have been conducted in other systems, but are understudied in elk (Aikens et al. 2017).

The decline of migratory behaviors has proven detrimental to ungulate populations globally (Wilcove and Wikelski 2008). Encroachment upon migratory routes as a result of increasing habitat loss and fragmentation has resulted in population crashes of ungulates traditionally dependent upon the fitness benefits of migration (Bolger et al. 2008). Shifts in vegetative phenology are anticipated due to climate change (Cremonese et al. 2017). This is likely to incur negative consequences for migratory ungulates, such as increases in phenological mismatch leading to reductions in fitness (Post & Forchhammer 2008, Rivrud et al. 2019, Aikens et al.

2020). Thus, preservation of systems and populations harboring intact migratory behaviors in the face of changing environments is a major goal in ungulate conservation (Bond et al. 2017). To better inform the protection of long-range movements in populations, it is necessary to characterize migratory patterns, both temporally and spatially (Kauffman et al. 2021). Even more important, understanding the phenological triggers and conditions signaling the timing and duration of migration can better equip managers to predict potential shifts in these parameters as a function of environmental factors (Rickbeil et al. 2019). Spatially, identification of highly trafficked migratory routes and the location and extent of seasonal ranges can aid decision makers hoping to target areas of highest conservation priority (Sawyer et al. 2009). Characterization of migratory phenological parameters and their drivers is therefore desirable from the perspective of the conservation of movement behaviors and species exhibiting them.

Elk (*Cervus canadensis*) exhibit high plasticity in the departure and arrival dates associated with their seasonal ranges, generally as a function of environmental conditions (Middleton et al. 2013, Rickbeil et al. 2019). Their marked plasticity and movement strategy diversity compared to other temperate migratory ungulates suggest that the determinants and parameters of their migratory timing are more flexible and likely more complex than in some other species (Xu et al. 2021). Spring migration phenology is of particular interest given the close tie between its initiation and spatiotemporal forage dynamics. In this chapter, I related spring migratory phenology to the timing of peak forage quality and investigated interindividual variation in forage access optimality in three migratory Rocky Mountain Elk herds. Using a multi-part framework, my analysis allows for exploration of the relationship between elk spring migratory phenology and the FMH, contributing to our understanding of the determinants of migratory timing and duration in ungulates more broadly. Additionally, this paper investigates heterogeneity in intraspecific optimization of resource access via a clustering analysis, quantifying trade-offs and illustrating high variability in migrant elk optimality.

METHODS

Study Area

See Chapter 1

Data

See Chapter 1

Estimation of Migratory Phenological Parameters

See Chapter 1

Selection of Migrants to Include

Though 223 migrants were identified in the data set, various data requirements necessary to investigate this goal excluded some individuals from being used. Individuals with data sets that started during a migration were filtered, as were individuals with less than two weeks of seasonal space use available on either side of a spring migration. Steamboat and Trinchera individuals were excluded from this analysis due to their comparatively low migrant sample sizes (Steamboat n = 13, Trinchera n = 17) and largely differing migratory patterns compared to other study areas (e.g. short distance elevational migrations lasting only a few days).

Covariates

I used a tripartite framework, extracting spatiotemporal covariates with respect to space use over three periods: 1) the two weeks prior to departure from the winter range, 2) the spring migration, and 3) the two weeks following arrival at the summer range (from here on referred to as pre-departure, during migration, and post-arrival respectively). Occurrence distributions calculated from continuous-time movement models were used to delineate space use in each period (Calabrese et al. 2016).

The distance between winter and summer ranges was determined by calculating the distance (in kilometers) between the centroids of the two-week periods of space use on either side of the spring migration. The duration of migrations was calculated as the difference in ordinal days between winter departure and summer arrival. Daily displacement was calculated by dividing the distance between seasonal ranges by migration duration. Instantaneous rate of green-up (IRG) metrics were derived from the MODIS09Q1 Version 6 MODIS/Terra Reflectance product (250 m, 8-day resolution, see chapter 1), giving measures of both interpolated daily IRG values and year-specific estimates of the ordinal day of peak annual IRG per pixel (Merkle et al. 2016). The mean ordinal day of peak annual IRG was calculated over the spatial area encountered during each of the three periods (represented by the respective occurrence distributions); additionally, the standard deviation was calculated to represent variability along the migratory corridor. Mean IRG optimality was calculated for each of the three periods.

Instantaneous rate of green-up optimality was calculated by:

$$OPT_{y,t,p} = 1 - (\max(IRG_{y,p}) - IRG_{y,t,p})$$

Where OPT is optimality, y is the year, t is the current day of the year, p is the pixel, and IRG is the instantaneous rate of green-up value.

Models, Statistics and Analysis

I generated summary statistics regarding departure dates, migration distances, migration duration, and daily displacements for each herd for comparison. Linear regression was used to investigate the relationship between daily displacements and distance.

To generate models investigating spring departure date and the duration of migration, I used five covariates as independent variables: the mean peak IRG date pre-departure, the mean peak IRG date during migration, the mean peak IRG date post-arrival, the standard deviation of peak IRG date along the migratory corridor, and the distance between seasonal ranges. As noted above, the pre-departure and post-arrival periods were two weeks on either side of the migration. I used a generalized linear mixed model (GLMM) framework with study area as a random intercept, implemented with the R package glmmTMB (Brooks et al. 2017). Candidate models included each combination of four-covariate models. I fit each candidate model (linear combinations of each covariate with no more than four covariates per model) and selected the top model using Akaike Information Criterion for small sample sizes (AICc; Burnham & Anderson, 2002). I removed covariates with a Variance Inflation Factor ≥ 5 and used Cook's Distance with a threshold of 0.2 to remove influential outliers (Dormann et al. 2013). I additionally fit simple herd-specific linear models using the same covariates as the top model to better investigate differences in response among study areas, because models fit with random slopes failed to converge.

To explore inter-individual variation in IRG optimality (i.e. optimization of exposure to IRG pre-, during-, and post-migration), I used model-based clustering from the R package mclust (Scrucca et al. 2016). Input covariates were the mean estimated optimalities per individual during each respective period. Top models and the optimal number of clusters were automatically selected via BIC. Cluster outputs were analyzed qualitatively for interpretation. I compared the distribution of herd-specific cluster composition with a chi-squared test.

RESULTS

I used location data from 131 individuals, with sample sizes varying by herd (Avalanche Creek, n = 40; Bear's Ears, n = 62; Uncompahgre Plateau, n = 29). A total of 78911 GPS points were used, with an average of ~602 locations per individual and a standard deviation of 220 locations. Herd-specific summary statistics are displayed in Table 2.1. Spring migratory routes are displayed in Figure 2.1.

The top model for spring departure date included mean peak IRG date (MPI) pre-departure, MPI during migration, the standard deviation of peak IRG date (SDPI) during migration, and the MPI post-arrival (Figure 2.2). The conditional R^2 value was 0.743. Mean peak IRG date pre-departure and MPI during migration had a positive effect on spring departure date. Herd-specific models produced differing responses (Table 2.2). The coefficient of mean peak IRG during migration was positive in Avalanche Creek and Uncompahgre Plateau. Standard deviation of peak IRG date during migration had a positive effect in Bear's Ears, and a negative effect in Uncompahgre Plateau.

The top model for migration duration included distance, MPI pre-departure, MPI during migration, and MPI post-arrival. The conditional R^2 value was 0.363. Distance and MPI post-arrival had positive effects on duration, while MPI pre-departure had a negative effect. Herd-specific models produced differing responses (Table 2.3). Mean peak IRG date post-arrival had a positive effect on duration in Bear's Ears and Avalanche Creek, while distance had a positive effect in Uncompahgre Plateau. No relationship was found between duration and daily displacements ($\boldsymbol{\beta} = 0.008$, $p = 0.98$).

The clustering algorithm produced two separate clusters: Cluster 1 and Cluster 2 (Figure 2.4). Cluster 1 had higher variation in optimality in all three periods compared to Cluster 2. Cluster 1 generally comprised individuals with mid-to-high optimality in one or two dimensions, with a lower value in remaining dimensions. Cluster 2, by contrast, generally consisted of individuals with mid-to-high optimality in two or all three dimensions and was more tightly clustered (Figure 2.5). Optimality for each period varied by cluster. The mean optimality for all three periods was higher in Cluster 2, while the standard deviation in optimality for all three periods was higher in Cluster 1. Cluster composition varied by herd, with differing proportions in each study area (Table 2.4). A chi-square test found evidence that the herd-specific distribution among clusters was unequal ($\chi = 24.092$, df = 2, $p < 0.001$).

DISCUSSION

Spatiotemporal dynamics in forage quality seemed to play an important role in influencing the phenology of spring migration in Colorado Rocky Mountain Elk. Elk appeared to adjust their migration in response to forage quality at differing periods of the migration, delaying departure with later corridor green-up and lengthening duration with later post-arrival green-up. My results suggest that elk may alter multiple aspects of their migratory phenology to facilitate heightened access to forage quality. This finding illustrates an impressive form of migratory plasticity observed in elk and offers a mechanism for resilience to environmental change. While individual variation existed in elk optimality, I did not observe variation in the period elk were optimizing, instead finding variation in overall optimality. Heterogeneity in interindividual optimality seems to exist along a gradient wherein a diversity of period-specific trade-offs appear viable.

Migration Timing and Duration

Spring departure date was positively affected by mean peak IRG date in the migratory corridor. This implies that migrants encountering regions with delayed peak green-up along their migratory route will depart from their winter range at a later date. Migratory elk are thus likely timing their departure date in response to forage quality along the migration itself, as would be predicted if individuals were engaging in ‘surfing’ according to the green-wave hypothesis of migration (Hebblewhite et al. 2008, Bischof et al. 2012). However, timing is likely additionally influenced by the date of snowmelt in combination with vegetative phenology (Rickbeil et al. 2019). It is also possible that forage quality on the winter range plays a role in triggering spring migration, as either perception of local conditions or memory of how local conditions correlate with future range conditions could act as triggers. Indeed, my model suggests a minor positive influence of green-up in the pre-departure period upon departure date. Note that these mechanisms are not necessarily mutually exclusive. My results support prior work demonstrating that IRG is likely to be an influential driver of ungulate migration, upholding the forage maturation hypothesis, and adds to literature observing surfing in elk specifically (Middleton et al. 2018, Aikens et al. 2020).

Mean peak IRG date following summer range arrival had a positive effect on migration duration. This indicates that migrants with summer ranges peaking at a later date take a longer time to perform their migration. One possibility is that elk are traveling along corridors more slowly in order to arrive at their summer range more optimally, so as to minimize phenology mismatch (i.e. the difference between peak green-up and their arrival). Another possibility is that elk are responding to current forage conditions along their migration route. I also found a positive effect of distance on duration, suggesting that on average migrants traversing greater distances take longer to do so. As might be expected, individuals with higher average daily displacements were significantly associated with shorter time spent along the corridor, but interestingly there is no significant relationship between distance and daily displacement. This could indicate that individuals don't increase the rate of their movement as a function of the distance they travel, but instead alter the speed of their migration to improve optimization of foraging or surfing.

Taken together, my models suggest that the determinants of migratory phenology in elk are multifaceted, with elk modulating timing of departure and duration of migration in response to resource conditions both along the migratory corridor and upon arrival at the summer range. This trade-off appears to shape the phenological parameters of migration in elk in these systems, implying multiple sources of plasticity and indicating response to both localized and anticipated conditions.

Elk Movement Optimality

The output of my cluster analysis showed that individuals vary in optimality along a multi-dimensional gradient, with each dimension representing optimality during a particular period of the migration (pre, during, post). Two clusters emerged: a highly optimized, low variation cluster, and a partially optimal, high-trade-off, high variation cluster. Given that ~62% of individuals belonged to the 'optimized' category, most elk in my dataset were seen to exhibit high overall optimality. This suggests that on average migratory elk have evolved a heightened level of precision in pursuing movements that maximize their access to high-quality forage during migratory events – impacting when to leave their winter range, how long to migrate, and when to arrive in their summer range. It also suggests that such precision lies along a continuum and that high diversity exists among migrants, with varying opportunities for optimality tradeoffs available and potentially viable.

According to optimization theory and its various applications in ecology (e.g. optimal foraging theory), it can be assumed as a null hypothesis that organisms have evolved movement behaviors aimed at acquiring resources at peak quality (Owen-Smith et al. 2010). This is rarely perfectly actualized in reality, but my analysis allows for individual-level estimation of how closely optimal foraging is achieved in the context of migration events. This framework can aid our understanding of how individual movements might relate to the green-wave, and discriminate between the variety of possible responses (Merkle et al. 2016). One can consider green-wave responses as a spectrum, from ‘lagging’ (delaying departure to prioritize winter range forage), to ‘surfing’ (prioritizing forage access along the corridor), to ‘jumping’ (prioritizing summer range forage access), and intermediate options (Bischof et al. 2012). A significant feature of this framework is its ability to elucidate the diversity and abundance of such ‘sub-strategies’. Sub-strategies optimizing different components of migratory movements can be specified along a three-dimensional gradient of optimality, between pre-departure optimization, route optimization, and post-arrival optimization. My results suggest high interindividual diversity along this gradient. This variation supports findings revealing high plasticity in elk movement compared to some other ungulates with more predictable sub-strategies (Sawyer et al. 2018, Xu et al. 2021), and articulates a specific form of plasticity. Such plasticity and diversity may aid elk in their ability to respond to future changes on the landscape (Rickbeil et al. 2019).

Though overall 62% of individuals were categorized in the ‘optimized’ cluster, percentages were not equal among study areas (Table 2.4). My analyses revealed stark differences in the overall optimality of different herds, with Avalanche Creek occurring nearly half and half among clusters, Bear's Ears primarily in the optimized cluster (82.2%), and Uncompahgre Plateau primarily in the sub-optimized cluster (68.9%). This implies that individuals in differing systems may be unequal in their average optimization of migratory events, likely owing to system-specific differences in forage phenology and topography. The herd-specific distribution among clusters is particularly of note given estimates of migratory frequency in these herds (see Chapter 1). Among these three populations, Bear's Ears has the highest overall optimality, and is the only herd estimated to be fully migratory. It is thus possible that optimality is stronger in populations wherein non-migratory strategies are absent, with an increased driver for migratory optimization in systems where facultative switching is less probable or potentially non-viable. This could relate to density-dependence, with partially migratory systems harboring additional factors that could less directly link migratory optimality to environmental conditions (e.g. optimality could be limited as a function of density thresholds). Additionally, the prevalence of more optimal movements may depend upon the nature of green-up in a system, with 'steeper' greenscapes encouraging and rewarding optimal movements (Aikens 2017).

Broader Implications

The timing of peak forage quality seems to be a strong driver of elk migratory movement, influencing both departure dates and migration duration. My results agree with the findings of Rickbeil et al. 2019, in that the peak date of green-up along the corridor is positively associated with departure dates. That this result holds in both the Colorado Rockies and the Greater Yellowstone Ecosystem (GYE) implies that this covariate is a particularly influential determinant of spring departure dates in elk. This finding indicates some level of surfing the green-wave in these systems, conflicting with literature not finding evidence of surfing in elk (Merkle et al. 2016), but supporting literature that did (Middleton et al. 2018). This suggests that surfing may not be a desirable tactic in all landscapes, likely as a function of the nature of the green-wave in systems, or that other trade-offs are more important (Aikens et al. 2017). Indeed, I found evidence against surfing in the Uncompahgre Plateau herd. This may relate to not only to the 'greenscape' in this system, but additionally to density dynamics, which as mentioned previously could potentially complicate green-wave response in partially migratory systems. My results overall imply a plastic modulation of departure date and duration that lead to a diversity of sub-strategies (migratory portfolios) and illustrate the highly adaptive nature of migratory elk. Surfing appears to drive migratory behavior in multiple herds, but not all, suggesting that surfing is not a universal mechanism, or is at least weaker in some systems than others.

My results indicate that elk attempt to optimize access to quality forage at every stage of the migration event – pre-departure, during migration, and upon arrival on summer range. Optimization on winter range and during migration could occur in response to localized conditions. However, the result of my duration model (indicating a response to forage phenology in the summer range) suggests that memory may play a role in migratory phenology, as elk appear to alter the duration of their migration as a function of non-localized anticipated conditions. The relative influences of local and memory-based responses are complex and commonly discussed in the literature, but my findings reiterate the importance of spatiotemporal memory in migration (Bracis et al. 2017, Merkle et al. 2019). Unfortunately, without a formal test for selection, it is difficult to show that elk are explicitly selecting for maximal IRG at fine scales compared to what's available, only that they are on average optimal in the timing of their movements overall. Thus, an explicit test for local selection could further elucidate the significance of local responses compared to the role of memory in influencing migratory phenology.

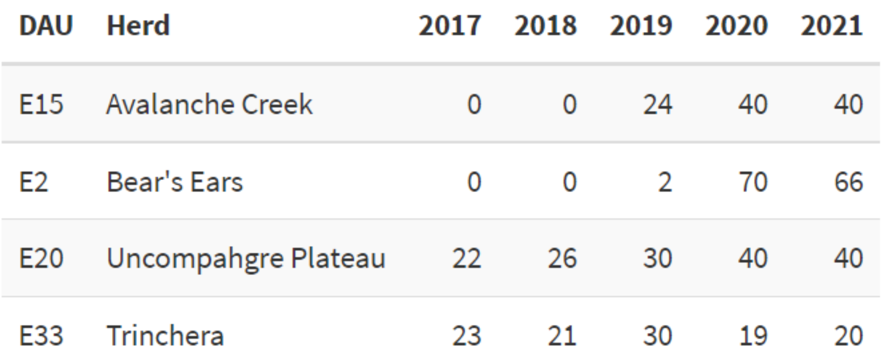
My clustering analysis revealed a continuum of sub-strategies among migratory elk, wherein trade-offs of optimality during discrete periods of migratory events could be quantified. My analysis indicated where an individual was along the three axes of optimality, revealing an abundance and diversity of sub-strategies. Various intermediate positions between ‘lagging’ and ‘jumping’ represent trade-offs in forage quality access throughout the migratory event. The resultant differences in overall access to forage quality are likely to influence fitness (Middleton et al. 2018). A multi-year longitudinal approach, with annual body condition estimates, parturition status, and quantification of optimality could potentially detect a difference in fitness among individuals within the continuum if present. However, the degree to which forage quality alone determines migrant fitness and migratory phenology should not be overstated, as a myriad of factors are also known to influence these variables (e.g., predation and hunting pressure, disease dynamics, snow, etc.).

Management Implications

The measurement of departure and arrival dates of migrants in these systems can act as a benchmark for future work to determine shifts in timing and duration of migrations, as well as potential increases in phenological mismatch. This is important baseline data, as it can allow subsequent studies to investigate the influences of climate change and increasing human modification of the landscape on animal movement. Mapping migratory routes should also inform current conservation efforts concerned with the intersection of corridors and potentially harmful human features. Determining theoretical drivers of departure date and duration will provide important insights for management, particularly in a world where vegetative phenology is at risk of changing due to climate change and alterations of hydrology (Aikens et al. 2020). Because the date of peak green-up along migratory corridors is a strong determinant of departure date, while the date of peak green-up upon summer range arrival is a strong determinant of duration, an alteration of green-up timing could shift migratory phenology in complex ways. Though I’ve shown that most elk in these systems optimize forage quality to a heightened degree, the speed at which they could adjust and maintain this optimality in quickly shifting conditions is uncertain. If such behavioral changes are delayed, it may have consequences for fitness and thus for population dynamics in populations with a high percentage of migrants. Understanding the rate at which vegetative phenology will shift over time, as well as quantifying the ways and rates at which migrants respond to such changes should prove to be a significant area of study in the near future, with various conservation implications. For example, studying this relationship should facilitate an increased awareness of where and when elk move in response to changing conditions, permitting up-to-date and spatiotemporally explicit management practices to better suit elk population needs in the face of phenological shifts.

EXHIBITS

Table 1.1 Year-specific elk captures in each herd.



DAU	Herd	2017	2018	2019	2020	2021
E15	Avalanche Creek	0	0	24	40	40
E2	Bear's Ears	0	0	2	70	66
E20	Uncompahgre Plateau	22	26	30	40	40
E33	Trinchera	23	21	30	19	20

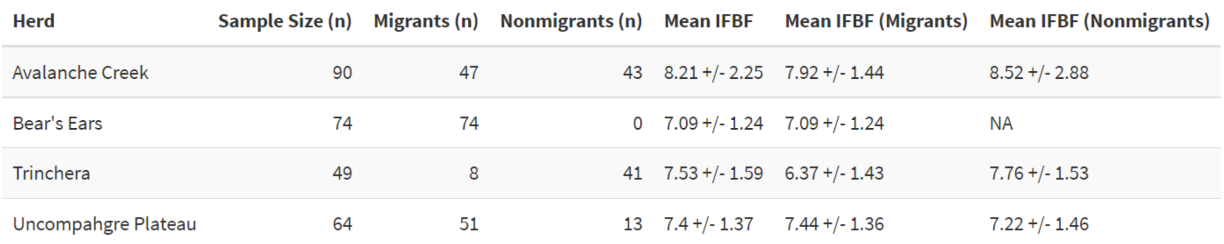
Table 1.2. Categories of covariates extracted and summarized at the seasonal range scale for individual elk for use analysis.

Covariate Categories	Covariates Summarized at the Seasonal Range Scale
Anthropogenic	Percent Cover Human Development, Road Length per Unit Area (km/km²), Percent Cover Crop
Land Cover/Habitat	Percent Cover Forest, Percent Cover Forest Edge, Percent Open Habitat, Hydrological Feature Length per Unit Area (km/km²), Mean Elevation (m)
NDVI	Mean NDVI Seasonality, Mean NDVI Predictability, Mean NDVI over the seasonal period, Mean IRG over the seasonal period
Snow	Mean Snow Seasonality, Mean Snow Predictability, Mean snow cover over the seasonal period

Table 1.3. Categories of covariates extracted from elk locations during seasonal periods for resource selection analysis.

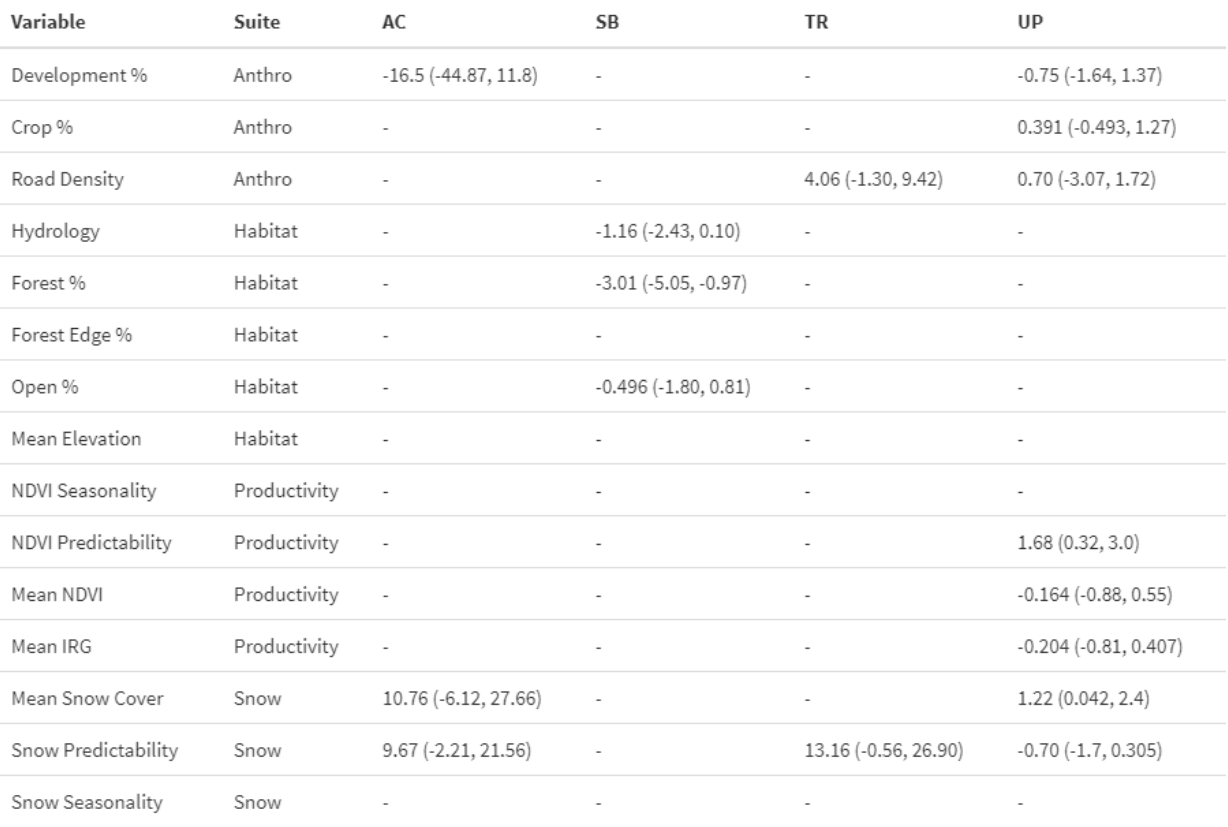
Covariate Categories	Covariates Extracted from Elk Locations for Resource Selection Functions
Anthropogenic	(Log)Distance to development, (Log)distance to roads
Land Cover/Habitat	(Log)Distance to hydrological feature, forest, open habitat, other habitat, Elevation
NDVI	NDVI, IRG, NDVI predictability
Snow	Snow cover, snow predictability

Table 1.4. Summary statistics for Ingesta-Free Body Fat (IFBF) analyses, including herd-specific and strategy-specific sample sizes, alongside herd-wide mean IFBF, and strategy-specific statistics within each herd. Mean estimates are followed by +/- the standard deviation. Note that body condition data was not collected from Steamboat elk.



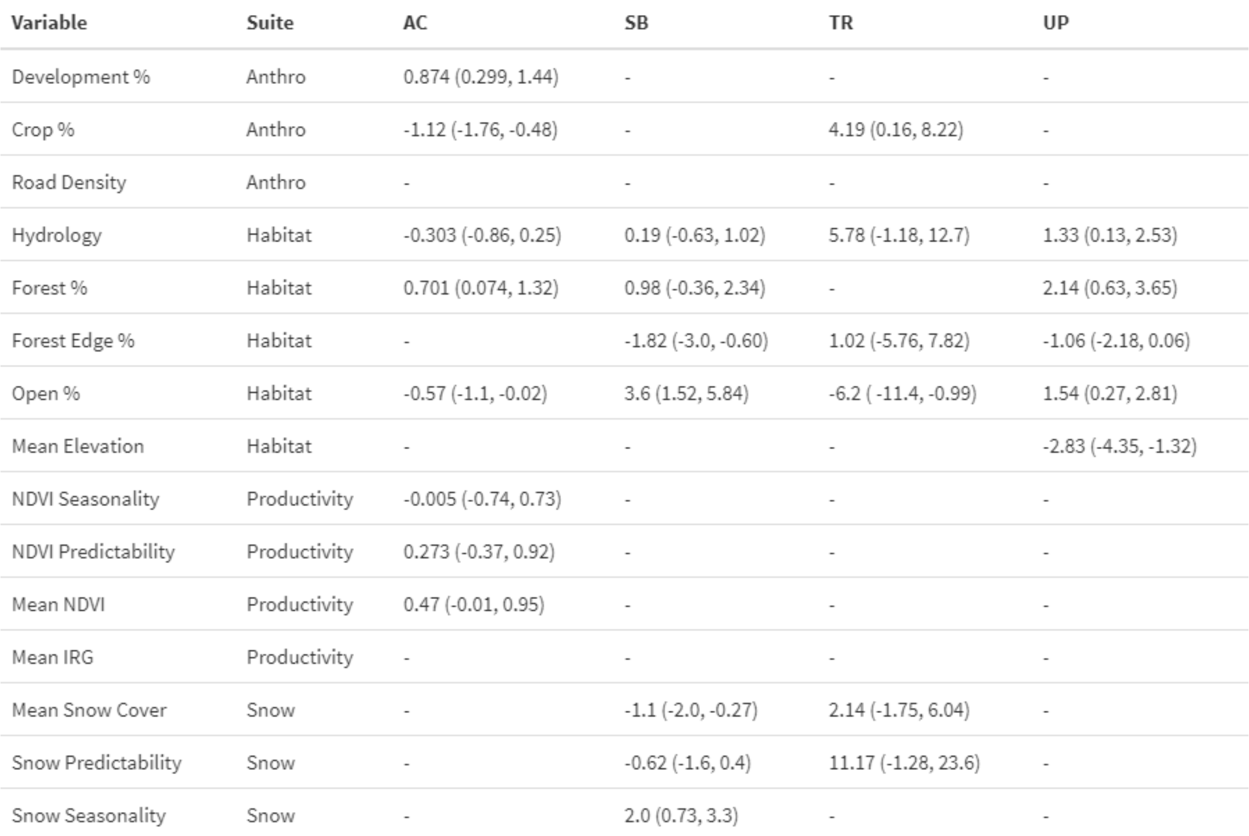
Herd	Sample Size (n)	Migrants (n)	Nonmigrants (n)	Mean IFBF	Mean IFBF (Migrants)	Mean IFBF (Nonmigrants)
Avalanche Creek	90	47	43	8.21 +/- 2.25	7.92 +/- 1.44	8.52 +/- 2.88
Bear's Ears	74	74	0	7.09 +/- 1.24	7.09 +/- 1.24	NA
Trinchera	49	8	41	7.53 +/- 1.59	6.37 +/- 1.43	7.76 +/- 1.53
Uncompahgre Plateau	64	51	13	7.4 +/- 1.37	7.44 +/- 1.36	7.22 +/- 1.46

Table 1.5. Parameter estimates for summer space use models. Estimates are listed alongside 95% confidence intervals, and dashes denote the absence of a covariate in a given study area model. Herds are listed by their acronyms (AC = Avalanche Creek, SB = Steamboat, TR = Trinchera, UP = Uncompahgre Plateau).



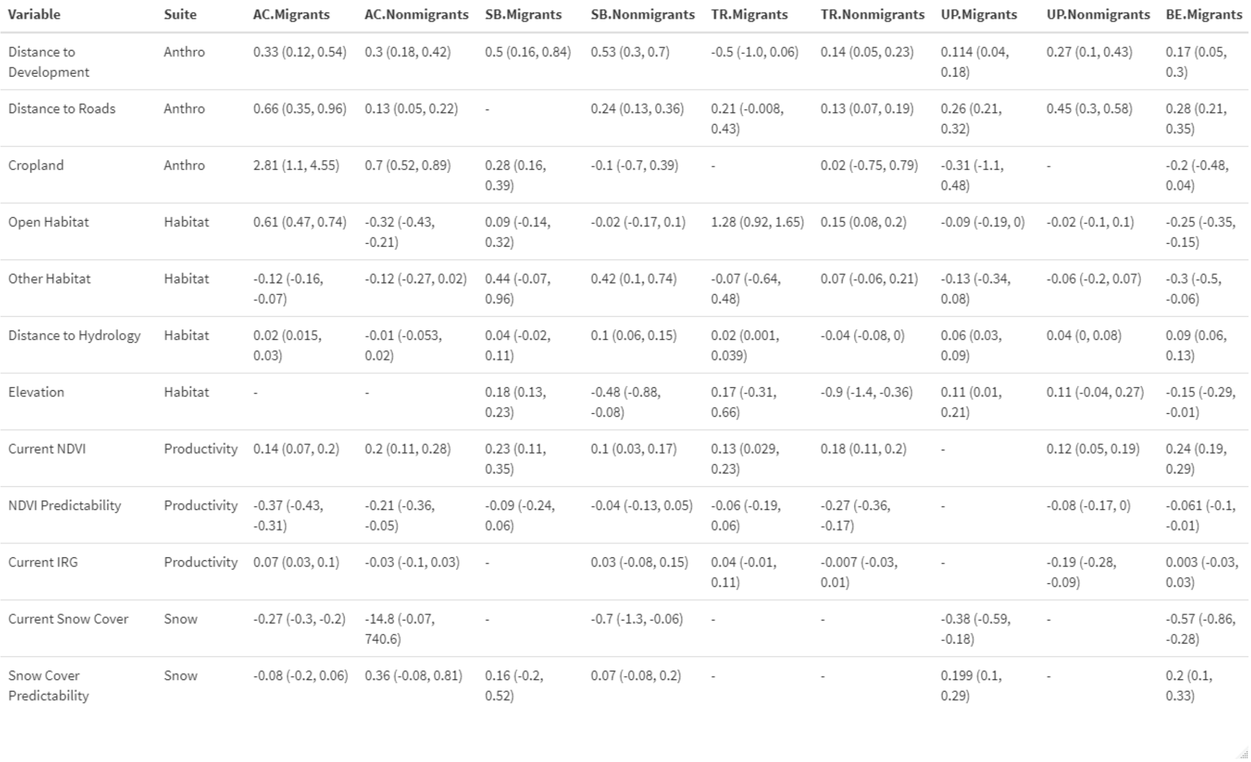
Variable	**Suite**	**AC**	**SB**	**TR**	**UP**
Development %	Anthro	-16.5 (-44.87, 11.8)	-	-	-0.75 (-1.64, 1.37)
Crop %	Anthro	-	-	-	0.391 (-0.493, 1.27)
Road Density	Anthro	-	-	4.06 (-1.30, 9.42)	0.70 (-3.07, 1.72)
Hydrology	Habitat	-	-1.16 (-2.43, 0.10)	-	-
Forest %	Habitat	-	-3.01 (-5.05, -0.97)	-	-
Forest Edge %	Habitat	-	-	-	-
Open %	Habitat	-	-0.496 (-1.80, 0.81)	-	-
Mean Elevation	Habitat	-	-	-	-
NDVI Seasonality	Productivity	-	-	-	-
NDVI Predictability	Productivity	-	-	-	1.68 (0.32, 3.0)
Mean NDVI	Productivity	-	-	-	-0.164 (-0.88, 0.55)
Mean IRG	Productivity	-	-	-	-0.204 (-0.81, 0.407)
Mean Snow Cover	Snow	10.76 (-6.12, 27.66)	-	-	1.22 (0.042, 2.4)
Snow Predictability	Snow	9.67 (-2.21, 21.56)	-	13.16 (-0.56, 26.90)	-0.70 (-1.7, 0.305)
Snow Seasonality	Snow	-	-	-	-

Table 1.6. Parameter estimates for winter space use models. Estimates are listed alongside 95% confidence intervals, and dashes denote the absence of a covariate in a given study area model. Herds are listed by their acronyms (AC = Avalanche Creek, SB = Steamboat, TR = Trinchera, UP = Uncompahgre Plateau).



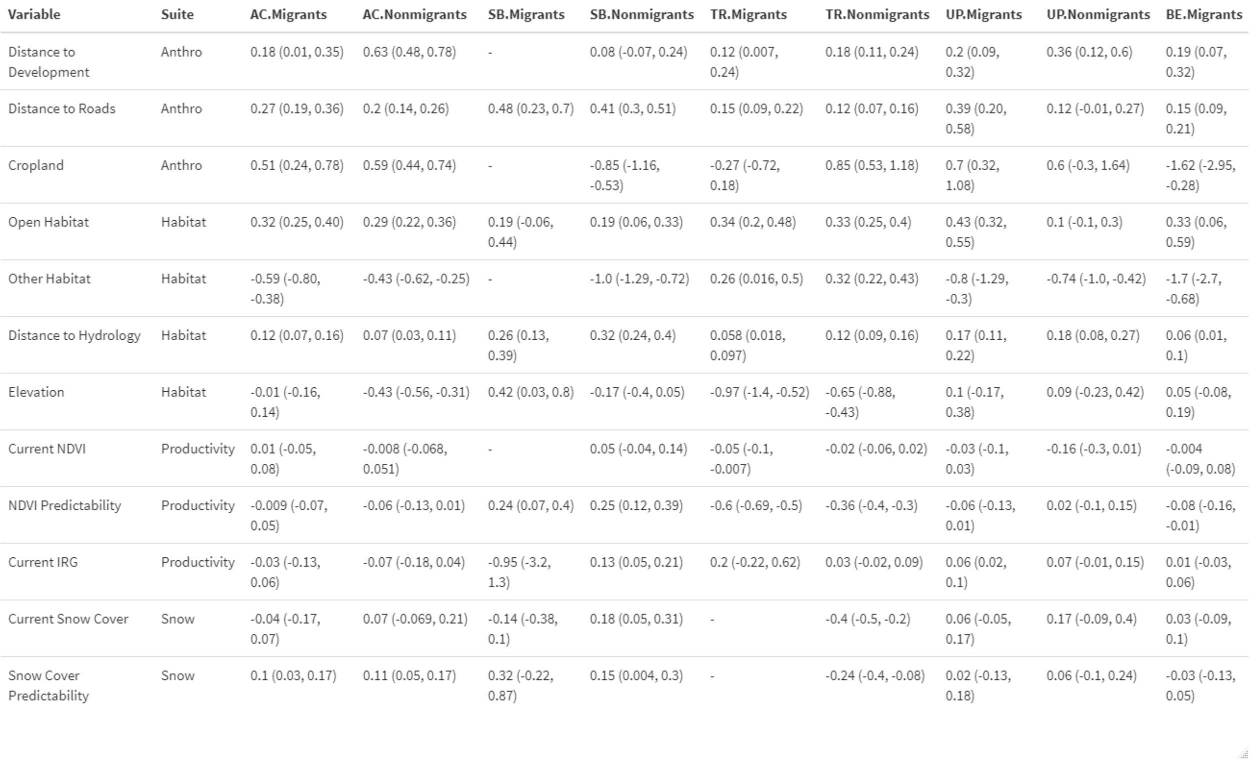
Variable	Suite	AC	SB	TR	UP
Development %	Anthro	0.874 (0.299, 1.44)	-	-	-
Crop %	Anthro	-1.12 (-1.76, -0.48)	-	4.19 (0.16, 8.22)	-
Road Density	Anthro	-	-	-	-
Hydrology	Habitat	-0.303 (-0.86, 0.25)	0.19 (-0.63, 1.02)	5.78 (-1.18, 12.7)	1.33 (0.13, 2.53)
Forest %	Habitat	0.701 (0.074, 1.32)	0.98 (-0.36, 2.34)	-	2.14 (0.63, 3.65)
Forest Edge %	Habitat	-	-1.82 (-3.0, -0.60)	1.02 (-5.76, 7.82)	-1.06 (-2.18, 0.06)
Open %	Habitat	-0.57 (-1.1, -0.02)	3.6 (1.52, 5.84)	-6.2 (-11.4, -0.99)	1.54 (0.27, 2.81)
Mean Elevation	Habitat	-	-	-	-2.83 (-4.35, -1.32)
NDVI Seasonality	Productivity	-0.005 (-0.74, 0.73)	-	-	-
NDVI Predictability	Productivity	0.273 (-0.37, 0.92)	-	-	-
Mean NDVI	Productivity	0.47 (-0.01, 0.95)	-	-	-
Mean IRG	Productivity	-	-	-	-
Mean Snow Cover	Snow	-	-1.1 (-2.0, -0.27)	2.14 (-1.75, 6.04)	-
Snow Predictability	Snow	-	-0.62 (-1.6, 0.4)	11.17 (-1.28, 23.6)	-
Snow Seasonality	Snow	-	2.0 (0.73, 3.3)	-	-

Table 1.7. Parameter estimates for strategy-specific summer resource selection function models. Estimates are listed alongside 95% confidence intervals and dashes denote the absence of a covariate in a given study area model. Herds are listed by their acronyms (AC = Avalanche Creek, BE = Bear's Ears, SB = Steamboat, TR = Trinchera, UP = Uncompahgre Plateau).



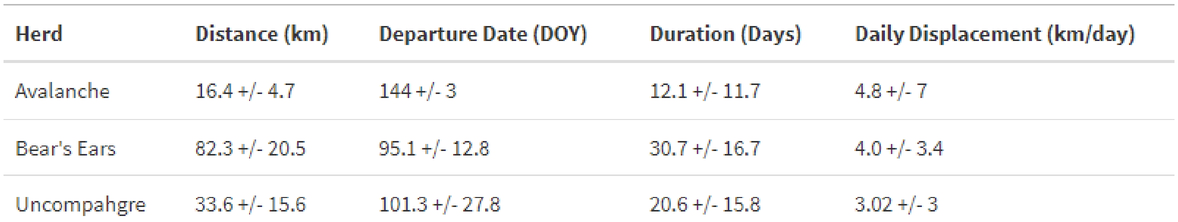
Variable	Suite	AC.Migrants	AC.Nonmigrants	SB.Migrants	SB.Nonmigrants	TR.Migrants	TR.Nonmigrants	UP.Migrants	UP.Nonmigrants	BE.Migrants
Distance to Development	Anthro	0.33 (0.12, 0.54)	0.3 (0.18, 0.42)	0.5 (0.16, 0.84)	0.53 (0.3, 0.7)	-0.5 (-1.0, 0.06)	0.14 (0.05, 0.23)	0.114 (0.04, 0.18)	0.27 (0.1, 0.43)	0.17 (0.05, 0.3)
Distance to Roads	Anthro	0.66 (0.35, 0.96)	0.13 (0.05, 0.22)	-	0.24 (0.13, 0.36)	0.21 (-0.008, 0.43)	0.13 (0.07, 0.19)	0.26 (0.21, 0.32)	0.45 (0.3, 0.58)	0.28 (0.21, 0.35)
Cropland	Anthro	2.81 (1.1, 4.55)	0.7 (0.52, 0.89)	0.28 (0.16, 0.39)	-0.1 (-0.7, 0.39)	-	0.02 (-0.75, 0.79)	-0.31 (-1.1, 0.48)	-	-0.2 (-0.48, 0.04)
Open Habitat	Habitat	0.61 (0.47, 0.74)	-0.32 (-0.43, -0.21)	0.09 (-0.14, 0.32)	-0.02 (-0.17, 0.1)	1.28 (0.92, 1.65)	0.15 (0.08, 0.2)	-0.09 (-0.19, 0)	-0.02 (-0.1, 0.1)	-0.25 (-0.35, -0.15)
Other Habitat	Habitat	-0.12 (-0.16, -0.07)	-0.12 (-0.27, 0.02)	0.44 (-0.07, 0.96)	0.42 (0.1, 0.74)	-0.07 (-0.64, 0.48)	0.07 (-0.06, 0.21)	-0.13 (-0.34, 0.08)	-0.06 (-0.2, 0.07)	-0.3 (-0.5, -0.06)
Distance to Hydrology	Habitat	0.02 (0.015, 0.03)	-0.01 (-0.053, 0.02)	0.04 (-0.02, 0.11)	0.1 (0.06, 0.15)	0.02 (0.001, 0.039)	-0.04 (-0.08, 0)	0.06 (0.03, 0.09)	0.04 (0, 0.08)	0.09 (0.06, 0.13)
Elevation	Habitat	-	-	0.18 (0.13, 0.23)	-0.48 (-0.88, -0.08)	0.17 (-0.31, 0.66)	-0.9 (-1.4, -0.36)	0.11 (0.01, 0.21)	0.11 (-0.04, 0.27)	-0.15 (-0.29, -0.01)
Current NDVI	Productivity	0.14 (0.07, 0.2)	0.2 (0.11, 0.28)	0.23 (0.11, 0.35)	0.1 (0.03, 0.17)	0.13 (0.029, 0.23)	0.18 (0.11, 0.2)	-	0.12 (0.05, 0.19)	0.24 (0.19, 0.29)
NDVI Predictability	Productivity	-0.37 (-0.43, -0.31)	-0.21 (-0.36, -0.05)	-0.09 (-0.24, 0.06)	-0.04 (-0.13, 0.05)	-0.06 (-0.19, 0.06)	-0.27 (-0.36, -0.17)	-	-0.08 (-0.17, 0)	-0.061 (-0.1, -0.01)
Current IRG	Productivity	0.07 (0.03, 0.1)	-0.03 (-0.1, 0.03)	-	0.03 (-0.08, 0.15)	0.04 (-0.01, 0.11)	-0.007 (-0.03, 0.01)	-	-0.19 (-0.28, -0.09)	0.003 (-0.03, 0.03)
Current Snow Cover	Snow	-0.27 (-0.3, -0.2)	-14.8 (-0.07, 740.6)	-	-0.7 (-1.3, -0.06)	-	-	-0.38 (-0.59, -0.18)	-	-0.57 (-0.86, -0.28)
Snow Cover Predictability	Snow	-0.08 (-0.2, 0.06)	0.36 (-0.08, 0.81)	0.16 (-0.2, 0.52)	0.07 (-0.08, 0.2)	-	-	0.199 (0.1, 0.29)	-	0.2 (0.1, 0.33)

Table 1.8. Parameter estimates for strategy-specific winter resource selection function models. Estimates are listed alongside 95% confidence intervals and dashes denote the absence of a covariate in a given study area model. Herds are listed by their acronyms (AC = Avalanche Creek, BE = Bear’s Ears, SB = Steamboat, TR = Trinchera, UP = Uncompahgre Plateau).



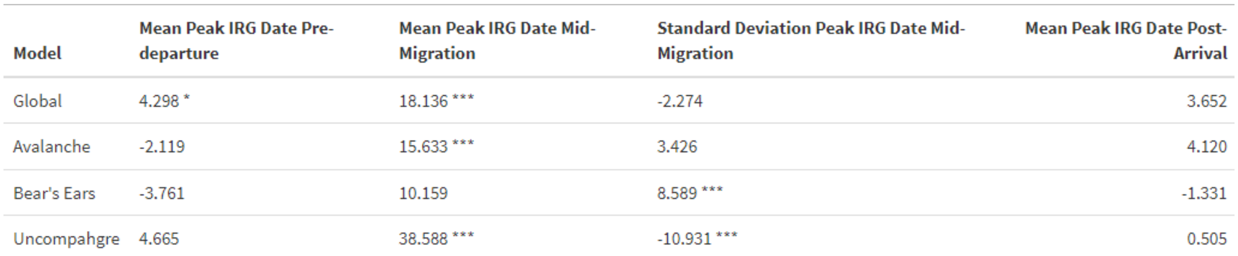
Variable	Suite	AC.Migrants	AC.Nonmigrants	SB.Migrants	SB.Nonmigrants	TR.Migrants	TR.Nonmigrants	UP.Migrants	UP.Nonmigrants	BE.Migrants
Distance to Development	Anthro	0.18 (0.01, 0.35)	0.63 (0.48, 0.78)	-	0.08 (-0.07, 0.24)	0.12 (0.007, 0.24)	0.18 (0.11, 0.24)	0.2 (0.09, 0.32)	0.36 (0.12, 0.6)	0.19 (0.07, 0.32)
Distance to Roads	Anthro	0.27 (0.19, 0.36)	0.2 (0.14, 0.26)	0.48 (0.23, 0.7)	0.41 (0.3, 0.51)	0.15 (0.09, 0.22)	0.12 (0.07, 0.16)	0.39 (0.20, 0.58)	0.12 (-0.01, 0.27)	0.15 (0.09, 0.21)
Cropland	Anthro	0.51 (0.24, 0.78)	0.59 (0.44, 0.74)	-	-0.85 (-1.16, -0.53)	-0.27 (-0.72, 0.18)	0.85 (0.53, 1.18)	0.7 (0.32, 1.08)	0.6 (-0.3, 1.64)	-1.62 (-2.95, -0.28)
Open Habitat	Habitat	0.32 (0.25, 0.40)	0.29 (0.22, 0.36)	0.19 (-0.06, 0.44)	0.19 (0.06, 0.33)	0.34 (0.2, 0.48)	0.33 (0.25, 0.4)	0.43 (0.32, 0.55)	0.1 (-0.1, 0.3)	0.33 (0.06, 0.59)
Other Habitat	Habitat	-0.59 (-0.80, -0.38)	-0.43 (-0.62, -0.25)	-	-1.0 (-1.29, -0.72)	0.26 (0.016, 0.5)	0.32 (0.22, 0.43)	-0.8 (-1.29, -0.3)	-0.74 (-1.0, -0.42)	-1.7 (-2.7, -0.68)
Distance to Hydrology	Habitat	0.12 (0.07, 0.16)	0.07 (0.03, 0.11)	0.26 (0.13, 0.39)	0.32 (0.24, 0.4)	0.058 (0.018, 0.097)	0.12 (0.09, 0.16)	0.17 (0.11, 0.22)	0.18 (0.08, 0.27)	0.06 (0.01, 0.1)
Elevation	Habitat	-0.01 (-0.16, 0.14)	-0.43 (-0.56, -0.31)	0.42 (0.03, 0.8)	-0.17 (-0.4, 0.05)	-0.97 (-1.4, -0.52)	-0.65 (-0.88, -0.43)	0.1 (-0.17, 0.38)	0.09 (-0.23, 0.42)	0.05 (-0.08, 0.19)
Current NDVI	Productivity	0.01 (-0.05, 0.08)	-0.008 (-0.068, 0.051)	-	0.05 (-0.04, 0.14)	-0.05 (-0.1, -0.007)	-0.02 (-0.06, 0.02)	-0.03 (-0.1, 0.03)	-0.16 (-0.3, 0.01)	-0.004 (-0.09, 0.08)
NDVI Predictability	Productivity	-0.009 (-0.07, 0.05)	-0.06 (-0.13, 0.01)	0.24 (0.07, 0.4)	0.25 (0.12, 0.39)	-0.6 (-0.69, -0.5)	-0.36 (-0.4, -0.3)	-0.06 (-0.13, 0.01)	0.02 (-0.1, 0.15)	-0.08 (-0.16, -0.01)
Current IRG	Productivity	-0.03 (-0.13, 0.06)	-0.07 (-0.18, 0.04)	-0.95 (-3.2, 1.3)	0.13 (0.05, 0.21)	0.2 (-0.22, 0.62)	0.03 (-0.02, 0.09)	0.06 (0.02, 0.1)	0.07 (-0.01, 0.15)	0.01 (-0.03, 0.06)
Current Snow Cover	Snow	-0.04 (-0.17, 0.07)	0.07 (-0.069, 0.21)	-0.14 (-0.38, 0.1)	0.18 (0.05, 0.31)	-	-0.4 (-0.5, -0.2)	0.06 (-0.05, 0.17)	0.17 (-0.09, 0.4)	0.03 (-0.09, 0.1)
Snow Cover Predictability	Snow	0.1 (0.03, 0.17)	0.11 (0.05, 0.17)	0.32 (-0.22, 0.87)	0.15 (0.004, 0.3)	-	-0.24 (-0.4, -0.08)	0.02 (-0.13, 0.18)	0.06 (-0.1, 0.24)	-0.03 (-0.13, 0.05)

Table 2.1: Summary statistics by herd, displaying spring migration distances, departure dates, durations, and daily displacements. Initial values are the mean followed by the standard deviation; estimates are rounded.



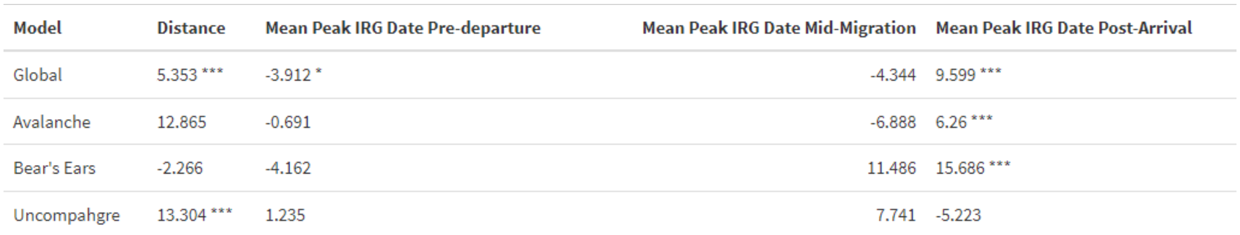
Herd	Distance (km)	Departure Date (DOY)	Duration (Days)	Daily Displacement (km/day)
Avalanche	16.4 +/- 4.7	144 +/- 3	12.1 +/- 11.7	4.8 +/- 7
Bear's Ears	82.3 +/- 20.5	95.1 +/- 12.8	30.7 +/- 16.7	4.0 +/- 3.4
Uncompahgre	33.6 +/- 15.6	101.3 +/- 27.8	20.6 +/- 15.8	3.02 +/- 3

Table 2.2: Parameter estimates for each covariate in global and herd-specific models, which used the same variables as the global model, for spring departure date. Note that a *** symbol following an estimate denotes significance ($p \leq 0.05$), while * denotes marginal significance ($p \leq 0.08$).



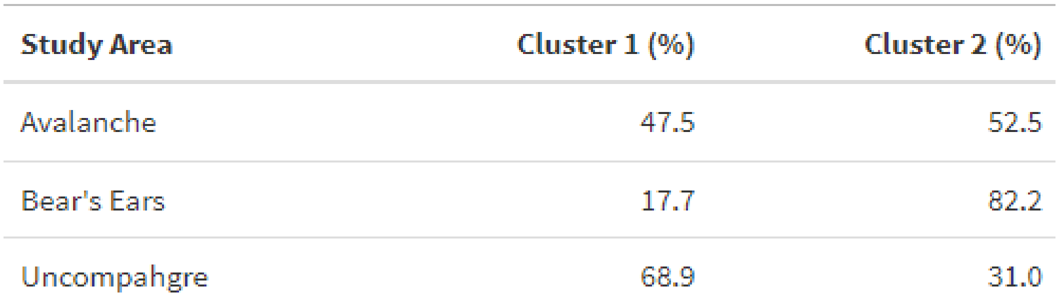
Model	Mean Peak IRG Date Pre-departure	Mean Peak IRG Date Mid-Migration	Standard Deviation Peak IRG Date Mid-Migration	Mean Peak IRG Date Post-Arrival
Global	4.298 *	18.136 ***	-2.274	3.652
Avalanche	-2.119	15.633 ***	3.426	4.120
Bear's Ears	-3.761	10.159	8.589 ***	-1.331
Uncompahgre	4.665	38.588 ***	-10.931 ***	0.505

Table 2.3: Parameter estimates for each covariate in global and herd-specific models, which used the same variables as the global model, for migration duration. Note that a *** symbol following an estimate denotes significance ($p \leq 0.05$), while * denotes marginal significance ($p \leq 0.08$).



Model	Distance	Mean Peak IRG Date Pre-departure	Mean Peak IRG Date Mid-Migration	Mean Peak IRG Date Post-Arrival
Global	5.353 ***	-3.912 *	-4.344	9.599 ***
Avalanche	12.865	-0.691	-6.888	6.26 ***
Bear's Ears	-2.266	-4.162	11.486	15.686 ***
Uncompahgre	13.304 ***	1.235	7.741	-5.223

Table 2.4: Percentage of individuals in each herd categorized as Cluster 1 or Cluster 2. Percentages are rounded to the nearest tenth.



Study Area	**Cluster 1 (%)**	**Cluster 2 (%)**
Avalanche	47.5	52.5
Bear's Ears	17.7	82.2
Uncompahgre	68.9	31.0

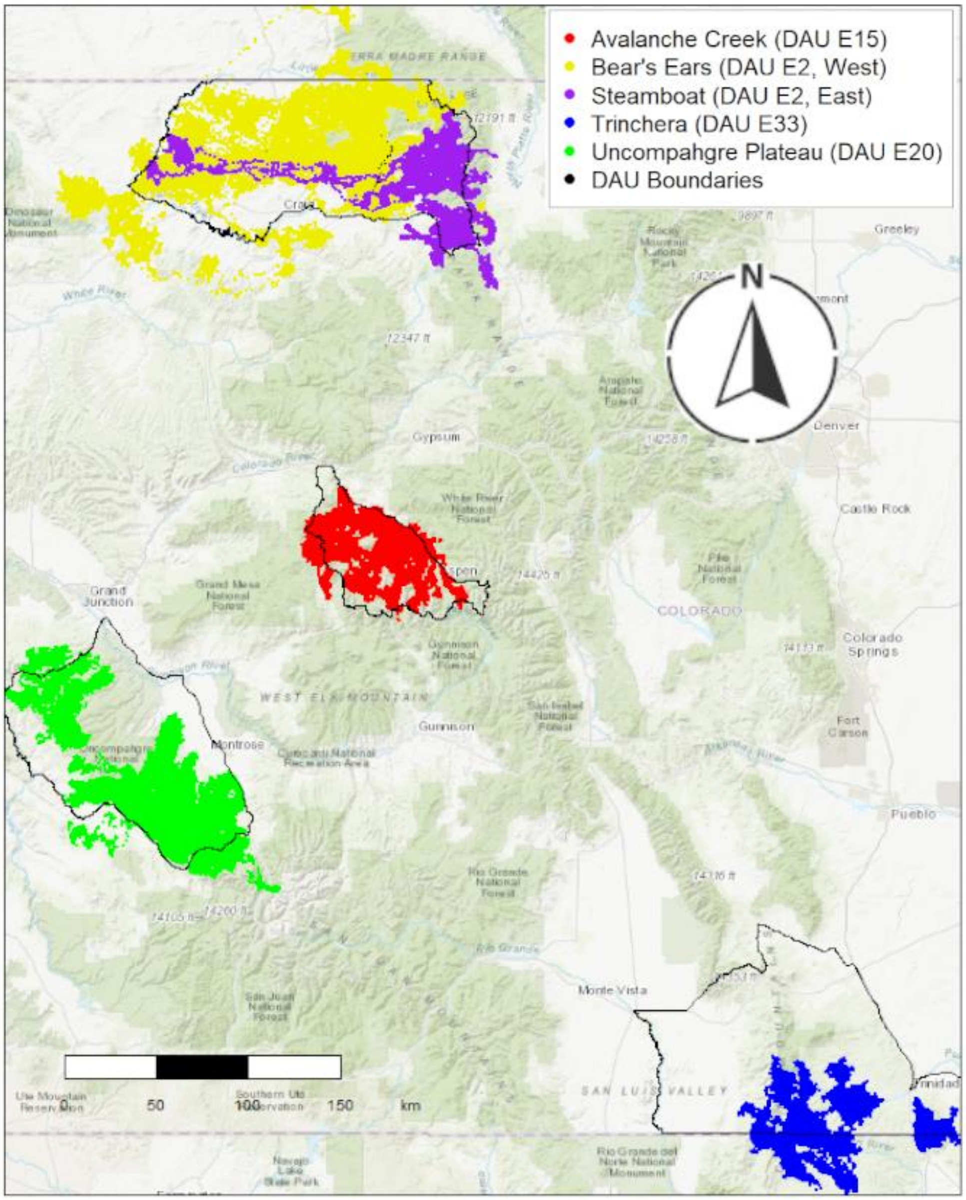


Figure 1.1. Map of study area in the state of Colorado. Black lines delineate the Colorado Parks and Wildlife Data Analysis Unit boundaries for each herd. Each colored point represents a location from an elk used in this study, with colors corresponding to specific herds: Avalanche Creek is shown in red, Bear’s Ears is shown in yellow, Steamboat is shown in purple, Trinchera is shown in blue, and Uncompahgre Plateau is shown in green.

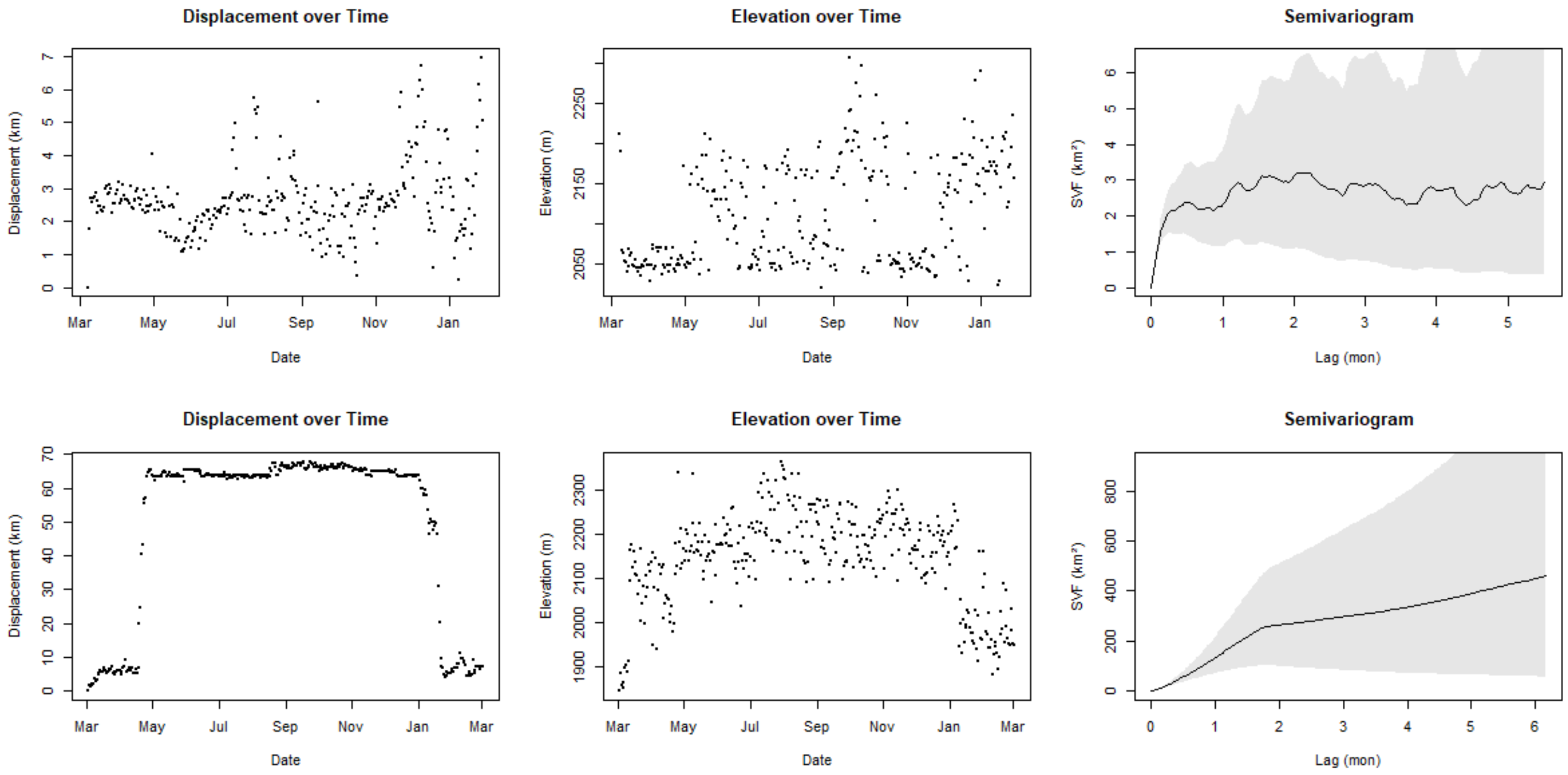


Figure 1.2. Graphs illustrating characteristic non-migratory and migratory behavior in two elk individuals. Displacement over time, elevation over time, and semivariograms are depicted for a non-migrant above and a migrant below. Qualitatively, timing of migratory events can be visually identified by sudden, persistent displacements across space and/or elevation gradients followed by a stable leveling off in the plot, signifying seasonal home ranging behavior. Non-migrants comparatively do not display clear migratory movement or strong patterns of discontiguous space use. Additionally, non-migrants produce asymptotic semivariograms, indicating

home ranging behavior throughout the duration of the tracking period (Fleming et al. 2017). Note the absence of a trend in the above individual, with an asymptotic semivariogram, and the clear migratory movement in the elk below moving nearly 70 kilometers between ranges.

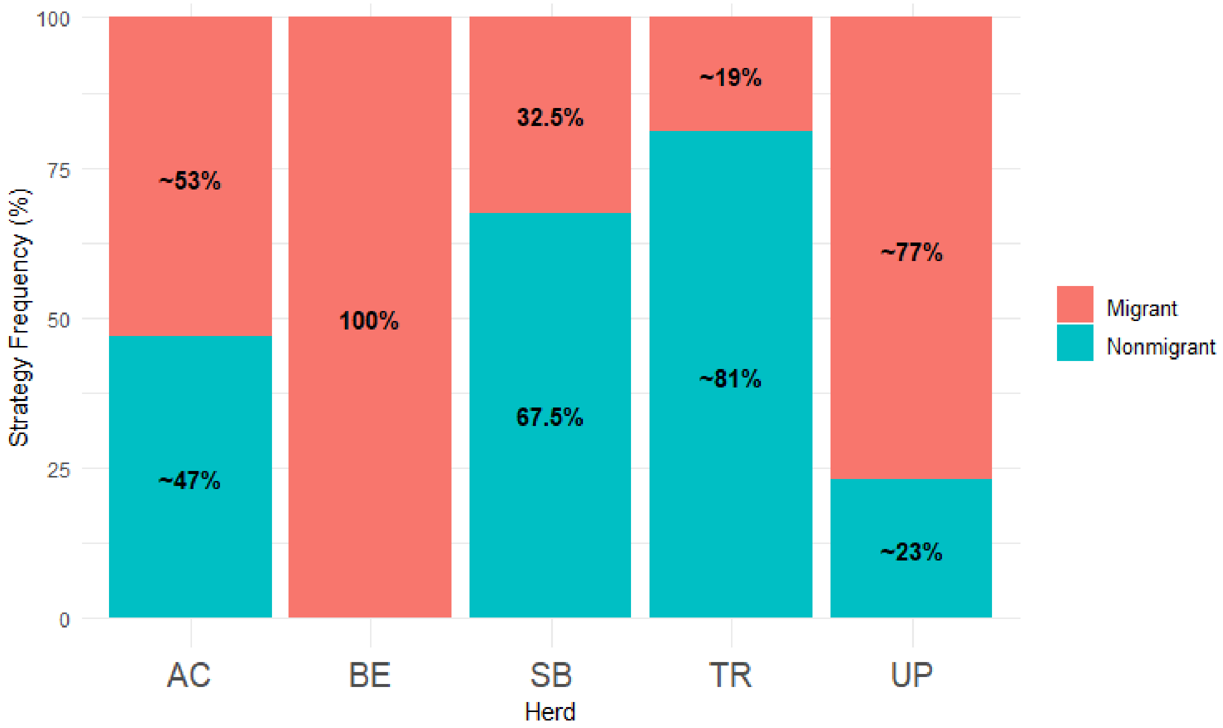


Figure 1.3. Bar plot showing movement strategy frequency estimates by study area, with percentages of differing strategies shown in bold. Strategy-specific sample sizes varied among study areas (Avalanche Creek: 49 migrants, 43 non-migrants; Bear's Ears: 74 migrants, 0 non-migrants; Steamboat: 13 migrants, 27 non-migrants; Trinchera: 17 migrants, 72 non-migrants; Uncompahgre Plateau: 71 migrants, 21 non-migrants). AC = Avalanche Creek, BE = Bear's Ears, SB = Steamboat, TR = Trinchera, UP = Uncompahgre Plateau.

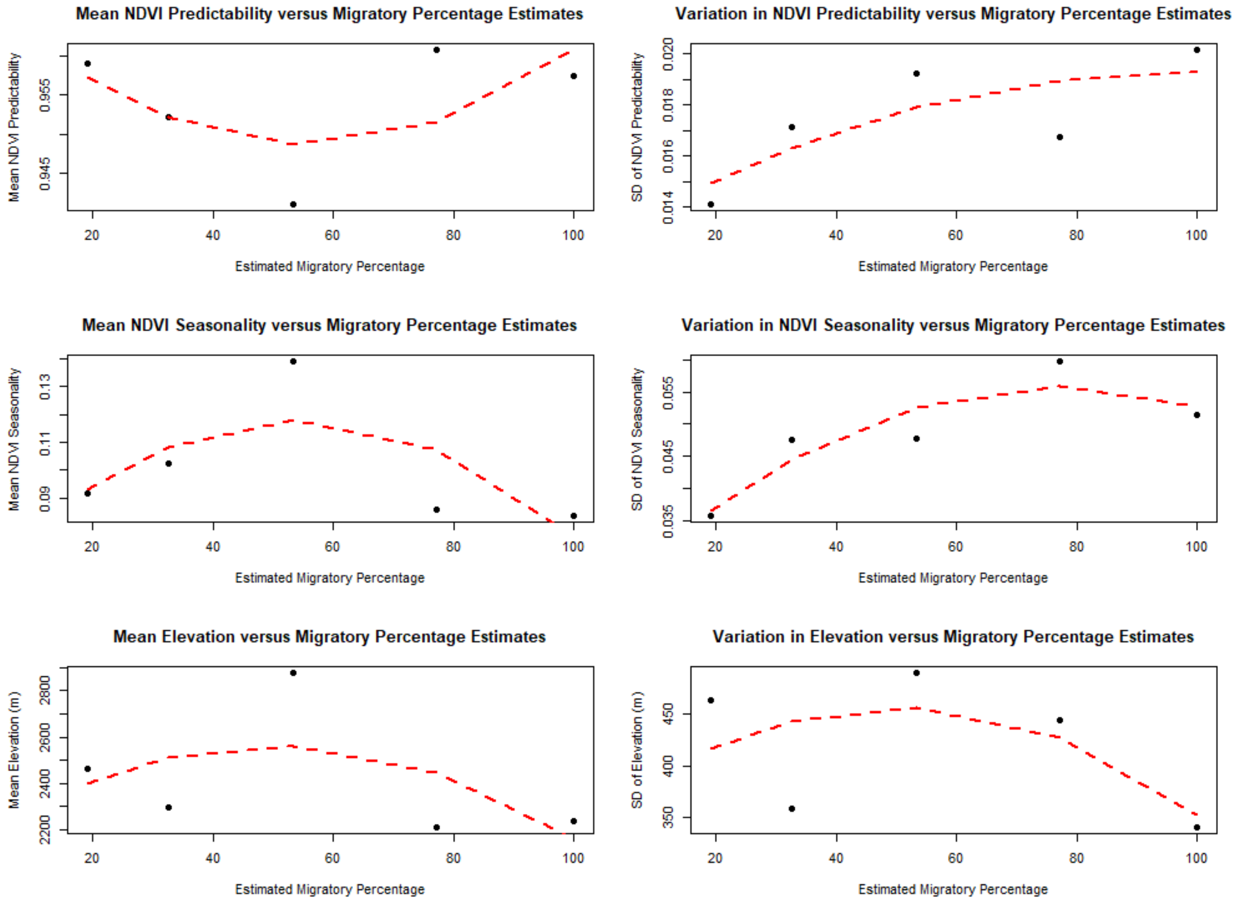


Figure 1.4. Metrics summarized at the landscape scale plotted against a continuum of estimated migratory percentage in each study area. Metrics include averages and variability in Normalized Difference Vegetation Index (NDVI) predictability, NDVI seasonality, and elevation over the full extent of each corresponding study area. LOESS curves fitted to the data are shown in red. From left to right, the herds are: Trinchera, Steamboat, Avalanche Creek, Uncompahgre Plateau, and Bear’s Ears.

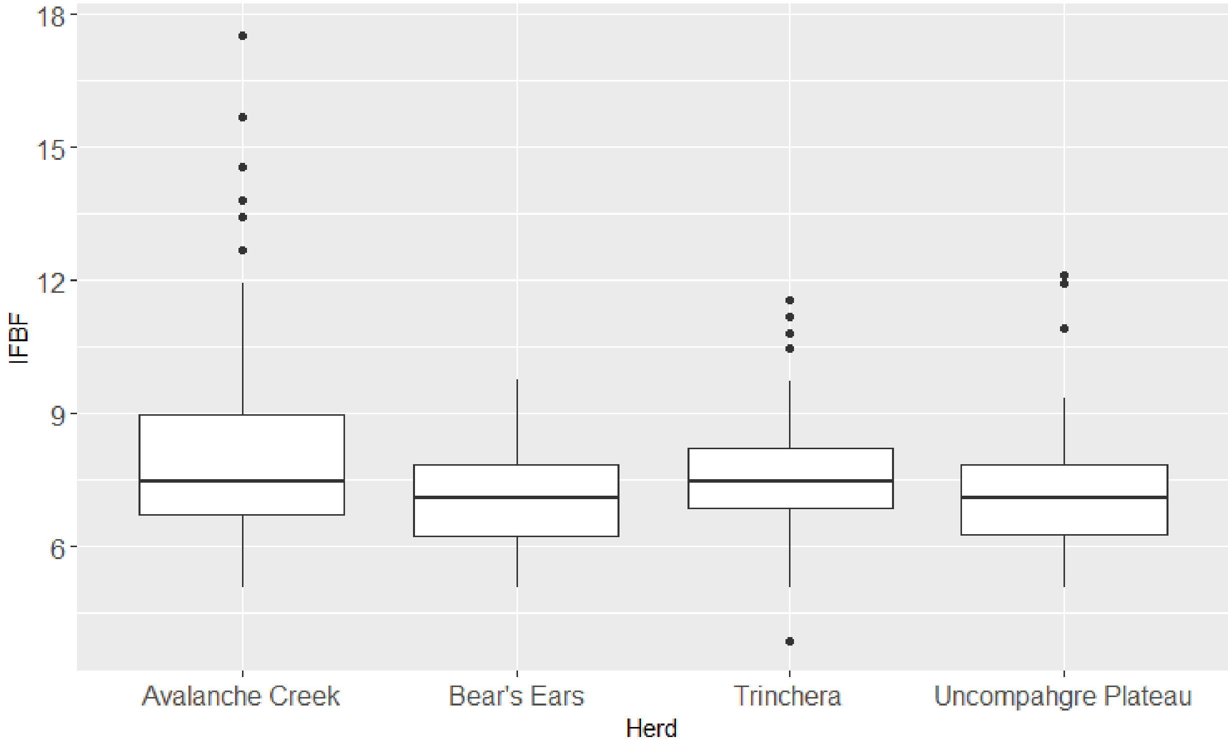


Figure 1.5. Box plot of Ingesta-free Body Fat distributions per herd. Ingesta-free Body Fat (IFBF) is on the y-axis, while herds are on the x-axis. Sample sizes varied by herd and were inclusive of all movement strategies. Avalanche Creek had n = 90, Bear’s Ears had n = 74, Trinchera had n = 49, and Uncompahgre Plateau had n = 64. Total sample size was n = 277.

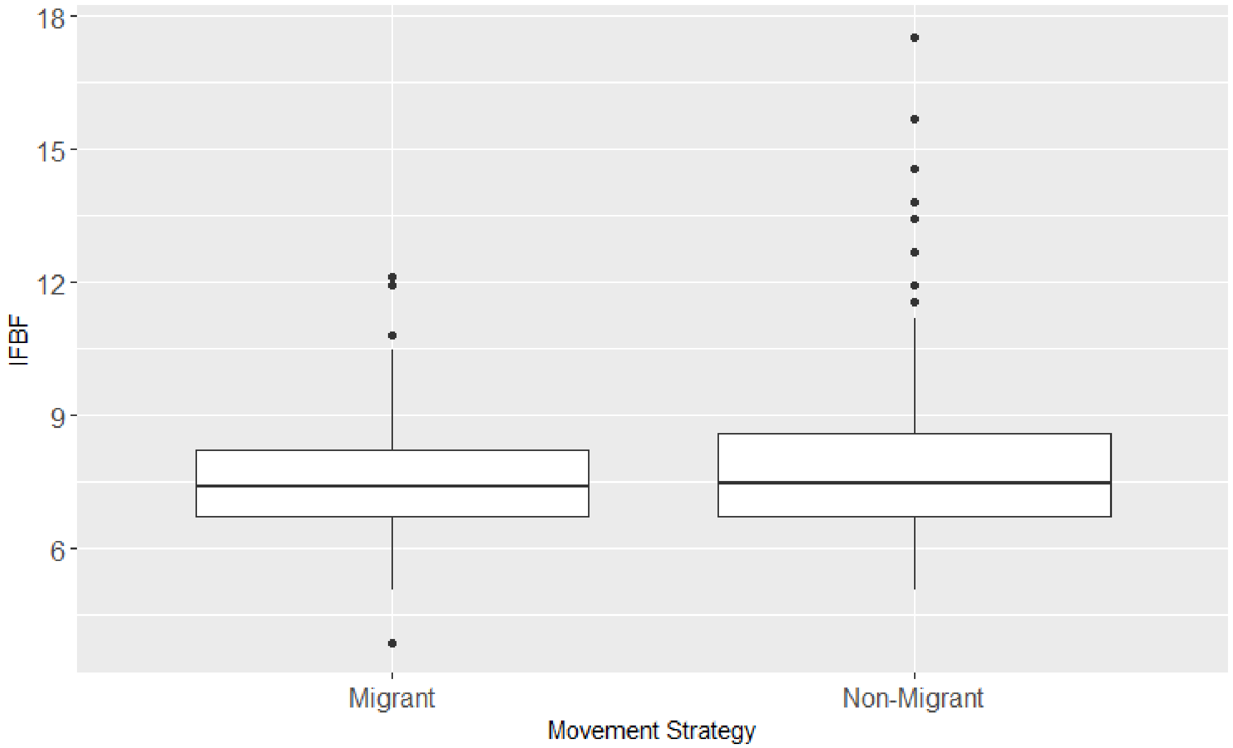


Figure 1.6. Box plot of Ingesta-free Body Fat distributions per strategy. Ingesta-free Body Fat (IFBF) is on the y-axis, while herds are on the x-axis. Sample sizes varied by movement strategy and were inclusive of all populations with the exception of Steamboat, for which there was no Ingesta-free Body Fat data. Migrant sample size was n = 180. Non-migrant sample size was n = 97.

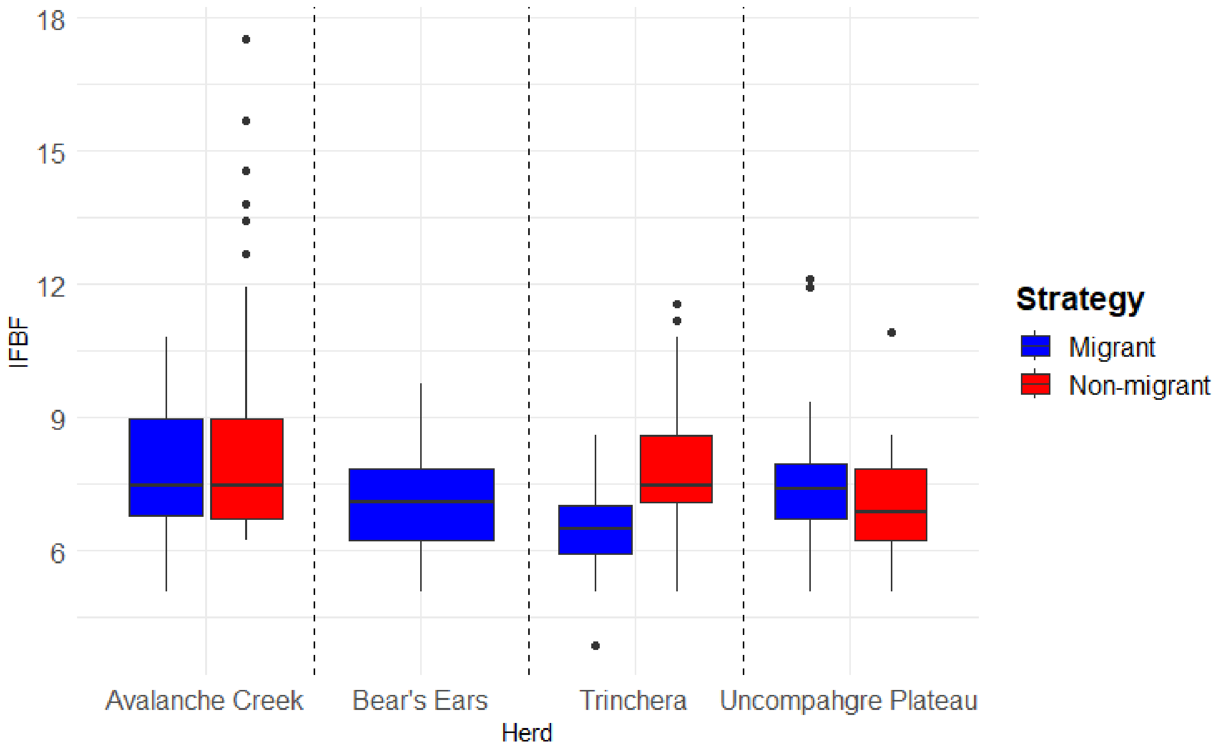


Figure 1.7. Box plot of Ingesta-free Body Fat estimate distributions by both herd and movement strategy. Ingesta-free Body Fat (IFBF) is on the y-axis, while herds are on the x-axis. Migrant distributions are shown in blue, while non-migrant distributions are shown in red. Differing herds are separated by vertical dotted black lines. Sample sizes varied by both herd and movement strategy. Avalanche Creek had n = 90, with 47 migrants and 43 non-migrants. Bear's Ears had n = 74, with 74 migrants. Trinchera had n = 49, with 8 migrants and 41 non-migrants. Uncompahgre Plateau had n = 64, with n = 51 migrants and n = 13 non-migrants.

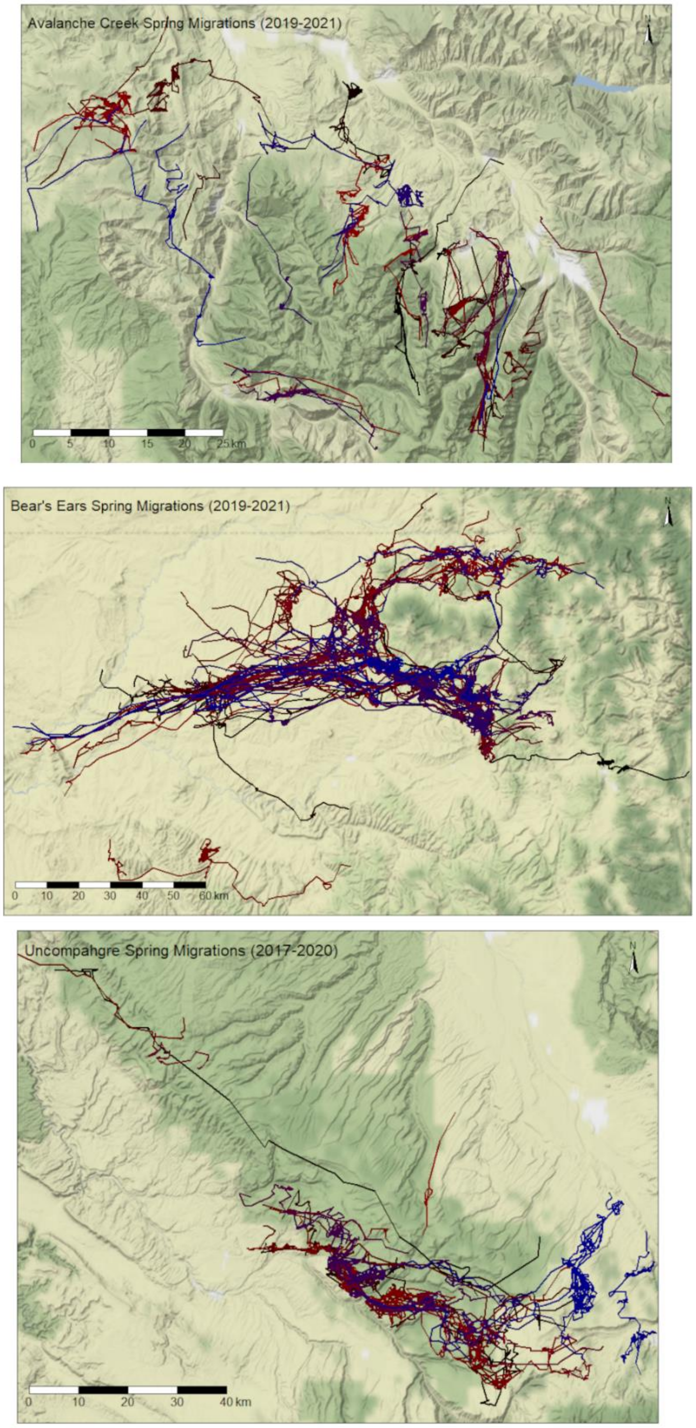


Figure 2.1. Distribution of spring migratory routes in three populations of elk in the Colorado Rocky Mountains between 2017 – 2021. Each contiguous line and color represents an individual migratory corridor. Top) Avalanche Creek herd, Middle) Bear's Ears herd, Bottom) Uncompahgre Plateau herd.

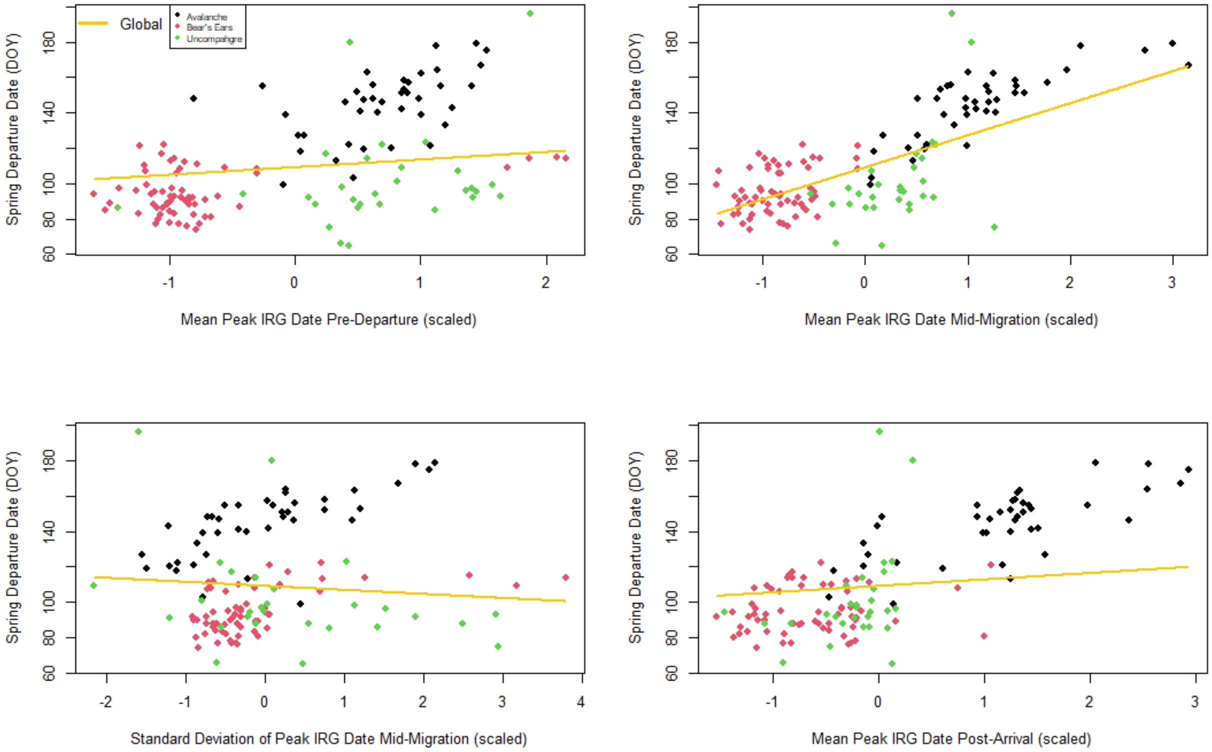


Figure 2.2: Estimated responses to each covariate in the top spring departure date model. The global model trend can be seen in gold. Dot colors represent herds: Avalanche Creek is black, Bear's Ears is red, and Uncompahgre Plateau is green. All independent variables are scaled.

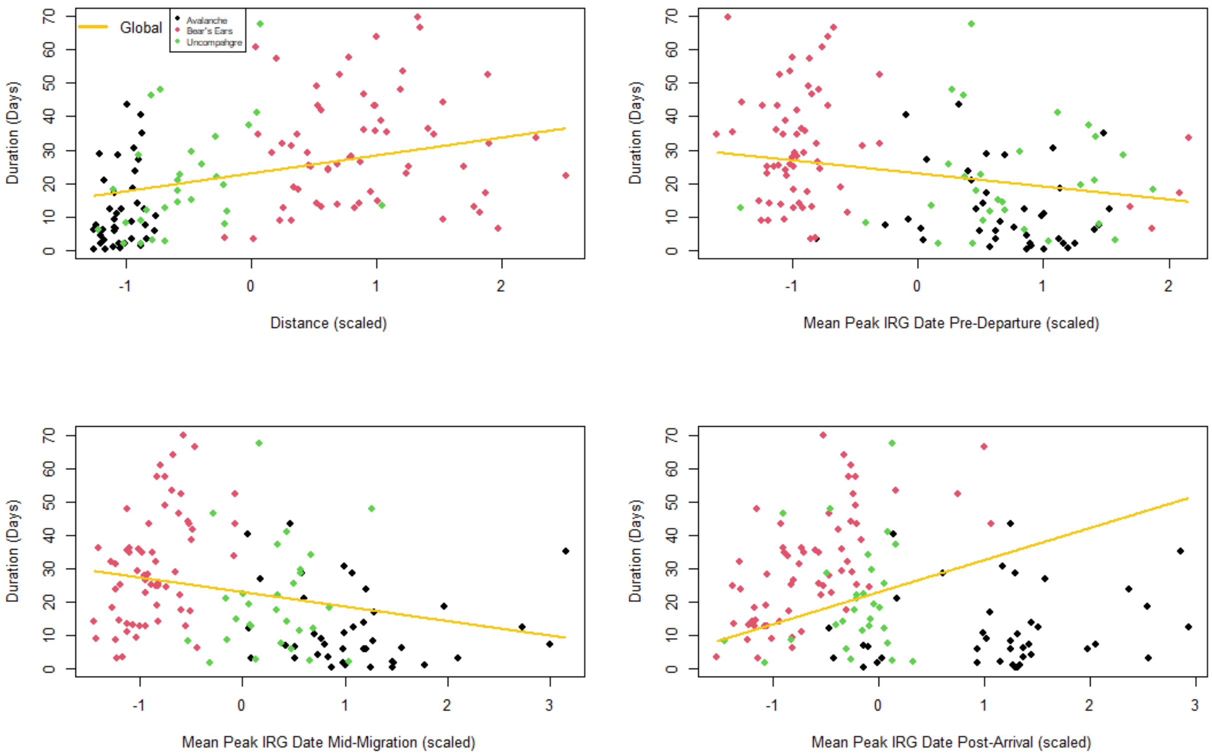


Figure 2.3: Estimated responses to each covariate in the top spring migration duration model. The global model trend can be seen in gold. Dot colors represent herds: Avalanche Creek is black, Bear's Ears is red, and Uncompahgre Plateau is green. All independent variables are scaled.

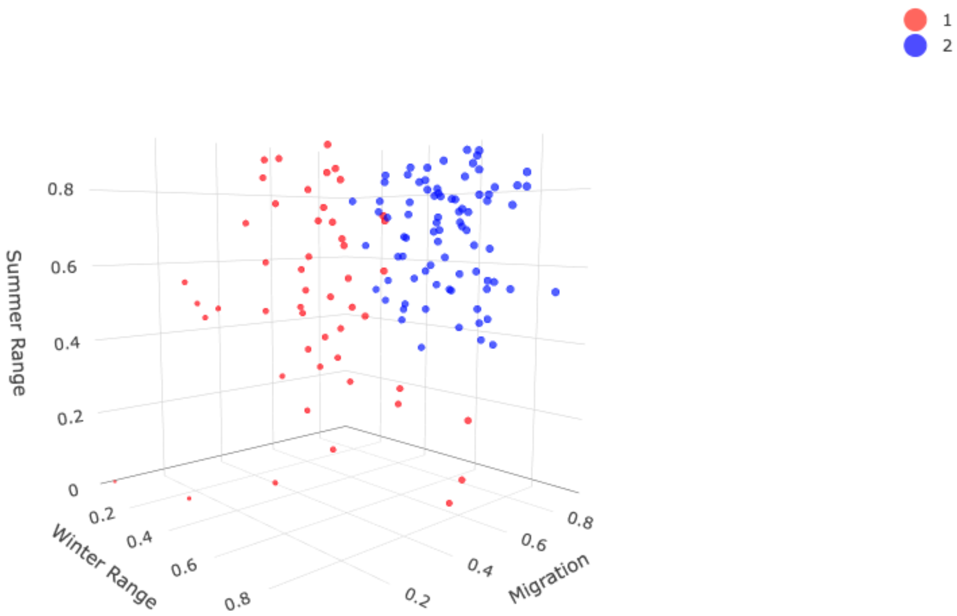


Figure 2.4: A 3D scatterplot illustrating the clustering and distribution of individual optimalities (the average difference between current and maximum Instantaneous Rate of Green-up at elk locations) along three axes: winter range (i.e. pre-departure), migration, and summer range (post-arrival). Two clusters are delineated, with cluster 1 (red) showing much higher variation and trade-offs between optimizing forage quality in one or more periods vs. others, while cluster 2 (blue) showed tighter clustering and on average higher mean optimality per period.

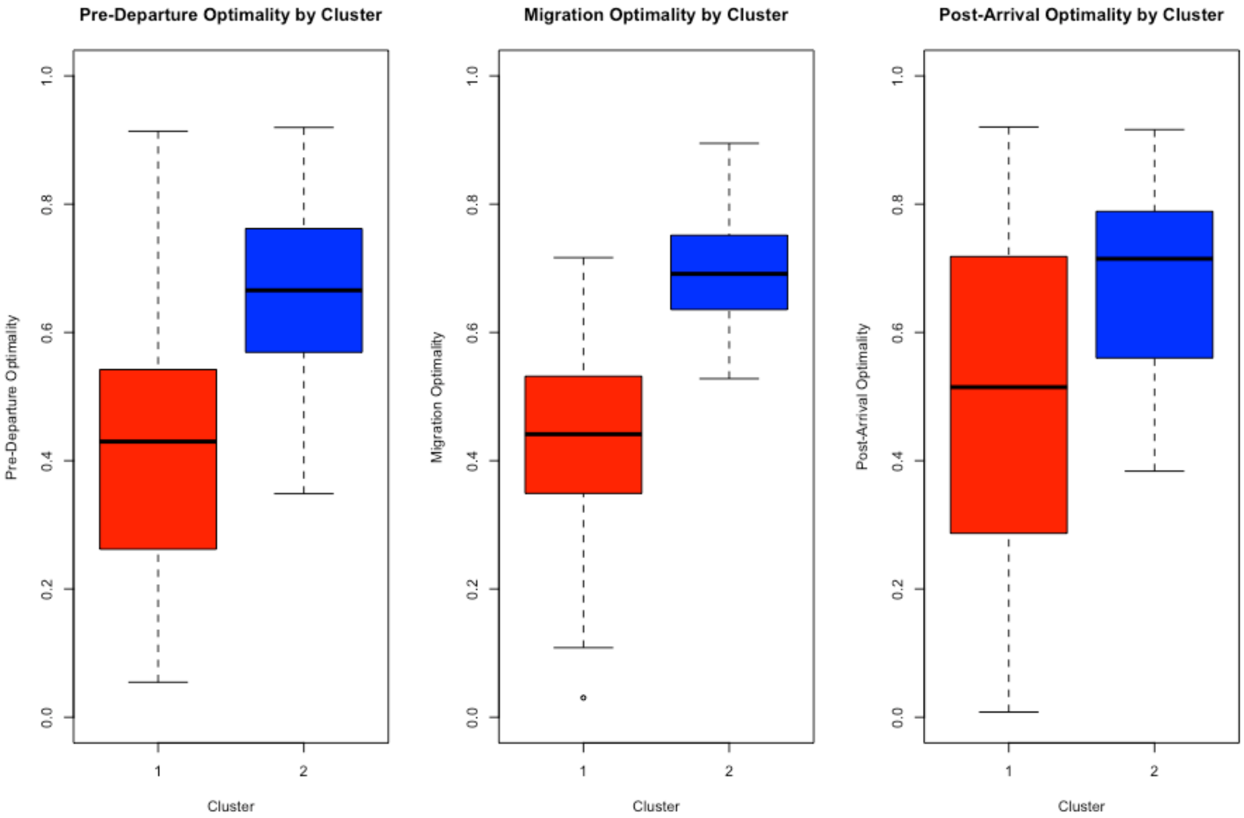


Figure 2.5: Boxplots of period-specific optimalities by Cluster. All plots are scaled to the same y-axis limits. Cluster 1 is shown in red, while Cluster 2 is in blue.

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