Drought reshuffles plant phenology and reduces the foraging benefit of green-wave surfing for a migratory ungulate

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Abstract
To increase resource gain, many herbivores pace their migration with the flush of nutritious plant green-up that progresses across the landscape (termed “green-wave surfing”). Despite concerns about the effects of climate change on migratory species and the critical role of plant phenology in mediating the ability of ungulates to surf, little is known about how drought shapes the green wave and influences the foraging benefits of migration. With a 19 year dataset on drought and plant phenology across 99 unique migratory routes of mule deer (Odocoileus hemionus) in western Wyoming, United States, we show that drought shortened the duration of spring green-up by approximately twofold (2.5 weeks) and resulted in less sequential green-up along migratory routes. We investigated the possibility that some routes were buffered from the effects of drought (i.e., routes that maintained long green-up duration irrespective of drought intensity). We found no evidence of drought-buffered routes. Instead, routes with the longest green-up in non-drought years also were the most affected by drought. Despite phenological changes along the migratory route, mule deer closely followed drought-altered green waves during migration. Migrating deer did not experience a trophic mismatch with the green wave during drought. Instead, the shorter window of green-up caused by drought reduced the opportunity to accumulate forage resources during rapid spring migrations. Our work highlights the synchronization of phenological events as an important mechanism by which climate change can negatively affect migratory species by reducing the temporal availability of key food resources. For migratory herbivores, climate change poses a new and growing threat by altering resource phenology and diminishing the foraging benefit of migration.

Keywords
climate change, migration, mule deer, normalized difference vegetation index, Odocoileus hemionus, the Green Wave Hypothesis, trophic mismatch, Wyoming
1 | INTRODUCTION

Altered phenology is a ubiquitous signature of climate change (Parmesan & Yohe, 2003), with implications for animal movement (Middleton et al., 2013), fitness (Lameris et al., 2018), species interactions, and ecosystem functioning (Deacy et al., 2017). When the availability of a key resource is dictated by phenology (e.g., fruiting, flowering), high-quality resources may only be available for a short window of time at a specific foraging location. By moving to exploit heterogeneity in resource phenology across space, mobile consumers can increase resource gain by 50%–1,000% (Armstrong, Takimoto, Schindler, Hayes, & Kauffman, 2016; Bronstein, Gouyon, Gliddon, Kjellberg, & Michaloud, 1990; Ruff et al., 2011), often exceeding potential resource gain that would result from increased resource abundance alone (Armstrong et al., 2016). Indeed, from fig wasps (superfamily Chalcidoidea) to grizzly bears (Ursus arctos; Deacy, Leacock, Armstrong, & Stanford, 2016; Schindler et al., 2013), mobile consumers increase resource acquisition by moving to exploit foraging resource pulses (Armstrong et al., 2016). Likewise, migration is an adaptive strategy that allows animals to exploit resource variability across seasonal ranges (Alerstam, Hedenstrom, & Akesson, 2003). Along the route itself, the way that resources propagate between seasonal ranges shapes the timing (Monteith et al., 2011), pace (Bauer, Van Dinther, Hegda, Klaassen, & Madsen, 2008; Sawyer & Kauffman, 2011), and the resulting foraging benefit of migration (Middleton et al., 2018). Despite growing concern about the influence of climate change on migratory taxa (Møller, Rubolini, & Lehikoinen, 2008), little is known about how climate influences the phenological pace and pattern of resources that herbivores exploit during migration (Aikens et al., 2017).

For many ungulates, high-quality forage is a fleeting resource, because the phenological stage of plant growth that maximizes energy intake occurs at intermediate biomass (hereafter green-up; Drent, Ebbeinge, & Weijand, 1978; Fryxell, 1991; van der Graaf, Stahl, Klimkowska, Bakker, & Drent, 2006). The flush of spring green-up that progresses across the landscape is often referred to as the “green wave.” The Green Wave Hypothesis conceptualizes the notion that herbivore migration manifests, in part, as a strategy to track the progression of young and nutritious plants via a behavior called “surfing the green wave” (Drent et al., 1978; van der Graaf et al., 2006). An accumulating body of evidence indicates that migratory ungulates that surf the green wave lengthen their exposure to high-quality food, increasing energy intake and fitness (Albon & Langvatn, 1992; Middleton et al., 2018; Mysterud, Langvatn, Yoccoz, & Stenseth, 2001). Relatedly, the Greenscape Hypothesis posits that the way the green wave progresses across the landscape should determine how well migrating ungulates surf and thus the foraging benefit of migration (Aikens et al., 2017). Specifically, the “greenscape,” or the phenological landscape characterized by the rate, duration, and order of green-up along an animal’s migratory route strongly influences how well individuals surf (Aikens et al., 2017). Migratory routes with prolonged green-up that progresses sequentially from one seasonal range to the other facilitate green-wave surfing, whereas routes with short green-up that progresses non-consecutively constrain surfing (Aikens et al., 2017). Quantifying greenscapes provides a tool to compare the phenological quality of routes (Aikens et al., 2017) and evaluate how the green wave is altered by climate. The effects of climate change include compression of spring green-up along elevational gradients (Vitasse, Signarbieux, & Fu, 2018), which may have consequences for migratory ungulates that track the progression of the green wave from low to high elevation.

Shifts in temperature and precipitation due to climate change will likely impact the green wave. Climate change is predicted to result in more frequent and severe drought in water-limited systems, which compose ~40% of the terrestrial landmass (Gosling & Arnell, 2016; IPCC, 2014; McLaughlin et al., 2017). Studies on the impact of climate change highlight climatic water balance—or the availability of moisture relative to its need—as a key driver of shifts in the distribution and phenology of plants (McLaughlin et al., 2017), sometimes playing a more important role than temperature alone (Crimmins, Dobrowski, Greenberg, Abatzoglou, & Mynsberge, 2011). Additionally, in mountainous systems, snow deposition strongly influences the components of the greenscape (Christianson, Klaver, Middleton, & Kauffman, 2013; Pettorelli, Mysterud, Yoccoz, Langvatn, & Stenseth, 2005), such that drought (e.g., reduced snowpack and spring rainfall) is likely to alter the progression of the green wave and the ability of migrants to surf. In topographically diverse areas, however, the effect of drought is likely to vary across space, potentially resulting in what have been termed “hydrologic refugia,” or mesic areas that are decoupled from climate because of unique hydrological processes (Dobrowski, 2011; McLaughlin et al., 2017). For migratory ungulates, routes that exhibit long green-up durations even during intense drought could serve as hydrologic refugia (hereafter drought-buffered routes) that would ameliorate the effects of drought on migratory ungulates. Although the concept of hydrologic refugia is appealing for conservation, whether drought-buffered routes exist in this system. For the first objective, we examined the impact of drought both across and within years. To investigate the effect of drought across years, we evaluated support for two alternative hypotheses: (a) to quantify the effect of drought on the pattern and progression of the green wave, and (c) to determine if drought-buffered routes exist in this system. For the first objective, we examined the impact of drought both across and within years. To investigate the effect of drought across years, we evaluated support for two alternative mechanisms by which drought influences green-wave surfing and the foraging benefit of migration. Specifically, we investigated if drought constrains how migrants surf the green wave, via either (a) a trophic mismatch (Post & Forchhammer, 2008; Visser, Noordwijk, Tinbergen, & Lessells, 1998) during migration or (b) a reduction in resource availability along the migratory route. In this analysis, we defined a trophic mismatch as a misalignment between migratory movements.
and peak green-up along the route. To disentangle these two potential mechanisms, we evaluated green-wave surfing during both the period when each animal was migrating and during a fixed time window representing the maximum period that green-up was available across years (hereafter 120-day period; Figure 1). Specifically, if drought causes a mistimed migration, animals should deviate farther from peak green-up during both the migration period and the 120-day period in dry years compared with wet years (as indicated by a shift in the distribution of Days-From-Peak away from zero for both time periods in Figure 1d). Alternatively, if drought compresses resource availability across time, but animals adjust their movements to track altered green waves during migration (Figure 1e), a decline in green-wave surfing will only occur during the 120-day period and not during the migration period (as indicated by a shift in Days-From-Peak away from zero only for the 120-day period in Figure 1f). Finally, to examine spatial heterogeneity in drought, we compared surfing across routes exposed to varying drought intensities within a given year.

2 | MATERIALS and METHODS

2.1 | Study area

Our study took place in western Wyoming, United States (42°25′N, 110°42′W), which has a semiarid climate. Mule deer migrate from low elevation winter ranges (~1,800–2,300 m), dominated by sagebrush steppe (Artemisia spp.) to mid (~2,300–2,750 m) or high (>2,750 m) elevation summer ranges, comprised of a mix of aspen (Populus tremuloides), sagebrush, conifer (Pinus spp.), and tall forb communities (Figure S1; Aikens et al., 2017).

2.2 | Green-wave surfing

We captured 99 adult (>1 year old), female mule deer and fitted them with GPS collars from 2013 to 2015. Animal capture and handling methods were approved by the Institutional Animal Care and Use Committee at the University of Wyoming (Protocol #20151204KM00135-01). Capture and collaring protocols were described in detail in Aikens et al. (2017). We used GPS movement data to quantify green-wave surfing and delineate migratory routes.

To quantify green-wave surfing, we used two metrics derived from the Instantaneous Rate of Green-up (IRG; Bischof et al., 2012). The IRG is a metric of spring green-up, which is derived from remotely-sensed Normalized Difference Vegetation Index (NDVI), a metric that has successfully been used to approximate vegetation growth and biomass (Petitorelli et al., 2005) as well as forage quality (Garrouette, Hansen, & Lawrence, 2016; Hamel, Garel, Fest-Aubin, Gaillard, & Cote, 2009) for ungulates in mountainous systems. Additionally, metrics derived from IRG were correlated strongly with on-the-ground metrics of forage quality in the Greater Yellowstone Ecosystem, where our study took place (Geremia et al., 2019). To calculate IRG, we cleaned and processed NDVI data (calculated from bands 1 and 2 of MOD09Q1, 250 m² pixels, 8 day temporal resolution) to reduce noise and bias from snow cover (Bischof et al., 2012; Merkle et al., 2016). We followed the methods of Bischof et al. (2012) with two deviations: (a) we used MOD09Q1 to calculate NDVI at an 8 day interval and (b) we used the snow flags from MOD09Q1 to set the dates when NDVI values were floored instead of using a fixed window (Merkle et al., 2016). We calculated...
IRG by taking the first derivative of a logistic curve fit to a time series of the processed NDVI data (Bischof et al., 2012). The resulting IRG curve peaks when the change in NDVI is most rapid—which occurs at intermediate biomass and peak green-up for the corresponding pixel (Bischof et al., 2012). According to the Forage Maturation Hypothesis, intermediate biomass should provide the highest quality forage for ungulates by balancing digestibility and intake rate (Fryxell, 1991).

We derived the following two metrics from the IRG curve: Days-From-Peak IRG and mean IRG. Days-From-Peak is calculated as the absolute difference in days between the date of peak IRG at a given location and the date that an individual used the location (Aikens et al., 2017). Days-From-Peak represents the behavioral component of surfing with a value of zero indicating perfect surfing, or a perfect match between date of peak green-up and date of animal use at a given location. We used the absolute value to avoid biasing the Days-From-Peak metric, so that positive values indicating late surfing did not cancel out negative values indicating early surfing when averaged together to calculate an overall metric of surfing behavior. The IRG value an individual experiences indexes potential resource gain by considering both deer behavior and the rate of green-up at a given point on the landscape (Aikens et al., 2017). For each GPS location, we extracted the value from the IRG curve that corresponded to the NDVI pixel visited on the date of animal use to quantify exposure to spring green-up. Because the IRG curve is scaled between zero and one, an IRG value of one represents the highest potential resource gain (Bischof et al., 2012). Use of both metrics allowed us to decompose the effect of drought on both the behavioral (Days-From-Peak) and resource gain (IRG) components of green-wave surfing (Aikens et al., 2017). We calculated IRG and Days-From-Peak for each GPS location. To avoid potential bias from unbalanced sample size resulting from different GPS collar fix schedules, we then calculated daily average IRG and Days-From-Peak for each animal-year (Aikens et al., 2017). We examined the degree to which forested pixels biased our green-wave surfing scores and found no evidence of bias (Appendix S2).

From the day-averaged surfing scores, we quantified green-wave surfing over three periods to assess the influence of drought on surfing. First, we calculated average green-wave surfing over a customized date range for spring migration of each individual-year as defined by Net Squared Displacement (i.e., the squared Euclidian distance between a reference point and subsequent relocations; see appendix S3 in Aikens et al., 2017 for details). We used green-wave surfing during the migration period to measure the influence of drought on surfing when animals are moving and actively seeking out green-up along their migratory routes. Second, we quantified surfing over a 120-day period centered on the median date of peak IRG for each year to compare net resource gain across years. We chose 120 days because this is the duration of spring green-up during the longest spring in our dataset (i.e., 2015). Since timing and pace of migration for ungulates are flexible, net resource gain during migration can vary considerably (Figure 2a; Monteith et al., 2011; Mysterud, 2013). For example, perfect surfing during a 5 day migration provides a lower total resource gain compared with perfect surfing during a 20 day migration. Thus, quantifying differences in net resource gain between a year with a short spring (and thus a shorter migration period) and a year with a long spring (and thus a longer migration period) requires a comparison of surfing beyond the window of migration, and across a consistent number of days (Figure 1). Third, to examine the effect of drought on green-wave surfing within a year, we...
calculated green-wave surfing during the spring green-up period for each year. We delineated the spring period based on the date range of peak IRG across the study area (Aikens et al., 2017; Merkle et al., 2019). This period represented the potential maximum time span during which a mule deer could experience the highest quality forage within a given year.

2.3 | Quantifying the greenscape

We used the methods described in Aikens et al. (2017) to quantify the greenscape of the 99 unique migratory routes from 2001 to 2019. Migratory mule deer in this system have strong fidelity to their migratory routes and use nearly the same route for most, if not all, of their life (Appendix S3; Merkle et al., 2019; Sawyer, Merkle, Middleton, Dwinnell, & Monteith, 2019). We therefore considered a migratory route to be a fixed trait of the animal, and used the observed migratory routes of mule deer to represent routes from the past, as well as routes likely used in the future. Thus, we extended the temporal window of our analysis examining the effect of drought on the greenscape to include 2001 (the earliest full year that the MODIS products are available) to 2019 (the last full year of MODIS data available). Using migratory routes delineated from GPS locations of individual deer, we calculated the duration of green-up as the difference between date of peak IRG at the beginning and end of each route—a metric that is strongly linked to green-wave surfing (Aikens et al., 2017). Additionally, we used the route-averaged “spring scale” as our metric of green-up rate for each route. Spring scale is a parameter estimated in the calculation of IRG. Specifically, when fitting the double logistic curve, following Bischof et al. (2012), two parameters are estimated: (a) the inflection point (the date of peak green-up), and (b) the scale parameter, which is the inverse of the rate of change in NDVI through time. This spring scale parameter can be interpreted as the time required to reach peak green-up, where large values represent more gradual green-up (Aikens et al., 2017; Bischof et al., 2012). Lastly, we calculated the order of green-up using Spearman’s rank correlation between the physical order of points along the route and the order those points greened up (Aikens et al., 2017). A value of one represents perfectly consecutive green-up and a value of zero represents nonconsecutive green-up.

2.4 | Drought data

We defined drought as a negative climate-water balance. We used the self-calibrated Palmer Drought Severity Index (sc-PDSI; spatial resolution: 0.04° [~4 km²], monthly time interval) from the West Wide Drought Tracker to estimate spring drought intensity (Abatzoglou, McEvoy, & Redmond, 2017). The sc-PDSI is a commonly used index of drought that has been corrected for more accurate comparisons of drought across space, in comparison with the original PDSI (Wells, Goddard, & Hayes, 2004). Both PDSI and sc-PDSI are metrics of drought which estimate water balance (the difference between the actual precipitation and the amount of water needed to achieve water balance; Palmer, 1965). A negative value for the sc-PDSI represents a negative climate–water balance (i.e., drought conditions) and positive values represent a positive climate–water balance (i.e., mesic conditions; Wells et al., 2004). The West Wide Drought Tracker utilizes monthly input data on temperature and precipitation from the Parameter-elevation Regressions on Independent Slopes Model in the calculation of the sc-PDSI (Abatzoglou et al., 2017). We extracted the sc-PDSI along each route during months corresponding to spring in a given year (using the same IRG-based method of delineating spring as described above) and calculated the average spring sc-PDSI for each year (2001–2019).

2.5 | Route-level response to drought

We examined the influence of drought on green-up duration (a key component of the greenscape) at the individual route level, using the 19 year time series of green-up data from the 99 unique routes. We focused on green-up duration as our metric of route quality because green-up duration sets a limit on the temporal availability of green-up along a migratory route, whereas green-up order does not. We defined a migratory route as drought-buffered if it remained high-quality across a range of drought intensities (Ashcroft, Gollan, Warton, & Ramp, 2012; Mackey et al., 2012). Being buffered from drought depends on two key components: quality and stability. To quantify the quality and stability of each route, we estimated the linear relationship between drought intensity and green-up duration along each route during 2001–2019 and extracted the intercept and slope of each regression. Because a value of zero for the sc-PDSI represents average conditions, the intercept of the route-level regression between sc-PDSI and green-up duration represents the baseline green-up duration expected under average conditions. We used this intercept to define the quality of each route. We used the slope of the regression to represent how variable the route was across a range of drought conditions (i.e., the stability of the route). Routes buffered from drought would be characterized by a long green-up duration (i.e., a large intercept) that is not variable across drought intensities (i.e., slope close to zero).

2.6 | Statistical analysis

We used linear mixed-effects models with a random intercept for individual ID to test for differences in surfing and exposure to spring green-up across drought and non-drought years. Year was specified as a factor, with 2013 (the drought year) as the reference year. We also examined the effect of drought across years, treating drought as a continuous variable (Appendix S4). To examine the effect of drought within a given year, we examined the relationship between drought intensity along individual routes and green-wave surfing in...
the spring (IRG and Days-From-Peak) using univariate linear regression for each year during 2013–2015. To quantify the influence of drought on the greenscape across a decadal scale of climate variability, we used univariate linear regression to examine the relationship between the average rate, duration, and order of green-up along the 99 unique routes and the average drought intensity of those routes, from 2001 to 2019. Because the distribution of green-up order was skewed, we arcsine transformed green-up order, before performing linear regression. We also used linear regression to examine the relationship between the quality and consistency of routes across a range of drought conditions.

3 | RESULTS

3.1 | Drought did not result in a trophic mismatch during migration

We assessed green-wave surfing across 3 years with variable spring weather. The 3 year period included a drought year (mean sc-PDSI in spring across all migratory routes = −2.1) with a short spring (67 days, 14 April to 20 June) in 2013, an intermediate spring that was wetter than average in 2014 (1.4 sc-PDSI; spring duration = 89 days, 2 April to 30 June), and a wet spring (2.2 sc-PDSI) with an unusually early (spring start = 14 February) and atypically long spring (120 days) in 2015 (Figure 2a).

During the migration period, deer closely tracked green-up in all years with a median Days-From-Peak of 10.36 in 2013 (drought year), 8.17 in 2014, and 13.23 in 2015 (Figure 2b). Animals surfed closer to the date of peak green-up in 2014 compared with 2013 (β = −2.30, SE = 0.84, p < .01; linear mixed effects model), but in 2015, animals surfed farther from peak green-up in comparison to 2013 (β = 2.78, SE = 0.88, p < .01; linear mixed effects model). The exposure of migrating mule deer to spring green-up was reduced in the drought year (median IRG in 2013 = 0.70) compared with non-drought years (median IRG in 2014 = 0.80; 2015 = 0.81; 2014 β ± SE = 0.098 ± 0.020, p < .0001; 2015 β ± SE = 0.11 ± 0.020, p < .0001; linear mixed-effects models; Figure 2c). Although deer surfed about 3 days farther from peak green-up during each day of migration in 2015 compared to the drought year of 2013 (Figure 2b,c), the unusually prolonged green-up rate in 2015 (average spring scale in 2015 = 16.6 days) resulted in 15.6% greater exposure to IRG during migration.

3.2 | Shorter springs reduce exposure to green-up

Drought resulted in poor surfing and low exposure to green-up during the standardized 120-day period (Figure 2). The dry year with a short spring resulted in low IRG (median in 2013 [drought year] = 0.52) compared with non-drought years with longer springs (median in 2014 = 0.60, β ± SE = 0.09 ± 0.015, p < .0001; median in 2015 = 0.69; β ± SE = 0.18 ± 0.015, p < .0001; linear mixed-effects models; Figure 2c). The degree to which deer movements were mismatched with peak green-up also was greater in the drought year (median Days-From-Peak in 2013 = 23.25) than in non-drought years (median Days-From-Peak in 2014 = 17.89, β ± SE = −5.43 ± 0.78, p < .0001; median in 2015 = 19.92, β ± SE = −3.31 ± 0.83, p < .01; linear mixed-effects models; Figure 2b).

Drought intensity (i.e., average sc-PDSI for each route during the spring period) varied considerably across individual migratory routes within the same year (Figure 3). Within a given year, deer migrating along drier routes consistently exhibited poorer surfing and

![Figure 3](image-url) The influence of within-year variability in drought on green-wave surfing across migratory routes in 2013 (orange; a, d; n = 58 routes), 2014 (green; b, e; n = 63 routes), and 2015 (purple; c, f; n = 63 routes). Green-wave surfing was quantified in terms of both potential resource gain, using the Instantaneous Rate of Green-up (IRG; a–c; maximum resource gain = 1) and behavior using Days-From-Peak green-up (d–f; perfect surfing = 0). Positive values for the sc-PDSI represent mesic conditions, whereas negative values represent dry conditions. Solid gray lines represent the fitted values and gray-dashed lines represent the 95% confidence intervals (fitted values ± 1.96 × SE)
often experienced lower exposure to green-up compared with wetter routes during the spring period (Figure 3). Although we did not detect a difference in average exposure to green-up across routes during the drought year, in the non-drought years, relatively wetter routes resulted in 21%–30% greater exposure to IRG than drier routes (Figure 3a–c).

### 3.3 Drought altered the pattern and progression of spring green-up

Drought compressed and reshuffled the green wave that progressed along migratory routes (Figure 4). Along the 99 unique migratory routes used by mule deer in the Wyoming Range, Wyoming, United States. A theoretical drought-buffered route is represented by the dotted line. The quality and variability of individual migratory routes were strongly correlated (the gray-dashed line represents the 95% confidence intervals, which were estimated from the standard error of the fitted values [solid gray line]). The variability of a route was quantified as the slope of the linear regression between the self-calibrated Palmer Drought Severity Index (sc-PDSI) and green-up duration of an individual migratory route, over a 19 year period (2001–2019; as shown in panel a). Route quality was estimated as the intercept from the same linear regression. For visualization, the variability of each route was assigned a value along a red–yellow–blue color ramp, where red colors indicate routes with the smallest slope, and blue colors represent routes with the largest slope.

### 3.4 No routes were buffered from drought

No routes exhibited consistently favorable green-up patterns as would be expected if they were buffered from drought. Specifically, no routes exhibited long green-up durations across a range of drought intensities, defined as a large intercept and a slope close to zero for the linear regression between drought intensity and green-up duration (Figure 5a). Instead, the quality and variability of migratory routes across a 19 year range in drought intensity were positively correlated (p < .001, r² = .35, β = 0.09; Figure 5). Specifically, high-quality routes in average years increased in quality during wet years but diminished in quality during drought years, whereas low-quality routes remained stable across a range of drought intensities (Figure 5).
Drought reduced exposure to spring green-up and decreased the benefit of green-wave surfing across years and along migratory routes (Figures 2 and 3). Instead of causing deer to be miscued with green-up (i.e., a trophic mismatch), drought constrained the opportunity to accrue forage resources during migration by reducing the amount of time that green-up was available (Figures 2 and 4). Drought altered the pattern and progression of spring green-up, resulting in reshuffled green waves that moved faster across the landscape, ultimately making it more difficult for mule deer to accrue forage resources during spring (Figures 2-4). Although there was variation in exposure to drought across individual migration routes (Figure 3), no routes were buffered from the effect of drought (Figure 5). Drought imposed a temporal constraint on green-wave surfing, thereby reducing the foraging benefit of migration. Climate change is expected to be unequal across space and time, likely altering landscape-level phenological gradients that migrating species exploit (Ahola et al., 2004; Both, 2010; Walther et al., 2002). Our work underscores the need to quantify the impact of climate change on resource phenology along migration corridors and to connect such changes to the foraging benefit of migration. We also demonstrate that a generalizable suite of metrics (i.e., the greenscape metrics of order, rate, and duration of phenological events) captures the key attributes of altered phenology that animals experience en route.

Considering a range of competing hypotheses regarding the mechanisms by which climate change affects migratory species is a foundational step toward effective conservation of animal migration (Knudsen et al., 2011). We evaluated two competing hypotheses on how drought alters the foraging benefit of ungulate migration: (a) a trophic mismatch or (b) a reduction in resource availability en route. One potential mechanism underlying a trophic mismatch is that the cue used to approximate resource availability (e.g., day length) no longer provides an accurate signal for the phenology of resources on a distant seasonal range (Durant, Hjermann, Ottersen, & Stenseth, 2007). Not all migratory animals, however, use indirect and inflexible cues to dictate behavior along the entire migratory journey (Winkler et al., 2014). For example, some species use local environmental cues (Ahola et al., 2004; Tøttrup et al., 2010; van der Graaf et al., 2006), previous experience (Thorup et al., 2007), or social information to guide migration (Knudsen et al., 2011; Newton, 2010). For ungulates, the timing and pace of migration are flexible, and are prompted mostly by plant phenology that migrants experience in the spring, not by proximate cues (Figure 2a; Monteith et al., 2011; Mysterud, 2013). Taken together, our findings indicate that drought reduces the foraging benefit of green-wave surfing by compressing and reshuffling spring green-up along migratory routes, not by causing migrants to be behaviorally mismatched with the arrival of spring on their summer ranges. For animals that are miscued, there is potential for behavioral adjustment or phenotypic plasticity to realign movements with resource peaks (Renner & Zohner, 2018). Nevertheless, a reduction in the temporal availability of resources provides fewer opportunities for adaptive changes in behavior (Armstrong, Schindler, Cunningham, Deacy, & Walsh, 2020; Deacy et al., 2017). Thus, altered phenological gradients that reduce resource availability en route should not be overlooked as a key threat to the persistence of ungulate migration.

We did not identify any routes that were buffered from the effect of drought. Instead, high-quality routes (i.e., routes with long green-up durations in average years) were the most variable across a range of drought intensities. We hypothesize that this trade-off between route quality and route stability in a variable environment contributes to the maintenance of a diversity of migratory tactics within populations. Indeed, trade-offs are a key mechanism driving the maintenance of behavioral differences among individuals (e.g., diet, space use; Bolnick et al., 2002; Nicholson, Bowyer, & Kie, 1997). For terrestrial herbivores, timing of migration is flexible (Kauffman, Meacham, Sawyer, Rudd, & Ostlund, 2018; Monteith et al., 2011), but at least for species like mule deer with high fidelity to their migratory routes (Appendix S3), the spatial location of their route is fixed (Merkle et al., 2019; Sawyer et al., 2019). Thus, the diversity of routes used by different individuals may persist because different routes yield variable benefits across years (Figure 5a). These individual differences are particularly important because populations with diverse forms of specialization, life-history strategy, or other forms of population diversity have high stability in the face of environmental change—a phenomenon called the portfolio effect (Schindler et al., 2010). Within the context of migration, a population comprised of individuals that use a diverse portfolio of migratory routes is predicted to be more stable in comparison to a population using a single migratory tactic (Lowrey et al., 2019). As climate change advances, a diversity of migratory tactics should promote population persistence (Ohlberger, Thackeray, Winfield, Maberly, & Völlestad, 2014; Schindler et al., 2010) and our work proposes one mechanism that may maintain such behavioral diversity.

Although our study focused on a single population of mule deer in Wyoming, our findings are relevant across a diversity of ungulate populations that move to seek plant green-up. From nomadic gazelles (Procopra gutturosa) in the eastern steppe of Mongolia (Mueller et al., 2008) to wildebeest (Connochaetes taurinus) in the Serengeti (Boone, Thirgood, & Hopcraft, 2006), moving long distances to exploit plant green-up is a common behavior (Merkle et al., 2016). Drought-induced changes to the greenscape are likely to influence migratory ungulate populations whose movements are fine-tuned to existing phenological patterns, a behavior that may take multiple generations and many decades to learn (Jesmer et al., 2018). Indeed, there is a well-established link between drought and poor population performance in ungulates in temperate and tropical systems (Gaillard et al., 1997; Mduma, Sinclair, & Hilborn, 1999; Middleton et al., 2013; Monteith et al., 2015). Our study indicates that reduced access to spring green-up during the growing season is one likely mechanism underlying this pattern,
with associated consequences for fitness. For example, migratory North American elk (Cervus elaphus) that surf closer to the date of peak green-up had greater body fat than their resident counterparts (Middleton et al., 2018). Decreased pregnancy and recruitment have been linked to increased drought intensity and reductions in the duration of spring green-up for elk (Middleton et al., 2013). Likewise, declines in recruitment of moose (Alces alces shirasi) were related to recent drought conditions that caused more rapid spring green-up (Monteith et al., 2015). Although climate change will continue to alter patterns of plant green-up, conservation efforts that minimize barriers to movement and reduce habitat fragmentation (Berger, 2004; Sawyer et al., 2013) can help ensure that migratory ungulates are able to access ephemeral forage resources (Monteith, Hayes, Kauffman, Copeland, & Sawyer, 2018). Integrative approaches to manage and conserve ungulate migration in a changing world should thus include explicit considerations of both the phenomenological quality of migratory corridors and the ability of animals to move freely across the landscape.

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AUTHOR CONTRIBUTIONS

E.O.A., M.J.K. and K.L.M. developed the research idea and study design. E.O.A. and J.A.M. analyzed the data. E.O.A., M.J.K. and K.L.M. developed the research idea and study design. E.O.A., M.J.K. and K.L.M. developed the research idea and study design. All authors collected the data, and S.P.H.D. managed the database. E.O.A. wrote the manuscript and all authors contributed to revisions.

DATA AVAILABILITY STATEMENT

MODIS data are publicly available through the NASA EARTHDATA database (https://search.earthdata.nasa.gov/search). Drought data are publicly available through the West Wide Drought Tracker (https://wrcc.dri.edu/wwdtt/batchdownload.php). GPS collar data are available upon request.

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E.O.A., M.J.K. and K.L.M. developed the research idea and study design. E.O.A. and J.A.M. analyzed the data. All authors collected the data, and S.P.H.D. managed the database. E.O.A. wrote the manuscript and all authors contributed to revisions.

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**Supporting Information**

Additional supporting information may be found online in the Supporting Information section.

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