Plasticity in elk migration timing is a response to changing environmental conditions


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Funding information
National Geographic Society, Grant/Award Number: Grant WW-100C-17; Knobloch Family Foundation; George B. Storer Foundation; Rocky Mountain Elk Foundation

Abstract
Migration is an effective behavioral strategy for prolonging access to seasonal resources and may be a resilient strategy for ungulates experiencing changing climatic conditions. In the Greater Yellowstone Ecosystem (GYE), elk are the primary ungulate, with approximately 20,000 individuals migrating to exploit seasonal gradients in forage while also avoiding energetically costly snow conditions. How climate-induced changes in plant phenology and snow accumulation are influencing elk migration timing is unknown. We present the most complete record of elk migration across the GYE, spanning 9 herds and 414 individuals from 2001 to 2017, to evaluate the drivers of migration timing and test for temporal shifts. The timing of elk departure from winter range involved a trade-off between current and anticipated forage conditions, while snow melt governed summer range arrival date. Timing of elk departure from summer range and arrival on winter range were both influenced by snow accumulation and exposure to hunting. At the GYE scale, spring and fall migration timing changed through time, most notably with winter range arrival dates becoming almost 50 days later since 2001. Predicted herd-level changes in migration timing largely agreed with observed GYE-wide changes—except for predicted winter range arrival dates which did not reflect the magnitude of change detected in the elk telemetry data. Snow melt, snow accumulation, and spring green-up dates all changed through time, with different herds experiencing different rates and directions of change. We conclude that elk migration is plastic, is a direct response to environmental cues, and that these environmental cues are not changing in a consistent manner across the GYE. The impacts of changing elk migration timing on predator–prey dynamics, carnivore–livestock conflict, disease ecology, and harvest management across the GYE are likely to be significant and complex.

KEYWORDS
climate change, forage, GPS, phenology, range, snow, telemetry, ungulate, Yellowstone
INTRODUCTION

Seasonal migration is an important behavioral strategy in multiple taxa, and an important ecological phenomenon in diverse ecosystems (Avgar, Street, & Fryxell, 2014; Bauer & Hoye, 2014; Harris, Thrigood, Hopcraft, Cromsigt, & Berger, 2009). Many species use seasonal migration to track emerging resources (Fryxell, Greever, & Sinclair, 1988), reduce predation risk (Hebblewhite & Merrill, 2009), or avoid disease and parasites (Altizer, Bartel, & Han, 2011). Migrations to track resources are often timed to coincide with peak plant and insect emergence (Aikens et al., 2017; Jonzén et al., 2006; Merkle et al., 2016), which are highly sensitive to climatic variation. Understanding the effects of environmental change on migration is critical for conservation because migrations play a role in many important ecosystem processes and services (Berger, 2004).

Most research exploring how changes in climate and phenology affect migration behavior has involved long-distance bird migrations (Jonzén et al., 2006; Visser, Perdeck, van Balen, & Both, 2009). Many neotropical migratory birds, cued by photoperiod, time their spring migrations to arrive on breeding grounds at peak insect emergence (Both, Bouwhuis, Lessells, & Visser, 2006; Both & Visser, 2001). Where climate change has led to earlier insect emergence, but migrants fail to track these changes, so-called “trophic mismatches” may emerge and cause population declines (Both, Van Asch, Bijlsma, Van Den Burg, & Visser, 2009; Both et al., 2006, 2010; Visser et al., 2009). However, there is growing evidence that some of these populations are adjusting their behavior, suggesting that migration, specifically migration timing, may be more plastic than previously expected (Jonzén, Hedenstrom, & Lundberg, 2007; Jonzén et al., 2006; Lameris et al., 2018) and highlighting a potential measure of resilience in the face of climate change.

Ungulate migrations are among the most dramatic of animal movements (Fryxell & Sinclair, 1988), and generally arise in response to spatial patterns of precipitation and plant emergence. In East Africa, for example, wildebeest migrate seasonally to exploit new grass growth in areas of high rainfall (Boone, Thrigood, & Hopcraft, 2006; Holdo, Holt, & Fryxell, 2009). In coastal Scandinavia, red deer time their migratory movements to higher elevations to exploit patchy snow melt which prolongs the emergence of plants via the so-called “green wave” (Albon & Langvatn, 1992; Bischof et al., 2012). In western North America, mule deer time their migration to track the green wave closely during spring migration (Aikens et al., 2017; Merkle et al., 2016; Sawyer & Kauffman, 2011). Though these and other studies have revealed some key drivers of ungulate migration, long-term, large-scale datasets are needed to fully understand the plasticity of this behavior and the potential influence of climate change on long-distance ungulate migrations.

In the Greater Yellowstone Ecosystem (GYE) of western North America, elk are the dominant ungulate and their populations (referred to here as herds) are partially migratory (Barker, Mitchell, Proffitt, & Devoe, 2018; Cole et al., 2015; Middleton et al., 2013). Migratory elk provide prey for large carnivores and scavengers, and support economically important harvests (Proffitt, Gude, Hamlin, & Messer, 2013). At the same time, these highly mobile elk harbor brucellosis (Cross, Cole, et al., 2010; Cross, Heisey, et al., 2010), which threatens domestic cattle, and their foraging can cause other conflicts such as damage to fences and crops on private land (Irby et al., 1996). Migration behavior has been studied at the individual herd level in GYE elk, revealing influences of snow accumulation (White et al., 2010), vegetation green-up (Merkle et al., 2016), harvest pressure (Proffitt et al., 2013), and supplemental feeding (Jones et al., 2014), but not at the ecosystem scale. Nor have the potential effects of recent drought and warming (Pederson et al., 2011; Shuman, 2012) been assessed with respect to elk migration, both of which have been hypothesized to influence elk reproduction (Middleton et al., 2013).

In this study, we first identify the primary environmental drivers of migration timing across the major herds of the GYE. Based on previous studies of individual populations (e.g., Jones et al., 2014; White et al., 2010), we expect that snow melt and vegetation green-up (influencing forage quality) will determine the timing of spring migration, while snow accumulation, summer biomass production (representing forage quantity), and hunting pressure will influence the timing of fall migration. We next test for temporal trends (2001-2015) in the timing of elk migration across the ecosystem. Due to earlier snow melt (Pederson et al., 2011) and later snow accumulation (Barnett et al., 2008) observed in the Rocky Mountains, we expect elk migrations will begin and end earlier in spring, and later in fall. Finally, we evaluate how key drivers of elk migration timing have changed through time and whether these changes are reflected in changes in observed elk migration timing across the GYE.

METHODS

2.1 Study area

The GYE is a 10.8 million ha, temperate ecosystem centered on the Yellowstone plateau and encompassing several surrounding mountain ranges (Noss, Carroll, Vance-Borland, & Wuerthner, 2002) (Figure 1). Its core, high-elevation habitats are dominated by alpine meadows, subalpine forests, and rocky slopes. The middle elevations are dominated by coniferous and deciduous forests, and the low elevations by shrub-steppe, grasslands, and agricultural fields. The climate is continental, with cold winters and warm summers.

This GYE is characterized by highly complex land ownership and management. Federal lands include Yellowstone and Grand Teton National Parks, 1.6 million ha of national forests, and extensive additional lands managed by the Bureau of Land Management, the US Fish and Wildlife Service, and the state-managed lands of Idaho, Montana, and Wyoming (Noss et al., 2002). Approximately 36% of the GYE is private land. Some mixed-use public and private lands are used for oil and gas development, ranching, amenity properties, and residential developments (Sawyer, Korfanta, Nielson, Monteith, & Strickland, 2017; Wright et al., 2003).
We defined nine partially migratory elk herds within the study area based on their winter and summer ranges (Figure 1). These herds winter in low-elevation shrub-steppe and grasslands on private and mixed-use public lands (Barker et al., 2018; Cole et al., 2015; Middleton et al., 2013). In spring, migratory individuals travel to high-elevation summer ranges in the national parks and forests, while resident individuals stay behind (Nelson et al., 2012). Though occasional long-distance dispersal events occur, the herds display high fidelity to their seasonal ranges.

2.2 Elk movement data

We aggregated GPS collar data for the nine elk herds examined here. Only adult, female elk are represented in the dataset due to agency emphasis on collaring and tracking females as drivers of population performance. Elk were captured via helicopter net-gunning and darting on their winter ranges between 2001 and 2015, and fitted with GPS collars that took locations once every 30 min to 24 hr for 1–3 years.
We used the program R (R Core Team, 2017) and the adeHabitatLT package (Calenge, 2006) to plot the net-squared displacement (NSD; Bunnefeld et al., 2011) for each individual elk. Net-squared displacement curves plot the straight-line distances between a starting point (the earliest point in the year in this case) and all subsequent points. Migration can be identified in NSD curves as an inverted curve where animals move away from a location then return later in a given time period, with migration start and end dates/times identified as the break points in the curve (Bunnefeld et al., 2011). For animals with multiple spring and/or fall migrations (i.e., more than 1 year of data), we randomly selected one spring and/or fall migration to avoid repeat sampling. This resulted in 231 spring migrations and 180 fall migrations (Table 1). We visually inspected the individual NSD profiles to determine start and end dates for spring and fall migrations (similar to Aikens et al., 2017).

We estimated individual home ranges before, during, and after spring and fall migrations using dynamic Browning Bridge Movement Models (dBBMM; Kranstauber, Kays, Lapoint, Wikelski, & Safi, 2012). We determined pre-migration and post-migration space use by assessing telemetry data 14 days prior to the start date and 14 days after the end date. During-migration space use was estimated by assessing all telemetry data occurring while an individual was migrating, resulting in three dBBMMs produced for each migration event. We defined individual home ranges using the 95% isopleth of the dBBMM utilization distributions. We distinguished migratory from resident elk, defining migratory individuals as those using nonoverlapping seasonal ranges (Middleton et al., 2013). All environmental variables were summarized at the home range scale by taking the mean value of all pixels falling with each home range.

### 2.3 | Environmental covariates
#### 2.3.1 | MODIS-derived environmental data

We assessed vegetation phenology, productivity, and canopy cover annually across the study period. Spring green-up and peak rate of change in vegetation greenness were derived from phenology curves (see Bischof et al., 2012; Merkle et al., 2016 for details) using the Normalized Difference Vegetation Index (NDVI) product (250 m spatial resolution) obtained from the Moderate Resolution Imaging Spectroradiometer’s (MODIS) suite of sensors. Phenology curves generally involve plotting of a measure of vegetation “greenness” (i.e., NDVI) throughout the year and identifying dates when changes in greenness occur. Phenology curves built using NDVI values throughout the year allow for spatially explicit phenological dates to be estimated at the pixel level including day of initiation of photosynthesis (green-up) and day of peak green-up. We obtained the initiation date of plant senescence from the MODIS Land Cover Dynamics product. We estimated the annual vegetation biomass production using the MODIS Net Primary Productivity (NPP) product (1 km spatial resolution) and the annual canopy cover using the MODIS Vegetation Continuous Fields product (250 m spatial resolution). All MODIS vegetation data is freely available and can be found at: https://e4ftl01.cr.usgs.gov/MOLT/.

We defined the date of spring snow melt as the first day in the first grouping of at least eight contiguous snow-free days on a pixel, and the date of fall snow accumulation as the first day in the first grouping of at least eight contiguous days with continuous snow cover. We estimated both snow variables using the MODIS Snow Cover product (500 m spatial resolution) which is binned at 8 day intervals and is available at: https://n5eil01u.ecs.nsidc.org/MOST/MOD10A2.006/.

#### 2.3.2 | Topography

We derived all topographic variables from the Shuttle Radar Topography Mission (SRTM) digital elevation model at a 30 m spatial resolution (Koch & Lohmann, 2000). We calculated slope and aspect directly from the SRTM digital elevation model. We converted aspect into eastness (sin of aspect) and northness (cosine of aspect) values ranging from −1 to 1 in both cases. We used slope to calculate a terrain roughness index (the mean of the differences between a focal cell and a queen's case neighborhood).

### 2.4 | Spatial covariates

We estimated an individual’s migration distance as the linear length of the migration period GPS locations. We measured two hunting metrics designed to represent hunting effects on migration timing during fall migrations: (a) whether an individual was in an active hunt area at the start of fall migration and (b) the proportion of time spent in an active hunt area during fall migration. Start and end dates of general hunting seasons were obtained from Idaho Department of Fish and Game, Montana Fish, Wildlife and Parks, and Wyoming Game and Fish Department.

#### 2.5 | Statistics

#### 2.5.1 | Environmental determinants of elk migration timing

We modeled winter range departure date, summer range arrival date, summer range departure date, and winter range arrival date

### Table 1 Sample sizes for spring and fall migrations by herd. Individuals with multiple migrations (i.e., more than 1 year of data) had 1 year randomly selected avoid repeat sampling

<table>
<thead>
<tr>
<th>Herd</th>
<th>Spring</th>
<th>Fall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blacktail</td>
<td>47</td>
<td>26</td>
</tr>
<tr>
<td>Clarks Fork</td>
<td>13</td>
<td>10</td>
</tr>
<tr>
<td>Cody</td>
<td>17</td>
<td>17</td>
</tr>
<tr>
<td>Jackson</td>
<td>40</td>
<td>40</td>
</tr>
<tr>
<td>Madison Valley</td>
<td>36</td>
<td>33</td>
</tr>
<tr>
<td>Northern</td>
<td>46</td>
<td>39</td>
</tr>
<tr>
<td>Paradise Valley</td>
<td>11</td>
<td>7</td>
</tr>
<tr>
<td>Sand Creek</td>
<td>15</td>
<td>8</td>
</tr>
<tr>
<td>Wiggins Fork</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>231</td>
<td>180</td>
</tr>
</tbody>
</table>
(date being represented by day of year [DOY]) against environmental covariates in linear mixed-effects models (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). For migrations arriving on winter range after December 31, DOY extended beyond 365 (i.e., January 5 would be DOY 370). These models were designed to allow for both perception and memory to influence migration timing. Ungulates can initiate migration due to the perception of local resource gradients or memory of previously available resource gradients. Using perception may help ungulates "surf" the green wave effectively (Aikens et al., 2017; Singh, Grachev, Bekenov, & Milner-Gulland, 2010). In contrast, drawing upon memory may help ungulates predict when and where beneficial foraging conditions may occur in future (Fagan et al., 2013), thus "jumping" the green wave (Bischof et al., 2012; Bracis & Mueller, 2017; Mueller, Fagan, & Grimm, 2011).

We included environmental variables in the winter- and summer range departure models which described current environmental conditions (perception component) or environmental conditions which an individual might anticipate given experience (i.e., future topography and forage conditions; memory component). We included spring phenological events (i.e., vegetation green-up) in the spring models and fall phenological events (i.e., plant senescence) in fall models. We did not include highly stochastic variables such as future snow accumulation or snow melt conditions in the departure models (Table 2). We included all conditions experienced after departure date in summer- and winter range arrival date models.

In fall, we considered hunting effects in the summer range departure date and winter range arrival date models as two covariates. The first was a binary variable describing whether an individual was in an active hunt area when it began to migrate. The second was an interaction term between mean canopy cover within fall migration corridors (representing security habitat; Proffitt, Grigg, Hamlin, & Garrott, 2009) and the proportion of fall migration the individual spent in active hunt areas. We scaled and centered all continuous variables prior to model-building and assessed continuous variables for multicollinearity prior to model construction using Pearson's r.

<table>
<thead>
<tr>
<th>Category</th>
<th>Winter range departure</th>
<th>Summer range arrival</th>
<th>Summer range departure</th>
<th>Winter range arrival</th>
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<tbody>
<tr>
<td>Forage</td>
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<td>Mig green-up</td>
<td>WR NPP</td>
<td>Mig NPP</td>
</tr>
<tr>
<td></td>
<td>WR NPP</td>
<td>Mig NPP</td>
<td>SR NPP</td>
<td>Mig NPP</td>
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<td></td>
<td>Mig green-up</td>
<td>Mig green-up</td>
<td>Mig senescence</td>
<td>Mig senescence</td>
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<td>Mig NPP</td>
<td>Mig NPP</td>
<td>Mig senescence</td>
<td>Mig NPP</td>
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<td></td>
<td>SR green-up</td>
<td>SR green-up</td>
<td>WR senescence</td>
<td>SR senescence</td>
</tr>
<tr>
<td></td>
<td>SR NPP</td>
<td>SR NPP</td>
<td>WR NPP</td>
<td>WR NPP</td>
</tr>
<tr>
<td>Security cover/ hunting</td>
<td>WR canopy cover</td>
<td>Mig canopy cover</td>
<td>SR canopy cover</td>
<td>PH*Mig canopy cover</td>
</tr>
<tr>
<td></td>
<td>Mig canopy cover</td>
<td>Mig canopy cover</td>
<td>PH*Mig canopy cover</td>
<td>PH*Mig canopy cover</td>
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<td></td>
<td>SR canopy cover</td>
<td>SR canopy cover</td>
<td>WR canopy cover</td>
<td>WR canopy cover</td>
</tr>
<tr>
<td>Topography</td>
<td>WR elevation</td>
<td>Mig elevation</td>
<td>WR elevation</td>
<td>Mig elevation</td>
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<tr>
<td></td>
<td>WR slope</td>
<td>Mig roughness</td>
<td>Mig roughness</td>
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<td></td>
<td>WR northness</td>
<td>Mig northness</td>
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<td></td>
<td>WR eastness</td>
<td>Mig eastness</td>
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<td>Mig eastness</td>
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<td></td>
<td>SR elevation</td>
<td>SR elevation</td>
<td>WR elevation</td>
<td>WR elevation</td>
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<td></td>
<td>SR slope</td>
<td>SR slope</td>
<td>WR slope</td>
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<td>SR northness</td>
<td>SR northness</td>
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<td></td>
<td>SR eastness</td>
<td>SR eastness</td>
<td>WR eastness</td>
<td>WR eastness</td>
</tr>
<tr>
<td>Snow</td>
<td>WR snow melt date</td>
<td>Mig snow melt date</td>
<td>Mig snow accumulation date</td>
<td>Mig snow accumulation date</td>
</tr>
<tr>
<td>Spatial</td>
<td>Migration distance</td>
<td>Migration distance</td>
<td>Migration distance</td>
<td>Migration distance</td>
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</tbody>
</table>
correlations and removed the least directly applicable variable of any pair exceeding $r = 0.8$.

Our model selection procedure began by adding all fixed effects, including interaction terms, in a linear model structure, then testing two models using a likelihood ratio test: herd identity as a random intercept and a model lacking a random intercept (Zuur et al., 2009). We also assessed all models for homoscedasticity, linearity, and normally distributed model residuals. Once we determined whether a random intercept was necessary, we removed the fixed effects coefficient or interaction term with the lowest $t$ value and tested the reduced model against the previous model using likelihood ratio tests (Zuur et al., 2009). We arrived at the final model when dropping any coefficient resulted in a significant decline in the reduced model's likelihood ratio. We tested all final models again for multicollinearity using variance inflation factors (VIF) and in no cases did any VIFs exceed a value of two (Zuur, Ieno, & Elphick, 2010). We assessed model fit using the Nakagawa and Schielzeth's (Nakagawa & Schielzeth, 2013) $R^2$ method applied to mixed models.

### 2.5.2 GYE-wide changes in elk migration timing

We tested for changes in elk migration timing across the GYE using generalized additive mixed models (Bolker et al., 2009) with herd as a random intercept. We tested this model structure against a model lacking a random intercept using likelihood ratio tests (Zuur et al., 2009). We included year as the fixed effect to test for changes in departure date and arrival date from winter and summer ranges. Due to potential bias associated with the Northern herd being the sole source of data for the years 2001 and 2002, we reran all models without Northern herd individuals to ensure results were consistent with models including all herds. We assessed all models for homoscedasticity and normally distributed model residuals.

### 2.5.3 Predicted herd-level changes in migration timing

We predicted herd-level changes in migration timing using the models relating environmental conditions to elk migration timing and annual environmental data from 2001 to 2015. We summarized all environmental variables included in the final models by herd summer and winter ranges, as well as along migration routes, by first compiling all GPS locations for each individual during winter and summer and then computing herd-level home ranges using Kernel density estimates and the 95% isopleth. The resulting herd ranges are inherently spatially static; however, White et al. (2010) demonstrated that Northern herd individuals displayed strong fidelity to particular summer and winter ranges which lends support to this assumption. We measured all stochastic environmental variables annually while topography, migration distance, and the proportion of days spent in an active hunt zone were held at their means. To assess whether any predicted herd-level migration timings had significantly changed from 2001 to 2015, we used generalized least squares (GLS) regression models relating the predicted migration timings to year (Zuur et al., 2009).

### 2.5.4 Temporal changes in important environmental cues

We tested for temporal changes in environmental conditions found to influence elk migration timing at the pixel level using Theil–Sen's nonparametric regression (Rickbeil et al., 2018; Sen, 1968) and Mann–Kendall tests (Kendall, 1955). This is a robust approach for estimating changes in time-series data which violate parametric assumptions. We examined herd level variation in rates of change in environmental conditions on both winter and summer ranges. We randomly sampled 200 Theil–Sen's slopes in each herd's range and used GLS models to test for differences between herd ranges on both winter and summer ranges while also accounting for spatially structured samples using a Gaussian spatial autocorrelation structure (Rickbeil, Hermosilla, Coops, White, & Wulder, 2017; Zuur et al., 2009). The use of a spatial autocorrelation structure allowed us to account for spatially structured Theil–Sen's slope samples within herd ranges.

### 3 RESULTS

We aggregated data from 414 collared elk within the 9 herds, resulting in a total sample of 231 spring migrations and 180 fall migrations from unique individuals. Elk migration distance ranged from 12 to 202 km. The mean departure from winter range was on DOY 131 (standard deviation (SD) = 24) while the mean arrival date on summer range was DOY 152 (SD = 23). The length of spring migration ranged from 2 to 90 days. The mean departure from summer range was DOY 300 (SD = 22) while the mean arrival on winter range occurred on DOY 306 (SD = 76). The length of fall migration ranged from 3 to 84 days.

### 3.1 Environmental determinants of migration timing

The fixed effects in all four migration models estimated migration timing with moderate-to-high levels of accuracy. Model fits ranged from marginal $R^2$ values of 0.44 to 0.72, indicating that individual elk across these nine herds respond to largely the same environmental cues governing migration timing. In all cases including herd as a random intercept resulted in improved model fit.

The final model of winter range departure date contained seven fixed effects (marginal $R^2 = 0.65$). Elk departed later from winter ranges with more available forage biomass (i.e., open, highly productive winter ranges) and later snow melt (Figure 2). This was balanced by individuals anticipating future forage opportunities specifically earlier green-up dates within migration corridors.

The final model of summer range arrival date contained four fixed effects (marginal $R^2 = 0.72$). Elk arrived later on summer ranges with later snow melt within migration corridors and on summer ranges
(Figure 2). Increasing migration distance and topographic roughness within the migration corridor also resulted in later arrival dates on summer ranges.

The final model of summer range departure date contained seven fixed effects, including an interaction term between canopy cover and the proportion of time spent in an active hunt area during migration (marginal $R^2 = 0.44$). Elk departed later from summer ranges with later snow accumulation; interestingly, elk departed earlier from more productive summer ranges (Figure 2). Individuals that were more exposed to hunting pressure (more time spent in open canopy active hunt areas) left summer range earlier.

The final model of winter range arrival date contained seven fixed effects including an interaction term between canopy cover and the proportion of time spent in an active hunt area during migration (marginal $R^2 = 0.45$). Elk arrived later on winter ranges when they migrated through corridors with later snow accumulation, and when their
winter ranges had later snow accumulation. Increasing canopy cover on winter range tended to promote earlier arrival dates (Figure 2). Like fall migration start dates, individuals that were more exposed to hunting pressure tended to arrive earlier on winter ranges.

### 3.2 | GYE-wide changes in migration timing

At the GYE scale, winter range departure date varied annually from 2001 to 2015 ($F = 4.22$, $p < 0.001$; Figure 3); however, winter range departure date in 2001 and 2015 was DOY 129 in both cases. Summer range arrival date varied in a similar fashion to winter range departure date ($F = 5.62$, $p < 0.001$); however, there was a slight increase in arrival date on summer range from DOY 144 in 2001 to 156 in 2015. No change in summer range departure date was detected ($F = 2.05$, $p = 0.15$). Arrival date on winter range however increased by almost 50 days, from DOY 285 in 2001 to 334 in 2015 ($F = 11.07$, $p < 0.001$). In all cases including herd as a random intercept resulted in improved model fit.

### 3.3 | Predicted herd-level changes in migration timing

Significant changes in the GLS modeled winter range departure dates were detected in the three most eastern herds—the Cody, Clarks Fork, and Wiggins Fork herds—with all three having later departure dates (approximately 10 days later across the 15-year period) from 2001 to 2015 (Figure 4). The Paradise Valley herd was the only herd to have significant predicted changes in summer range departure date and winter range arrival date, with both becoming earlier from 2001 to 2015.

### 3.4 | Temporal changes in important environmental cues

We detected spatiotemporal changes in the three most important and dynamic environmental conditions relating to migration timing: snow melt, snow accumulation, and spring green-up. The rate
of change in snow melt date varied by herd on summer \( (F = 40.65, p < 0.001) \) and winter ranges \( (F = 71.12, p < 0.001) \), with the western herds showing significant advancement and the eastern herds showing significant delay—though the rates of change were larger on winter than summer range (Figure 5). Similarly, the rate of change in snow accumulation date varied by herd on summer \( (F = 8.22, p < 0.001) \) and winter ranges \( (F = 24.45, p < 0.001) \), with western herds seeing slightly later snow accumulation, or no change, on summer range. On winter range, the eastern herds, except the Wiggins Fork herd, all experienced early snow accumulation dates overall. Green-up date became earlier in five of nine predominantly western herds on winter range \( (F = 2.76, p = 0.005) \). On summer range, however, green-up date became earlier on only one herd range and became later on two eastern herds' winter ranges \( (F = 2.18, p = 0.02) \).

4 | DISCUSSION

Despite the spatial separation of the nine herd's summer and winter ranges, our findings revealed a large shared response across the nine major migratory elk herds in the GYE to important environmental cues influencing when elk started or ended their seasonal migrations. This suggests that elk migration timing across the GYE is structured to a large extent by bottom-up processes governing forage and snow conditions, regardless of herd, supporting the prediction that plasticity in ungulate migration behaviors may be a resilient strategy allowing ungulates to adapt to changing climatic conditions. The decision to depart winter range reflected a trade-off between immediate and future foraging conditions, indicating that local resources and anticipated future foraging opportunities were both important factors governing when individuals migrated off winter range. Once an individual began migrating, arrival on summer range was strongly influenced by the timing of snow melt. We found that summer range departure also reflected trade-offs between present and future conditions—specifically, local forage versus future exposure to hunting pressure, which represents a top-down pressure. An individual's arrival back to winter range was largely dictated by snow accumulation and, again, exposure to hunting.

The interannual variation in migration timing, particularly winter range departure date and summer range arrival date, indicates a significant plasticity in elk migration timing. Given the strength of the winter range departure model and summer range arrival model, this variation is likely a direct result of interannual variation in snow melt and/or spring green-up. The ability of elk to adjust their migration timing to match environmental conditions suggests that, through migration, elk can maintain their access to high-quality forage even as climate change alters when and where these conditions occur.
This result echoes recent studies of bird migrations which highlight a greater degree of flexibility in response to changing conditions than originally believed (Jonzén et al., 2006, 2007; Lameris et al., 2018). Though the mechanisms underlying this flexibility in birds and ungulates differ, insights from both suggest a measure of resilience to a changing climate.
The GYE-level winter range departure, summer range arrival, and summer range departure date models all agreed to a large degree with the predicted changes in herd-level migration timing. The predicted changes in winter range departure date in the three most eastern herds were likely due to significantly later snow melt conditions on winter range. Unsurprisingly, the east–west gradient in the direction and strength of changes in snow melt and green-up dates resulted in an east–west gradient in predicted departure dates from winter range. However, when considering spring migration as a whole, 17 out of 18 models (with the majority being nonsignificant) indicated that winter range departure and summer range arrival dates are becoming later (the exception being the arrival date on summer range for the Blacktail herd which had a nonsignificant earlier arrival date). This may indicate a GYE-wide pattern of later spring migration dates which is not able to be fully detected across a relatively short (15 year) study period. Jonzén et al. (2007) demonstrated how prebreeding mortality, territories, and environmental conditions result in an optimal migration strategy of delaying a response to shifting seasonal resources in migrant bird species. Similar complex responses may be resulting in delayed responses to shifting environmental cues for elk across the GYE.

A major unexplained result is the significantly later winter range arrival date detected at the GYE scale versus the predicted changes in winter range arrival date using environmental covariates. Winter range arrival date estimated directly using telemetry data suggested winter range arrival dates are on average 50 days later in 2015 than in 2001. However, our predictions of migration timing based on environmental conditions could not account for this dramatic change in timing. This gap suggests that we omitted a major environmental factor in our model or that the trend is not a result of environmental changes. One possibility is that snow accumulation date does not fully account for the effect of snow. Snow depth affects elk movement patterns (Sweeney & Sweeney, 1984); if snow depth patterns are changing in manner which is inconsistent with snow accumulation dates, then this could be a factor influencing the large delay in winter range arrival date detected here. Alternatively, we posit that this change may be a result of top-down factors such as changing hunting pressure and nonhuman predation pressure. The timing and extent of human hunting pressure on elk changes annually across the GYE (Proffitt et al., 2013) and may have changed directionally during our study. The influence of hunting pressure has been previously shown to affect elk habitat selection, with elk selecting for cover habitats and habitat with reduced or no human access (Proffitt et al., 2009, 2010, 2013). Wolf and bear populations have increased in the past two decades in the GYE, and effects on elk demography are well documented (e.g., Middleton et al., 2013).

Our results indicate that elk engage, to some degree, in “green-wave” surfing; individuals delayed departure from winter range when green-up occurred later during migration. In a recent multispecies study of green-wave surfing, Merkle et al. (2016) found some evidence of this behavior in elk, but the association was weaker than in other tested ungulate species (e.g., mule deer). Individuals leaving winter range later when green-up along migration routes also occurs later could either be a result of perception of current conditions or, alternatively, memory of how conditions on winter range associate with green-up during migration. If green-up occurs in an ordered manner along migration corridors, then perception of local conditions would allow for individuals to adjust timing to match green-up timing, similar to Aikens et al.’s (2017) study of mule deer green-wave surfing in Wyoming. However, if green-up occurs in a disordered or patchy manner, similar to Bischof et al.’s (2012) study of red deer in Scandinavia, then some form of memory of local conditions informing how individuals anticipated green-up in migration corridors is likely, supporting theory of memory of current conditions informing how animals predict future conditions (Bracis & Mueller, 2017; Fagan et al., 2013).

The degree of variation in changes in snow melt, snow accumulation, and vegetation green-up dates on summer and winter ranges represents a significant challenge for both migratory elk and elk management. We established that the environmental cues which result in spring and fall migration are shared to a large degree across herds in the GYE. However, the direction of changes in snow melt, snow accumulation, and green-up are not consistent across herds or seasonal ranges. If migratory elk continue to react to these environmental cues in a similar fashion in the future and these directional changes in snow melt, snow accumulation, and vegetation green-up continue, we can expect increasing asynchrony in migration timing among different herds across the GYE. Climate projections indicate warming and drying across the GYE into the 21st century (Westerling, Turner, Smithwick, Romme, & Ryan, 2011). Reduced snowfall in spring and/or fall will likely mean prolonged periods of time spent on summer ranges.

The timing of elk migrations we describe here determines the seasonal redistribution of thousands of herbivores throughout the GYE every year. These animals play many roles in the ecosystem, as consumers, prey animals, big game, and disease vectors. Carnivore–livestock conflict, specifically wolf predation on cattle, depends on migratory elk migration timing, specifically when elk migrate off winter ranges thus removing an important prey species from local wolf packs (Laporte, Muhly, Pitt, Alexander, & Musiani, 2010). This is hypothesized to result in an increase in wolf depredation events on cattle as wolves shift from hunting elk to cattle (Nelson et al., 2012). The transmission of zoonotic disease between elk and cattle depends on conmingling levels at particular times of the year (Cross, Cole, et al., 2010; Cross, Heisey, et al., 2010). Specifically, in the case of brucellosis, the amount of time elk and cattle coningle in late winter and spring is the primary driver of transmission risk and changing migration timings will clearly alter this dynamic (Cross, Cole, et al., 2010; Cross, Heisey, et al., 2010; Merkle et al., 2018). Harvest management is another area of potential concern. Most GYE elk populations are partially migratory, and hunting seasons are often timed to promote harvest of resident elk and avoid migrant elk, or to maintain a target ratio of migrant: resident harvest. Improved understanding and continued monitoring of herd-specific migration timings should
allow for proactive harvest planning to focus harvest pressure on the desired elk subpopulations.

Globally, long-distance ungulate migrants are declining (Berger, 2004; Bolger, Newmark, Morrison, & Doak, 2008; Wilcove & Wikelski, 2008), including barren-ground caribou (Vors & Boyce, 2009), bison (LaLiberte & Ripple, 2004), wildebeest (Homewood et al., 2001; Ogutu & Owen-Smith, 2003), and mule deer (Sawyer et al., 2017) populations. The causes are varied but include habitat loss and fragmentation—including barriers to migration (Sawyer, Lindzey, & McWhirter, 2005), resource development (Sawyer et al., 2017), predation (Hervieux, Hebblewhite, Stepnisky, Bacon, & Boutin, 2015), harvest, and climate change (directly [Ogutu & Owen-Smith, 2003] and indirectly [Sharma, Couturier, & Côté, 2009; Wilcove & Wikelski, 2008]) have all been implicated in the declines of migratory ungulates. Similarly, migratory elk in certain GYE herds are declining in absolute numbers (Middleton et al., 2013) and as a proportion of herd size (Cole et al., 2015) and similar environmental and anthropogenic factors have been put forward as causal reasons for the declines in population recruitment (Middleton et al., 2013, 2018). Understanding the drivers of migration behavior is an important step in predicting how future changes in environment will impact the migratory segments of these herds. Finally, applying our knowledge of changes in migration timing to investigate access to forage, predator–prey dynamics, and migrant elk demographics will allow for a more complete picture of the effects of changing climates for future management of elk across the GYE.

ACKNOWLEDGEMENTS

Numerous cooperators shared elk movement data, including the Wyoming Game and Fish Department, Montana Fish, Wildlife and Parks, Idaho Department of Fish and Game, US National Park Service (Yellowstone and Grand Teton National Parks), US Fish and Wildlife Service (National Elk Refuge), and the Wildlife Conservation Society. Dan MacNulty and Dan Stahler provided important feedback during the development of this manuscript. We thank the many biologists and pilots who were involved in collecting data for this project. ADM and GJMR received funding for this work from the National Geographic Society (Grant WW-100C-17), the Knoebel Family Foundation, the George B. Storer Foundation, and the Rocky Mountain Elk Foundation. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

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How to cite this article: Rickbeil GJM, Merkje KA, Anderson G, et al. Plasticity in elk migration timing is a response to changing environmental conditions. *Glob Change Biol*. 2019:00:1–14. https://doi.org/10.1111/gcb.14629