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RESEARCH ARTICLE

Native forage mediates influence of irrigated agriculture on migratory behaviour of elk

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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 migratory behaviour are not well-understood.
2. We quantified associations between hypothesized drivers of partial migration and the likelihood of migration for individual ungulates that experienced a range of environmental conditions and anthropogenic influences.
3. We evaluated the effects of forage variation, conspecific density, and human land uses on migratory behaviour of 308 adult female elk in 16 herds across western Montana.
4. We found irrigated agriculture on an individual's winter range reduced migratory behaviour, 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 beneficial native 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 behaviour may decline as a result.

KEYWORDS
agricultural subsidy, *Cervus canadensis*, forage maturation, land use, migration, Montana, partial migration, ungulate

1 | 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 behaviour of ungulates across the world has been altered or lost in recent decades, spurring interest in understanding how behaviours may change in the future (Bolger, Newmark, Morrison, & Doak, 2008; Wilcove & Wikelski, 2008). Several studies contrast the fitness benefits of different behaviours in partially migratory populations to draw inference about potential future changes in ungulate behaviour (Hebblewhite & Merrill, 2011; Rolandsen et al., 2017; 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 behaviour 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.

Partial migration in ungulates is not expressed as a simple dichotomy of migration vs. residency; individual behaviours can fall along a continuum that also includes intermediate migratory behaviours (e.g., moving short distances or for short times, or making several movements within the same season). Despite widespread recognition of these intermediate behaviours (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 behavioural extremes. As a result, we lack a clear understanding of how the factors that influence migratory behaviour of ungulates produce the full range of behaviours 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; Hebblewhite, Merrill, & McDermid, 2008), 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 behaviours when forage varies less predictably. Because behaviours of ungulates can range from residency to migration even where individuals experience similar variations in forage, the forage maturation hypothesis alone cannot explain the full range of migratory behaviours observed in ungulate populations.

Theory predicts that partial migration should occur under conditions of density dependence or frequency dependence (Kaitala, Kaitala, & Lundberg, 1993; Taylor & Norris, 2007), but empirical evidence conflicts 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 out-compete or displace others from areas of limited resources (Gauthreaux, 1982). Studies of ungulates, however, reveal that high conspecific density may increase (Peters et al., 2017), have no effect on (Eggeman, Hebblewhite, Bohm, Whittington, & Merrill, 2016) or even decrease (Mysterud et al., 2011) migratory behaviour. 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. Distinguishing between the effects of social constraints and resource limitations on migratory behaviour of ungulates requires explicitly assessing conspecific density in conjunction with the resources and other benefits provided on the shared range.

In mountainous regions, the shared range on which resident ungulates remain year-round is often the low-elevation overwintering area (e.g., Found & St. Clair, 2016; Hebblewhite et al., 2008; Middleton et al., 2013). Humans tend to use low-elevation areas more intensively than higher-elevation areas (Haggerty, Epstein, Stone, & Cross, 2018; Skovlin, Zager, & Johnson, 2002), and human use often alters the resources available to ungulates. For example, conversion of valley bottoms to irrigated agricultural land provides high-quality forage resources (Barker, Mitchell, Proffitt, & Devoe, 2019; Lande, Loe, Skjærli, Meisingset, & Mysterud, 2014; Mould & Robbins, 1981) that may encourage ungulates to remain in low elevations throughout the year (i.e., the agricultural subsidy hypothesis). Alternatively, or in addition, lower elevations may provide a survival benefit where higher densities of human populations or structural developments exclude large carnivores (i.e., the human shield hypothesis; Berger, 2007; Knopff, Knopff, Boyce, & St Clair, 2014; Linke, McDermid, Fortin, & Stenhouse, 2013; Oakleaf et al., 2006). Because conversion of ungulate winter range for human uses is predicted to increase into the future (Thompson & Henderson, 1998), explicitly assessing the influence of human land use on migratory behaviour of ungulates could prove particularly useful for understanding and predicting future behavioural changes.

The primary goal of this study was to quantify associations between hypothesized drivers of partial migration and migratory behaviour of individual ungulates across a range of environmental conditions and anthropogenic influences. Migratory behaviour 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 behaviour of elk is therefore of interest from both a theoretical and an applied perspective.

We used Global Positioning System (GPS) collar data collected from 308 adult female elk in 16 herds to assess individual migratory behaviours. We evaluated 5 non-exclusive hypotheses currently posited to explain partial migration in ungulates: the forage maturation, competitive release, social fence, agricultural subsidy and human shield hypotheses (Table 1). We predicted that forage variation, conspecific density, human land uses or combinations of these drivers would affect migratory behaviour of elk (Appendix S1, Supporting Information). Our results advance theories of partial migration while identifying potential means of influencing elk migratory behaviours to achieve management and conservation goals.

TABLE 1 Hypothesized explanations for partial migration in ungulates

Hypothesis	Predictions	References
Forage		
Forage maturation: 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)
Conspecific density		
A) Competitive release: Individuals out-compete 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)
B) Social fence: 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)
Shared range resources		
A) Agricultural subsidy: Ungulates are less likely to migrate from low elevations because irrigated agricultural areas 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)
B) Human shield: Ungulates are less likely to migrate from low elevations because predators are excluded from these human-dominated areas	Elk are less likely to migrate when the intensity of human use inside their winter range is high	Berger (2007), Hebblewhite and Merrill (2009)

Note: Predictions in bold were best-supported in explaining variation in behaviour of 308 adult female elk in 16 herds across south-western Montana, USA, 2006–2016. Hypotheses labelled A) were the best-supported of the 2 within the category.

2 | MATERIALS AND METHODS

Our study area spanned approximately 85,000 km^2 across south-western Montana, USA (44°–47° N and 109°–115° W; Figure 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 4,000 m in the south-east. Temperatures ranged from −8.2 to 17.6°C, and yearly precipitation ranged from 101 to 2,082 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 south-eastern 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 south-eastern 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*).

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 1 year of data for each herd and 2 randomly selected locations per day per individual (one between 0800 and 2000 hr and the other between 2000 and 0800 hr) to assess migratory behaviour. 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 net squared displacement (NSD; Bunnefeld et al., 2011) to classify individual behaviours as resident, migrant or intermediate (i.e., neither resident nor migratory) using a combination of pre hoc and post hoc rules (Appendix S2). We assessed behaviour using the migrateR package (Spitz, Hebblewhite, & Stephenson, 2017) in Program R version 3.4.0 (R Development Core Team, 2017). We defined migrants as animals that moved at least 8.7 km from their starting winter location prior to the end of summer, remained for up to 8 months and then made a return trip to the same or a different winter range. Our migration distance

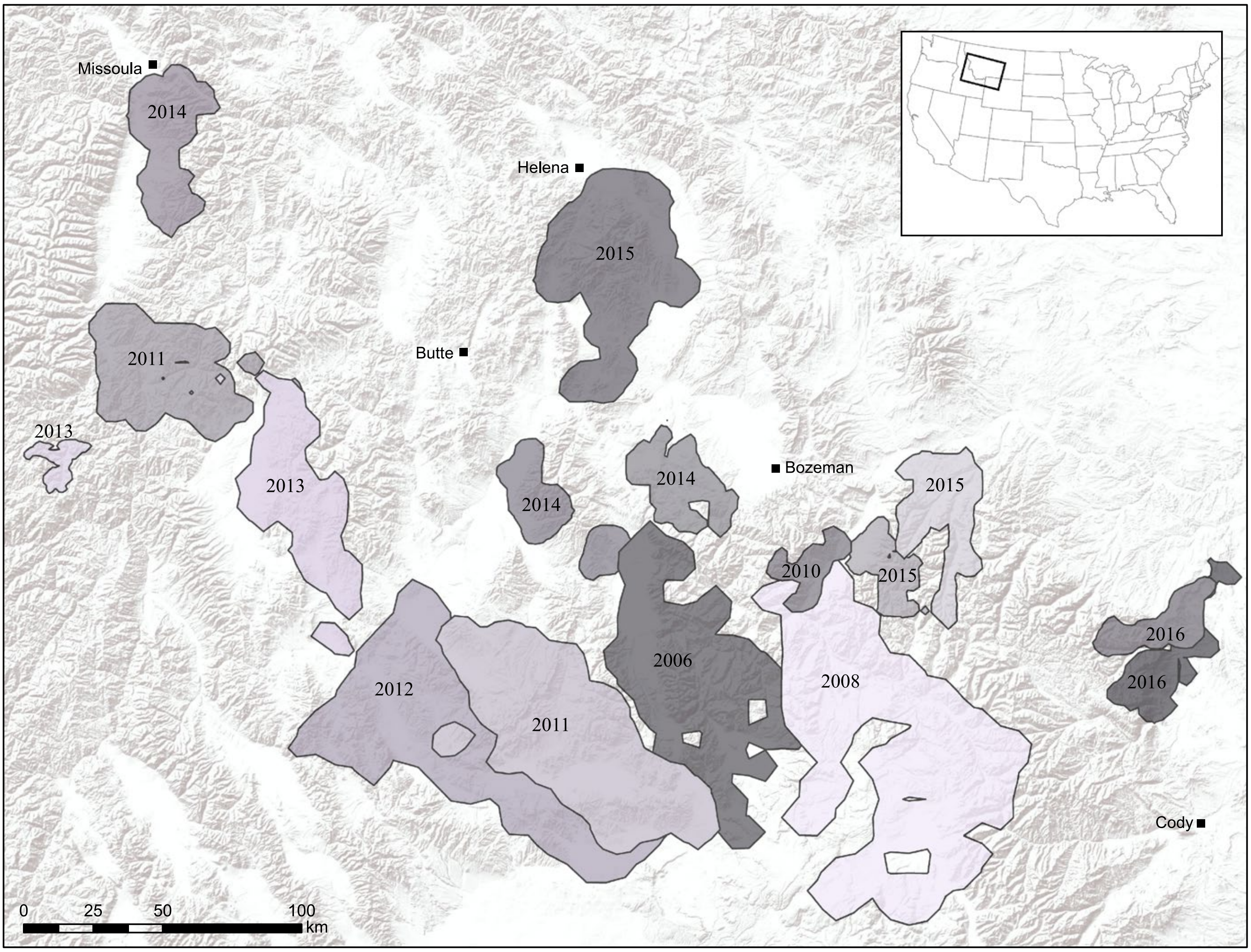

FIGURE 1 Yearly ranges of 16 elk herds across western Montana, USA, 2006–2016

cut-off corresponds to a δ parameter >75 in migratory behaviour models, which we identified as the most appropriate cut-off across our study system based on visual assessments of individual displacement plots.

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

$$logit(Pr(Y_i \leq j)) = \Theta_j - \beta_1 X_{i1} \ldots - \beta_n X_{in} - \upsilon(Herd_i); i = 1, \ldots n; j = 1, \ldots ,J - 1$$

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, υ represents a normally distributed random effect of Herd, and i represents an individual. We used flexible thresholds to represent behavioural categories that were ordered but not necessarily equidistant from one another. 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 collar location data. 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 250 m MODIS 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–August for that herd during the year of interest) to be available to any individual within the herd. We used locations from all collared 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. Further, because photosynthetic pigments correlate well with forage quality for elk (Christianson & Creel, 2015), maximum NDVI can serve as a proxy for both quality and quantity of forage.

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 used NDVI amplitude because it represents the peak increase in photosynthetic activity above the baseline, thereby capturing how forage varies during the growing season relative to non-growing season conditions. 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 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. Because complete-coverage counts can underestimate herd numbers when canopy cover reduces sightability, we used MODIS MOD44B Vegetation Continuous Fields per cent tree cover data to assess canopy cover on the winter ranges of each herd to determine whether herd estimates were likely to be affected by sightability.

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. These 2 measures of human land use are independent of each other, because an elk could have access to irrigated agriculture on a winter range composed of many or few parcels of land.

We developed 19 a priori models representing 5 hypotheses posited to explain partial migration in ungulates, including biologically relevant combinations of each (Appendix S1). We used AIC corrected for small sample size (AICc) to assess relative support for models, considering models with ΔAICc ≤4 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).

3 | RESULTS

We assessed migratory behaviour of 308 adult female elk in 16 herds across south-western Montana during 2006–2016, using data from 5 to 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 travelled up to 110 km from their initial starting locations, but movement distances varied considerably among individuals and were strongly positively skewed (median = 22 km, IQR = 30 km). The length of time spent on summer range varied similarly (median = 104 days, IQR = 94 days).

Migratory behaviours varied within and among herds. On average, herds were composed of 62% ± 30% (SD) migrants, 16% ± 14% intermediates and 22% ± 21% residents. The percentage of migrants within a herd ranged from 19% to 100% (Table 2). Among herds, the relative index of conspecific density varied widely, spanning an order of magnitude. Median canopy cover on winter ranges of all herds was <38%, and no more than 13% of any herd winter range exceeded 50% canopy cover, suggesting sightability was relatively high and comparable among herds (Anderson, Moody, Smith, Lindzey, & Lanka, 1998; Samuel, Garton, Schlegel, & Carson, 1987). 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. Within herds, the maximum forage available on individuals' winter ranges during summer differed from 3 to 31 NDVI digital numbers (DN), and the intensity of human land use ranged from 0.003 to 0.357.

Migratory individuals tended to live in areas where forage varied more predictably from year to year, to have relatively better forage outside their winter range during the summer growing season and to experience higher conspecific density during winter than

TABLE 2 Number of adult female elk studied in 16 herds across south-western Montana, USA, 2006–2016; relative index of conspecific density during the winter at the beginning of the year; and proportion of migratory, intermediate and resident behaviour

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

non-migrants. Mean predictability of forage variation was 2.85 for migrants vs. 3.40 for both intermediates and residents. The median difference in forage (i.e., maximum NDVI) was 3 DN for migrants vs. 1 DN for residents or intermediates. The median index of conspecific density was 8.12 for migrants vs. 1.75 for intermediates and 1.14 for residents. Access to agricultural areas did not differ strongly among behaviour types; 64% of migrants, 63% of intermediates and 59% of residents had irrigated agriculture on their winter ranges. The median number of unique landowners per km^2 on an individual's winter range was 0.009 for migrants, 0.005 for intermediates and 0.020 for residents.

We found similar support for 2 models (ΔAICc ≤ 4) in explaining variation in individual migratory behaviours. Likelihood ratio tests indicated that including the random effect of herd improved model fit ($p < 0.001$ in both cases). The best-supported model (ΔAICc = 0, $\omega_i = 0.58$, $\log(L) = -232.76$) included the effects of forage predictability, relative forage outside the winter range, irrigated agriculture and an interaction between irrigated agriculture and the relative forage outside the winter range (Nagelkerke pseudo-$R^2 = 0.31$; Figure 2), supporting the forage maturation and agricultural subsidy hypotheses. The second-best-supported model (ΔAICc = 2.29, $\omega_i = 0.19$, $\log(L) = -233.91$) included the effects of forage predictability, irrigated agriculture, conspecific density and an interaction between irrigated agriculture and conspecific density (Nagelkerke pseudo-$R^2 = 0.30$), supporting the forage maturation, agricultural subsidy and competitive release hypotheses.

The best-supported model indicated the odds of an elk migrating rather than exhibiting other behaviours increased as forage varied more predictably (OR = 6.28, 95% CI = 1.84, 21.40) but decreased by 54% if an elk had irrigated agriculture on its winter range (OR = 0.46, 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 ($n = 12$; Figure 3).

Similarly, the second-best-supported model indicated the odds of an elk migrating rather than exhibiting other behaviours 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). This model also indicated 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 ($n = 11$).

4 | DISCUSSION

Despite substantial variation in behaviour among individuals and among herds, we found common effects of native forage, irrigated agriculture and conspecific density on migratory behaviour of elk in the majority of herds we studied. The predicted effects of these factors on intermediate behaviours more closely matched their predicted effects on resident than on migratory behaviours. 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 predictable availability of beneficial forage outside elk winter range can mediate the influence of irrigated agriculture on migratory behaviour.

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 conspecific density increased the likelihood of migration only for individuals that overwintered in irrigated agricultural areas, suggesting agricultural land provided a desirable but limited resource for elk. Irrigated agriculture provides higher-quality forage than many other plant communities in the Rocky Mountains (Barker, Mitchell, Proffitt, & Devoe, 2019); 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 studies that have not found increased likelihood of migration at high conspecific density (Eggeman et al., 2016; Mysterud et al., 2011).

Although 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 assessments of partial migration often rely on an assumption that individuals achieve similar fitness during the shared season. Investigation into relative fitness benefits of different behaviours during the shared season could improve theoretical understanding and predictions of behavioural changes in partially migratory populations. Explicitly including intermediate behaviours in analyses may provide a more nuanced understanding of the conditions under which intermediate behaviours are most likely to increase. Because costs and benefits of movement can vary yearly, and because ungulates can change behaviours between years, long-term monitoring of individuals would provide the strongest understanding of fitness consequences (Clutton-Brock & Sheldon, 2010).

Management and conservation goals often aim to preserve or increase migratory behaviour 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. Because the influence of forage on migratory behaviour 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 behaviour of individuals. Our study indicates that strategies to improve forage on migratory summer ranges may prove most effective if such improvements can ensure predictable forage availability. Efforts to bolster resilience of vegetative communities (i.e., maintain or improve the stability of vegetative communities in the face of change) may help ensure reliable availability of forage (Holling, 1973). Such efforts might include retaining 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, Mitchell, Proffitt, & Devoe, 2019), managing disturbances to maintain a mosaic of early-successional vegetative

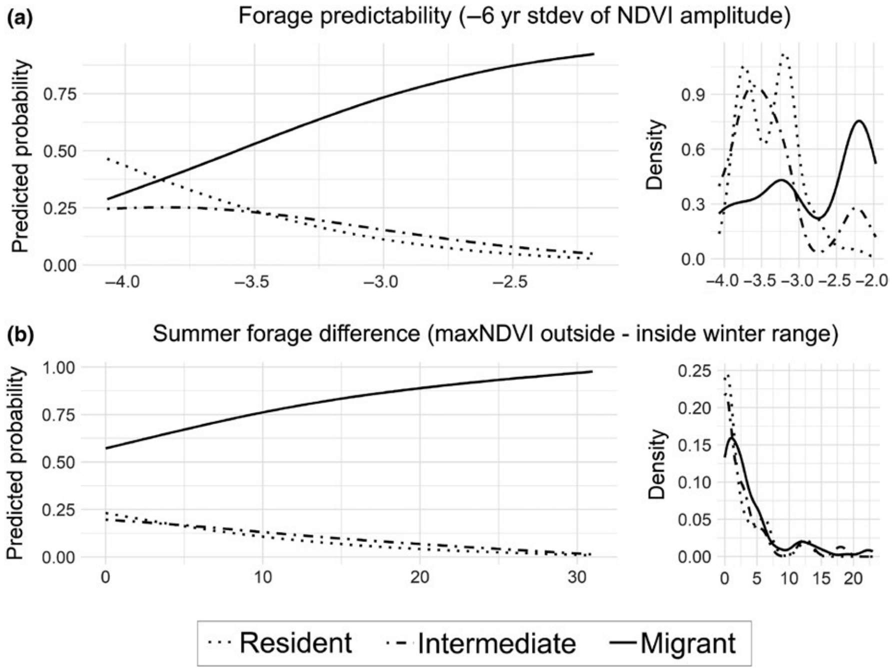

FIGURE 2 Results of best-supported model explaining migratory behaviour of 308 elk in 16 herds across south-western Montana, USA, 2006–2016, and smoothed histograms of the raw data. Elk were increasingly likely to migrate rather than remain resident as forage varied more predictably (panel a). Elk that 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)

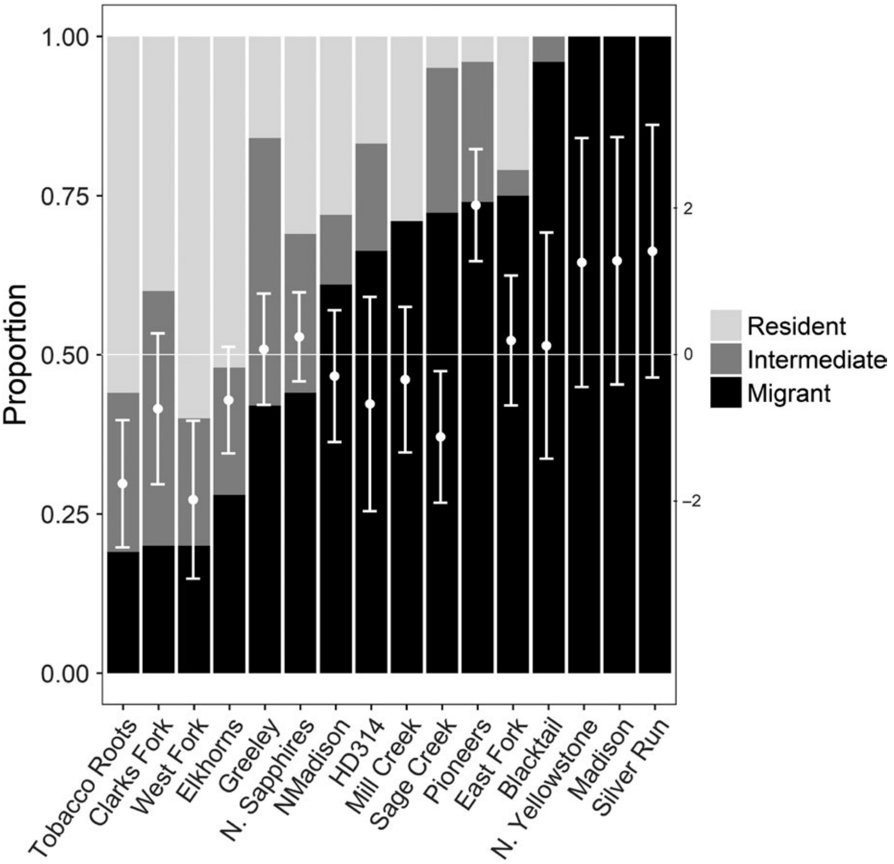

FIGURE 3 Proportion of migratory, intermediate and resident elk in 16 herds across south-western Montana, USA, 2006–2016, along with the effect of herd (random effect estimate ± 95% CI) in logistic regression models associating vegetation characteristics with individual migratory behaviours. Despite wide variation in proportions of behaviours among herds, the majority of herds responded similarly to vegetation characteristics (i.e., CI of herd effect overlapped 0)

communities across the summer ranges of migratory elk could improve both the quality and predictable availability of forage for migrants. Fire management (Barker, Mitchell, Proffitt, & Devoe, 2019) and timber management (Scotter, 1980) may prove useful in manipulating ungulate forage resources, although additional work is needed to fully assess effects of such practices (Cook, Cook, Davis, & Irwin, 2016).

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 commonly 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 just as effectively exclude or remove predators despite their lower intensity of human use (Musiani et al., 2004). If so, human-provided refugia from predation could act synergistically with human-provided forage in reducing the likelihood of migration in agricultural areas. 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).

World-wide declines in migratory behaviour 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 behaviour of elk will decline as a result. It remains to be seen, however, whether affected populations would become entirely resident under such circumstances. The ability of elk to change behaviour between years (Eggeman et al., 2016) may allow migratory behaviours to persist through times when the benefits of migration are reduced. If elk can most effectively capitalize on unpredictable forage variation by changing behaviour yearly based on external conditions, then migration should be retained even if the relative proportion of migrants in the population declines in some years. Alternatively, or additionally, intermediate behaviours may prove particularly beneficial if they allow increased behavioural flexibility in the face of changing external conditions. Our finding that the drivers of intermediate behaviours aligned more closely with those of resident than migrant behaviours suggests that decreasing migration could result in increasing prevalence of intermediate behaviours rather than entirely resident populations.

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AUTHORS' CONTRIBUTIONS

All authors conceived the ideas and designed methodology. K.J.B. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and have final approval for publication.

DATA ACCESSIBILITY

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.9582536 (Barker, Mitchell, & Proffitt, 2019).

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