

Supplemental feeding alters migration of a temperate ungulate

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Abstract. Conservation of migration requires information on behavior and environmental determinants. The spatial distribution of forage resources, which migration exploits, often are altered and may have subtle, unintended consequences. Supplemental feeding is a common management practice, particularly for ungulates in North America and Europe, and carryover effects on behavior of this anthropogenic manipulation of forage are expected in theory, but have received limited empirical evaluation, particularly regarding effects on migration. We used global positioning system (GPS) data to evaluate the influence of winter feeding on migration behavior of 219 adult female elk (*Cervus elaphus*) from 18 fed ranges and 4 unfed ranges in western Wyoming. Principal component analysis revealed that the migratory behavior of fed and unfed elk differed in distance migrated, and the timing of arrival to, duration on, and departure from summer range. Fed elk migrated 19.2 km less, spent 11 more days on stopover sites, arrived to summer range 5 days later, resided on summer range 26 fewer days, and departed in the autumn 10 days earlier than unfed elk. Time-to-event models indicated that differences in migratory behavior between fed and unfed elk were caused by altered sensitivity to the environmental drivers of migration. In spring, unfed elk migrated following plant green-up closely, whereas fed elk departed the feedground but lingered on transitional range, thereby delaying their arrival to summer range. In autumn, fed elk were more responsive to low temperatures and precipitation events, causing earlier departure from summer range than unfed elk. Overall, supplemental feeding disconnected migration by fed elk from spring green-up and decreased time spent on summer range, thereby reducing access to quality forage. Our findings suggest that ungulate migration can be substantially altered by changes to the spatial distribution of resources, including those of anthropogenic origin, and that management practices applied in one season may have unintended behavioral consequences in subsequent seasons.

Key words: carryover effects; elk; feedgrounds; migration; nutritional condition; partial migration; plant phenology; stopover; supplemental feeding; ungulates; Wyoming.

INTRODUCTION

Long-distance migration is a phenomenon observed across numerous taxa that allows individuals to exploit spatiotemporal variation of resources and potentially reduce the risk of predation (Fryxell and Sinclair 1988). This strategy, however, is diminishing across the globe (Wilcove and Wikelski 2008) even in the midst of calls for increased protection. Numerous factors threaten the persistence of long-distance migration, including anthropogenic barriers (e.g., roads), habitat loss, and changes in resource distribution (e.g., agricultural fields, supplemental feeding, and climate change [Bolger et al. 2008, Middleton et al. 2013, Sawyer et al. 2013]). Conserving

animal migration amid rapidly changing landscapes requires a better understanding of the causes and consequences of seasonal movements.

Migration evolved as a means to exploit seasonally available resources (Fryxell and Sinclair 1988). For example, migratory ungulates access high-quality forage because plants in early phenological stages are high in protein and energy, but low in fiber, making them easy to digest (Albon and Langvatn 1992). Access to high-quality forage increases body fat of migrants, potentially enhancing demography and population growth (Mysterud et al. 2001, Hebblewhite et al. 2008). Ungulates in temperate regions migrate seasonally as cold temperatures and deep snow force ungulates down to lower elevations in autumn; in spring, ungulates move up in elevation, following nutritious new growth (Albon and Langvatn 1992, Parker et al. 2009).

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Because access to seasonal resources is a key driver of migration (Fryxell and Sinclair 1988, Hebblewhite et al. 2008), modifying resource availability on seasonal ranges holds the potential to alter migration. Land management practices can increase the year-round forage benefit of winter ranges. For example, winter habitat enhancements and access to hay fields increased numbers of resident elk in Alberta, Canada (Hebblewhite et al. 2006). Supplemental feeding in winter delayed spring migration of mule deer (*Odocoileus hemionus*) in Utah, USA (Peterson and Messmer 2007). Meanwhile, climate change is altering the timing and length of forage production in many high-elevation mountain ranges (Middleton et al. 2013). Alterations to forage resources are increasingly common, but their influence on migration remains poorly understood.

Nutritional condition is the mechanism by which resources are integrated across seasons, with gains and losses in one season carrying over to subsequent seasons (Monteith et al. 2013). Strong carryover effects have been documented in numerous taxa, providing the mechanism for altered resource levels on one seasonal range to influence the year-round behavior of migrants. Many foraging decisions are state dependent (Parker et al. 2009) as are migratory behaviors (Monteith et al. 2011). For example, avian migrants in better condition are able to migrate and arrive earlier on summer range, which enhances reproductive success and survival (Marra and Holberton 1998). Mule deer in the Sierra Nevada of California, USA, that were in good nutritional condition likely enhanced nutrient gain by remaining on summer ranges longer in autumn (Monteith et al. 2011). Anthropogenic factors that alter forage resources may have unintended carryover effects by altering nutritional condition and behavior in subsequent seasons (Dean et al. 2004, Parker et al. 2009).

Supplemental feeding is a common management practice utilized around the world on numerous taxa (Appendix A: Table A1) and represents a land-use change that alters resource distribution with a potential carryover effect on migratory behavior (Sahlsten et al. 2010). There is a long history of feeding ungulates during winter in Europe and North America, with common goals to reduce private property damage, and maintain or increase herd size by enhancing overwinter survival despite habitat loss through increased anthropogenic development and agriculture (Smith 2001, Putman and Staines 2004). While individual body condition and demography can be enhanced by winter feeding (Peterson and Messmer 2007), little is known about the potential consequences to year-round foraging strategies, including migratory behavior.

Among the most intensive ungulate feeding operations are those of elk in Wyoming, USA, conducted by the Wyoming Game and Fish Department (WGFD) and the United States Fish and Wildlife Service. Large numbers of elk (>20 000) have been fed baled, loose-leaf hay and alfalfa pellets at 23 sites known as feedgrounds,

during every winter (generally December–April) since 1912 (Appendix A: Plate A1; Smith 2001). Wyoming feedgrounds were established in locations that serve to intercept elk migrating down from high-elevation public lands before they reach private lands in valley bottoms where they can damage stored crops and potentially transmit diseases to domestic livestock; brucellosis is of particular concern (Cross et al. 2007, Scurlock and Edwards 2010). The long-term feeding of migratory elk in Wyoming, not all of which attend feedgrounds, has essentially created a landscape-scale experiment in the alteration of seasonal forage resources and its' impact on migration. There was concern, however, that this anthropogenic manipulation of forage resources, as well as other impacts (e.g., hunting, development), would severely alter elk migration patterns (Allred 1950). We know that some traditional routes have been lost (Allred 1950, Cromley 2000), but an evaluation of the impacts to other aspects of migration are lacking.

We evaluated the influence of augmented forage resources during one season on the year-round migratory behavior of North American elk, a migratory ungulate typical of temperate regions. Because resources are integrated across seasons (Marra et al. 1998, Monteith et al. 2013), we hypothesized that enhancing winter resources through supplemental feeding would carry over to alter the migration ecology of elk that attend feedgrounds. We used a GPS data set of elk movements from 18 feedgrounds and 4 native winter ranges (representing 280 elk-years; Fig. 1) to evaluate the influence of winter feeding on migration. We predicted that elk attending feedgrounds (hereafter referred to as "fed") would employ a different migratory tactic than elk utilizing native winter range (hereafter referred to as "unfed"). We hypothesized that unfed elk would exit winter in poorer nutritional condition, and subsequently adjust their migratory behavior to maximize access to high-quality forage. We also expected that migration distances of unfed elk would be greater than fed elk, because feedgrounds act to shortstop migration.

STUDY AREA AND METHODS

We evaluated the influence of seasonal resource alteration on the migration ecology of elk in the Rocky Mountains of western Wyoming at the southern extent of the Greater Yellowstone Ecosystem (Fig. 1). The study area encompassed the Wind River, Gros Ventre, Wyoming, Salt, and Snake River mountain ranges, with feedgrounds located primarily in the foothills. Fed elk were sampled from 18 of the 22 state-run feedgrounds (Fig. 1; Appendix A: Table A2) to achieve a representative distribution across the study area. Feedground operation commences at the discretion of the feeder when elk begin to congregate at the feeding site and cessation typically occurs once most elk have departed. Winter feeding is known to have physiological (Schmidt and Hoi 2002) and demographic (Tarr and Pekins 2002) effects on ungulates, and thus represents a profound and

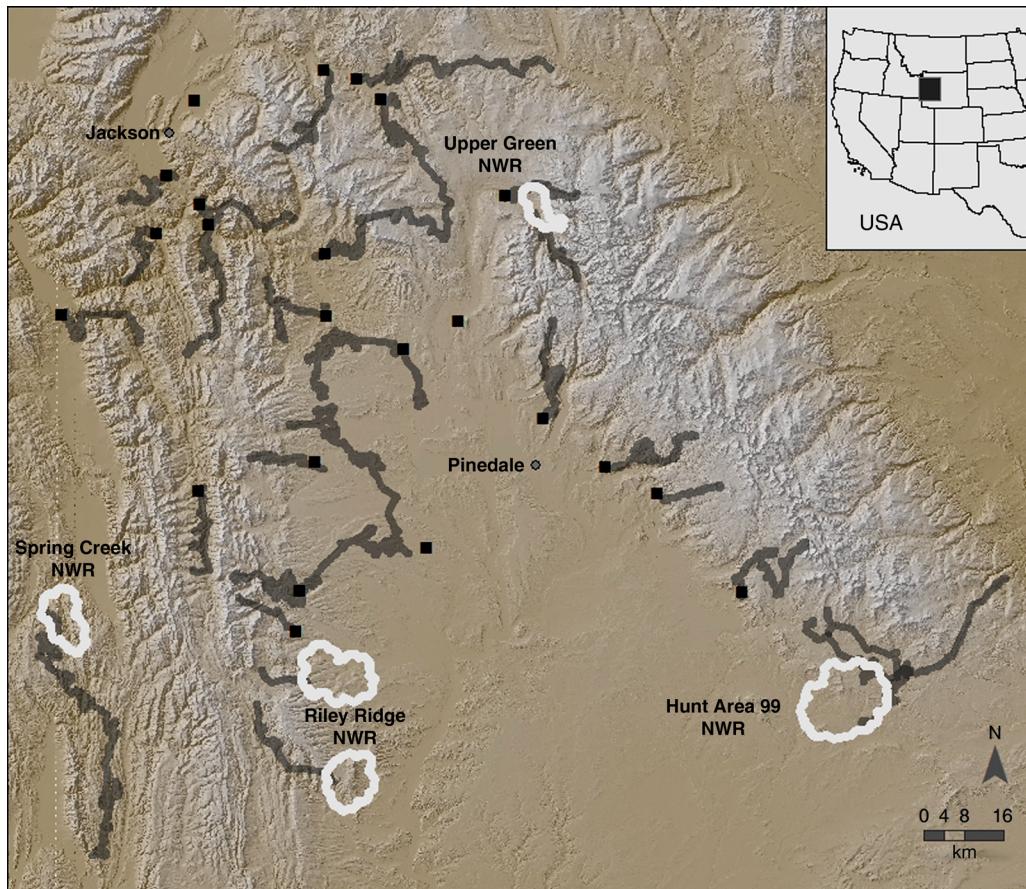


FIG. 1. Study area in the Rocky Mountains of western Wyoming, USA. Elk were captured and monitored on feedgrounds (black squares) and adjacent native winter ranges (NWR; white polygons). Examples of common migration routes are depicted with dark gray lines.

consistent alteration of resources that occurs during only one season. Unfed elk were sampled from four native winter ranges: the northern and southern end of the Wind River Mountain range, the Gannett Hills in the Salt Mountain range and the southern portion of the Wyoming range (Fig. 1; Appendix A: Table A2). Movement data from unfed elk in the southern portion of the Wyoming range was collected from 2009 to 2011 in a separate study. Elevations ranged from 1700 to 3500 m. Vegetation was typical of the Intermountain West with summer ranges of mixed conifer, aspen (*Populus tremuloides*), and meadows. Winter ranges of fed elk included herbaceous species, shrubs, conifer, and agriculture, while the winter range of unfed elk was primarily riparian areas with willow (*Salix* sp.), sagebrush–steppe, aspen, and conifer. Regional climate is typified by long, cold winters and brief, warm summers (Appendix A: Fig. A1).

Elk capture

During January through March in 2007–2011 we captured adult (>1 year old), female elk at 18 feedgrounds via corral traps or ground darting and chemical

immobilization (Scurlock and Edwards 2010; Appendix A). For unfed elk, we captured adult females via helicopter net-gunning (Leading Edge Aviation, Lewiston, Idaho, USA) during January 2010 and March 2011 on three native winter ranges. We fit elk with GPS radio collars (Lotek Wireless, Newmarket, Ontario, Canada) programmed to record locations every 30 (fed elk) or 60 (unfed elk) minutes for one (fed elk) or two (unfed elk) years. Automatic drop-off mechanisms allowed collar retrieval in the field. We removed one residual upper canine from most elk for age determination by cementum annuli analysis, and assigned all elk to one of three age classes: 2–5, 6–9, or ≥10 yr. All elk were handled in accordance with protocols approved by the University of Wyoming Institutional Animal Care and Use Committee and following recommendations of the American Society of Mammalogists (Sikes et al. 2011).

Movement strategy

Data were split by year, so that unfed elk collared for two years or fed elk collared twice represented two elk-years. Movement strategy (i.e., migration, residency, etc.) was allowed to vary between years, treating every

elk-year as independent with regard to the individual's behavior. Although some individuals ($n=40$ individuals; 18%) in our sample were monitored for two years, we assumed this repeated sampling did not have an undue influence on our analysis (Monteith et al. 2011), because migration timing of individuals can fluctuate widely between years due to annual variation in weather. We initially employed movement models using net squared displacement (NSD) developed by Bunnefeld et al. (2011) in an effort to identify movement strategies and quantify migration parameters of individual elk (Bischof et al. 2012, Singh et al. 2012). The models, however, failed to converge for many elk or clearly misidentified movement strategy for others. Therefore, we visually inspected NSD profiles and movement patterns in GIS to categorize movement strategies as: migrant, disperser, resident, and other. We classified an elk as a migrant if it had distinct, nonoverlapping seasonal ranges with localization, and returned to the same winter range (Cagnacci et al. 2011). In contrast, a disperser migrated but returned to a different winter range. Resident elk exhibited overlapping seasonal ranges and lacked a seasonal movement event. Elk were classified as "other" if they exhibited ambiguous or multi-strategy patterns. We used a chi-square test to compare migration tendencies of fed vs. unfed elk. Only migrant and disperser elk were used for subsequent analyses of migration pattern. Elk that died or dropped their collars prior to completing autumn migration ($n = 30$) were excluded from analyses of autumn migration.

Timing of migration

Seasonal range polygons were created from elk locations using 90% contours derived from Brownian Bridge Movement Models using the BBMM package (Nielson et al. 2012) in R (R Development Core Team 2012). Departure from one range was identified as the date an elk made directed movement away from one seasonal range and did not return, whereas arrival date was identified when elk ceased directed movement and localized on the other seasonal range. If an elk made a directed movement away from one seasonal range, localized for a period of time, but then continued migrating to a higher elevation and localized again, we considered the first break to be a stopover. We calculated migration distance as a simplified Euclidean trajectory using the Ramer-Douglas-Peucker algorithm in the rgeos package (Bivand and Rundell 2012) with a radius of 1 km. Given a set of sequential locations, the algorithm calculates a length using fewer locations given a specified buffer radius, within which locations are consolidated as one. Starting and ending points were the centroids of winter and summer range polygons for each elk.

Migration modeling

Many of the migration metrics, such as date of departure from winter range and date of arrival to

summer range within the same year, lack independence. Therefore, we used principal component analysis (PCA) of migration metrics to derive independent, composite variables representing migration (Appendix B: Table B1). We then performed a multivariate analysis of variance (MANOVA) on principal components 1–4 to assess the difference in migration pattern between fed and unfed elk (Zar 1999). Following a significant main effect in MANOVA, we used canonical correlation analysis to identify the factors primarily responsible for that significance, and included those variables in a separate ANOVA, with the same main effect. Doing so allowed us to evaluate the general migration patterns of fed and unfed elk, which we then used to guide subsequent analyses.

The PCA analyses indicated general differences in arrival to and departure from summer range between fed and unfed elk; therefore, we used time-to-event modeling to evaluate the influence of environmental and individual variables on time of arrival to and departure from summer range in Program MARK (Fieberg and Delgiudice 2008, Monteith et al. 2011). Doing so enabled us to account for effects of weather, plant phenology and feedground operation (i.e., dates elk were being fed) that may confound a direct comparison of fed and unfed migration patterns. We buffered the migration window for modeling to include the migration event (i.e., relocation points) of all elk; spring encounter histories occurred between 1 March and 31 July, and autumn encounter histories occurred between 1 August and 31 December. We used known-fate models with the logit-link function to estimate the daily probability of not migrating as a function of the variables; we then subtracted the result from one to calculate the daily probability of migrating (Fieberg and Delgiudice 2008, Monteith et al. 2011).

Predictor variables

We included fed and unfed elk as a categorical covariate, and feedground operation as a time-dependent variable. We obtained daily weather variables for both winter and summer ranges of individual elk from DayMET, an interpolated and extrapolated data set of daily meteorological observations that produces gridded (1×1 km) estimates of daily weather, including temperature ($^{\circ}\text{C}$; maximum, minimum, average), precipitation (mm/d), and snow water equivalence (SWE; Thornton et al. 2012). We included metrics of plant phenology, which are highly influenced by and correlated with snow cover and have been shown to drive spring migration (Monteith et al. 2011, Bischof et al. 2012). To estimate plant phenology, we used an 8-day composite of moderate resolution imaging spectroradiometer (MODIS) data from which normalized difference vegetation index (NDVI) was calculated at 250-m² resolution (NASA Land Processes Distributed Active Archive Center [LP DAAC] 2012). Daily NDVI values were estimated using linear interpolation between

weekly values for the entire winter and summer range of each elk. In addition to the absolute daily value of weather and NDVI, we also calculated a metric of change based on the difference between a daily value and the average during the previous 14 days, because ungulate migration is often initiated by changing environmental conditions (Monteith et al. 2011). Initial predictor variables included both absolute and relative change for all weather metrics and NDVI on both winter and summer range, migration distance, feedground operation (last [Spring] and first [Autumn] date of feeding), elevation of summer range, age category, capture area (categorical), and a status variable of fed vs. unfed. We also included year as a variable to account for any interannual variation in migration that was not adequately explained by our environmental predictor variables.

Model selection

We used Pearson's correlation coefficients to detect pairs of collinear predictor variables that could not be included in the same model ($|r| > 0.6$; Long et al. 2009). All variables on summer range were highly correlated with variables on winter range (average $|r| = 0.73$), and since we were modeling migration patterns with respect to summer range (summer arrival and departure), we retained only summer range variables. For arrival to summer range, weather and NDVI were highly correlated (all $|r| > 0.68$) and we chose to retain only NDVI because spring plant phenology is a well-known driver of ungulate migration (Albon and Langvatn 1992). For modeling departure from summer range there was a similar correlation issue and we chose to drop NDVI and retain weather variables based on their relevance from previous research (Fieberg et al. 2008). Collinearity issues between daily measures and the metric of relative change for both minimum temperature and SWE resulted in the retention of daily measures only.

We used an information theoretic approach for model selection and to evaluate variable importance, by calculating Akaike information criterion corrected for small sample sizes (AIC_c) and Akaike weights (w_i) for each model (Burnham and Anderson 2002). Before formal model selection, we fit a global model that included all uncorrelated predictor variables and relevant interactions (Appendix B: Table B2). We then excluded variables that were clearly uninformative (i.e., 85% confidence intervals overlapped zero) from further analyses (Arnold 2010). We assessed over-dispersion using the new global model by adjusting the variance inflation factor, $\hat{\epsilon}$ and investigating any changes in β estimates, model rank or AIC weight; no changes were detected and we concluded that the global model was not over-dispersed (Burnham and Anderson 2002). Next, we modeled all possible combinations of those remaining predictor variables and examined models within $2 \Delta AIC_c$ units of the top model; models $\leq 2 \Delta AIC_c$ units from the top model with at least one

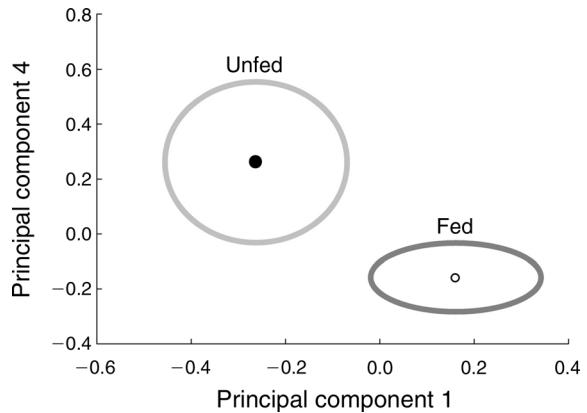


FIG. 2. Principal component 1 vs. principal component 4. Ellipses outline 95% of the data. Principal component 1 represented arrival to, departure from and duration on summer range, with limited influence of duration on spring and autumn stopovers. Principal component 4 consisted of migration distance and arrival on winter range.

additional parameter and essentially the same maximized log likelihood were deemed noncompetitive and eliminated from further consideration (Burnham and Anderson 2002, Long et al. 2009). To evaluate specific seasonal patterns and depict relationships between a specific predictor variable and a response variable, we used the top model and modeled expected effects of the variable of interest within the observed range, while holding other variables constant (Monteith et al. 2013).

RESULTS

Movement strategy and migration pattern

We evaluated movement during 280 elk-years (116 unfed, 164 fed) from 219 individual elk collared during 2007–2011 to assess movement strategies. We identified 204 migrants (65% unfed, 79% fed), 31 dispersers (13% unfed, 10% fed), 37 resident (21% unfed, 7% fed), and 8 other (1% unfed, 4% fed) patterns. Movement strategies between fed and unfed elk differed ($\chi^2 = 16.29, n = 280, df = 3, P = 0.001$), with 9.2 more migrants and 9.7 fewer residents for fed elk than expected compared with unfed elk. We documented 236 spring (90 unfed, 146 fed) and 207 autumn (75 unfed, 132 fed) migration events. Stopovers were used by a greater percentage of fed elk than unfed elk during both spring (56% vs. 48%) and autumn migrations (49% vs. 42%). Migration distance was significantly shorter for fed elk (35.4 ± 2.3 km) than unfed elk (54.6 ± 5.9 km). While there is high variation among individuals, the general migration patterns of fed and unfed elk, based on principal components 1–4 differed significantly ($F_{4,191} = 4.72, P = 0.0012$); canonical correlation analysis indicated the significant effect of fed status was attributed primarily to PC1 and PC4 (Fig. 2). Separate one-way ANOVAs for PC1 and PC4 indicated that fed elk spent less time on summer range by arriving later and departing earlier than unfed elk (PC1; $F_{1,194} = 8.58, P = 0.0038$), and that fed elk

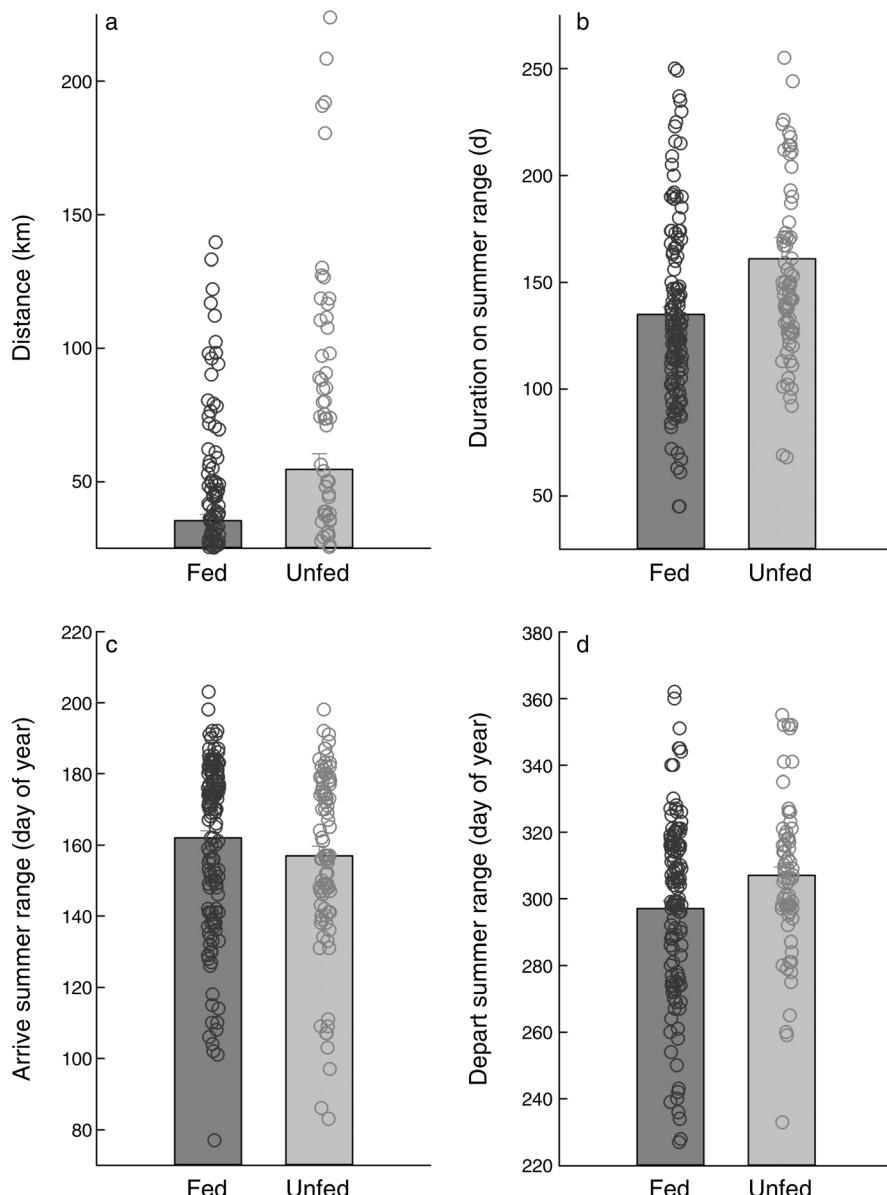


FIG. 3. Summary statistics (mean + SE) overlaid with individual data points for fed (dark gray circles) and unfed (light gray circles) elk for spring migration (a) distance, (b) duration on summer range, and (c) arrival and (d) departure from seasonal ranges (day of year), western Wyoming, USA, 2007–2011.

migrated shorter distances and arrived back on winter range earlier than unfed elk (PC4; $F_{1,194} = 8.52$, $P = 0.0039$; Fig. 3). Although fed and unfed elk departed and returned to winter range on similar dates, on average, fed elk migrated 19.2 km less, arrived to summer range 5 days later, resided on summer range 26 fewer days and departed 10 days earlier than unfed elk. Consequently, fed elk used stopovers for 11 more days in spring and 13 more days in autumn than unfed elk (Appendix B: Table B3).

Arrival to summer range

Following initial variable assessment of models for arrival to summer range, we removed the following variables because their 85% CIs included zero: age category, year, fed/unfed status, capture area, elevation, migration distance and relative change for NDVI. The new global model included daily NDVI, feedground operation (last [spring] and first [autumn] date of feeding), and an interaction between NDVI and feedground operation. That global model also was the top model, receiving 93.4% of the Akaike weight. The model

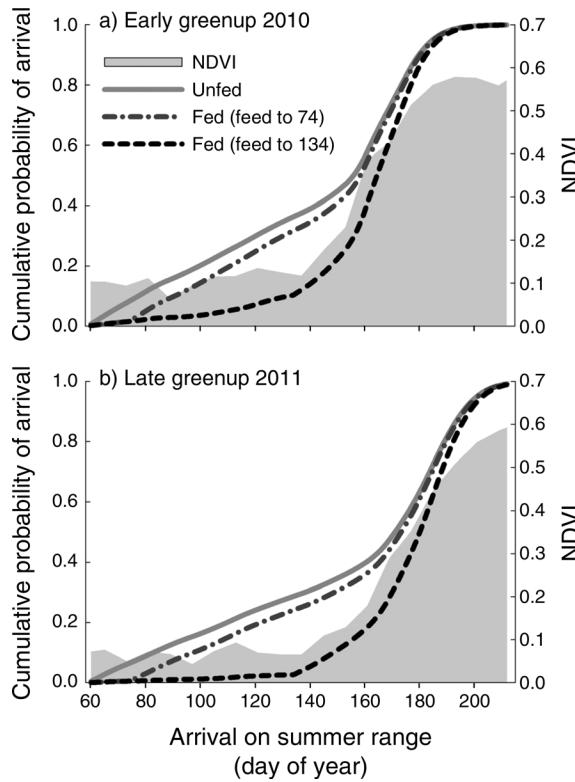


FIG. 4. Model estimates of the cumulative probability of arrival to summer range relative to Julian date for unfed and fed elk under two scenarios of feedground operation (end on day of year 74 and 134), and average daily normalized difference vegetation index (NDVI) relative to day of year during two years with contrasting rates of increase in NDVI: (a) early and (b) late.

indicated a positive response to changes in NDVI (estimate $\beta = 7.25$, 95% CI = 6.58–7.92), a negative response to feedground operation ($\beta = -4.33$, 95% CI = -6.87 to -1.79), and the positive interaction term between NDVI and feedground ($\beta = 25.96$, 95% CI = 7.57–44.35) indicated that responsiveness of elk to changes in NDVI differed between elk that were being fed and those that were not. Notably, the status variable of fed vs. unfed elk was not significant ($\beta = 0.16$, 95% CI = -0.12–0.43), but the time-specific feedground operation variable was highly significant indicating that migration of fed elk was delayed while being fed. Following cessation of feeding, however, fed elk functioned much like unfed elk, whose daily probability of migration increased with NDVI (Fig. 4). Feeding had an overriding influence on the positive effects of NDVI until NDVI reached a threshold value of 0.17, at which point our model indicated fed elk became responsive to NDVI, even if feedgrounds were still operating, and began to arrive on summer range. During early green-up, when NDVI values increased above that threshold value before the end of feeding, fed elk arrived on summer range earlier than in years with late green-up (see day of year 140 in Figs. 4a, b, and 5). Model

estimates of the daily probability of arrival relative to day of year when feedground operation ceased indicated that arrival of fed elk to summer range was suppressed by feedground operation, particularly during years when plant phenology was delayed (Fig. 5).

Departure from summer range

Initial variable reduction (based on 85% CIs) for models of departure from summer range removed the following variables: age category, year, capture area, migration distance, and feedground operation. This resulted in a new global model with the following predictor variables: fed/unfed status, elevation, daily minimum temperature, daily precipitation, daily SWE, and an interaction between fed/unfed status and daily minimum temperature. Following the evaluation of all possible combinations of those variables, we initially considered two models that had 72.4% and 27.4% of the AIC_c weight. The second model (model 2; $\Delta\text{AIC}_c = 1.94$) had daily SWE as an additional variable, but had approximately the same maximum log likelihood as the top model, and the 85% CI for SWE overlapped zero. Therefore, we deemed model 2 noncompetitive and removed it from consideration. The daily probability of departing summer range was influenced by elevation, fed/unfed status and changes in weather severity, specifically decreasing minimum temperature ($\beta = -0.15$, 95% CI = -0.17 to -0.12) concurrent with increasing precipitation ($\beta = 0.09$, 95% CI = 0.07–0.11; Fig. 6). Migratory pulses were observed following these weather events, but fed elk were more responsive ($\beta = 0.40$, 95% CI = 0.04–0.76) with a larger proportion departing summer range than unfed elk (for raw data pattern, see Appendix C: Fig. C1). The interaction between fed status and minimum temperature was negative ($\beta = -0.04$, 95% CI = -0.08 to -0.01), indicating a stronger migratory response of fed elk to

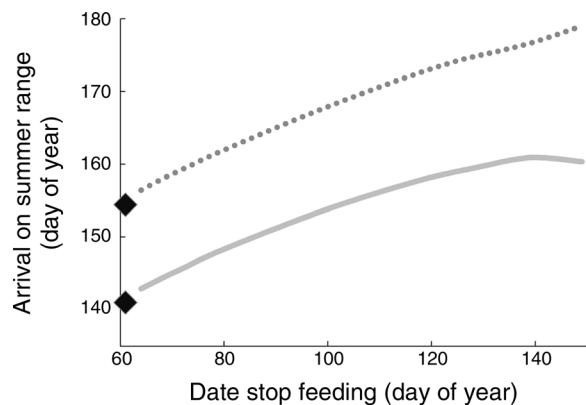


FIG. 5. Predicted mean arrival on summer range from model estimates of the daily probability of arrival relative to Julian date when feedground operation ceased during two years with contrasting timing of increase in NDVI: early, 2010 (solid line) and late, 2011 (dotted line), Wyoming, USA. Black diamonds represent the average arrival date for unfed elk.

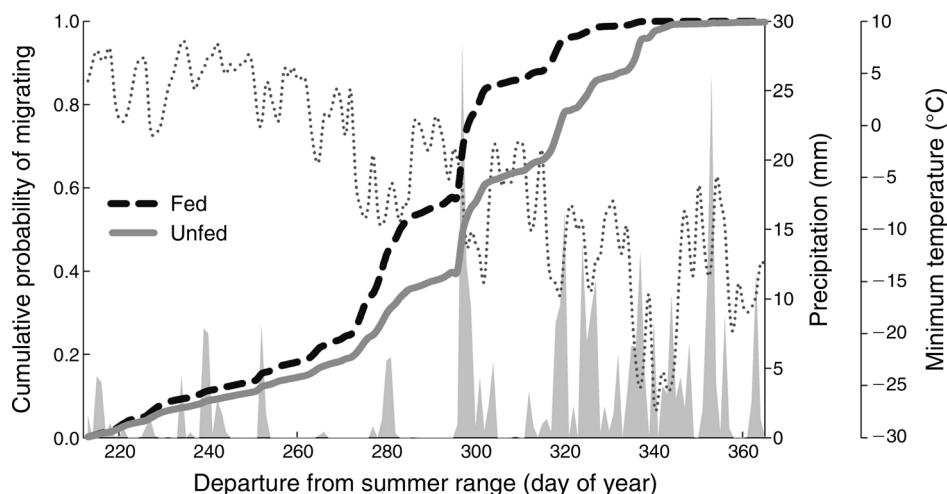


FIG. 6. Cumulative daily probability of departure from summer range for fed and unfed elk (dashed and solid lines, respectively) relative to day of year during a cold and wet autumn, Wyoming, USA. Dotted line represents minimum temperature ($^{\circ}\text{C}$) and gray shading represents precipitation (mm). Migratory pulses coincided with decreasing temperature and increasing precipitation (e.g., day of year 280, 295).

cold temperatures than unfed elk. Elevation also contributed to the daily probability of departure, with elk at high elevation departing earlier ($\beta = 0.95$, 95% CI = 0.44 to 1.47).

DISCUSSION

We observed consistent differences in the migratory patterns of fed and unfed elk (Figs. 2 and 3). Differences in timing were driven by an altered response to the environmental cues of migration, with fed elk being less responsive to plant green-up in spring and more responsive to cold temperatures and precipitation events in autumn than unfed elk. Overall, these findings suggest that, at least in this system, supplemental feeding on winter range (the non-growing season) alters the extent to which migratory elk exploit available resources during the growing season. We infer this to be partly caused by carryover effects of winter supplemental feeding, as departure from winter range was similar among fed and unfed elk, but arrival to, and departure from, summer range was not. Our study also implies that management strategies meant to alleviate resource shortages in one season (e.g., winter) may have a lasting influence on the year-round foraging behavior of migratory species.

Migration was the dominant movement strategy for both fed and unfed elk, as expected for a temperate ungulate (Mysterud et al. 2001). Although winter feeding in Wisconsin led to a decrease in the proportion of migratory white-tailed deer (*Odocoileus virginianus*; Lewis and Rongstad 1998), we did not detect an increase in residency among fed populations. Previous work has shown that the incidence of migration can be conditional and dependent upon weather severity, topographic variability, and local density on a seasonal range

(Cagnacci et al. 2011, Mysterud et al. 2011). Circumstances may not facilitate fed elk becoming resident, because feedgrounds offer limited cover, are on public lands that receive heavy use (e.g., hunting), and often are adjacent to private property where tolerance for elk is low. Importantly, our findings indicate that although winter feeding has changed patterns of elk migration, it has not yet altered the propensity to migrate.

Both fed and unfed elk interrupted their migrations with one or two stopovers, but stayed at those stopovers for extended periods of time ($\bar{x} \geq 34$ days). Such extended stays are at odds with the classic notion of stopovers as brief respites (i.e., <1 week) used for recuperation (McGuire et al. 2012) or refueling (Bayly et al. 2013). Mule deer adjacent to our study area used multiple stopovers, but averaged just 3.6 days per stopover (H. Sawyer, personal communication). While all elk departed winter range at approximately the same time, fed elk tended to linger nearby, often traveling <5 km from the feedground. Such long stopovers may reduce the risk of being caught in late-winter storms or deep snow by delaying arrival to summer range. For elk that are supplementally fed, stopovers may act more as transitional range that allows elk to escape a high-density winter range while maintaining close proximity to the feeding site.

That unfed elk migrated an average of 19.2 km farther than fed elk was expected, considering that feedgrounds were established along historical migration routes to intercept elk before reaching private land at lower elevation (Smith 2001). Historical records of elk migrations indicate that current patterns of migration were altered long ago by ranching, fencing, hunting and feedground establishment (Allred 1950, Cromley 2000). While efforts were made to push elk to feedgrounds

when they were first established, elk now typically arrive and stay of their own accord, indicating that the forage offered at feedgrounds has altered cultural patterns of migratory behavior.

Unfed elk responded more strongly to spring green-up, allowing them to arrive earlier on summer range compared to fed elk (Fig. 4). This suggests that unfed elk are tracking phenology and gaining access to newly emergent plant growth (Sawyer and Kauffman 2011, Bischof et al. 2012), while fed elk are delayed by winter feeding. Tracking phenological gradients in plant growth is critical because forage quality declines over summer as plants mature and senesce (Albon and Langvatn 1992, Tollefson et al. 2011). Delayed arrival of fed elk to summer range suggests that feedground use may cause elk to be mismatched with growing-season phenology of their forage.

In autumn, fed elk demonstrated a heightened sensitivity to daily changes in temperature and precipitation (Fig. 6), which are known to trigger autumn migration (Monteith et al. 2011). By leaving at the first sign of winter weather, fed elk minimize their risk of being caught at high elevation in deep snow and cold temperatures. Unfed elk appear to accept the risk and remain on summer range to prolong access to high-quality forage. Sawyer and Kauffman (2011) observed common use of autumn stopovers in mule deer and suggested that such behavior might reduce risk while prolonging access to quality forage, by allowing animals to slowly move down the mountain to safeguard against early season storms. Fed elk exited winter with slightly more body fat than unfed elk (Jones 2013), which may mean that fed elk can afford to employ a risk-averse strategy on summer range. On the other hand, fed elk likely have cultural knowledge of winter feeding, causing them to leave summer range early in pursuit of a reliable forage source. Ironically, this behavior could limit the full exploitation of forage during the growing season by fed elk, and may contribute to dependence on winter feeding, lengthening, and thus increasing, costs of feeding programs. Although hunting pressure can also influence the timing of elk migrations (Conner et al. 2001, Grigg 2007), refuges from hunting on winter range were rare in our study area. In addition, hunting pressure in this system is evenly distributed with similar start dates for all fed and unfed elk. Thus, we suspect that hunting pressure did not play a strong role in triggering autumn migration for elk in our study population.

Fed elk spent nearly a month (26 ± 3.6 days; mean \pm SE) less on summer range. This is a striking difference that may influence intake of quality forage. Plant quality is much higher when plants are young (Albon and Langvatn 1992), and even slight differences in diet quality over time can have multiplicative effects on energy reserves (White 1983, Cebrian et al. 2008). Indeed, access to quality forage in spring and early summer enhances autumn body mass and demography

in ungulates (Herfindal et al. 2006). Similar to our findings, semi-domestic reindeer (*Rangifer tarandus*) that were supplementally fed during winter did not respond to early plant phenology to migrate, and failed to increase their summer body mass as much as unfed reindeer (Ballesteros et al. 2013). While feedground attendance may buffer fed elk against drastic winter fat loss and starvation, reduced access to high-quality summer range may reduce their ability to capitalize on years of high forage production.

Our work indicates that winter feeding has carryover effects on foraging ecology and seasonal range use of elk that should be considered when evaluating this management action. Benefits of increased overwinter survival may be offset somewhat by decreased nutritional gain on summer range. Elk feeding in Wyoming is within the brucellosis endemic area, and prolonged time on winter or nearby transitional ranges may necessitate a reevaluation of cattle turn-out dates to reduce the risk of interspecific disease transmission. Our migration models indicate that earlier cessation of feedground operation would encourage fed elk to migrate and spend more time on summer range, thereby increasing access to high-quality forage and maximizing their distance from cattle. Shortening the feeding season also would reduce intraspecific disease transmission, because feedgrounds crowd elk and expose them to higher disease risk (Cross et al. 2007, Scurlock and Edwards 2010).

Conservation of migration is a concern worldwide, and while much attention has been paid to the threat of conspicuous barriers such as fences and roads (Bolger et al. 2008), very little research has addressed the consequences of landscape-level alteration of seasonal resources. In our study, alteration of forage resources through supplemental feeding on one seasonal range had clear, far-reaching consequences for elk migration, with effects on timing and seasonal range use that carried over between seasons. Just as migration is a behavioral strategy animals use to exploit seasonal variation in resources, anthropogenic factors that alter the availability of seasonal resources have the potential to disrupt migratory systems.

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is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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SUPPLEMENTAL MATERIAL

Appendix A

A table documenting the use of supplemental feeding around the world and supplemental study area information, including a picture of elk on a feedground in western Wyoming, additional capture area information, a climograph of the study area, and detailed method descriptions of elk chemical immobilization ([Ecological Archives A024-204-A1](#)).

Appendix B

Detailed description and tables for principal component analysis, migration modeling, and summary migration statistics ([Ecological Archives A024-204-A2](#)).

Appendix C

Figure showing the raw data for autumn migration in the study area during 2009 ([Ecological Archives A024-204-A3](#)).