



Research Article

Land Management Alters Traditional Nutritional Benefits of Migration for Elk

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ABSTRACT Ungulates typically migrate to maximize nutritional intake when forage varies seasonally. In western North America, however, increasing numbers of ungulates reside on low-elevation winter range year-round rather than migrating. These residents often occupy irrigated agricultural areas, but it is not known whether the nutrition provided by agricultural land exceeds that gained by migration. We evaluated the nutrition available to a partially migratory population of elk (*Cervus canadensis*) in west-central Montana where some individuals summered on low-elevation agricultural lands, whereas others summered on traditional higher-elevation ranges. We sampled elk forage plants from ground plots and adult female elk movements from global positioning system (GPS) collar locations during late summer for 2 years. We tested for differences in the nutrition provided by 11 vegetative communities commonly available to elk in the Rocky Mountains and the nutrition available in areas used by individuals whose behaviors ranged from residency to migration. We found the nutrition available to elk decreased along the continuum from resident to migratory behavior, contrary to our hypothesis that all behaviors would provide access to equivalent forage quality. The relatively small summer home ranges of migrants suggest other factors (e.g., decreased competition) may compensate for their lower nutritional value, because the size of a home range is often inversely related to its fitness benefits. We found 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. Excluding elk from irrigated agricultural areas should therefore reduce nutritional incentives for elk to reside at low elevations year-round. Additionally, fire in higher-elevation dry forests may temporarily increase forage quality for elk and improve nutritional benefits of migratory behavior. Our results indicate land management practices can affect nutritionally mediated fitness benefits of differing behaviors in partially migratory populations of ungulates. © 2018 The Wildlife Society.

KEY WORDS *Cervus canadensis*, elk, forage quality, land use, Montana, nutrition, partial migration.

In temperate climates, ungulates typically migrate from winter ranges during spring to track growth of highly nutritious emergent vegetation into higher-elevation summer range. Access to high-quality forage is 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).

When elk (*Cervus canadensis*) forego seasonal migration, they tend to remain resident in these low-elevation valley bottom areas (Hebblewhite et al. 2008, Middleton et al. 2013, Found and St. Clair 2016).

Increasing numbers of elk that reside on private agricultural land year-round present a common management challenge in the western United States due to potential issues of crop damage, disease transmission to livestock, and reduced public hunting opportunities (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 (Krausman et al. 2014), managers often seek to encourage migration off low-elevation private lands. If resident elk benefit from high-quality forage in

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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 help increase prevalence of migratory behavior and reduce property damage issues on private lands.

Resident ungulates usually comprise part of a partially migratory population in which behavior of individuals can fall along a continuum from residency to migration (Luccarini et al. 2006, Hebblewhite et al. 2008, Cagnacci et al. 2011, Middleton et al. 2013). Partial migration represents an evolutionarily stable strategy under which both resident and migratory behaviors should persist within the same population (Lundberg 1987). Different behaviors can allow individuals to achieve equal fitness, consistent with predictions of partial migration as an ideal free distribution (Fretwell and Lucas 1969, Hebblewhite and Merrill 2011). In some partially migratory populations, however, fitness differences can result in reduced prevalence (Middleton et al. 2013, Cole et al. 2015) or even loss (Harris et al. 2009) of some behaviors over time. Therefore, when increasing numbers of ungulates exhibit resident behavior, it is not always clear whether prevalence of migratory behavior is also increasing (i.e., the overall population is growing) or whether migratory behavior is declining (i.e., the relative prevalence of resident behavior is increasing). In the absence of historical data on prevalence of different behaviors, assessing relative fitness benefits of migration and residency can provide insight into whether migratory behaviors may be declining. Additionally, such assessment can improve theoretical understanding of the conditions under which different behaviors are maintained within the same population.

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/g 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 have lower survival 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 which native vegetative communities provided forage of similar quality to that of irrigated agriculture during late summer and 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, USA, where natural survival and pregnancy rates should be influenced primarily by nutritional intake. The risk of predation is

relatively low for adult females; grizzly bears (*Ursus arctos*) do not inhabit the area, and gray wolves (*Canis lupus*) occurred sporadically (Montana Fish, Wildlife and Parks 2014). Because previous work in our study area did not suggest nutrition was limiting to elk in this population (Proffitt et al. 2016), we hypothesized that partial migration in the North Sapphires represented an ideal free distribution in which fitness benefits were equivalent across behavioral strategies. Thus, we predicted that native vegetative communities at high elevations would provide digestible energy (i.e., nutrition) similar to that provided by irrigated agriculture at low elevations during late summer, and we predicted that 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, where the elk population has increased from <250 individuals in the 1960s to nearly 1,000 in 2015 (Edwards et al. 2015, Montana Fish, Wildlife and Parks 2017). Estimates of recruitment vary annually and have averaged approximately 25 calves/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 potential issues of crop damage and reduced public hunting opportunities (Montana Fish, Wildlife and Parks 2017).

The North Sapphire Mountains have relatively low elevational relief compared to other mountain ranges in the Rocky Mountain region; elevations in the study area ranged from approximately 1,000 m to 3,000 m. Yearly temperatures ranged from -5 °C to 25 °C (PRISM [Parameter-elevation Regressions on Independent Slopes Model] Climate Group 2016). Land ownership included a matrix of public lands (59%) and publicly accessible corporate timber lands (3%) that dominated the higher-elevation summer range traditionally used by migratory elk, and privately owned residential and agricultural lands (38%) that dominated the valley-bottom elk winter range. Mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), moose (*Alces alces*), and bighorn sheep (*Ovis canadensis*) were sympatric with elk. Resident 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 or corn fields with additional grasses (e.g., cheatgrass [*Bromus tectorum*]) and forbs (e.g., bladder campion [*Silene latifolia*]) interspersed at lower abundance. Non-irrigated agricultural areas most commonly consisted of wheat-related or rye-related grasses (e.g., crested wheat grass [*Agropyron cristatum*], blue wild rye [*Elymus glaucus*], couch grass [*E. repens*], intermediate wheatgrass [*Thinopyrum intermedium*]).

Bluebunch wheatgrass (*Pseudoroegneria spicata*) and fescues (rough fescue [*Festuca campestris*], Idaho fescue [*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 malva-ceus*), 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 area, 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 we 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 further divided each forest type into 3 successional stages based on fire history (burned 1–5 yr ago, burned 6–15 yr ago, and burned >15 yr ago). We included an additional classification for dry forests to represent recent prescribed burns (1–5 yr ago) to account for potential differences between prescribed burns and wildfires.

We identified summer forage species based on fecal plant fragment analyses of pellet samples. We collected fresh composite fecal pellet samples (i.e., ≤ 20 pellets <48 hr old from 7–10 individual elk) from ≥ 4 sampling sites every 16 days from June to October in 2014 and 2015. We used global positioning system (GPS) collar locations recorded within 24 hours to identify sampling sites, which included areas used by resident and migratory individuals. When feasible, we visited areas used by >1 collared individual to increase the likelihood of attaining sufficient sample size from multiple individuals. We defined forage species as those comprising 95% of the diet.

We collected forage species in each phenological stage (emergent, flowering, fruiting, mature, senescent). We collected graminoid and forb species >1 cm above the ground to represent the available foraging height for an elk. We collected the current years' growth of leaves and stems for forage shrubs. We estimated dry matter digestibility (Robbins et al. 1987a, b; Hanley et al. 1992) for each phenological 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)

measured as kcal/g of forage using an equation developed by Cook et al. (2016).

We measured composition and phenological stage of forage species at 752 vegetation plots located within the yearly range of elk. Plots were proportionally allocated to landcover types, then stratified within landcover types based on aspect and slope (Krebs 1989). We completed all vegetation sampling within a 6-week period during the time of peak vegetative growth (15 Jul–31 Aug) and considered each of these samples to represent late summer. We estimated DE at each vegetation plot as the weighted mean of digestible energy (DE) values for each forage species in each phenophase; we included all forage species and phenophases 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 DE 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 DE.

Classification of Migratory Behaviors

We captured elk by helicopter, using either net-gunning or chemical immobilization consistent with Montana Fish, Wildlife and Parks Animal Care and Use Committee protocol 19-2013. We fitted GPS collars on 45 adult female elk in February 2014 and 3 additional elk in February 2015 (Lotek Wireless, Ontario, Canada, IridiumTrack M 3D). We programmed collars to record locations 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 [UDs]) estimated from summer (Jul–Aug) and winter (Feb–Mar) 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 (VI) between seasonal 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., VI of 95% UD_s = 0). We defined residents as individuals whose core use areas overlapped (i.e., VI of 50% UD_s > 0). We defined all other individuals as intermediates (i.e., VI of 50% UD_s = 0 and VI 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, and we determined the average elevation at which each behavior group was located by calculating the mean elevation of all individual locations.

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 VI between core use areas, then by VI 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.

Access to Nutrition Across Migratory Behaviors

We developed a model of forage quality using generalized linear regression to predict phenophase-specific DE in 30×30 -m units 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 model of the most explanatory covariates from an initial global model of 8 standardized covariates that may influence vegetative growth: 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 Normalized Difference Vegetation Index (NDVI) amplitude. All covariates had a Pearson's correlation coefficient < 0.6 . We predicted DE across the study area using unstandardized estimates of the covariates included in the top model, creating one model of the forage available to elk during late summer.

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

We used a generalized linear model with the average daily DE to which individuals had access 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 DE to which residents, intermediates, and migrants had access each day to assess trends in relative access to nutrition throughout late summer. To compare inferences based on categorical and continuous classifications of migratory behavior, we examined the relationship between the predicted DE 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 in which resident, intermediate, and migratory individuals 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 compare models that included and did not include migratory status as the explanatory variable to determine whether

migratory behavior was important in explaining the number of days an individual had access to each category of forage quality.

RESULTS

Nutritional Quality of Vegetative Communities

We sampled 34 forage species in 5 phenology stages to estimate 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 DE. 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). 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 landcover types ($P=0.03$ for mesic forests burned within 5 years; $P=0.02$ for mesic forests burned 6–15 years prior; $P<0.01$ for remaining 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 comprised 26.3% and 21.6% of the population in 2014 ($n=38$) and 2015 ($n=37$), respectively. Intermediates comprised 47.4% and 51.4% of the population in 2014 and 2015, respectively. Migrants comprised 26.3% and 27.0% of the population in 2014 and 2015, respectively. We

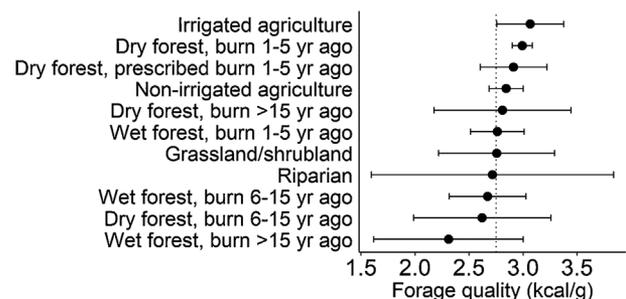


Figure 1. Mean forage quality (kcal of digestible energy/g of dietary forage) available to elk in 11 vegetative communities in the North Sapphire Mountains, Montana, USA, summer (Jul–Aug) 2014 and 2015. The dotted vertical line represents the quality of forage considered adequate to support survival and reproductive needs of adult female elk, based on studies of other populations (Cook et al. 2004). Error bars represent 95% confidence intervals.

did not observe any switching between migratory and resident behaviors for individuals with 2 years of location data ($n = 34$), although we observed residents and migrants switching to or from intermediate behaviors between years ($n = 11$ and $n = 7$, respectively). Five elk died during the study ($n = 2$ residents, $n = 3$ intermediates) because of 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 $29.2 \pm 20.3 \text{ km}^2$ for migrants, $58.5 \pm 19.1 \text{ km}^2$ for intermediates, and $67.2 \pm 25.4 \text{ km}^2$ 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 (Fig. 2). The average elevation at which each behavior group was located during late summer was $1,690 \pm 197 \text{ m}$ for migrants, $1,561 \pm 211 \text{ m}$ for intermediates, and $1,410 \pm 148 \text{ m}$ 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 km to 15.5 km.

Access to Nutrition Across Migratory Behaviors

The top model predicting DE across the study area during late summer included landcover type, slope, canopy cover, solar radiation, and elevation as covariates ($r^2_{\text{adj}} = 0.26$). The model indicated forage quality decreased with elevation and canopy cover and increased with solar radiation and slope. Approximately 55% ($n = 1,943$) of GPS-collar locations were recorded in areas predicted to provide adequate ($\geq 2.75 \text{ kcal/g}$) forage quality, 43% ($n = 1,531$) were in areas of marginal ($2.40\text{--}2.75 \text{ kcal/g}$) forage quality, and 2% ($n = 67$) were in areas of poor ($\leq 2.40 \text{ kcal/g}$) forage quality. On average, residents accessed areas predicted to provide $2.84 \pm 0.15 \text{ kcal/g}$ (range = $2.34\text{--}3.14$), intermediates accessed areas providing $2.77 \pm 0.18 \text{ kcal/g}$ (range = $2.15\text{--}3.09$), and migrants accessed areas providing

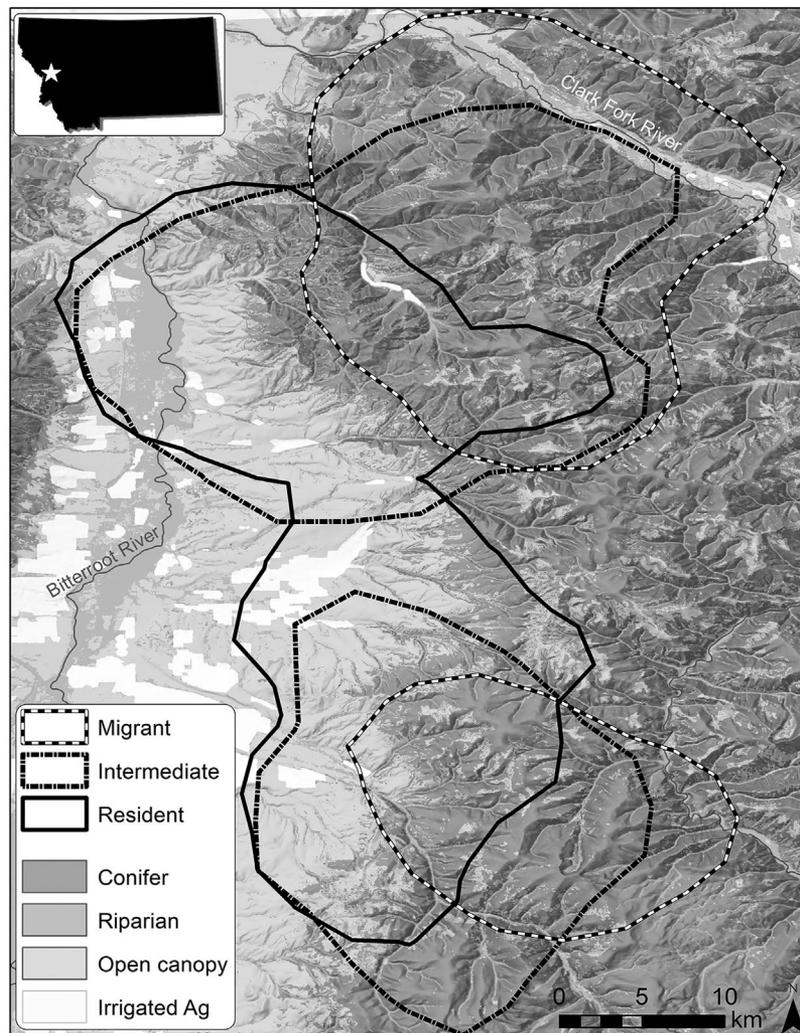


Figure 2. Aggregated group home range areas used by resident, intermediate, and migratory elk during late summer (Jul–Aug) in the North Sapphire Mountains, Montana, USA, 2014–2015. Migrants tended to use higher-elevation coniferous areas that did not include irrigated agricultural (Ag) land.

2.66 ± 0.15 kcal/g (range = 2.18–3.06) of DE daily during late summer.

Average access to nutrition decreased across the continuum from residency to migration (Fig. 3). Migrants had access to lower forage quality than residents or intermediates ($P < 0.001$ in both cases) during late summer; access to forage quality differed to a lesser degree 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. Daily access to nutrition for migrants showed a seasonal decline, whereas resident and intermediate daily access to nutrition exhibited stable or increasing trends (Fig. 4). Residents used irrigated agricultural areas an average of 30 ± 8 days during the 45-day late summer period, compared to 20 ± 14 days for intermediates and 2 ± 4 days for migrants.

Migratory behavior explained 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 behavior did not play a strong role in explaining 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 residents and intermediates ($P < 0.001$ in both cases). Residents and intermediates differed little 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. Migrants had access to marginal forage quality for more days than residents ($P < 0.01$) and intermediates ($P = 0.05$), and 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

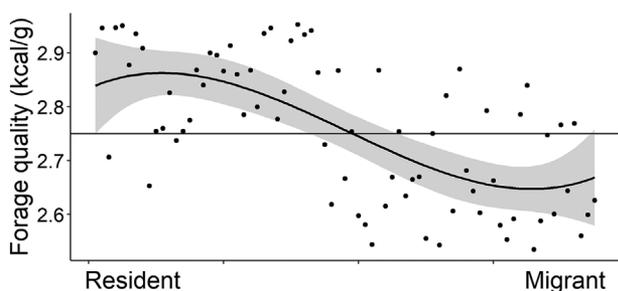


Figure 3. The average quality of forage (kcal of digestible energy/g of available forage) to which adult female elk had access during late summer (Jul–Aug) decreased with increasing strength of migratory behavior in the North Sapphire Mountains, Montana, USA, 2014–2015. The horizontal line represents 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). The shaded area illustrates the 95% confidence interval.

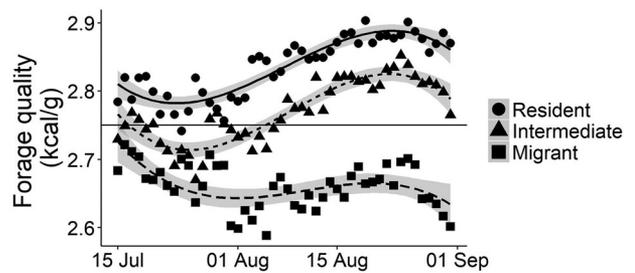


Figure 4. Daily forage quality (kcal of digestible energy/g of available forage) to which resident, intermediate, and migratory elk in a partially migratory population had access during late summer (Jul–Aug) in the North Sapphire Mountains, Montana, USA, 2014–2015. The horizontal line represents the 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). The shaded area illustrates the 95% confidence interval.

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 access to equivalent nutrition, 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 the nutrition accessed by elk that exhibited 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 <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 reduce survival of adult females but may result in reduced fecundity or recruitment for migrants. In contrast to residents and intermediates, 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); 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). 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 frequency of resident behavior to increase under 1 of 2 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 recruit fewer individuals into the migratory portion of the population.

Alternatively, because the size of a home range is typically inversely related to its fitness benefits (Mitchell and Powell 2007, Owen-Smith et al. 2010), the relatively small summer home ranges of migrants suggest that 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, for example by selecting high-quality forage plants at spatial scales finer than we evaluated (Cook et al. 2016). Further, migrants could benefit from lower conspecific density and therefore reduced competition for nutritional resources. Our results suggest that residents experienced higher conspecific density. Although size of aggregated summer home ranges and total numbers of elk were very similar for residents and migrants, individual home ranges of residents were much larger than those of migrants, implying residents experienced 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 for either reason the 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 DE 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 of late summer nutrition captured forage quality as perceived by an elk.

We focused our analysis on the late summer time period because of 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 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 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. 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 access to nutrition.

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