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Home Is Where the Food Is: Causes and Consequences of Partial Migration in Elk

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HOME IS WHERE THE FOOD IS:
CAUSES AND CONSEQUENCES OF PARTIAL MIGRATION IN ELK

By

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HOME IS WHERE THE FOOD IS: CAUSES AND CONSEQUENCES OF PARTIAL MIGRATION IN ELK

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Migratory and non-migratory ungulates often coexist in partially migratory populations, but the mechanisms that drive and maintain different migratory behaviors within the same herd are poorly understood. In western North America, increasing numbers of elk (*Cervus canadensis*) reside on low-elevation winter range year-round. These residents can cause issues associated with crop damage, potential for disease transmission to livestock, and reduced effectiveness of harvest management strategies. Because migrants transfer nutrients, alter carnivore distributions, and structure vegetative communities across seasonal ranges, reductions in migratory behavior raise ecological as well as management-related concerns. This work investigated the factors affecting migratory behavior of female elk and assessed the nutritional consequences of different behaviors. In our study of a partially migratory elk population in west-central Montana, we found that migrants had access to lower-quality forage during summer than their non-migratory counterparts. In our broader-scale study of 16 elk herds across western Montana, we found that migratory behavior of individuals was best-explained by a combination of native forage, irrigated agriculture, and conspecific density. Together, these results reveal a strong influence of irrigated agriculture on migratory behavior of elk. Migration is commonly considered a strategy to increase access to high-quality forage; our results reveal that irrigated agriculture can alter the traditional nutritional benefits of migration by providing high-quality forage at low elevations throughout the year. Although elk were less likely to migrate if they overwintered in irrigated agricultural areas, predictable availability of better forage elsewhere mitigated that effect. Thus, maintaining or improving the quality of forage available on migratory summer ranges should encourage migratory behavior, as should excluding elk from irrigated agricultural areas. Given the importance of nutritional intake during late summer and fall to elk fecundity and calf survival, improving the forage available to migrants could go beyond preserving current behaviors to effectively increase prevalence of migration where irrigated agriculture has subsidized increasing numbers of resident ungulates.

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Most importantly, my parents David and Debbie and brother Tim have been vital to whatever minimal success I have achieved thus far in my life. They have encouraged every one of my hare-brained pursuits with unwavering love and enthusiasm. I would dedicate this thesis to them, but that would make Mom feel obligated to read the whole thing, which she should not do under any circumstances. Instead I dedicate it to KimBerly McCoy, under the condition that neither of us has to read the other's thesis in its entirety.

This work was significantly improved by several anonymous acquaintances' helpful feedback on my attempts to have a life outside of grad school.

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Introduction and Overview

When ungulates migrate, they transfer nutrients (Hobbs 1996), alter carnivore distributions (Henden et al. 2014), and structure vegetative communities across seasonal ranges (McNaughton 1984, Holdo et al. 2007). Ungulate migration therefore connects disparate habitats (Shaw 2016) and affects ecological processes across trophic levels (Holdo et al. 2011). In recent decades, changing climate and anthropogenic influences have altered or reduced migratory behavior of many ungulates worldwide (Wilcove and Wikelski 2008, Harris et al. 2009). In western North America, increasing numbers of ungulates residing on private land year-round raise not only ecological but also management-related concerns (Haggerty and Travis 2006) due to issues of crop damage, potential for disease transmission to livestock, and reduced public hunting opportunities (e.g., Montana Fish, Wildlife and Parks 2004, Idaho Department of Fish and Game 2014, Utah Division of Wildlife Resources 2015). To mitigate these management challenges and ensure continued ecosystem functioning, managers and conservationists often seek to maintain or increase migratory behavior of ungulates.

Strategies to conserve migratory behavior often focus on conserving geographic areas that serve as migration corridors (Berger 2004, Sawyer et al. 2009), but continued availability of migration corridors does not guarantee continued migration. Prevalence of resident behavior has increased in some partially migratory populations where migrants still travel along traditional routes (Middleton et al. 2013, Cole et al. 2015). Thus, successful conservation of migratory behavior will rely on efforts to conserve not only corridors but also behaviors themselves. Influencing behavior requires an understanding of both the factors driving the behavior and its resultant consequences to the individual.

Partially migratory populations, in which only a portion of individuals migrate seasonally (Chapman et al. 2011), can provide insight into both the evolutionary drivers and the ecological consequences of differing migratory behaviors. Empirical and theoretical studies of partial migration have focused largely on birds, fish, and insects (Dingle and Drake 2007) and thus may not adequately describe behavior of ungulates (Bolger et al. 2008). For example, migratory behavior appears to be under stronger genetic control in avian species (Berthold 1999) than in ungulates; individuals in several ungulate taxa have been noted to switch behaviors between years (e.g., pronghorn, White et al. 2007; wildebeest, Maddock 1979; and elk, Eggeman et al. 2016). Additionally, rather than exhibiting a strict dichotomy, behavior of ungulates can range along a continuum from residency to migration (Cagnacci et al. 2011). Intermediate behaviors, such as short movements between overlapping seasonal ranges or brief times spent on migratory ranges, are relatively understudied. A more complete understanding of partial migration would therefore be gained from studies that explicitly incorporate the full continuum of migratory behaviors in ungulates.

The overarching goal of this thesis was to advance ecological theories of partial migration while providing helpful information to natural resource professionals working to manage populations of migratory ungulates. Elk (*Cervus canadensis*) display wide variation in migratory behavior (Irwin 2002) and therefore served as an appropriate study species in which to address my research questions. Specifically, I sought to determine why elk exhibit different migratory behaviors and whether different behaviors can provide individuals similar fitness benefits. I included intermediate behaviors in all analyses to provide a more nuanced assessment of variation in ungulate behavior.

In Chapter 1, I investigated whether different migratory behaviors provided elk access to similar nutrition during late summer, because nutritional intake during this season is particularly critical for reproduction and survival of adult female ungulates. I tested for differences in a) the quality of forage provided by different vegetative communities in the Rocky Mountains, and b) the quality of forage available to residents, intermediates, and migrants in a partially migratory population of elk in western Montana. Although access to high-quality nutrition is commonly considered the primary benefit of migration, I found that the quality of forage to which elk had access decreased along the continuum from resident to migratory behavior. Nutritional consequences of intermediate behaviors were more similar to those of residents than of migrants. Results suggest that conversion of ungulate winter range to irrigated agriculture can alter historic nutritional benefits of migration. Recently-burned dry forests provided forage quality equivalent to that of irrigated agriculture, revealing a potential for habitat manipulations to maintain or improve the nutrition available on summer ranges of migrants.

In Chapter 2, I asked which of 7 non-exclusive hypotheses currently posited to explain migration of ungulates best explained behavior of female elk in 16 herds across western Montana. I found that native forage, irrigated agriculture, and conspecific density had consistent effects on behavior of individuals. The predicted effects of these factors on intermediate behaviors more closely matched their effects on resident than on migratory behaviors. Elk were more likely to migrate when the forage available during the growing season varied predictably between years, and they were less likely to migrate when they had access to irrigated agriculture on their winter range. However, elk that had access to better forage outside their winter range during the growing season were more likely to

migrate away from irrigated agricultural areas. Because elk in multiple herds responded similarly to forage-related cues across a range of environmental conditions and anthropogenic influences, changes to forage across broad geographic areas should have similar effects on migratory behavior of individuals.

Overall, my work reveals that irrigated agriculture provides a strong nutritional incentive for elk to forego seasonal migration, but this effect on migratory behavior can be mitigated by the predictable presence of high-quality forage outside agricultural areas. Land management practices that maintain or improve forage quality on summer ranges of migrants could therefore increase both the likelihood of migration and the nutritional benefits of migratory behaviors. Because vegetative communities in earlier seral stages and with lower canopy cover typically provide the highest-quality forage for elk, fire management or timber management (e.g., revegetation, logging, thinning, or mechanical treatments) may help improve forage on migratory summer ranges. Maintaining a mosaic of successional stages in mesic forests may prove particularly helpful based on my finding that only early-successional mesic forests provided nutrition adequate to support healthy reproduction in elk. Alternatively, or in addition, excluding elk from irrigated agriculture throughout the year should reduce prevalence of resident behaviors. Although behavior of ungulates is often considered to fall along a continuum from residency to migration, I found that both the causes and consequences of intermediate behaviors aligned more closely with those of resident than migratory behaviors.

Because this work represents a collaborative effort that would have been impossible without assistance, and because thesis chapters were designed for publication in scientific journals, I use the collective “we” through the remainder of the thesis.

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Chapter 1: Nutritional Consequences of Partial Migration in a Montana Elk Population

As of March 26, 2018 this manuscript is in review at the Journal of Wildlife Management with Michael Mitchell, Kelly Proffitt, and Jesse DeVoe as coauthors.

Abstract

Most ungulate populations are partially migratory and include both migrants and residents. Increasing numbers of ungulates remaining resident on privately-owned agricultural land year-round present a common management challenge in parts of western North America due to issues of crop damage and reduced public hunting opportunities. Migration is commonly considered a strategy to increase access to high-quality forage, but it is unclear whether ungulates that remain resident in irrigated agricultural areas have access to lower-quality forage than ungulates that migrate. We evaluated the nutrition available to a partially migratory population of elk (*Cervus canadensis*) in west-central Montana where individuals summered on both low-elevation agricultural lands and traditional higher-elevation ranges. We sampled elk forage plants from ground plots and adult female elk movements from bihourly GPS collar locations for 2 years, and we tested for differences in 1) the quality of forage provided by 11 vegetative communities commonly available to elk in the Rocky Mountains, and 2) the quality of forage available in areas used by residents and migrants during late summer. Irrigated agriculture provided the highest forage quality in low elevations, but recently-burned (1-6 yr prior) dry forests at higher elevations provided forage quality approximately equivalent to that of irrigated agriculture. Fire may therefore temporarily increase forage quality for elk on native forests and improve nutritional benefits of migratory behavior. Additionally, excluding elk from irrigated agricultural areas may reduce nutritional incentives for elk to

remain resident year-round. Elk that migrated had access to lower forage quality than elk that did not migrate; we hypothesize this nutritional difference could result in lower fecundity for migrants based on studies of other elk populations. Our results indicate land management practices can affect the nutritionally-mediated fitness benefits of differing behaviors in partially migratory populations of ungulates.

Introduction

In temperate climates, ungulates typically migrate from winter ranges during spring to track growth of highly-nutritious emergent vegetation into higher-elevation summer range (Bischof et al. 2012). Most ungulate populations are partially migratory, however, and behavior of individuals ranges across a continuum from residency to migration (Luccarini et al. 2006, Hebblewhite et al. 2008, Cagnacci et al. 2011, Middleton et al. 2013). Partial migration can represent an evolutionarily stable strategy under which both resident and migratory behaviors should persist within the same population (Lundberg 1987). It is not always clear, however, whether all behaviors allow individuals to achieve equal fitness, or whether one type of behavior makes the “best of a bad situation” by achieving sufficient though not equal fitness (e.g., surviving but not reproducing in all years; Lundberg 1988, Holt and Fryxell 2011).

Access to high-quality forage has historically been considered a primary benefit of migration for herbivores (Fryxell and Sinclair 1988, Boyce 1991), but land use practices can alter nutritional landscapes such that ungulates may not need to migrate to find high-quality forage. For example, conversion of valley bottoms to irrigated agricultural land can provide alfalfa, corn, and other nutritious crops at low elevations throughout the summer (Mould and Robbins 1981). Elk (*Cervus canadensis*) that do not

migrate tend to remain resident in these low-elevation valley bottom areas year-round (Hebblewhite et al. 2008, Middleton et al. 2013, Found and St. Clair 2016).

Increasing numbers of elk that reside on private agricultural land present a common management challenge in the western United States due to issues of crop damage and reduced public hunting opportunities (e.g., Montana Fish, Wildlife and Parks 2004, Idaho Department of Fish and Game 2014, Utah Division of Wildlife Resources 2015). When resident ungulates exceed levels tolerated by humans (e.g., Krausman et al. 2014), managers often seek to encourage movement off low-elevation private lands. If residents benefit from high-quality forage in irrigated agricultural areas (Lande et al. 2014), management strategies to create or conserve areas of equivalent or better forage quality on higher-elevation public lands may provide a means of encouraging migratory behavior and reducing property damage issues on private lands. Such strategies would benefit from an understanding of the relative quality of forage provided by native vegetative communities and irrigated agricultural lands.

When residents comprise part of a partially migratory population, it is not always clear whether an apparent increase in the number of residents is due to a relative increase in resident behavior (i.e., the proportion of migrants in the population is decreasing) or to a growing population (i.e., numbers of residents and migrants are increasing proportionally). In the absence of historical data on relative proportions of residents and migrants in a population, assessing relative fitness benefits of migration and residency can provide insight into whether migratory behaviors may be declining. Survival and reproduction of ungulates is particularly affected by nutritional intake during late summer and fall (Bender et al. 2008, Cook et al. 2013, Monteith et al. 2014). Residents and

migrants typically forage in different areas throughout late summer, with migrants returning to areas used by residents during fall (Middleton et al. 2013, Eggeman et al. 2016).

Where ungulates have access to adequate quantities of forage, the quality of forage (i.e., digestibility) most strongly affects their fitness (Cook et al. 2004). Adult female elk that consistently consume < 2.75 kcal of digestible energy (DE) per gram of forage during late summer and fall may fail to become pregnant until later in the breeding season, and those consuming < 2.40 kcal/g may not become pregnant at all and may exhibit lower survival rates than elk that consistently consume higher-quality forage (Cook et al. 2004, 2013, 2016). Thus, comparing the quality of forage available to residents and migrants can provide insight into whether one type of behavior might confer higher fecundity or survival.

The objectives of our study were to determine 1) which native vegetative communities provided forage of similar quality to that of irrigated agriculture, and 2) whether female elk that exhibited different migratory behaviors had access to different qualities of forage during late summer. We studied a partially migratory population of elk in the North Sapphire Mountains of west-central Montana, where the risk of predation is relatively low for adult females. Grizzly bears (*Ursus arctos*) do not inhabit the area, and presence of gray wolves (*Canis lupus*) has been sporadic (no active packs documented in the area since 2012, although individual wolves occasionally traveled through the study area; Montana Fish, Wildlife and Parks 2014). Natural survival and pregnancy rates in this population should therefore be driven primarily by nutritional intake. If fitness of elk is equivalent across behavioral strategies, we hypothesized nutrition available to elk

exhibiting different migratory behaviors would also be equivalent. Thus, we predicted that 1) native vegetative communities at high elevations would provide digestible energy similar to that provided by irrigated agriculture at low elevations during late summer, and 2) the digestible energy to which adult female elk had access would not differ among individuals employing a continuum of migratory behaviors.

Study area

Our study area encompassed 2,400 km² of the North Sapphire Mountains in west-central Montana. The population of elk inhabiting the North Sapphire Mountains has grown from < 250 individuals in the 1960s to nearly 1,000 in 2015 (Edwards et al. 2015, Montana Fish, Wildlife and Parks 2015). Estimates of recruitment vary annually and have averaged approximately 25 calves per 100 adult females during the past 5 years (Edwards et al. 2015). Anecdotal evidence suggests resident behaviors may have increased in recent years, and local landowners and sportsmen have voiced concerns about current elk distributions (Montana Fish, Wildlife and Parks 2017).

Elevations in the study area ranged from 1000 m to 3000 m, and yearly temperatures ranged from -5 °C to 25 °C (PRISM). Land ownership included a matrix of public lands (59%) and publicly accessible corporate timber lands (3%) that dominated the higher-elevation traditional summer range, and privately-owned residential and agricultural lands (38%) that dominated the valley-bottom traditional winter range. Mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), moose (*Alces alces*), and bighorn sheep (*Ovis canadensis*) were sympatric with elk. Carnivores included mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), and American black bear (*Ursus americanus*).

Riparian areas, agricultural lands, and grasslands dominated low elevations, transitioning to shrub- and conifer-dominated ecosystems at high elevations. Riparian areas were primarily cottonwood-dominated (*Populus* spp.) forested areas. Irrigated agricultural areas consisted mostly of alfalfa hay (*Medicago sativa*) or corn (*Zea mays*) fields with additional grasses and forbs interspersed at lower abundance (e.g., *Bromus tectorum*, *Silene latifolia*). Non-irrigated agricultural areas most commonly consisted of wheat-related or rye-related grasses (e.g., *Agropyron cristatum*, *Elymus glaucus*, *E. repens*, *Thinopyrum intermedium*). Bluebunch wheatgrass (*Pseudoroegneria spicata*) and fescues (*Festuca campestris*, *F. idahoensis*) dominated natural grasslands. Shrublands included sage-steppe and deciduous ecosystems. Sage-steppe areas were dominated by big sagebrush (*Artemisia tridentata*), antelope bitterbrush (*Purshia tridentata*), and rabbitbrush (*Chrysothamnus viscidiflorus*). Ninebark (*Physocarpus malvaceus*), chokecherry (*Prunus* sp.), serviceberry (*Amelanchier alnifolia*), and ocean spray (*Holodiscus discolor*) constituted the dominant deciduous shrubs. Dry forests were typically dominated by ponderosa pine (*Pinus ponderosa*) at lower elevations and by Douglas fir (*Pseudotsuga menziesii*) at higher elevations. Mesic forests were dominated by either lodgepole pine (*Pinus contorta*) or a mix of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Unlike other mountain ranges in this region, the North Sapphire Mountains lie at relatively low elevation and do not include substantial alpine meadows.

Methods

Nutritional Quality of Vegetative Communities

To evaluate potential effects of land management practices on nutritional resources for elk during late summer, we compared the average forage quality available in 11 landcover types identified in the study area. Landcover types consisted of riparian areas, agricultural areas (classified as either irrigated or non-irrigated), open canopy grasslands and shrub lands, and forests. We classified forests as either mesic or dry, and each classification was further divided into 3 successional stages based on fire history (burned 1-5 years ago, burned 6-15 years ago, and burned >15 years ago). Dry forests included an additional classification for recent prescribed burn (1-5 years ago) to account for potential differences between prescribed burns and wildfires.

We identified summer forage species using level B (>5% prevalence in diet) fecal plant fragment analyses of pellet samples. We collected fresh composite fecal pellet samples from at least 4 sites (including areas used by resident and migratory individuals) every 16 days from June-October in 2014 and 2015. Each composite sample consisted of up to 20 fresh (< 48 hour old) pellets from 7-10 individual elk. We defined forage species as those comprising 95% of the total diet.

We collected forage species in each phenological stage (emergent, flowering, fruiting, mature, and senescent). We estimated dry matter digestibility (Robbins et al. 1987*a, b*, Hanley et al. 1992) for each stage using sequential detergent fiber analysis (Van Soest 1982; Wildlife Habitat and Nutrition Lab, Washington State University, Pullman, WA, USA). We converted dry matter digestibility to digestible energy (DE; Cook et al. 2016) measured as kilocalories per gram of forage (kcal/g).

We measured composition and phenological stage of forage species at 752 randomly-established vegetation plots located within the yearly range of elk, stratified by

landcover type, aspect, and slope. We completed all vegetation sampling within a 6-week period during the time of peak vegetative growth (Jul 15 – Aug 31) and considered each of these samples to represent the late summer time period as a whole. We estimated digestible energy at each vegetation plot as the weighted mean of digestible energy values for each forage species in each phenophase; we included all forage species and phenophases in order to characterize the nutrition generally available to elk across the landscape. We compared forage quality in different landcover types using a generalized linear model in which digestible energy was the response variable and landcover type was a categorical explanatory variable. We used irrigated agriculture as the reference category to which we compared the effect of all other landcover types on digestible energy.

Classification of Migratory Behaviors

We captured elk by helicopter, using either net-gunning or chemical immobilization, consistent with Montana Fish, Wildlife and Parks ACUC protocol 19-2013. We fitted Global Positioning System (GPS) collars on 45 adult female elk in February 2014 and 3 additional elk in February 2015 (Lotek Wireless, IridiumTrack M 3D). We programmed collars to record a location every 2 hours and to drop off after 104 weeks. We used elk-years as the sampling unit for analyses.

We classified migratory behavior of individuals as resident, intermediate, or migrant based on overlap of kernel seasonal home ranges (i.e., utilization distributions; UD_s) estimated from summer and winter location data using the ad hoc href smoothing factor and the same grid cell size for each individual (Fieberg and Kochanny 2005). We used the `adehabitatHR` package in Program R version 3.3.2 (R Development Core Team

2016) to calculate volume of intersection between seasonal (summer, Jul – Aug; and winter, Feb – Mar) home ranges (95% UD_s), and between core use areas (50% UD_s) within each individual's seasonal home ranges. We defined migrants as individuals whose seasonal home ranges did not overlap (i.e., volume of intersection of 95% UD_s = 0). We defined residents as individuals whose core use areas overlapped (i.e., volume of intersection of 50% UD_s > 0). We defined all other individuals as intermediates (i.e., volume of intersection of 50% UD_s = 0 and volume of intersection of 95% UD_s > 0). We also calculated the size of the aggregated summer home range for each behavior group as the area of a 95% UD estimated using locations of all individuals exhibiting that behavior.

Despite recognition that migratory behavior often exists along a continuum from residency to migration, few studies explicitly address the full continuum. Therefore, in addition to categorizing individuals as resident, intermediate, or migrant we also ranked individual behaviors along a continuum ranging from residency to migration. We ranked individuals first by volume intersection between core use areas, then by volume intersection between home ranges, and finally by Euclidean distance between centroids of seasonal ranges, such that lower volume intersection values and longer distances between centroids both indicated stronger migratory behavior.

Nutritional Access Across Migratory Behaviors

We developed a predictive model of forage quality by using generalized linear regression to predict phenophase-specific digestible energy across the study area as a function of spatial covariates (K.M. Proffitt, Montana Fish, Wildlife and Parks, unpublished data). We used bidirectional stepwise selection to identify a top predictive model from an initial

global model that included 8 standardized covariates: landcover type, elevation, slope, canopy cover (LANDFIRE 2012), compound topography index (CTI), solar radiation index (total solar radiation at the landscape scale, calculated using the Area Solar Radiation tool in ArcMap 10.2), spring precipitation (PRISM Climate Group 2016), and NDVI amplitude. All covariates had a Pearson's correlation coefficient < 0.6 . We predicted digestible energy across the study area using unstandardized estimates of the covariates included in the top model, creating one predictive model of the forage available to elk during late summer.

We extracted the predicted digestible energy values at elk locations recorded by GPS collars, and we averaged the values each day to estimate the quality of forage to which each individual had access each day. We calculated average daily digestible energy as the average of all days during late summer for each individual. We excluded locations from our analyses that were recorded during the warmest times of day (1400h – 1800h) when elk were more likely to be resting than actively foraging (Merrill 1991).

We used a generalized linear model with average daily digestible energy as the response variable and migratory status of individuals as the explanatory variable to determine whether residents, intermediates, and migrants had access to different qualities of forage during late summer. We also plotted the average daily digestible energy to which residents, intermediates, and migrants had access each day to assess trends in relative nutritional access throughout late summer. To compare inferences based on categorical and continuous classifications of migratory behavior, we examined the relationship between the predicted digestible energy values at GPS collar locations and

migratory behavior, treating behavior as a continuum ranging from residency to migration.

We used negative binomial regression models to compare the number of days individual resident, intermediate, and migratory elk had access to adequate ($DE \geq 2.75$), marginal ($2.40 - 2.75$ DE), and poor ($DE \leq 2.40$) forage quality, using the number of days' access as the response variable. We used a likelihood ratio chi-square test to determine whether migratory behavior was a significant predictor of the number of days' access to forage quality by comparing models that included and did not include migratory status as the explanatory variable.

Results

Nutritional Quality of Vegetative Communities

We sampled 34 forage species in 5 plant phenology stages to estimate digestible energy (DE). Graminoids provided an average of 2.94 ± 0.29 [SD] kcal/g, forbs provided an average of 2.89 ± 0.49 kcal/g, and shrubs provided an average of 2.54 ± 0.56 kcal/g of digestible energy. Irrigated agricultural land and dry forests recently burned by wildfire consistently provided adequate forage quality for elk (i.e., 95% CI of mean DE > 2.75 kcal/g). Non-irrigated agriculture, dry forests recently burned by prescribed fire, and recently-burned mesic forests consistently provided at least marginal forage quality (i.e., 95% CI of mean DE > 2.40 kcal/g).

On average, irrigated agricultural land provided the highest quality of forage for elk (3.07 ± 0.15 kcal/g), and mesic forests burned >15 years ago provided the lowest forage quality (2.31 ± 0.35 kcal/g; Fig. 1.1). Forage quality did not strongly differ between irrigated agricultural land and recently-burned dry forests, regardless of whether

burns resulted from natural wildfires ($p = 0.67$) or prescribed burning ($p = 0.19$). We found evidence that irrigated agricultural land provided higher forage quality than any of the other vegetative communities ($p = 0.03$ for mesic forests burned within 5 years; $p = 0.02$ for mesic forests burned 6-15 years prior; $p < 0.01$ for remaining landcover types).

Classification of Migratory Behaviors

We estimated seasonal home ranges and core use areas for 46 adult female elk in 1 to 2 years resulting in a total of 75 elk-years. We classified 24% as residents ($n = 18$), 49% as intermediates ($n = 37$), and 27% as migrants ($n = 20$). Residents composed 26.3% and 21.6% of the population in 2014 ($n = 38$) and 2015 ($n = 37$), respectively. Intermediates composed 47.4% and 51.4% of the population in 2014 and 2015, respectively. Migrants composed 26.3% and 27.0% of the population in 2014 and 2015, respectively. We did not observe any switching between migratory and resident behaviors for individuals with 2 years of location data ($n = 34$), although both residents and migrants were observed switching to or from intermediate behaviors between years ($n = 11$ and $n = 7$, respectively). A total of 5 elk died during the study ($n = 2$ residents, $n = 3$ intermediates), due to hunting-related mortalities ($n = 4$) or unknown causes ($n = 1$). The small number of mortalities precluded our ability to assess differences in survival between groups.

On average, sizes of individual summer home ranges were 29.2 ± 20.3 [SD] km^2 for migrants, 58.5 ± 19.1 km^2 for intermediates, and 67.2 ± 25.4 km^2 for residents. The size of aggregated group summer home ranges was 589.7 km^2 for migrants, 744.2 km^2 for intermediates, and 544.7 km^2 for residents. Volume of intersection between winter and summer home ranges across all elk-years ranged from 0 to 42%. Volume of intersection between winter and summer core use areas ranged from 0 to 18%. Euclidean

distance between centroids of winter and summer home ranges across all elk-years ranged from 1.4 to 15.5 km.

Nutritional Access Across Migratory Behaviors

The top model predicting digestible energy included landcover type, slope, canopy cover, solar radiation, and elevation as covariates ($r^2_{\text{adj.}} = 0.26$). Forage quality was predicted to decrease with increasing elevation and canopy cover and to increase with increasing solar radiation and slope. Approximately 55% ($n = 1943$) of GPS collar locations were recorded in areas predicted to provide adequate (≥ 2.75 kcal/g) forage quality, 43% ($n = 1531$) were in areas of marginal (2.40 – 2.75 kcal/g) forage quality, and 2% ($n = 67$) were in areas of poor (≤ 2.40 kcal/g) forage quality. On average, residents accessed areas predicted to provide 2.84 ± 0.15 kcal/g (range 2.34 – 3.14), intermediates accessed areas providing 2.77 ± 0.18 kcal/g (range 2.15 – 3.09), and migrants accessed areas providing 2.66 ± 0.15 kcal/g (range 2.18 – 3.06) of digestible energy daily during late summer.

Average nutritional access decreased monotonically across the continuum from residency to migration (Fig. 1.2). Migrants had access to lower forage quality than residents or intermediates ($P < 0.001$ in both cases) during late summer, but access to forage quality did not differ as strongly between residents and intermediates ($P = 0.05$). The forage quality to which migrants had access was consistently lower than the forage quality to which intermediates or residents had access on each day throughout the summer, and migrant daily nutritional access showed a seasonal decline whereas resident and intermediate daily nutritional access exhibited stable or increasing trends (Fig. 1.3). Residents accessed irrigated agricultural areas an average of 30 ± 8 days during the 45-

day late summer time period, compared to 20 ± 14 days for intermediates and 2 ± 4 days for migrants.

Migratory behavior was a predictor of the number of days an individual had access to adequate and marginal forage quality ($\chi^2_2 = 18.30, p < 0.001$ and $\chi^2_2 = 12.14, p = 0.002$, respectively) during late summer, but migratory status did not play a strong role in predicting the number of days an individual had access to poor forage quality ($\chi^2_2 = 5.24, p = 0.07$). On average, residents, intermediates, and migrants had access to adequate forage quality for 37 days (95% CI = 2, 51), 28 days (95% CI = 2, 34), and 13 days (95% CI = 10, 19), respectively. Migrants had access to adequate forage quality for fewer days than both residents and intermediates ($P < 0.001$ in both cases). We found no evidence that residents and intermediates differed in the number of days they had access to adequate forage quality ($p = 0.14$). On average, residents, intermediates, and migrants had access to marginal forage quality for 11 days (95% CI = 8, 17), 19 days (95% CI = 15, 26), and 30 days (95% CI = 22, 45), respectively. We found evidence that migrants had access to marginal forage quality for more days than residents ($P < 0.01$) and intermediates ($P = 0.05$) and that intermediates had access to marginal forage quality for more days than residents ($P = 0.02$) during late summer. On average, residents, intermediates, and migrants had access to poor forage quality for <1 day (95% CI = 0.61, 0.8), 1.0 day (95% CI = 0.5, 2.0), and 1.3 days (95% CI = 0.6, 3.3).

Discussion

Contrary to our prediction that migratory and resident behaviors would provide equivalent nutritional access, we found the quality of forage available to elk decreased along the continuum from resident to migratory behavior. Elk that migrated had access to

the lowest forage quality throughout late summer, on average each day and for more total days. We found relatively weak evidence for differences between intermediates and residents, indicating nutritional access provided by intermediate behaviors was more similar to that of residents than migrants. Irrigated agricultural areas contributed strongly to the nutritional differences we observed, providing 8 – 33% higher forage quality than other vegetative communities. Higher-elevation dry forests that burned less than 6 years prior to our study, however, provided forage quality approximately equal to that of irrigated agricultural areas.

Our results suggest the quality of forage available to elk in the North Sapphires during late summer was not likely to negatively affect survival of adult females but may result in reduced fecundity or recruitment for migrants. We found elk rarely accessed areas predicted to provide $DE < 2.40$ kcal/g, the value below which survival of adult elk in other populations was affected (Cook et al. 2004, 2013, 2016). Indeed, none of the few mortalities we observed appeared related to malnutrition. In contrast to residents and intermediates, however, migrants most commonly accessed areas providing $DE < 2.75$ kcal/g, which may be insufficient to support lactation and rapid growth of calves (Cook et al. 2004, 2013, 2016). We therefore hypothesize that fecundity or recruitment of migrants may be lower than that of residents, thereby reducing the fitness of migrants in this population. If our hypothesis is correct, we would expect relative abundance of resident behavior to increase under one of two possible scenarios, assuming available forage quality remains consistent. First, migrants may alter their behavior in subsequent years (Eggeman et al. 2016), switching to intermediate or resident behaviors to improve their fitness. Second, migrants may continue to migrate in subsequent years but, to the extent

that migration is a genetic or learned behavior, recruit fewer individuals into the migratory portion of the population.

Alternatively, the smaller summer home ranges of migrants compared to those of residents and intermediates indicate migrants may gain other benefits from the areas they occupy despite the lower forage quality available to them. For example, migrants could decrease overall energy expenditure by foraging and bedding within the same general area rather than traveling to and from irrigated agricultural plots each day. Migrants may also behaviorally compensate for being located in areas of lower forage quality by increasing foraging rates or selecting high-quality forage plants at fine spatial scales (Cook et al. 2016). Further, migrants could benefit from lower conspecific density and therefore reduced competition for nutritional resources. The aggregated group summer home range of residents was very similar in size to that of migrants, as were the total numbers of residents and migrants. Residents, however, had much larger individual home ranges than migrants, suggesting more overlap with other individuals and thus higher conspecific density.

The energetic benefits that migrants may gain from potential reductions in foraging effort or intraspecific competition suggest that available forage quality may provide an incomplete measure of nutritional intake for elk. If nutritional intake of migrants exceeds that predicted by our model, nutritional benefits of migration may be more similar to those of residents and intermediates than our results suggest. We estimated available nutrition using mean digestible energy to characterize the average quality of forage generally available to elk across the landscape, recognizing that elk can make fine-scale foraging decisions that allow them to consume higher-quality forage than

is broadly available. The very small percentage of elk locations (< 3%) recorded in areas we predicted to provide poor-quality forage lends support to our assumption that our model captured forage quality as perceived by an elk.

We focused our analysis on the late summer time period due to the particularly strong effect of summer and fall nutrition on pregnancy rate and overwinter survival of ungulates (Bender et al. 2008, Cook et al. 2013, Monteith et al. 2014). If migrants in this population effectively take advantage of the highly-nutritious fresh vegetative growth that proceeds from low to high elevations during spring (Sawyer and Kauffman 2011, Bischof et al. 2012, Merkle et al. 2016), the quality of forage available to migrants could potentially exceed that available to residents or intermediates during early summer as the growing season progresses. Because vegetation is most nutritious and digestible earliest in the growing season, however, we expected both residents and migrants to have access to good-quality forage during spring.

Nutritional similarities between irrigated agricultural land and recently-burned dry forests suggest fire management may serve as a tool to temporarily increase forage quality in high-elevation areas that comprise traditional summer range for migrants. Additional work may uncover other opportunities to manipulate the nutrition available to elk outside of low-elevation winter range. Disturbances such as thinning and logging, for instance, could affect growth of forage plants in forest understories (Scotter 1980). In general, forests in earlier seral stages and with more open canopies provide higher forage quality for elk, particularly at high elevations (Cook et al. 2016). More work is needed, however, to fully assess the effects of different logging techniques and thinning practices on elk nutritional resources (Cook et al. 2016) and to compare the effects of timber and

fire management. Additionally, the extent to which the quality of forage available in alpine ecosystems differs from that in irrigated agricultural lands remains largely unexplored; our study area lacked alpine meadows commonly used by migratory elk in other populations (Morgantini and Hudson 1989, Luccarini et al. 2006).

Management Implications

In our study area, recently-burned forests dominated by Douglas fir or Ponderosa pine provided equivalent forage quality to that of irrigated agriculture. Therefore, allowing wildfires in these forests to burn when socially, economically, and ecologically feasible could help improve forage quality in higher-elevation areas and thus increase the nutritional benefits of migratory behavior. The inherent patchiness and unpredictability of wildfires, however, may preclude the ability of managers to effectively use fire as a tool to increase forage quality in some areas. Excluding elk from irrigated agricultural land likely provides an effective means of limiting resident behaviors; other low-elevation vegetative communities did not provide similar forage quality and are thus less likely to support year-round use by elk. Harvest management strategies may also reduce the likelihood of resident behaviors becoming more prevalent in areas where elk have access to irrigated agriculture. Ensuring the risk of harvest for residents is similar to or higher than that of migrants could help offset potential differences in reproduction caused by the differences we observed in nutritional access.

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Figures

FIGURE 1.1. Mean forage quality (kcal of digestible energy/g of dietary forage, \pm standard deviation) available to elk in 11 vegetative communities in the North Sapphire Mountains, Montana, USA, during summer (Jul–Aug) 2014 and 2015. The dotted vertical line represents the quality of forage considered adequate to support survival and reproductive needs of adult female elk, based on studies of other populations (Cook et al. 2004).

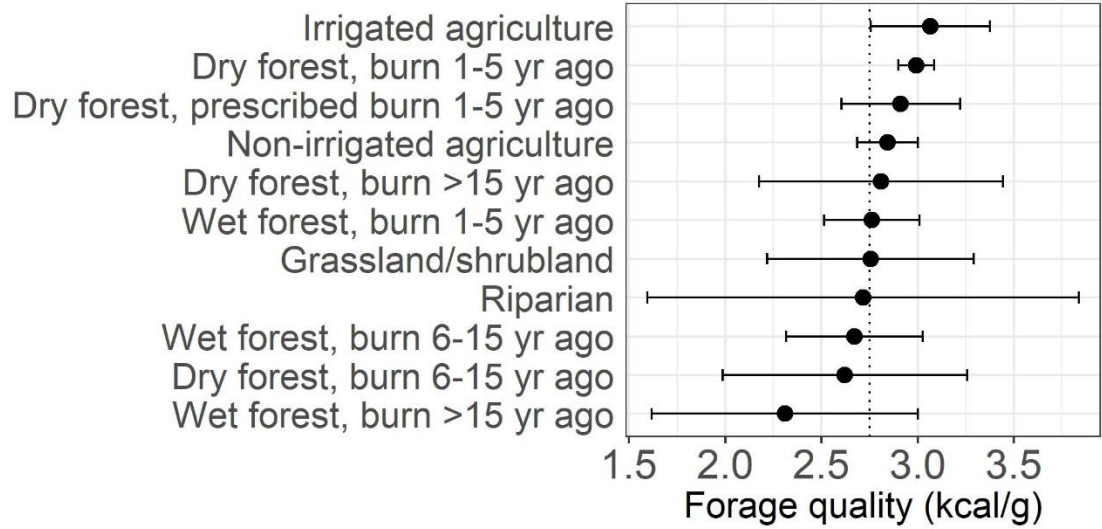
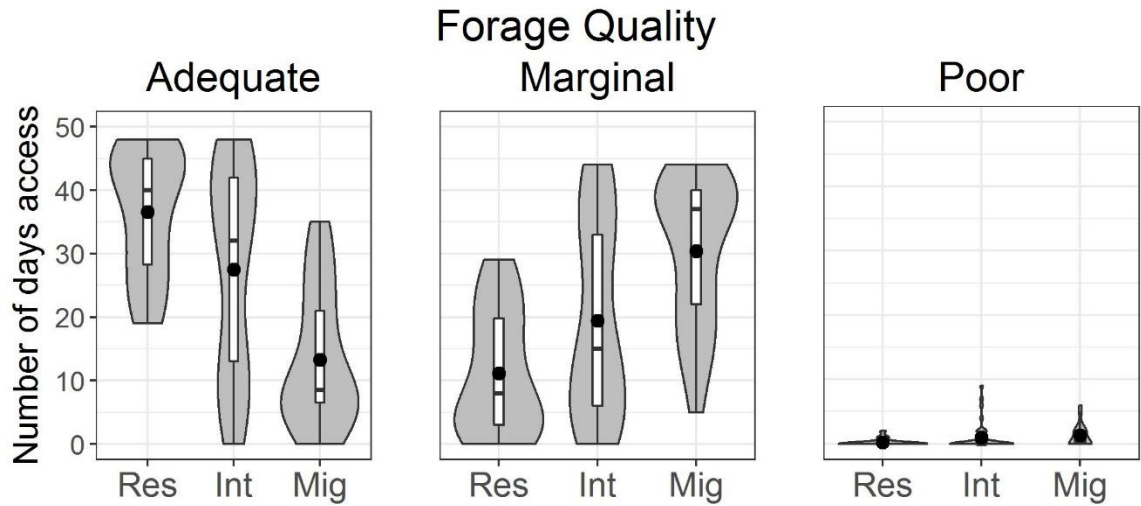


FIGURE 1.3. Number of days that resident (Res), intermediate (Int), and migratory (Mig) elk in a partially migratory population had access to adequate (≥ 2.75 kcal/g), marginal ($2.40 - 2.75$ kcal/g), and poor forage quality (< 2.40 kcal/g) during late summer (Jul–Aug) in the North Sapphire Mountains, Montana, USA, 2014–2015. Plots combine traditional box-and-whisker plots (white) representing the 5-number summary (minimum, first quartile, median, third quartile, and maximum) with kernel density estimates (gray) representing a mirrored probability density of the data. Black dots represent mean values.



Chapter 2: Native Forage Mediates Influence of Irrigated Agriculture on Migratory Behavior of Elk

This chapter is formatted for submission to a peer-reviewed scientific journal with Drs. Michael Mitchell and Kelly Proffitt as coauthors.

Abstract

1. Ungulates migrate to maximize nutritional intake when forage varies seasonally.

Populations of ungulates often include both migratory and non-migratory individuals, but the mechanisms driving individual differences in behavior are not well-understood.

2. We quantified associations between hypothesized drivers of partial migration and migratory behavior of individual ungulates that experienced a range of environmental conditions and anthropogenic influences.

3. We evaluated the effects of forage variation, conspecific density, animal age, and human land use on migratory behavior of adult female elk in 16 herds across western Montana.

4. We found irrigated agriculture on an individual's winter range reduced migratory behavior, but individuals were more likely to migrate away from irrigated agricultural areas if better forage was available elsewhere or if they experienced high conspecific density on their winter range. When the forage available during the summer growing season varied predictably between years, elk were more likely to migrate regardless of whether they had access to irrigated agriculture.

5. Our study shows that predictable availability of high-quality forage can encourage migration even for ungulates with irrigated agriculture on their winter range.

Perturbations that can affect the forage available to ungulates include wildfires, timber harvest, livestock grazing, and changing weather patterns. If these or other disturbances

negatively affect forage on summer ranges of migrants, or if they cause forage to vary unpredictably across space and time, our results suggest migratory behavior may decline as a result.

Introduction

Migration of large ungulates plays an important role in ecosystem functioning (Holdo, Holt, Sinclair, Godley, & Thirgood, 2011) by transferring nutrients (Hobbs, 1996), structuring vegetative communities (Holdo, Holt, Coughenour, & Ritchie, 2007; McNaughton, 1984), and altering presence of large carnivores (Henden, Stien, Bardsen, Yoccoz, & Ims, 2014) over broad spatial and temporal scales. Migratory behavior of ungulates across the world has been altered or lost in recent decades, spurring interest in understanding how behaviors may change in the future (Bolger, Newmark, Morrison, & Doak, 2008; Wilcove & Wikelski, 2008). Several studies contrast the fitness benefits of different behaviors in partially migratory populations to draw inference about potential future changes in ungulate behavior (Hebblewhite & Merrill, 2011; Rolandsen et al., 2016; White, Barten, Crouse, & Crouse, 2014). Benefits of migration, however, may change over time (Middleton et al., 2013; Wilcove & Wikelski, 2008). Therefore, a more complete understanding of migratory behavior requires insight into the factors associated with an animal's decision to migrate, not only investigation into the consequences after the decision has been made.

Although partial migration is the most common form of behavior in migratory populations (Chapman, Broenmark, Nilsson, & Hansson, 2011), the mechanisms driving differences in individual behaviors of ungulates remain largely undefined. Despite widespread recognition that ungulate behavior can range along a continuum from

residency to migration (e.g., Cagnacci et al., 2011; Mueller et al., 2011; Mysterud et al., 2011; Singh, Börger, Dettki, Bunnefeld, & Ericsson, 2012), most theoretical and empirical studies of partial migration focus on the behavioral extremes (i.e., migration vs. residency). As a result, we lack a clear understanding of how the factors that influence migratory behavior of ungulates produce the full range of behaviors we observe.

Whereas the influence of nutritional resources on ungulate migration is fairly well-understood, influences of other factors remain less clear. Studies across disparate species and ecosystems demonstrate support for the forage maturation hypothesis (Bastille-Rousseau et al., 2017; Mueller et al., 2011), which posits that herbivores migrate to increase access to high-quality forage where vegetative conditions vary spatially and temporally (Fryxell, 1991). Under this hypothesis, individuals are expected to migrate when forage varies predictably and to remain resident or exhibit other behaviors when forage varies less predictably. Three additional factors may alter or interact with the influence of forage on ungulate migration: conspecific density, animal age, and human land use practices.

Theory predicts partial migration should occur under conditions of density dependence or frequency dependence (Kaitala, Kaitala, & Lundberg, 1993; Taylor & Norris, 2007). Empirical evidence conflicts, however, regarding the influence of density on migration of ungulates. Many studies of other taxa (e.g., birds, newts) support the competitive release hypothesis (Chapman, Brönmark, Nilsson, & Hansson, 2011), which posits that migration is more likely at high densities because some individuals outcompete or displace others from areas of limited resources (Gauthreaux, 1982). Some studies of ungulates, however, have found high density may not affect migration

(Eggeman, Hebblewhite, Bohm, Whittington, & Merrill, 2016) or may even reduce migratory behavior (Mysterud et al., 2011). Reduced migration at high density supports the social fence hypothesis (Matthysen, 2005), which posits that individuals constrain their movement to avoid negative social interactions with unrelated conspecifics.

Empirical evidence further conflicts regarding the influence of animal age on migratory behavior. Some studies suggest older ungulates are less likely to migrate due to increased difficulty of movement (i.e., movement propensity hypothesis; Singh et al., 2012), whereas others indicate older ungulates are more likely to migrate (Eggeman et al., 2016). Migrants move through areas where they may experience high predation risk and where forage benefits may differ from year to year (Hebblewhite & Merrill, 2011; Middleton et al., 2013); residency involves inherently less risk because animals remain in known areas rather than traveling long distances where the benefits of movement are uncertain. Thus, the increased likelihood of migration for older animals is consistent with the terminal investment hypothesis, which asserts that older individuals invest less in their own survival and are therefore more likely to exhibit risky behaviors (T. H. Clutton-Brock, 1984).

In addition to uncertainty regarding the effects of conspecific density and age, we also lack a clear understanding of the effects of human land use practices on migratory behavior. In mountainous regions, conversion of land for human uses is most prevalent on low-elevation winter range of ungulates (Haggerty, Epstein, Stone, & Cross, 2018; Skovlin, Zager, & Johnson, 2002). Ungulates that do not migrate often remain resident in these low elevations year-round (e.g., Found & St. Clair, 2016; Hebblewhite, Merrill, & McDermid, 2008; Middleton et al., 2013), but their primary motivation for doing so is not

always clear. When low-elevation areas are converted to irrigated agricultural land, the nutritional benefit of high-quality agricultural forage (Lande, Loe, Skjærli, Meisingset, & Mysterud, 2014; Mould & Robbins, 1981) may encourage ungulates to reside on winter range throughout the year (i.e., agricultural subsidy hypothesis). Alternatively, or in addition, the higher densities of human populations or structural developments at low elevations may provide a survival benefit by excluding large carnivores (Knopff, Knopff, Boyce, & St. Clair, 2014; Linke, McDermid, Fortin, & Stenhouse, 2013; Oakleaf et al., 2006) and therefore reducing risk of predation (i.e., human shield hypothesis; Berger, 2007).

Conversion of ungulate winter range for human uses is predicted to increase into the future (Thompson & Henderson, 1998), as are climate changes that may affect vegetation and other factors that influence migratory behavior (IPCC, 2014). Changing climate and land use practices are commonly-cited causes of global reductions in migratory behavior of ungulates (Bolger et al., 2008; Wilcove & Wikelski, 2008). Anticipating how migratory behaviors will change in the future therefore relies on an accurate understanding of how ungulates respond to changing vegetative conditions and land use practices. Adaptation of a migratory animal to changing conditions relies in part on the primary drivers of its migratory behavior, but these drivers can be difficult to discern across the range of conditions experienced by a species (Shaw, 2016).

The primary goal of our study was to quantify associations between hypothesized drivers of partial migration and migratory behavior of individuals that experienced a range of environmental conditions and anthropogenic influences. Migratory behavior of elk (*Cervus canadensis*) varies widely within and among populations (Irwin, 2002); elk

therefore serve as a model species in which to study variation in migration. In some areas, recent increases in prevalence of resident ungulates have resulted in economic and social challenges (Krausman, Christensen, McDonald, & Leopold, 2014) due to issues of crop damage (Bunnell, Wolfe, Brunson, & Potter, 2002), potential for disease transmission to livestock (Cheville, McCullough, Paulson, & Council, 1998), and reduced public-land hunting opportunities (Proffitt, Thompson, Henry, Jimenez, & Gude, 2016). Identifying factors that influence migratory behavior of elk is therefore of interest from both a theoretical and an applied perspective.

We used GPS collar data collected from 308 adult female elk in 16 herds to assess individual migratory behaviors. We evaluated 7 non-exclusive hypotheses currently posited to explain partial migration in ungulates: the forage maturation, competitive release, social fence, terminal investment, movement propensity, agricultural subsidy, and human shield hypotheses (Table 1). We predicted that forage variation, conspecific density, animal age, human land uses, or combinations of these drivers would affect migratory behavior of elk (Supplementary Material Appendix A). Our results advance theories of partial migration while identifying potential means of influencing elk migratory behaviors to achieve management and conservation goals.

Study area

Our study area spanned approximately 85,000 km² across southwestern Montana, USA (44°–47° N and 109°–115° W; Fig. 1). The area lies in the central Rocky Mountains in a temperate ecosystem characterized by warm summers and cold, snowy winters. Elevations ranged from about 860 m in the northwest to 4000 m in the southeast.

Temperatures ranged from -8.2 to 17.6 °C, and yearly precipitation ranged from 101 to 2082 mm, during the years of the study (PRISM Climate Group, 2018).

Low-elevation intermountain basins and valleys often included cottonwood-dominated (*Populus spp.*) riparian corridors. Conversion of low-elevation areas to agricultural uses was common throughout the region. Agricultural uses included pivot-irrigated fields typically consisting of alfalfa hay (*Medicago sativa*) and non-irrigated fields consisting of wheat-related or rye-related grasses (e.g., *Agropyron cristatum*, *Elymus glaucus*, *E. repens*, *Thinopyrum intermedium*). Native vegetative communities included low-elevation grasslands, sage-steppe and deciduous shrubs, conifer-dominated montane forests, and alpine meadows.

Land ownership varied widely, with low-elevation areas more likely to be privately-owned and higher elevations more likely to be publicly-owned. In addition to agricultural areas, privately-owned lands consisted of residential and exurban developments. Publicly-accessible land was primarily managed by federal agencies including the United States Forest Service, Bureau of Land Management, and National Park Service. The area included portions of 13 National Forests. Herds in the southeastern portion of the study area also had access to Yellowstone National Park, which concentrates human disturbance along limited road corridors.

Mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), moose (*Alces alces*), pronghorn (*Antilocapra americana*), and bighorn sheep (*Ovis canadensis*) were sympatric with elk. Bison (*Bison bison*) also occurred in the southeastern portion of the study area. Carnivores common across the study area included cougars (*Puma concolor*), bobcats (*Lynx rufus*), coyote (*Canis latrans*), wolves (*Canis lupus*), and

American black bear (*Ursus americanus*). All elk herds with the exception of the three most westerly herds were also exposed to grizzly bears (*U. arctos*).

Methods

Adult female elk were captured by helicopter during winter using either net-gunning or chemical immobilization, consistent with Montana Fish, Wildlife and Parks Animal Care and Use protocols. Elk were fitted with GPS collars programmed to collect at least 1 location per day. We excluded locations recorded during days when the herd was being captured. We used one year of data for each herd and 2 randomly-selected locations per day per individual (one between 0800 – 2000 hr and the other between 2000 – 0800 hr) to assess migratory behavior. We only included individuals with at least 9 months of locations (i.e., those that had an opportunity to complete one full annual migration including a return trip).

We used a combination of pre-hoc and post-hoc classification rules to identify individual behaviors as resident, intermediate, or migrant using net squared displacement (NSD; Bunnefeld et al., 2011). NSD uses Akaike's information criterion (AIC; Burnham & Anderson, 2004) to determine whether a model of resident, nomadic, dispersal, mixed-migratory, or migratory behavior best represents the daily squared distance an animal moved from a starting location. We used relative net squared displacement (rNSD) in the migrateR package (D. B. Spitz, Hebblewhite, & Stephenson, 2017) in Program R version 3.4.0 (R Core Team, 2017) to find the most parsimonious starting location from which to calculate subsequent displacement values. We altered default model parameter constraints to allow migrants to remain on their summer range for up to 8 months. We excluded models of nomadism from consideration in model selection, because this model

type is most commonly misclassified by NSD techniques (Bunnefeld et al., 2011; Peters et al., 2017). We used post-hoc classification rules (see below) to classify nomadic behaviors as intermediate. We also excluded mixed-migrant models (representing migrants that return to a different wintering area) from consideration in model selection and classified these behaviors as migrants post-hoc for 2 reasons. First, model selection often inappropriately favored their increased complexity. Second, model parameters could not account for a return trip to a different wintering area that was further away from summer locations than the original wintering area.

After identifying the best-supported rNSD model of behavior for each individual, we used post-hoc rules to finalize behavior classifications based on parameter estimates. We used post-hoc rules rather than constraining parameters prior to fitting models in order to improve model convergence (Derek B. Spitz, Hebblewhite, & Stephenson, 2017). We defined migrants as animals that moved at least 8.7 km from their starting location (i.e., δ parameter > 75) prior to the end of summer (i.e., Θ parameter > 270 days from start date) and made a return trip to the same or a different winter range. Animals that made a return trip to a different winter range that was further from their summer locations than their initial winter range were represented by “resident” models with $\delta > 900$; we classified these individuals as migrants post-hoc. We defined residents as individuals who did not move more than 6.7 km (i.e., δ parameter < 45); thus, we classified animals as resident if their best-supported model indicated they “dispersed” or “migrated” less than 6.7 km. We classified dispersers, animals that did not migrate until after summer ended (i.e., did not complete a spring migration), and animals that exhibited other behaviors that were neither characteristic of migration nor residency as

intermediate. Behaviors uncharacteristic of migration and residency were represented by individuals whose best-supported model indicated they “migrated” between 6.7 and 8.7 km (i.e., $45 > \delta < 75$) or “resided” within an area in which daily movements exceeded 6.7 km (i.e., $45 > \delta$).

We used logistic regression models with behavior as an ordered categorical response ranging from residency to migration to assess the influences of forage, conspecific density, age, and human land use on migratory behavior of elk. We used the `clmm` and `clmm2` functions in the `ordinal` package (Christensen, 2015) and included herd as a random effect to account for the differing numbers of individuals captured in each herd. Models followed the form

$$\text{logit}(\Pr(Y_i \leq j)) = \Theta_j - \beta_1 X_{i1} \dots - \beta_n X_{in} - v(\text{Herd}_i); \quad i=1, \dots, n; \quad j=1, \dots, J-1$$

where Y represents an ordinal response, J represents a response category (i.e., resident, intermediate, or migrant), Θ_j represents thresholds between response categories, β represents the coefficient estimate for covariate X , v represents a normally-distributed random effect of Herd, and i represents an individual. We used flexible thresholds between behavioral categories. We used likelihood ratio tests to assess whether the random effect of herd improved model fit to a degree that merited the increased model complexity.

We estimated covariates to represent the conditions each elk experienced during winter prior to a potential spring migration. We delineated winter home ranges for each individual as 95% kernel utilization distributions (UDs) estimated from location data

collected during the first season of the year. To capture conditions experienced immediately prior to spring, and because some herds were captured during February, we delineated winter home ranges using only February locations. We used the ad hoc href smoothing factor and the same grid cell size for each individual in each herd (Fieberg & Kochanny, 2005) in the adehabitatHR package (Calenge, 2006).

We used two metrics derived from 250m Landsat Normalized Difference Vegetation Index (NDVI) data as proxies for elk forage. First, to quantify relative forage outside an elk's winter range during summer (i.e., the forage the elk could access by leaving its winter range as opposed to remaining resident) we used maximum NDVI, which represents the peak level of photosynthetic activity each growing season. We calculated the difference in forage by subtracting the maximum NDVI value within the individual's winter range from the maximum NDVI value outside the winter range. We considered any area within the herd's growing season range (i.e., 100% minimum convex polygon [MCP] of all elk locations recorded May – Aug for that herd during the year of interest) to be available to any individual within the herd. We used locations from all elk (not only the subset of individuals with at least 9 months of locations) to estimate herd-level ranges. We used an MCP to avoid including areas located on the other side of highways that elk did not typically cross. We used maximum NDVI because it measures native vegetative communities on a scale comparable to that of irrigated agriculture. Maximum NDVI is calculated independently of baseline NDVI values recorded during the non-growing season, which are typically higher on irrigated agricultural land than in other areas.

Second, to determine how predictably forage varied across space and time, we quantified variation in NDVI amplitude across the herd's growing season range. We calculated the standard deviation of NDVI amplitude in each pixel of each herd's growing season range, using values from the year of the study and each of the 5 years prior. We then averaged standard deviations across the herd's growing season range to estimate one value of forage variation across space and time (Mueller et al., 2011). We used NDVI amplitude because it represents the peak increase in photosynthetic activity above the baseline, thereby capturing how forage varies relative to non-growing season conditions.

We estimated individuals' ages during capture using tooth eruption and wear. We classified elk as Old if their age was estimated to be >10 yrs. This number corresponds to cutoffs generally used in field estimations and to literature values associated with age classes of adult females (R. C. Cook et al., 2013).

We estimated herd sizes from yearly aerial complete-coverage surveys conducted by Montana Fish, Wildlife and Parks biologists as part of routine survey and inventory projects. We created an index of conspecific density by dividing the estimated herd size by the area of the herd's winter range (i.e., 95% UD of all elk locations recorded during February in the winter of interest); values were unitless because they represent a relative index of density rather than an exact measure of elk per unit area. When nearly half (>45%) of individuals in one herd also used another herd's winter range, we combined counts and home ranges to estimate a shared density index that included both herds. Although complete-coverage counts can sometimes underestimate herd numbers, elk in our study area primarily overwinter in open-canopy areas. Sightability should therefore

be relatively high and should be comparable between herds. The wide variation in estimated herd sizes, which spanned an order of magnitude, is likely greater than potential error among estimates.

We used land ownership data to quantify human land use within individual elk winter ranges. We downloaded recent ownership data from the online Montana cadastral database (Montana State Library, 2017); we received older cadastral data for each year through 2006 via email from Montana State Library GeoInfo. To characterize land use in the small area of Wyoming that fell within our study area, we used georeferenced parcel boundaries (ArcGIS REST Services, 2017), a land ownership map (United States Geological Survey, 2017), and aerial imagery in which irrigated agricultural areas were clearly visible. First, we classified individuals as either having or not having access to irrigated agriculture on their winter range (i.e., acres of irrigated agriculture on parcels within the winter range > 0). Second, we calculated an index of the intensity of human land use to serve as a proxy for exclusion of large carnivores. We calculated this index by dividing the number of unique landowners on an individual's winter range by the area of the winter range.

We developed 26 *a priori* models representing 7 hypotheses posited to explain partial migration in ungulates, including biologically relevant combinations of each (Supplementary Material Appendix A). We removed individuals that were missing age estimates before we compared models. We used AIC corrected for small sample size (AICc) to assess relative support for models, considering models with $\Delta\text{AICc} \leq 2$ to be supported (Burnham & Anderson, 2004). We report maximized log-likelihood ($\log(L)$), number of estimable parameters (K), and Akaike weights (ω_i) of supported models.

Because traditional methods of estimating R^2 values do not apply to ordinal logistic regression models, we used Nagelkerke's pseudo- R^2 to assess goodness-of-fit (Nagelkerke, 1991).

Results

We assessed migratory behavior of 308 adult female elk in 16 herds across southwestern Montana during 2006-2016, using data from 5-34 individuals per herd (Table 2). We classified 63.6% of elk as migratory ($n = 196$), 15.6% as intermediate ($n = 48$), and 20.8% as resident ($n = 64$). Migrants traveled up to 110 km from their initial starting locations, but movement distances varied considerably among individuals and were strongly positively skewed (median = 22km, IQR = 30km). The length of time spent on summer range varied similarly (median = 104d, IQR = 94d). Migratory behaviors varied among herds; the percentage of migrants within a herd ranged from 19-100% (Fig. 2). On average, herds were composed of $62 \pm 30\%$ (SD) migrants, $16 \pm 14\%$ intermediates, and $22 \pm 21\%$ residents.

The relative forage outside an elk's winter range during summer was strongly positively skewed and ranged from 0-31 maximum NDVI digital numbers (DN; median = 2, IQR = 6). Median difference in forage was 3 DN for migrants vs. 1 DN for residents or intermediates. Predictability of forage variation across the growing season ranges of all herds averaged 3.04 ± 0.68 (SD) standard deviations of NDVI amplitude (range 4.07 – 1.98). Forage varied most predictability for migrants (median = 2.85 for migrants vs. 3.40 for both intermediates and residents). Age was not estimated at capture for 10 individuals. Approximately 14% ($n = 43$) of the elk for whom age was estimated ($n = 298$) were older than 10 yrs. Migrants were more likely to be old than were intermediates

or residents (20% > 10 yrs vs. 5% and 7%, respectively; $\chi^2_2 = 10.90$, $p = 0.004$). Conspecific density indices were positively skewed and ranged from 1.04 to 46.41 (median = 6.51, IQR = 13.32). Migrants tended to experience higher conspecific density during winter than intermediates or residents (median = 8.12 vs. 1.75 and 1.14, respectively). About 63% of individuals had access to irrigated agriculture on their winter range ($n = 194$); access to agricultural areas did not differ strongly among behavior types (64% of migrants, 63% of intermediates, and 59% of residents had irrigated agriculture on their winter ranges). The unique landowners per km² on an individual's winter range varied from 0.0002 – 0.3625 (median = 0.0091, IQR = 0.0203).

The conditions that individuals experienced during winter varied within herds. As few as 27% of individuals in a herd accessed the irrigated agricultural land that was available on the herd winter range; 1 herd winter range did not include irrigated agriculture. The percentage of elk in a herd that had access to irrigated agriculture varied from 0-100% (median = 74%, IQR = 44%). Within herds, the maximum forage available on individuals' winter ranges during summer differed from 3 – 31 DN among individuals, and the intensity of human land use differed from 0.003 to 0.357 among individuals.

We found similar support for 2 models ($\Delta\text{AICc} \leq 2$) in explaining variation in individual migratory behaviors. Because neither model included the Age covariate, we report model estimates after rerunning the models using all individuals, including those missing age estimates ($n = 308$). Likelihood ratio tests indicated that including the random effect of herd improved model fit ($p < 0.001$ in both cases).

The best-supported model ($\Delta\text{AICc} = 0$, $\omega_i = 0.31$, $\log(L) = -224.34$) included the effects of forage predictability, relative forage outside the winter range, irrigated

agriculture, and an interaction between agriculture and the relative forage outside the winter range (Nagelkerke pseudo- $R^2 = 0.31$; Fig. 3), supporting the forage maturation and agricultural subsidy hypotheses. The odds of an elk migrating rather than displaying other behaviors increased as forage varied more predictably (OR = 6.28, 95% CI = 1.84, 21.40) but decreased by 55% if an elk had irrigated agriculture on its winter range (OR = 0.45, 95% CI = 0.21, 0.99). The odds of an elk migrating away from a winter range that included irrigated agriculture increased as the relative forage available elsewhere increased (interaction term between irrigated agriculture and relative forage OR = 1.17, 95% CI = 1.05, 1.29). The effect of herd was indistinguishable (i.e., 95% CI of herd effect overlapped 0) for 75% of the herds studied ($n = 12$; Fig. 2).

The second-best-supported model ($\Delta AICc = 1.10$, $\omega_i = 0.18$, $\log(L) = -224.89$) included the effects of forage predictability, irrigated agriculture, conspecific density, and an interaction between agriculture and conspecific density (Nagelkerke pseudo- $R^2 = 0.30$), supporting the forage maturation, agricultural subsidy, and competitive release hypotheses. Similar to the best-supported model, the odds of an elk migrating rather than displaying other behaviors increased as forage varied more predictably (OR = 5.64, 95% CI = 1.58, 20.17) but decreased by 57% if an elk had irrigated agriculture on its winter range (OR = 0.43, 95% CI = 0.19, 1.00). The odds of an elk migrating away from a winter range that included irrigated agriculture increased as conspecific density on the winter range increased (interaction term between irrigated agriculture and conspecific density OR = 1.20, 95% CI = 1.04, 1.40). The effect of herd was indistinguishable for 69% of the herds studied ($n = 11$).

Discussion

Despite substantial variation in behavior among individuals and among herds, we found common effects of native forage, irrigated agriculture, and conspecific density on migratory behavior of elk in the majority of herds we studied. The predicted effects of these factors on intermediate migratory behaviors more closely matched their predicted effects on resident than on migratory behaviors. Presence of irrigated agriculture on an elk's winter range reduced the likelihood of migration, but elk were more likely to migrate away from irrigated agricultural areas if better forage was available elsewhere during the summer growing season or if conspecific density was high. Migration was also more likely where forage varied predictably from year to year. Our results therefore support the forage maturation, agricultural subsidy, and competitive release hypotheses and reveal that availability of predictably good forage outside elk winter range can mediate the influence of irrigated agriculture on migratory behavior.

Management and conservation goals often aim to preserve or increase migratory behavior of ungulates (Berger, 2004; Sawyer, Kauffman, Nielson, & Horne, 2009). We found that maintaining or improving the forage available on traditional migratory summer ranges can encourage migration even where elk have access to irrigated agriculture. Generally, areas with less canopy cover and in earlier seral stages provide relatively high nutrition for ungulates, but additional work is needed to fully assess effects of land management practices on elk forage (J. G. Cook, Cook, Davis, & Irwin, 2016). These practices might include fire management (Barker et al. unpublished data) or timber management such as revegetation, logging, thinning, or mechanical treatments (Scotter, 1980). Because we found the influence of forage on migratory behavior

remained largely consistent across a range of environmental conditions and anthropogenic influences, changes to forage across broad geographic areas should have similar effects on migratory behavior of individuals.

Management strategies to improve forage on migratory summer ranges may prove most effective if such improvements can ensure reliable forage availability. Our findings revealed a strong positive association between the likelihood of an elk migrating and how predictably forage varied from year to year. The forage available to elk can vary due to changing climate and weather patterns, land use practices such as timber management or energy development, and stochastic events such as wildfires and tree disease outbreaks. Efforts to bolster resilience of vegetative communities (i.e., improve the stability of vegetative communities in the face of change) may help ensure reliable availability of forage (Holling, 1973). Such efforts might include maintaining structural diversity in forests, conserving biodiversity and connectivity, and controlling invasive species (Fischer, Lindenmayer, & Manning, 2006). Additionally, given the relatively high nutritional quality of early seral-stage vegetative communities (Barker et al. unpublished data), managing disturbances to maintain a mosaic of early-successional vegetative communities across the summer ranges of migratory elk could improve both the quality and predictable availability of forage for migrants.

Though animals in the same partially migratory population are typically thought to experience similar conditions during the season in which individuals use the same or similar areas (Holt & Fryxell, 2011), we found elk in the same herd experienced different conditions during the shared winter season. For example, when portions of a herd's winter range were converted to irrigated agriculture, not all elk accessed that agricultural

land during winter. Theory-based predictions of migratory behavior often rely on an assumption that individuals achieve similar fitness during the shared season.

Investigation into the fitness benefits of different behaviors during the shared season could improve theoretical understanding and predictions of behavioral changes in partially migratory populations. Because costs and benefits of movement can vary yearly, and because ungulates can change behaviors between years, long-term monitoring of individuals would provide the strongest understanding of fitness consequences (T. Clutton-Brock & Sheldon, 2010).

Our results corroborate theoretical assertions that density and frequency dependence are necessary for the evolution and persistence of partial migration (Lundberg, 2013; Taylor & Norris, 2007). We found that conspecific density increased the likelihood of migration only for individuals that overwintered in irrigated agricultural areas, suggesting agricultural land provides a desirable but limited resource for elk. Irrigated agriculture provides higher-quality forage than many other plant communities in the Rocky Mountains (Barker et al. unpublished data); therefore, these findings agree with predictions of partial migration as an ideal free or ideal despotic distribution (Fretwell & Lucas, 1969; Griswold, Taylor, & Norris, 2011). Assessing interactions between forage and density fell outside the scope of other elk studies that have not found increased likelihood of migration at high conspecific density (Eggeman et al., 2016; Mysterud et al., 2011).

In addition to nutritional benefits, agricultural areas may also provide a benefit of reduced risk of mortality. Although areas with high densities of human populations or heavily-travelled roads and trails are predicted to most strongly exclude large carnivores

under the human shield hypothesis (Berger, 2007; Knopff et al., 2014; Oakleaf et al., 2006), agricultural areas may also effectively exclude or remove predators despite their relatively lower intensity of human use (Musiani et al., 2004). If so, human-provided refugia from predation risk could act synergistically with human-provided forage resources in reducing the likelihood of migration. Additionally, privately-owned lands that restrict hunter access can reduce the risk of mortality due to human hunting, the primary cause of mortality for adult elk in this region (Brodie et al., 2013).

We did not find support for the movement propensity hypothesis, which posits that old age limits an animal's ability to undertake long seasonal movements. Rather, our finding that migratory elk tended to be older than residents and intermediates aligns more closely with the terminal investment hypothesis, which predicts that older elk should undertake risky migrations to improve their likelihood of reproductive success. It remains unclear, however, whether migration allows individuals to realize this hypothesized reproductive benefit. Other studies of elk that migrated into Yellowstone National Park during summer found that pregnancy rates and calf-cow ratios were lower for migrants than for residents (Middleton et al., 2013). If recruitment is also lower for migrants in other herds in our study area, and if migration is an inherited or learned trait, the older age of migrants may reflect an increasing age structure of migratory portions of populations that has arisen as a result of this lower recruitment.

Worldwide declines in migratory behavior of ungulates are commonly attributed to changes in climate and land use practices (Bolger et al., 2008; Wilcove & Wikelski, 2008). If these changes cause forage to vary unpredictably between years, or if they negatively affect forage on migratory summer ranges more strongly than on lower-

elevation winter ranges during the summer growing season, our results suggest migratory behavior of elk will decline as a result. It remains to be seen, however, whether migratory behavior would effectively be lost in affected populations. Partially migratory populations in which individuals employ a diversity of migratory tactics may be well-poised to respond effectively to changing external conditions. Migration is not a fixed trait in ungulates; elk can and do change behaviors between years (Eggeman et al., 2016). If elk can most effectively capitalize on unpredictable forage variation by changing their behavior yearly based on external conditions, then genetic and learned components of migration should be retained even if the relative proportion of migrants in the population declines in some years. Alternatively, or additionally, intermediate behaviors may become more prevalent in the future if they allow increased behavioral flexibility in the face of changing external conditions. Thus, if benefits of migration are reduced or become inconsistent in the future, ungulate populations may not become entirely resident as a consequence.

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Tables

TABLE 2.1. Hypothesized explanations for partial migration in ungulates. Predictions in bold were best-supported in explaining variation in behavior of 298 adult female elk in 16 herds across southwestern Montana, USA, 2006-2016. Hypotheses labeled A) were the best-supported of the 2 within the category.

Hypothesis	Predictions	References
<u>Forage</u>		
<i>Forage maturation:</i> Movements of herbivores are driven primarily by availability of forage	Elk are more likely to migrate when forage varies predictably and is better outside their winter range during the growing season.	Fryxell 1991, Mueller et al. 2011
<u>Conspecific density</u>		
<i>A) Competitive release:</i> Individuals outcompete or displace others to gain access to a limited amount of high quality resources	Elk are more likely to migrate when conspecific density is high during the shared season.	Taylor and Norris 2007, Chapman et al. 2011
<i>B) Social fence:</i> Movement is constrained by high density of unrelated conspecifics due to potentially negative social interactions	Elk are less likely to migrate when forage is better outside their winter range during the growing season if conspecific density is high.	Mysterud et al. 2011
<u>Animal age</u>		
<i>A) Terminal investment:</i> Older individuals invest more in reproduction and are thus more likely to undergo risky migration	Elk are more likely to migrate if they're old.	Clutton-Brock 1984, Eggeman et al. 2016
<i>B) Movement propensity:</i> Older individuals are less likely to migrate because movement is more difficult	Elk are less likely to migrate if they're old.	Singh et al. 2012
<u>Human influence</u>		
<i>A) Agricultural subsidy:</i> Ungulates are less likely to migrate from human-dominated areas because humans provide high-quality forage	Elk are less likely to migrate when they have access to irrigated agriculture on their winter range.	Middleton et al. 2013
<i>B) Human shield:</i> Ungulates are less likely to migrate from human-dominated areas because humans exclude predators	Elk are less likely to migrate when the intensity of human use inside their winter range is high.	Berger 2007, Hebblewhite and Merrill 2009

TABLE 2.2. Number of adult female elk studied in 16 herds across southwestern Montana, USA, 2006 – 2016; proportion of the herd that was at least 10 years old during the year of the study; relative index of conspecific density during the winter at the beginning of the year; and the proportions of migratory, intermediate, and resident behavior in the herd.

Herd	Year	n	≥ 10 yr. old (ppn)	Relative Density	Migrant (ppn)	Intermediate (ppn)	Resident (ppn)
Madison	2006	27	0.22	46	1.00	0.00	0.00
N. Yellowstone	2008	27	0.44	15	1.00	0.00	0.00
Silver Run	2016	5	0.60	2	1.00	0.00	0.00
Blacktail	2011	23	0.14	3	0.96	0.04	0.00
East Fork	2011	24	0.35	8	0.75	0.04	0.21
Pioneers	2013	27	0.00	2	0.74	0.22	0.04
Sage Creek	2012	22	0.05	3	0.73	0.23	0.05
Mill Creek	2015	17	0.06	17	0.71	0.00	0.29
HD314	2010	6	0.33	15	0.67	0.17	0.17
N. Madison	2014	18	0.11	10	0.61	0.11	0.28
N. Sapphires	2014	36	0.09	1	0.44	0.25	0.31
Greeley	2015	19	0.00	7	0.42	0.42	0.16
Elkhorns	2015	25	0.04	1	0.28	0.20	0.52
Clarks Fork	2016	10	0.10	24	0.20	0.40	0.40
West Fork	2013	10	0.10	8	0.20	0.20	0.60
Tobacco Roots	2014	16	0.00	1	0.19	0.25	0.56

Figures

FIGURE 2.1. Yearly ranges of 16 elk herds across western Montana, USA, 2006 – 2016.

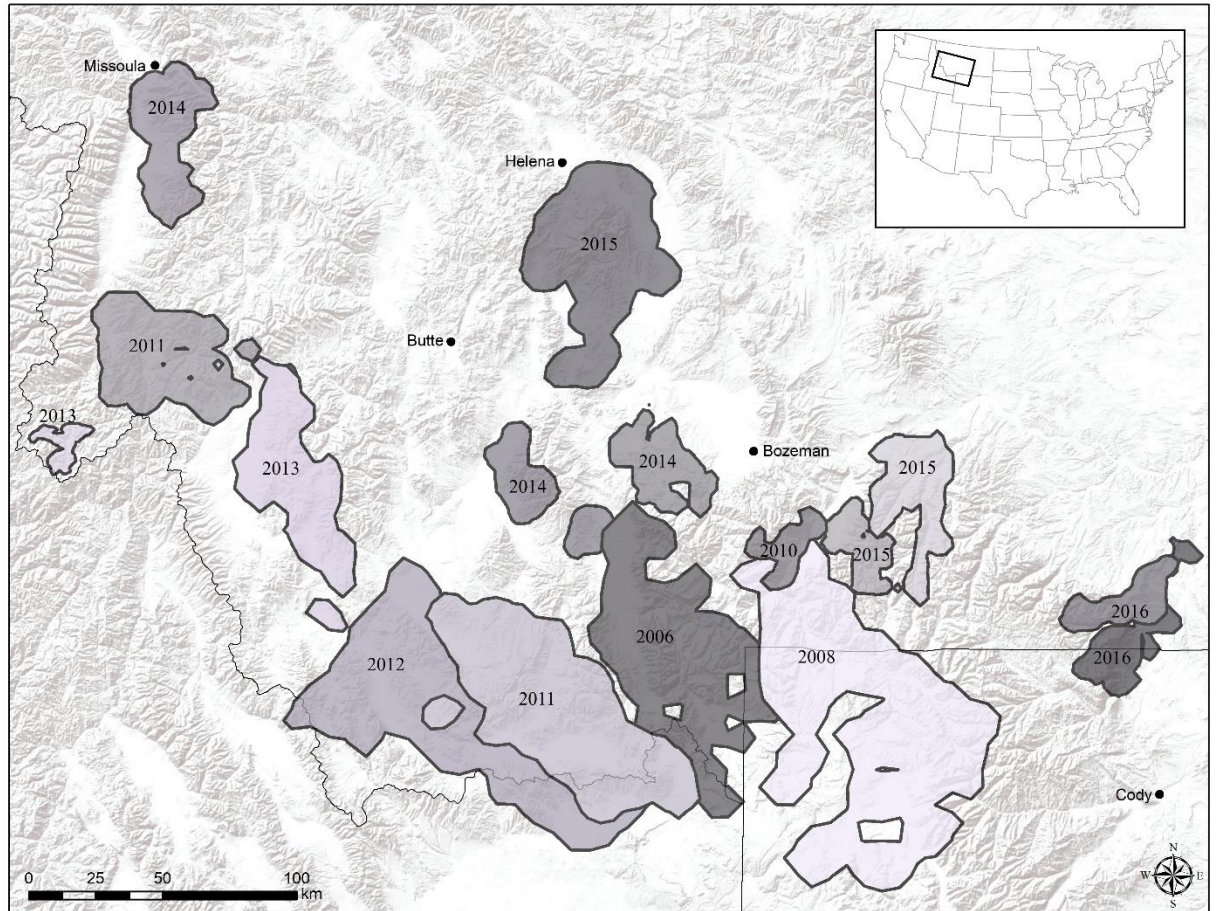


FIGURE 2.2. Proportion of migratory, intermediate, and resident elk in 16 herds across southwestern Montana, USA, 2006 – 2016, along with the effect of herd (random effect estimate \pm 95% CI) in logistic regression models associating vegetation characteristics with individual migratory behaviors. Despite wide variation in proportions of behaviors among herds, the majority of herds responded similarly to vegetation characteristics (i.e., CI of herd effect overlapped 0).

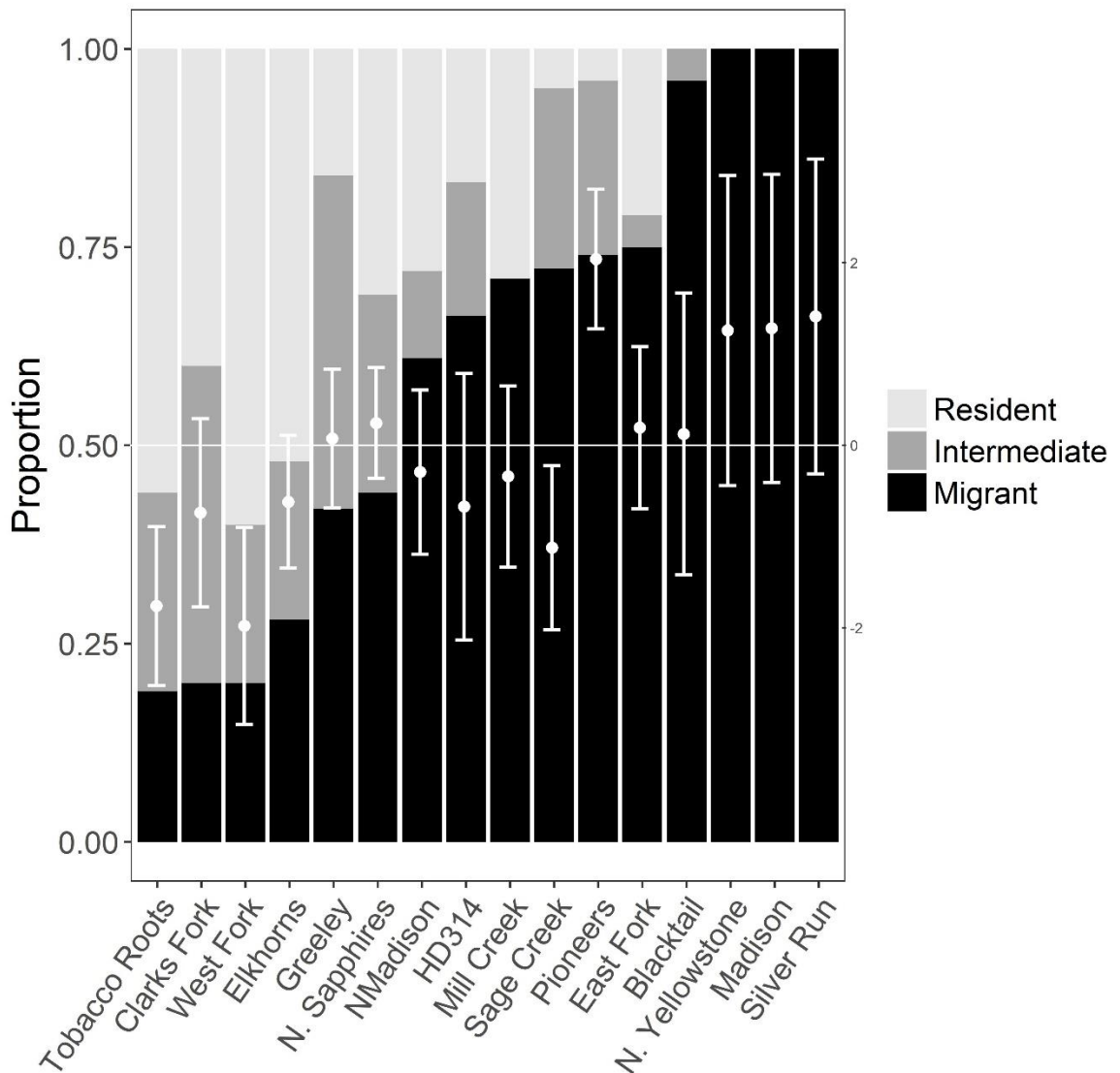
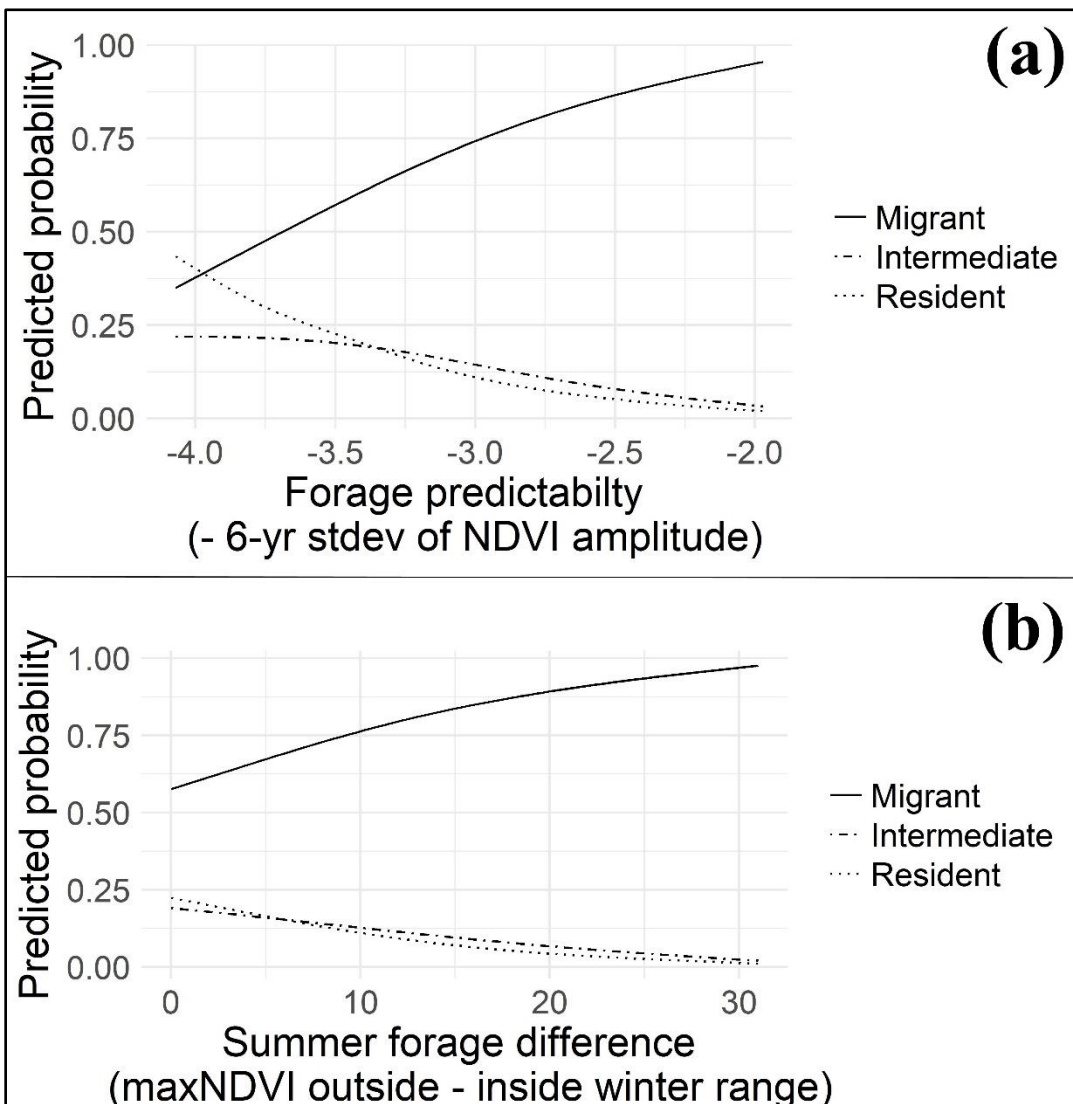


FIGURE 2.3. Results of best-supported model explaining migratory behavior of 308 elk in 16 herds across southwestern Montana, USA, 2006-2016. Elk were increasingly likely to migrate rather than remain resident as forage varied more predictably (panel a). Elk that had access to irrigated agriculture on their winter range were less likely to migrate, but these elk were more likely to migrate away from irrigated agriculture as the forage available outside the winter range more strongly exceeded that inside the winter range during the summer growing season (panel b).



Supplementary material

Appendix A – Migratory behavior models

TABLE A1. Akaike's model selection criterion (AICc), number of estimable parameters (K), AICc weight (ω_i), and maximized log-likelihood ($\log(L)$) for 26 *a priori* models used to test relative support for 7 hypotheses posited to explain partial migration in ungulates. Models were estimated using data from 298 elk in 16 herds across southwestern Montana, USA, 2006-2016. We considered models with $\Delta\text{AICc} \leq 2$ to be supported (Burnham and Anderson 2004).

Model covariates	Biological explanation	ΔAICc	K	ω_i	$\log(L)$
predFor + deltaFor + irrig + deltaFor*irrig	Elk are more likely to migrate if forage varies predictably and is better outside their winter range. Elk are less likely to migrate if they have access to irrigated agriculture on their winter range, unless forage is better outside their winter range	0.00	7	0.31	-224.34
predFor + irrig + Dens + irrig*Dens	Elk migrate when forage varies predictably and remain resident for the agricultural forage, but agricultural fields can only support so many elk	1.10	7	0.18	-224.89
predFor + deltaFor	Elk migrate if forage varies predictably and is better outside their winter range	3.19	5	0.06	-228.02
predFor + deltaFor + Old	Elk migrate if forage varies predictably and is better outside winter range, but they are more or less likely to migrate if they are old	3.41	6	0.06	-227.09
predFor + deltaFor + densOwn	Elk migrate if forage varies predictably and is better outside winter range, but they remain resident for the lower mortality risk	3.74	6	0.05	-227.25
predFor + deltaFor + Dens	Elk migrate if forage varies predictably and is better outside winter range, but they are more or less likely to migrate at high conspecific density	3.82	6	0.05	-227.30
predFor + deltaFor + Old + Dens	Elk migrate if forage varies predictably, is better outside winter range, they are old, and conspecific density is high	4.20	7	0.04	-226.43

predFor + deltaFor + deltaFor*predFor	Elk migrate if forage varies predictably only when forage is better outside winter range	4.85	6	0.03	-227.81
predFor + deltaFor + irrig	Elk are less likely to migrate under FMH conditions if they have access to irrigated agriculture on their winter range	5.08	6	0.02	-227.93
predFor + deltaFor + densOwn + deltaFor*predFor	Elk only remain resident for the lower mortality risk if forage is also better on winter range during the growing season	5.18	7	0.02	-226.93
predFor + deltaFor + densOwn + Old + densOwn*Old	Elk migrate if forage varies predictably and is better outside winter range, unless they're old and remain resident for the lower mortality risk	5.22	8	0.02	-225.89
predFor + deltaFor + Old + deltaFor*Old	The influence of age changes depending whether forage is better outside winter range	5.28	7	0.02	-226.98
irrig + Dens + irrig*Dens	Elk remain resident for the agricultural forage, but agricultural fields can only support so many elk	5.45	6	0.02	-228.11
predFor + deltaFor + Dens + deltaFor*Dens	The influence of conspecific density changes depending whether forage is better outside winter range	5.51	7	0.02	-227.09
predFor + deltaFor + densOwn + deltaFor*densOwn	Elk remain resident for the lower mortality risk only when forage is worse outside winter range anyway, or they are more likely to remain resident when forage is better outside the winter range if there's lots of human use	5.57	7	0.02	-227.12
predFor + irrig + densOwn + irrig*densOwn	Elk migrate when forage varies predictably and remain resident for the agricultural benefit only if humans do not use the area intensively	5.81	7	0.02	-227.24
predFor + irrig + Old + Dens + Old*Dens	Elk migrate when forage varies predictably and remain resident for the agricultural forage, but agricultural areas can only support so many elk, and older elk are better competitors	5.98	8	0.02	-226.27
predFor + deltaFor + Old + Dens + Old*Dens	Elk migrate because some elk outcompete others from limited	6.30	8	0.01	-226.43

	forage and older elk are better competitors				
densOwn + irrig + Dens + irrig*Dens	Elk remain resident for both agricultural forage and lower mortality risk, but agricultural areas can only support so many elk	6.93	7	0.01	-227.80
predFor + deltaFor + irrig + predFor*irrig	Elk migrate when forage varies predictably and is better outside their winter range unless they have access to irrigated agriculture on their winter range	7.12	7	0.01	-227.90
densOwn	Elk remain resident for the lower mortality risk	7.45	4	0.01	-231.19
irrig	Elk remain resident just for the agricultural forage	8.81	4	0.00	-231.87
densOwn + Old + densOwn*Old	Elk remain resident for the lower mortality risk unless they're old	9.05	6	0.00	-229.91
deltaFor	Elk migrate if forage is better outside their winter range (no matter how predictably it varies)	9.17	4	0.00	-232.05
densOwn + irrig + Dens + densOwn*Dens	Elk remain resident for both agricultural forage and lower mortality risk, but human-dominated areas can only support so many elk	9.42	7	0.00	-229.05
densOwn + irrig	Elk remain resident for the lower mortality risk and the agricultural forage	9.43	5	0.00	-231.14

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