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ARTICLE

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Diverse migratory portfolios drive inter-annual switching behavior of elk across the Greater Yellowstone Ecosystem

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Abstract

A growing body of evidence shows that some ungulates alternate between migratory and nonmigratory behaviors over time. Yet it remains unclear whether such short-term behavioral changes can help explain reported declines in ungulate migration worldwide, as opposed to long-term demographic changes. Furthermore, advances in tracking technology reveal that a simple distinction between migration and nonmigration may not sufficiently describe all individual behaviors. To better understand the dynamics and drivers of ungulate switching behavior, we investigated 14 years of movement data from 361 elk in 20 herds across the Greater Yellowstone Ecosystem (GYE). First, we categorized yearly individual behaviors using a clustering algorithm that identified similar migratory tactics across a continuum of behaviors. Then, we tested seven hypotheses to explain why some ungulates switch behaviors, and we evaluated how behavioral changes affected the proportions of different behaviors across the system. We identified four distinct behavioral tactics: residents (4.8% of elk-years), short-distance migrants (53.7%), elevational migrants (21.9%) and long-distance migrants (19.6%). Of the 20 herds, 18 were partially migratory, and 5 had all four movement tactics present. We observed switches between migratory tactics in all sets of consecutive years during our study period, with an average of 22.5% of individual elk changing movement tactics from one year to the next. Elk in herds with higher movement tactic diversity were significantly more likely to switch tactics and often responded more effectively to adverse environmental conditions, compared to those in herds with low movement tactic diversity. During our study period, switching increased the prevalence of both short- and long-distance migrants, decreased the prevalence of elevational migrants, and had no effect on the prevalence of residents. Our findings suggest that rather than

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contributing to the declining migratory behavior found in the GYE, switching behavior may enable greater resiliency to continuously changing environmental and anthropogenic conditions.

KEYWORDS
elk, GPS tracking, Greater Yellowstone Ecosystem, migratory plasticity, migratory portfolios, migratory tactic, movement ecology, partial migration, switching behavior

INTRODUCTION

Partial migration, in which varied migratory and nonmigratory movements occur in a single population (Chapman et al., 2011; Lundberg, 1988), occurs across taxa, including invertebrates (Hansson & Hylander, 2009), fish (O'Neal & Stanford, 2011), birds (Lundberg, 1988), and mammals (Berg et al., 2019; Gowan et al., 2019). Partial migration can be maintained by demographic processes driven by differential fitness benefits of migratory tactics (e.g., Cole et al., 2015; Hebblewhite & Merrill, 2011) or by behavioral plasticity driven by interacting intrinsic factors (e.g., genes [Pulido, 2011], animal age [Clutton-Brock, 1984], and reproductive status [Berg et al., 2019]) and extrinsic influences (e.g., forage availability [Fryxell & Sinclair, 1988], climate [Xu et al., 2021], anthropogenic influence [Barker, Mitchell, & Proffitt, 2019], and sociocultural learning [Dodson, 1988]). A clear grasp of the drivers of behavioral plasticity is a critical, yet often missing, first step to understanding adaptations of migratory species amid rapid climatic and anthropogenic change (Middleton et al., 2020; Xu et al., 2021).

Advanced tracking of animal movements has revealed growing evidence of individuals switching between migratory and nonmigratory tactics from one year to the next, suggesting that behavioral plasticity may play a key role in maintaining partial migration. For ungulates in particular, recent work indicates many individuals switch migratory tactics, although switching rates vary considerably within and among species (e.g., mule deer [*Odocoileus hemionus*], Sawyer et al., 2018; van de Kerk et al., 2021; bighorn sheep [*Ovis canadensis*], Lowrey et al., 2020; Spitz et al., 2018). Because few studies have investigated the drivers of switching behaviors, the causes of variation in this behavioral plasticity are not well understood (Denryter et al., 2021; Lowrey et al., 2020; Picardi et al., 2020). For instance, reported switching rates of elk (*Cervus canadensis*) range from 0% for one herd in the eastern Greater Yellowstone Ecosystem (GYE; Middleton et al., 2013) to 0.2% for another in the southern GYE (Cole et al., 2015), to 23% for a herd in Banff National Park (BNP) (Eggeman et al., 2016), and up to 53% for one set of consecutive years in the North Sapphire Mountains in Montana (Barker, Mitchell, Proffitt, & DeVoe, 2019). Such wide variation among switching rates may be attributable to varying habitat conditions across the different studies, but may also be due to methodological differences in defining migratory behaviors.

Although researchers historically classified ungulates as either migratory or resident (Fryxell & Sinclair, 1988; Middleton et al., 2013), recent studies harnessing new technology and larger datasets challenge this simple dichotomy by illuminating a diversity of movement tactics in ungulates (Barker, Mitchell, Proffitt, & DeVoe, 2019; Denryter et al., 2021; Lowrey et al., 2020; van de Kerk et al., 2021). For example, Lowrey et al. (2020) classified short- and medium-distance migration as intermediate tactics along a spectrum of migratory tactics ranging from residency to long-distance migration in bighorn sheep (*O. canadensis*). Similarly, van de Kerk et al. (2021) identified seven movement tactics in mule deer, and Denryter et al. (2021) identified two elevational migration tactics in Sierra Nevada bighorn sheep (*O. canadensis sierrae*). A more complete understanding of behavioral plasticity, therefore, requires a close examination of switching among several migratory tactics.

Behavioral plasticity in ungulate migration can be influenced by environmental changes, sociocultural learning, and human land uses (Xu et al., 2021). Ungulates generally migrate to decrease predation and disease risk, lessen exposure to severe seasonal weather, and increase access to forage (Kauffman et al., 2021). In temperate northern ecosystems, ungulates tend to move from lower elevation winter ranges to higher elevation summer ranges where prolonged snowmelt extends the time of vegetative growth (Fryxell & Sinclair, 1988). Uphill movement of the leading edge of high-quality greening vegetation in spring (i.e., the green wave) therefore plays a key role in regulating migratory behavior (Bischof et al., 2012; Fryxell, 1991; Merkle et al., 2016). As climate change accelerates, the processes that ungulates use to prolong access to forage may be disrupted, leading to increased likelihood of spatiotemporal mismatches with peak forage (Middleton et al., 2013; Post & Forchhammer, 2008). Furthermore, increasing variation in snow depth and the timing of snowmelt can alter the costs of energy expenditure for animals moving through the spring landscape (Laforge et al., 2021; Rickbeil et al., 2019).

Accumulated herd-level knowledge of environmental fluctuations typically results in a higher prevalence and diversity of migratory tactics in ungulate populations (Dodson, 1988; Jesmer et al., 2018; Lowrey et al., 2020). For example, extant herds of bighorn sheep are more migratory and have higher switching rates than their recently restored counterparts (Lowrey et al., 2020), and elk in larger groups are more likely to switch tactics (Eggeman et al., 2016). It is clear that social learning plays a key role in influencing migratory behavior (Jesmer et al., 2018; Lowrey et al., 2020; Nelson, 1998), but its role in driving migratory plasticity has yet to be fully explored.

Recent declines and changes in ungulate migration have coincided with rapid changes in human land use across the United States, especially near protected areas (Davis & Hansen, 2011), yet no studies have examined anthropogenic influences on switching behavior. Increases in land development to meet the needs of the growing human population (Davis & Hansen, 2011) can disrupt migration timing and movement rates (Sawyer et al., 2020; Wyckoff et al., 2018) and can serve as refuge from predators (Hebblewhite et al., 2005; Wilmers & Levi, 2013). Furthermore, the availability of high-quality forage in agricultural lands and government-run feeding areas on ungulate winter ranges has reduced the migratory propensity (Barker, Mitchell, Proffitt, & DeVoe, 2019; Lewis & Rongstad, 1998) and distance (Jones et al., 2014) in some populations.

In ungulate populations across North America, declining migration and increasing residency have been associated with management challenges as larger aggregations of wildlife on agricultural lands increase crop damage and heighten the risk of disease transmission to livestock (Cole et al., 2015; Hebblewhite et al., 2006; Middleton et al., 2013; Rayl et al., 2021). Elk in particular create considerable management challenges because of their relatively high body mass and tendency to congregate in large herds. Despite their management challenges, elk also hold considerable ecological, economic, and cultural value, with herds sustaining recovering large carnivores including the gray wolf (*Canis lupus*), grizzly bear (*Ursus arctos horribilis*), and mountain lion (*Puma concolor*), as well as substantial human harvest (Haggerty & Travis, 2006; Middleton et al., 2020). To date, elk in some areas have lost over 50% of historical migration routes (Berger, 2004), while the number and proportion of migratory individuals have declined in some herds (Cole et al., 2015; Middleton et al., 2013). Assessing whether these declines are a result of short-term behavioral switches rather than more permanent long-term alterations would therefore fill a critical gap in ecological theory while helping natural resource professionals anticipate movement tactics to more effectively manage ungulates under changing environmental and anthropogenic conditions.

To date, there have been no multi-population studies examining how and why ungulates switch between diverse migratory tactics. As a result, the role of behavioral plasticity in changing ungulate migratory tactics remains poorly understood. Here, we define switching as an individual changing migratory tactics from one year to the next. We used GPS location data from 361 individual elk in 20 herds spanning the GYE to characterize the full variety of plasticity in migratory tactics and to evaluate drivers of switching behavior. Based on the spatiotemporal breadth of the dataset, we expected to see a wide range of migratory tactics, including residency, short-distance migration, and long-distance migration (Cole et al., 2015; Middleton et al., 2013), and switching between tactics driven by environmental fluctuations, social learning, anthropogenic influences, or a combination of these factors. We tested seven nonmutually exclusive hypotheses to explain the drivers and directionality of switching behavior (Table 1).

METHODS

Study area and movement data

Our study spanned nearly 150,000 km^2 of the GYE, including northwestern Wyoming, eastern Idaho, and southern Montana (Figure 1). Centered around Yellowstone and Grand Teton National Parks, the area encompasses surrounding national forests and tribal lands, as well as a mosaic of agricultural lands, energy infrastructure, and rapidly expanding urban and suburban development (Hansen & Phillips, 2018; Rickbeil et al., 2019). Elk in the GYE mainly spend the winter in lower elevation grasslands and shrublands on a mix of multiuse public and private lands, where they experience the highest amount of anthropogenic-influenced habitat, including residential and energy development, agricultural land, and feeding grounds in some portions of Wyoming (Gigliotti et al., 2022; Rickbeil et al., 2019). Many elk migrate in spring towards higher elevation alpine meadows and coniferous forests in less developed national parks or forests, where they spend the summer before returning to winter ranges in fall or early winter (Middleton et al., 2013).

We used GPS collar data collected between 2006 and 2020 from 361 adult female elk in 20 herds. Our dataset contained 840 elk-years (defined as an individual's arrival date at a winter range up to the return to the winter range in the subsequent year), with fix rates ranging from 30 min to 48 h. This dataset is a subset of movement data

TABLE 1 Hypotheses, explanations, and predictions regarding the causes and directionality of individual elk switching among migratory tactics in the Greater Yellowstone Ecosystem, USA.

Theme	Hypothesis	Explanation	Prediction	References
Environment	Green-wave	Migrants follow fresh vegetative growth to prolong access to high-quality forage	Spatiotemporal mismatch between green-up and migration will increase shifts away from residency as animals alter behavior to increase nutritional intake	Middleton et al. (2018); Merkle et al. (2016)
	Energy expenditure	Deep snow impedes migratory movement due to increased energetic demands	Deeper snow will reduce likelihood of leaving the winter range and will increase shifts away from migratory tactics	Parker et al. (1984); Singh et al. (2012)
Social	Cultural knowledge transmission	Accumulated herd-level knowledge of diverse migratory tactics increases prevalence of switching behavior in response to environmental changes	Elk in herds with diverse migratory portfolios will have increased switching rates in all directions	Lowrey et al. (2020); Jesmer et al. (2018)
Anthropogenic	Human shields	Proximity to humans reduces predation risk on winter range relative to summer range	High levels of developed land in the winter range increases shifts away from migratory tactics	Wilmers and Levi (2013); Hebblewhite et al. (2005)
	Human disturbance	Residential and energy development alter or disrupt migration	High levels of developed land in the migratory range increases shifts away from migratory tactics	Wyckoff et al. (2018); Sawyer et al. (2020)
	Agricultural subsidy	Agricultural vegetation provides nutritional benefit on winter ranges	More access to agriculture on the winter range increases shifts away from migratory tactics	Barker, Mitchell, Proffitt, and DeVoe (2019); Barker, Mitchell, and Proffitt (2019);Wilmers and Levi (2013)
	Deliberate forage provisioning	Ungulate feed grounds decrease migratory distance and propensity	Access to feed grounds increases shifts away from migratory tactics	Jones et al. (2014); Lewis and Rongstad (1998)

from the 26 known GYE herds for which GPS data have been collected (Gigliotti et al., 2022), using data only from individuals with at least two consecutive years of movement data (20 of the 26 herds).

Classification of movement tactics and switch events

To identify migratory tactics, we first classified each elk-year as either resident (with no distinct seasonal movements) or nonresident by manually reviewing adjacent interactive plots (e.g., https://gabezuckerman.shinyapps.io/ExampleMigrationClassification/) of net squared displacement (NSD; Bunnefeld et al., 2011), elevation change, and a map of GPS relocations for each elk-year. To identify migratory tactics from the nonresident elk-years, we plotted migratory distance as the *x*-axis and elevation change as the *y*-axis and used *k*-means clustering to classify tactics along this spectrum with residency (0, 0) on one end and long-distance migration at the other ([max. elevation change, max. distance], inset graph Figure 1; Lowrey et al., 2020). Thus, we did not use a predetermined number of migratory tactics; instead, we found the optimal number of clusters and used these clusters to guide the classification of nonresident behaviors (see Appendix S1; Lowrey et al., 2020). For each nonresident elk-year, we visually identified the timing of spring and fall migrations based on departure from or arrival to clustered GPS points on the map coupled with a change in slope of the NSD or elevation change curves. We measured migration distance as the

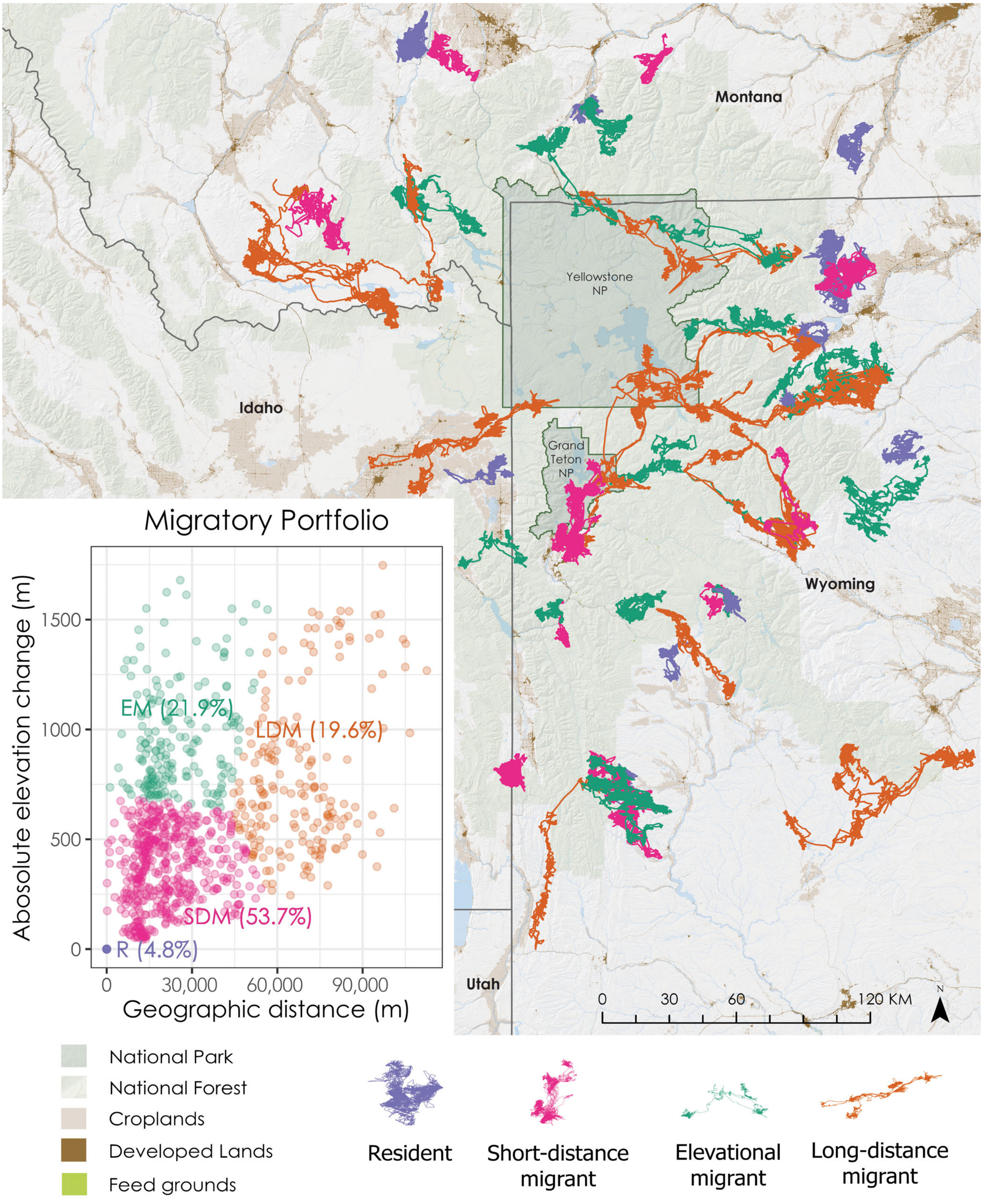

FIGURE 1 Map of study area across the Greater Yellowstone Ecosystem (GYE), with the GYE level migratory portfolio (inset) and example yearlong paths from each of the four migratory movement tactics identified across the area. R, resident; SDM, short-distance migrant; EM, elevational migrant; LDM, long-distance migrant; NP, National Park.

diameter of the smallest circle encompassing the 99% isopleth of a Brownian Bridge movement model (BBMM) for the movement data during the spring migration for each nonresident elk-year (Sawyer et al., 2009). Similarly, we measured the absolute elevation change between GPS locations recorded during the dates of the spring migration. We labeled a set of consecutive years a switch event if an individual elk had a different tactic in the second year from the first.

Covariate extraction

We extracted a yearlong normalized difference vegetation index (NDVI) from 8-day, 250-m resolution MODIS/Terra Surface Reflectance satellite imagery (Vermote, 2015). Using the irg r-package (R Core Team, 2019; Robitaille, 2020), we found an instantaneous rate of green-up (IRG) at each GPS relocation during the spring migration, as defined by the timing of that tactic classification (or, for resident elk, during average herd-level migration dates). To measure spatiotemporal match between presence and peak green-up, we found the days-from-peak green-up (DFP) for each GPS relocation by finding the absolute difference between the day the pixel was accessed by the animal and the day it reached its maximum IRG value (Aikens et al., 2017). We used the mean DFP for each elk-year's spring migratory period to represent that elk-year's green-wave tracking. Low DFP values indicate spatiotemporal alignment between an elk's location in space and time and high-quality, greening vegetation at that same location in space and time (i.e., green-wave surfing), while high DFP values represent a spatiotemporal mismatch with peak forage opportunities.

We extracted snow depth for each GPS relocation from the Snow Data Assimilation System (SNODAS), a modeled remote sensing snow product with a 1 km spatial resolution and a daily temporal resolution, using Google Earth Engine in Python (Gorelick et al., 2017; National Operational Hydrologic Remote Sensing Center, 2004; Python Software Foundation, https://www.python.org/). We measured the maximum snow depth encountered in the winter range, defined as the individual elk's 99% isopleth of the BBMM of the movement data between the end of the first year's fall migration and the start of the second year's spring migration (or, for residents, the herd-level average dates).

We calculated herd-level migratory diversity using Shannon's *H* diversity index (Lowrey et al., 2020). This metric provides a single value that represents the relative proportions of the movement tactics within a given herd. The maximal value is determined by the total number of movement tactics, with higher values representing herds with higher migratory diversity.

We used the Land Change Monitoring, Assessment, and Projection (LCMAP), a 30-meter resolution land cover product (Pengra et al., 2020), to extract human land use data. LCMAP is a yearly product spanning from 1985 to 2017. As our study's temporal range was 2006–2020, we used the 2017 land cover product for 2018, 2019, and 2020. We separately extracted the proportion of developed land in each elk-year's spring migratory period and winter ranges by dividing the area of pixels designated as "developed" by the total area of the corresponding ranges. We also used LCMAP to calculate the proportion of cultivated agricultural land in each elk-year's winter range following a similar procedure, using pixels designated as "cropland." We used a modified version of the Wyoming Game and Fish Department's Feed Ground Locations shapefile, manually updated for increased spatial accuracy, to identify elk winter ranges that contained access to supplemental winter feed grounds (WGFD, https://wgfd.wyo.gov/Wildlife-in-Wyoming/Geospatial-Data/Big-Game-GIS-Data).

Modeling switch events

We fit 29 candidate logistic regression models for all seven hypotheses and biologically relevant combinations with the binary response variable of whether an elk exhibited a switch in migratory tactics (yes/no) using scaled and centered covariates. We ensured covariates had a variance inflation factor (VIF) <2 (Eggeman et al., 2016; Zuur et al., 2010). We fit separate sets of models for each tactic as they vary in responses to habitat change (Eggeman et al., 2016). We used the caret package to fit models (Kuhn, 2020) and selected top models using Akaike information criterion adjusted for small sample size ($\mathrm{AIC_c}$; Anderson & Burnham, 2002; Burnham & Anderson, 2004) based on a delta$\mathrm{AIC_c}$ value of 2. We used the Matthews Correlation Coefficient (MCC) to evaluate model fit because it is well suited for imbalanced datasets, with −1, 0, and 1 representing perfect misclassification, random chance, and perfect classification, respectively (Chicco & Jurman, 2020). We identified covariates as significant if their 85% confidence interval did not overlap with 0 (Arnold, 2010).

RESULTS

Classification of movement tactics and switch events

Results of the cluster analysis revealed four movement tactics in 361 adult female elk across the GYE (Figure 1). Of the 840 elk-years (mean = 2.3 elk-years per elk), we identified 40 elk-years as residents (R, 4.8%; $n = 22$ elk). The remaining 800 elk-years clustered into an optimal $k = 3$ groups using *k*-means (Appendix S1), which we identified as short-distance migrants (SDMs), elevational migrants (EMs), and long-distance migrants (LDMs). SDMs comprised the majority of elk-years ($n = 451$ elk-years, 53.7%; 229 elk), traveled less than 55 km between seasonal ranges, and experienced a maximum elevation change of 675 m. EMs were the second most common tactic ($n = 184$ elk-years, 21.9%; 112 elk) and traveled no more than 57 km between seasonal ranges, ranging between 645 and 1680 m of elevation change. EM and SDM traveled similar distances between ranges but differed in the elevation change between ranges. LDMs ($n = 165$ elk-years, 19.6%; 91 elk) traveled between 44 and 113 km between seasonal ranges, and had elevation changes up to 1750 m. Of the 20 herds, only 5 had elk that exhibited all four tactics, although there was a moderate correlation (Pearson's $r = 0.56$) between the number of elk-years represented in a herd and the number of tactics present (Appendix S2). Of the remaining 15 herds, 9 herds had 3 tactics, 4 herds had 2 tactics, and 2 herds had only 1 tactic. In well-represented herds (with >25 elk-years), there were typically one or two dominant tactics, which were always one of the three migratory tactics.

We observed instances of switching behavior in every year of our 15-year study period. In the 478 sets of consecutive elk-years from the 361 elk, switches between tactics occurred 105 times, resulting in an overall switch rate of 22%. Of the 361 elk in 20 herds, 92 elk in 16 herds accounted for all of the switches in movement tactics. Annually, switching occurred at a mean rate of 22.5%, with a standard deviation of 11% (7% minimum in 2011–2012; 50% maximum in 2007–2008). EMs switched tactics at the highest rate, changing in 41 out of 108 chances (38%), while LDMs switched at the lowest rate (12.8%). Residents switched in 6 out of 23 chances (26%) and SDMs switched in 41 out of 256 chances (16%). The small sample size of switches from resident behavior precluded our ability to evaluate the drivers of these switch events. The 86 elk monitored for more than two consecutive years switched in 52 out of 203 chances (26%) with 12 elk switching more than once.

Switching behaviors altered the study area-wide proportions of different migratory tactics. Over the course of the study period, switching accounted for the loss of eight EMs (41 switches from EM, only 33 switches to EM), while increasing the balance of LDMs and SDMs by four each (17 switches from LDM, 21 switches to LDM; 41 switches from SDM, 45 switches to SDM; Figure 2). Residents had an equal number of switches in both directions. Nearly all switches were to or from intermediate tactics (defined as EM/SDM, as opposed to R/LDM, which lie on the ends of the behavioral continuum). There were only two instances of extreme switching, with one elk switching from R to LDM in 2008–2009 and another switching from LDM to R in 2019–2020.

Modeling switch events

Elevational migrants

We found support for six models explaining switching from an EM tactic (including the null model), but only the top-ranked model had informative covariates (AIC_c weight = 0.15; log-likelihood = −68.42; $K = 4$; MCC = 0.21; Appendix S3: Table S1). Based on this model, switching was influenced by the interaction between the proportion of developed lands in the winter range and herd-level movement tactic diversity. Considering the two covariates separately, EMs with low levels of developed land on their winter range or in herds with low movement diversity were more likely to switch tactics. However, elk in herds with high movement diversity were more likely to switch at high levels of winter range development, whereas those in herds with low or average movement diversity were more likely to switch at low levels of development (Figure 3; Appendix S3: Table S1).

Short-distance migrants

The only supported model of switching from an SDM tactic explained switching as a function of the interaction between the proportion of developed land on the spring migratory route and herd-level migratory diversity (AIC_c weight = 0.97; log-likelihood = −92.45; $K = 4$; MCC = 0.25). Only the herd-level movement diversity covariate was significantly different from zero, indicating the likelihood of switching from an SDM tactic increased as movement tactic diversity increased (see Appendix S3: Table S2). The covariates for both spring migratory route developed land and the interaction term were not informative.

Long-distance migrants

There were five competitive models of the drivers that influenced switching from an LDM tactic (including the null model). The best-supported model was a function of the interaction between winter range

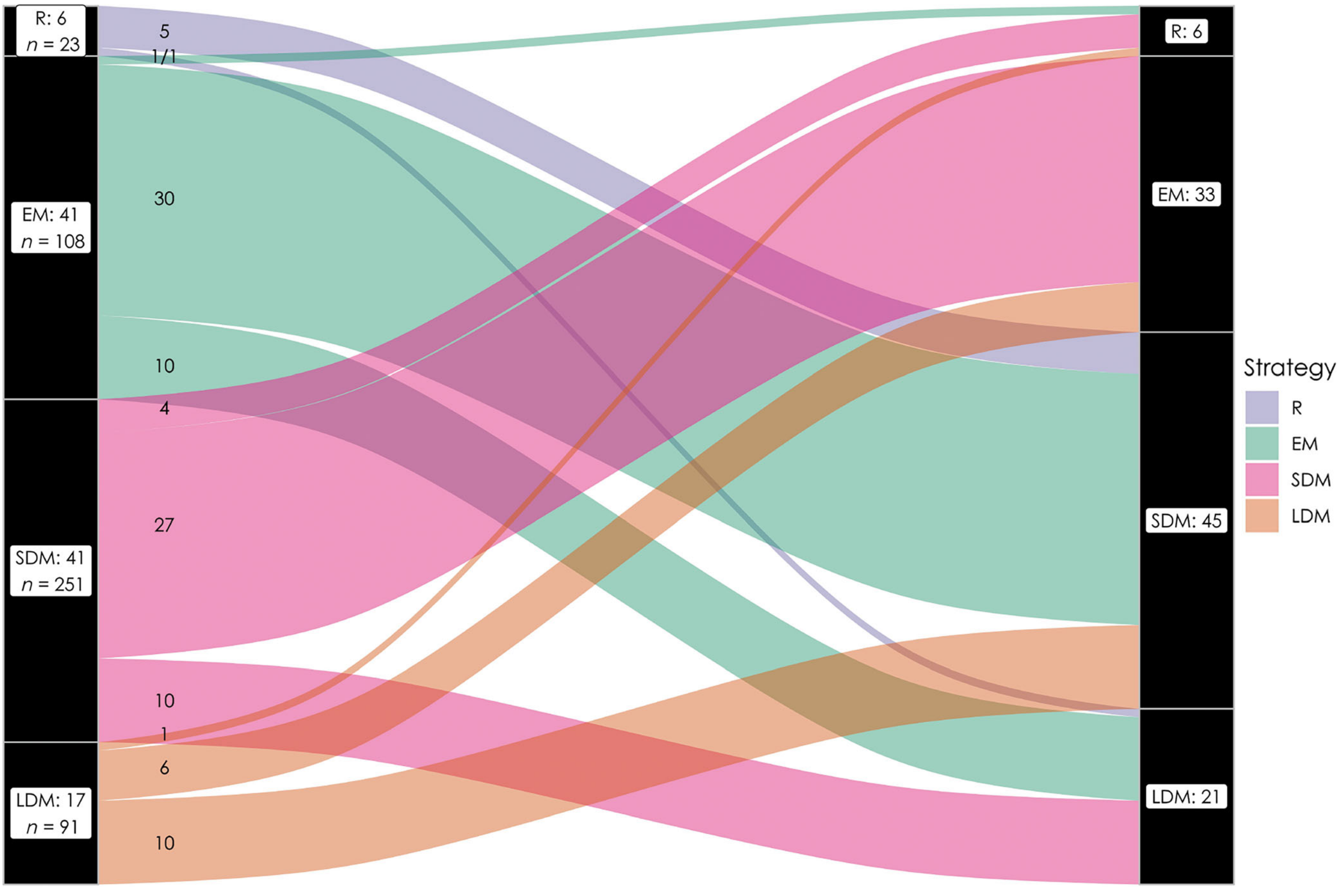

FIGURE 2 Direction and frequency of migratory switching behavior from one year (left axis) to the next (right axis) over 478 consecutive elk-years across the Greater Yellowstone Ecosystem, USA, 2006–2020. For each tactic, the numbers on the left side represent the number of individuals that switched tactics (top) and the total number of individuals that began a set of consecutive years with that tactic (bottom). The numbers on the right side represent the number of individuals that switched to that particular tactic. Residents (R) switched tactics in 26% of chances; elevational migrants (EMs) switched tactics most often (38% of opportunities); short-distance migrants (SDMs) in 16% of chances; and long-distance migrants (LDMs) in 12.5% of chances. Most changes only moved a single step along the migratory continuum (e.g., R to SDM or R to EM, as opposed to R to LDM or LDM to R), although there were two instances of extreme (LDM to R or vice versa) switches.

snow depth and herd-level movement tactic diversity (AIC_c weight $= 0.17$; log-likelihood $= -39.62$; $K = 4$; $\text{MCC} = 0.31$; Appendix S3: Table S3). Based on this model, the likelihood of switching increased as snow depth and herd-level movement diversity increased when holding the other covariates at their mean values. The likelihood of switching from an LDM tactic increased as snow depth increased when herd-level movement tactic diversity was at average or low values (Figure 4). However, LDM in herds with high movement tactic diversity were more likely to switch at low and intermediate snow depths (Figure 4). The three remaining supported models indicated an increased likelihood of switching as the proportion of developed land on the spring migratory route increased (see Appendix S3: Table S3). One of these models also indicated that the likelihood of switching from an LDM tactic decreased as snow depth increased, similar to the “High” herd-level diversity line in Figure 4.

Residents

We were unable to model resident switching behavior due to the small sample size ($n = 6$ switching events).

DISCUSSION

Combining movement data from 20 herds spanning a broad range of environmental conditions and anthropogenic influences revealed diversity and plasticity of movement tactics used by elk across the GYE. Our classification method identified more migratory tactics and higher rates

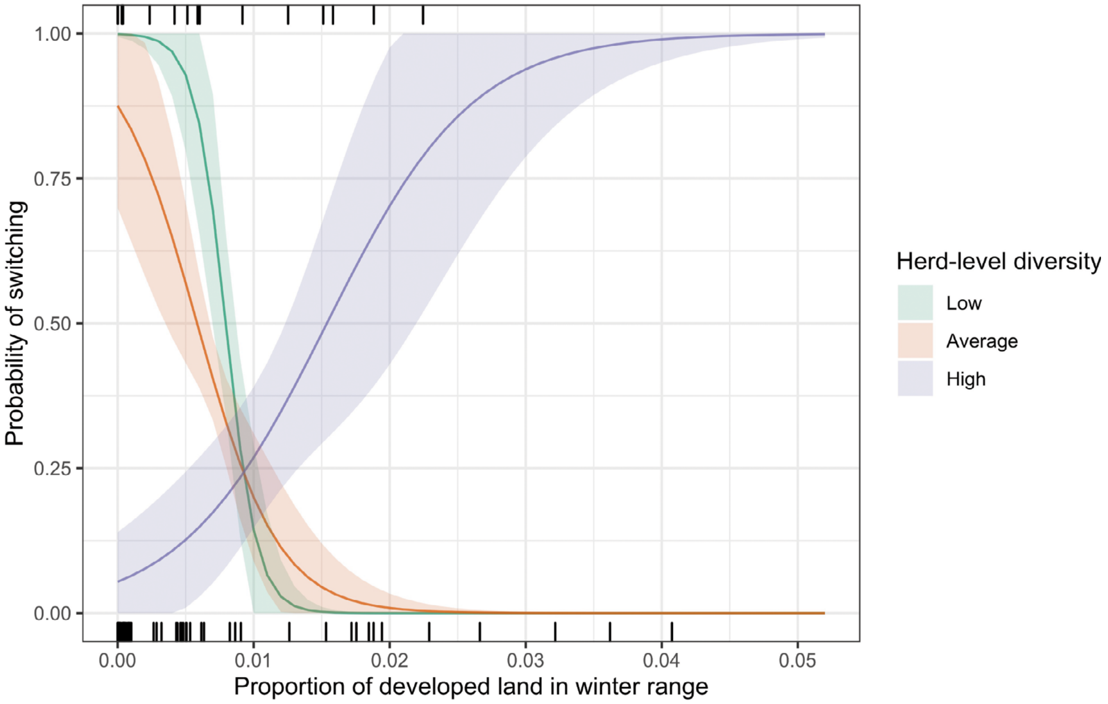

FIGURE 3 Predicted rates of switching from an elevational migration tactic for elk in the Greater Yellowstone Ecosystem, USA, 2006–2020 (based on 41 switches in 108 sets of consecutive years). Elk in herds with high movement tactic diversity were more likely to switch at higher levels of winter range development, whereas those in herds with low or average values were more likely to switch at lower levels of development. The rug plots show the distribution of data used to fit the models, with bars on the top indicating switch events and bars on the bottom indicating nonswitching events.

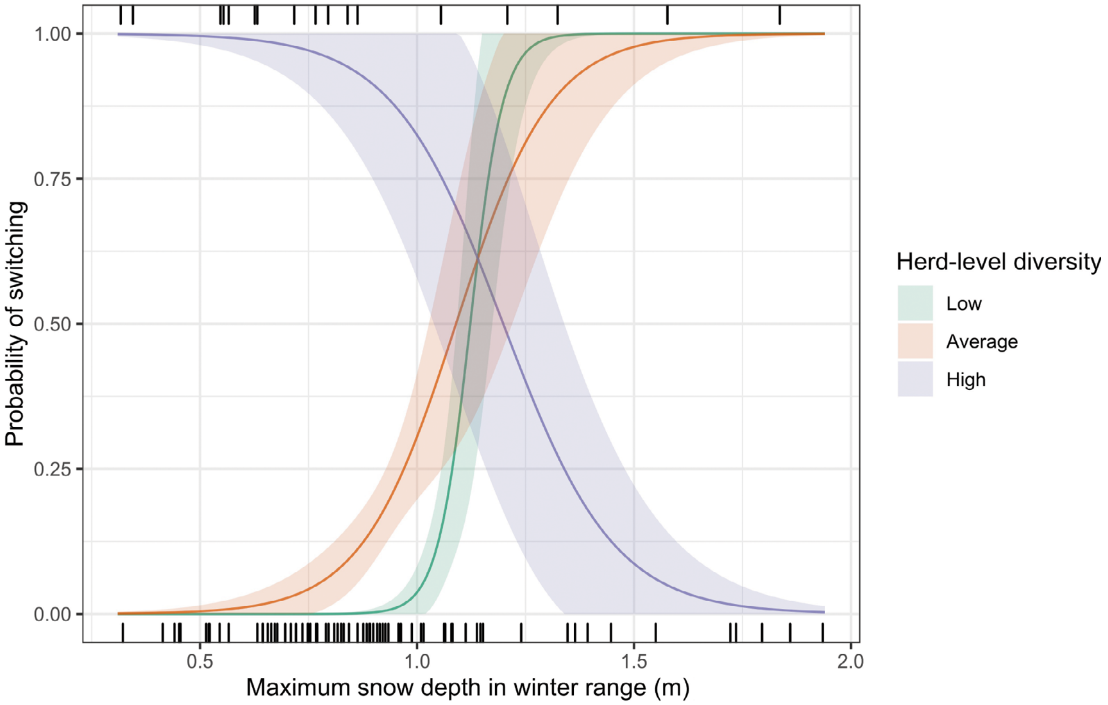

FIGURE 4 Predicted switch rates of long-distance migrants (LDMs) in the Greater Yellowstone Ecosystem, USA, 2006–2020 (based on 17 switches in 91 sets of consecutive years). LDM in herds with low or average movement tactic diversity levels were much more likely to switch at higher winter range snow depths. LDM in herds with high movement tactic diversity levels were much more likely to switch at low or intermediate levels of snow in the winter range. The rug plots show the distribution of data used to fit the models, with bars on the top indicating switch events and bars on the bottom indicating nonswitching event.

of switching among tactics than previously reported in the system (Cole et al., 2015; Middleton et al., 2013). Herd-level migratory tactic diversity was a key driver of switching behavior and was significantly associated with the probability of switching from all migratory tactics. Diverse migratory portfolios offer more opportunities for within-generation knowledge transmission, thereby enabling animals to make more flexible decisions to adapt to a changing environment (Keith & Bull, 2017; Lowrey et al., 2020). We found evidence of diverse migratory portfolios in 18 of the 20 herds we studied, with five herds exhibiting all four movement tactics (residency, short-distance migration, elevational migration, and long-distance migration).

Based on the number of switches among the four movement tactics during our study period, the proportion of migrant behaviors increased, indicating that switching is not contributing to the declines. In migratory behavior that have been reported across the GYE and similar systems (Cole et al., 2015; Hebblewhite et al., 2006; Middleton et al., 2013). If increasing residency is happening across the system, our results indicate that switching is not increasing the proportion of residents. However, migratory subpopulations in many herds continue to decline, suggesting that behavioral changes alone are not keeping pace with differing fitness between tactics (Cole et al., 2015; Hebblewhite et al., 2006; Middleton et al., 2013). This could be due to migrants suffering from lower survival, reduced recruitment, or both relative to their nonmigratory counterparts (Cole et al., 2015). It is possible that switching may play a role in the increase in residency if animals first switch from a migratory tactic, then benefit from increased fitness that encourages continued residency following the initial switch, though our data do not address fitness.

Our findings add to the growing body of work showing that the primary herbivore in this important ecosystem is capable of responding dynamically to differing natural and anthropogenic environments. Very few switches between residents and LDMs took place during our study (2% of all switching was either LDM to R or R to LDM), suggesting that switching functions as a short-term adjustment rather than a mechanism for large changes in behavior. In fact, of the 12 elk that switched multiple times, all but one eventually switched back to their original tactic. Even for elk that did not switch tactics, few remained in exactly the same position on the migratory spectrum from one year to the next. This is likely because ungulates exhibit multiple types of plasticity that may alter their position on the spectrum. In addition to switching migratory tactics, ungulates can make changes to migratory routes or shift migration timing in response to habitat changes (Xu et al., 2021). Elk in the GYE have been shown to shift both spatial and temporal dimensions of migration in response to changing snow conditions and predation risk, as well as human land use and harvest pressure (Jones et al., 2014; Rickbeil et al., 2019; White & Garrot, 2013). Migratory plasticity is necessary for the long-term persistence of migratory behavior as it serves as a buffer to climatic and anthropogenic-induced habitat change (Xu et al., 2021). Indeed, human disturbances on the winter and spring migratory ranges were some of the most commonly supported extrinsic drivers of switching behavior, influencing switching from both EM and LDM tactics. Together, our results suggest that human land uses are altering ungulate migration, but individuals within herds may have the ability to share information and adapt to these changing conditions]

Elk in herds with a high diversity of movement tactics exhibited differential switching responses at extreme levels of human disturbance and climatic variation. Contrary to our expectation that higher movement tactic diversity would be associated with higher switching rates, we found that elk in herds with lower movement tactic diversity were far more likely to switch from LDM if their winter ranges had deeper snow. We speculate this result may reveal an assumption that the entire migration will be too energetically costly based on the immediate presence of deep snow on the winter range for LDM in herds with low movement tactic diversity (Parker et al., 1984). However, LDMs in herds with high movement tactic diversity were very unlikely to switch at high snow depths, potentially because more culturally transmitted landscape knowledge gave them insight that immediate local conditions may not hold true for the entirety of the migration. In fact, these LDMs were more likely to switch at low winter range snow depths, possibly because low snow levels could be a learned indication of shortened green-wave surfing potential during a long migration. Indeed, cultural knowledge transmission is key to successfully prolonging forage benefits through migration, with ungulate populations increasing their migratory propensity and green-wave surfing ability as they spend more time in a landscape (Jesmer et al., 2018). Thus, we speculate that maintaining diverse migratory portfolios and the cultural knowledge transmission they enable may help retain long-term migratory knowledge amidst continuing environmental and anthropogenic changes (Jesmer et al., 2018; Middleton et al., 2020).

Land development influenced the likelihood of elk switching among tactics, but the influence differed based on an individual's location along the migratory spectrum. While this was not a pattern we predicted, we found LDMs responded to development along their migration routes, whereas elk with intermediate tactics responded to development on their winter ranges. For LDMs, development levels as low as 3% on the migratory route were likely to lead to a switch from migration. Similarly, low thresholds have been identified in mule deer, which avoid migrating through areas with 3% surface cover of energy development (Sawyer et al., 2020). As anthropogenic land use is projected to dramatically increase in the GYE over the remainder of the century (Hansen & Phillips, 2018), limiting development in winter ranges and on spring migratory routes may help reduce switching away from migratory tactics (Middleton et al., 2020).

While there has been recent evidence of diverse migratory tactics and ensuing migratory plasticity in other species, our results contrast with those of several foundational GYE elk studies due to differences in sample size and methodological advances. The spatiotemporal breadth of our study combined with the use of a migratory spectrum that did not rely on predefined migratory tactics (e.g., NSD) led us to identify diverse migratory and switching behaviors similar to those found by Barker, Mitchell, Proffitt, and DeVoe (2019) and Lowrey et al. (2020), rather than those found based on the traditional dichotomy of migrant and resident tactics. In turn, the identification of more diverse migratory tactics led to more switches than previously believed to occur. Both Middleton et al. (2013) and Cole et al. (2015) found no evidence of switching in GYE elk but looked only at individual herds and identified fewer annual movement tactics. While Eggeman et al. (2016) found annual switching levels in BNP comparable to this study (BNP: 15% vs. GYE: 23%), their results would have likely been even closer had they considered switching among more than just migrants and residents. When Barker, Mitchell, Proffitt, and DeVoe (2019) included an intermediate tactic on a migratory spectrum, annual switching rates jumped to over 50%, albeit from only a single set of consecutive years from 34 individuals. Our results of a 22% switching rate place elk switching behavior closer in frequency to many other North American ungulates, including moose (21%; White et al., 2014), white-tailed deer (39%; Sabine et al., 2002), and mule deer (51%; van de Kerk et al., 2021).

Interestingly, despite the well-known influence of forage on ungulate migratory behavior (Aikens et al., 2017; Fryxell & Sinclair, 1988; Merkle et al., 2016), we did not find support for any of our bottom-up hypotheses related to switching between tactics. This result adds to recent work that has revealed nuanced and sometimes inconsistent influences of foraging on behavioral plasticity. For example, Eggeman et al. (2016) found that forage conditions influenced switching from a resident tactic but had little effect on migrant switching, and Xu et al. (2021) did not find a clear relationship between changing forage conditions and migratory tactic changes in either spatial or temporal dimensions. We hypothesize that our lack of support for bottom-up hypotheses may indicate that the influence of forage is incorporated within the influence of other related factors—for example, the effect of snow on prolonged access to high-quality forage (Laforge et al., 2021) or changes in anthropogenic land use altering forage availability (Sawyer et al., 2020; Wyckoff et al., 2018). Alternatively, or additionally, the influence of forage may prove stronger in combination with other intrinsic factors for which we were unable to account, such as animal reproductive status, body condition, age, or sex (Berg et al., 2019; Eggeman et al., 2016; Peters et al., 2019). It is also possible that our metric of day-from-peak green-up did not sufficiently capture aspects of forage conditions that influence elk movement behavior.

While our study included a large sample size, affording a significant advance in our picture of diversity and plasticity across this system, there were several limitations. Although this is the most comprehensive sample of multiyear elk movement data from the GYE, it is possible our results under- or overestimated switching rates given that we lacked multiple years of consecutive data from 6 of the 26 known herds in the ecosystem (Gigliotti et al., 2022). Similarly, it is possible that relatively minor shifts in distances traversed and/or elevation changes were denoted as switches due to the automated classification of migratory tactics. While this could result in changes in tactic that do not have considerable biological consequences, our approach is justified as it is objective, reproducible, and does not rely on predefined behaviors (Lowrey et al., 2020). We were also limited by a lack of information about age, animal abundance, reproductive status, and male movement data. Future studies monitoring the vital rates of herds or migratory tactics could help link switching events with fitness or demographic consequences (Lowrey et al., 2020). Additionally, due to the lack of long-term data for individuals, we were unable to evaluate the permanence of shifts in tactics and therefore cannot make predictions about long-term trends in migratory behavior. Regardless, our findings provide considerable support for the idea that diverse migratory portfolios, and the cultural knowledge transmission they enable lead to increased migratory propensity that can make ungulates more resilient and adaptable to changing conditions over the short term.

Conserving ungulate migratory behavior is an arduous, multifaceted task (Brakes et al., 2019) that can be made easier by protecting diverse migratory tactics and the flexible switching behavior they facilitate. For instance, by limiting disturbance and development on critical winter ranges and migratory routes that are determined specifically for each of the various migratory tactics, natural resource professionals can protect movement tactic diversity (Brakes et al., 2019; Lowrey et al., 2020;

Middleton et al., 2020; Whitehead, 2010). In general, management actions that facilitate cultural knowledge transmission and support multiple behavioral tactics will likely prove most effective in encouraging continued migration amidst changing environmental conditions and anthropogenic influences.

AUTHOR CONTRIBUTIONS

Arthur D. Middleton and Gabriel R. Zuckerman conceived the idea for this research. Gabriel R. Zuckerman led the writing and performed the analyses. Kristin J. Barker contributed initial formative feedback, Laura C. Gigliotti and Kristin J. Barker contributed to the analyses, and Arthur D. Middleton provided insight throughout the process. All authors gave valuable feedback on the manuscript, and many shared field data collected by their institution.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The novel code for the statistical analyses performed in this manuscript (Zuckerman, 2023) is available from Zenodo: https://doi.org/10.5281/zenodo.7746946. The movement data used in this study are not publicly available, as they are primarily owned by the state in which they occur or by the universities that collected the data. The movement data were obtained for this project by undertaking numerous data sharing memorandums of understanding (MOU) with various state agencies, universities, and researchers that did not include the public dispersal of the data. For data requests regarding the Madison, North Madison, Mill Creek, Silver Run, Blacktail, and Greeley herds, please reach out to Justin Gude (jgude@mt.gov) or Kelly Proffitt (kproffitt@mt.gov) from the Montana Department of Fish, Wildlife and Parks. A formal memorandum of understanding may be required for data use. For data requests regarding the Northern Herd, please reach out to Daniel Stahler (dan_stahler@nps.gov) from the Yellowstone Center for Resources or Daniel MacNulty (dan.macnulty@usu.edu) from the Department of Wildland Resources and Ecology Center, Utah State University. A formal memorandum of understanding may be required for data use. For data requests regarding the Clarks Fork herd, please reach out to Matthew Kauffman (mkauffman@usgs.gov) from the U.S. Geological Survey; Wyoming Cooperative Fish and Wildlife Research Unit. A formal memorandum of understanding may be required for data use. For data requests regarding the Cody herd, please reach out to Tony Mong (tony.mong@wyo.gov) from the Wyoming Game and Fish Department or Arthur Middleton (amiddleton@berkeley.edu) from UC Berkeley. A formal memorandum of understanding may be required for data use. For data requests regarding the Jackson herd, please reach out to Eric Cole (eric_cole@fws.gov) from the National Elk Refuge; US Fish and Wildlife Service, or Ben Wise (benjamin.wise@wyo.gov) from the Wyoming Game and Fish Department. A formal memorandum of understanding may be required for data use. For data requests regarding the Targhee herd, please reach out to Mark Hurley (mark.hurley@idfg.idaho.gov) from the Idaho Department of Game and Fish. A formal memorandum of understanding may be required for data use. For data requests regarding the Wiggins Fork herd, please reach out to Daryl Lutz (daryl.lutz@wyo.gov) from the Wyoming Game and Fish Department. A formal memorandum of understanding may be required for data use. For data requests regarding the Gooseberry herd, please reach out to Eric Maichack (eric.maichak@wyo.gov) from the Wyoming Game and Fish Department. A formal memorandum of understanding may be required for data use. For data requests regarding the Green River, Afton, Fall Creek, Hoback, Pinedale, South Wind River, and Piney herds, please reach out to Brandon Scurlock (brandon.scurlock@wyo.gov) from the Wyoming Game and Fish Department. A memorandum of understanding may be required for data use. Other datasets utilized for this research were retrieved from MODIS/Terra Surface Reflectance satellite imagery (https://cmr.earthdata.nasa.gov/search/concepts/C193529944-LPDAAC_ECS.html; Vermote, 2015); the Snow Data Assimilation System (SNODAS; https://nsidc.org/data/g02158/versions/1; National Operational Hydrologic Remote Sensing Center, 2004); the Land Change Monitoring, Assessment, and Projection (LCMAP; https://www.usgs.gov/special-topics/lcmap/lcmap-data-access; Pengra et al., 2020); and an updated version of the Wyoming Game and Fish Department's Feed Ground Locations shapefile (original: https://wgfd.wyo.gov/Wildlife-in-Wyoming/Geospatial-Data/Big-Game-GIS-Data; updated: https://github.com/gabezuckerman/Plasticity1/tree/main/covariates/feed/data). For each of the previously mentioned open-source datasets, the query details are discussed in the *Covariate extraction* section in the *Methods*.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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