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Original Investigation

Relating the movement of a rapidly migrating ungulate to spatiotemporal patterns of forage quality

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ABSTRACT

Migratory ungulates exhibit recurring movements, often along traditional routes between seasonal ranges each spring and autumn, which allow them to track resources as they become available on the landscape. We examined the relationship between spring migration of mule deer (*Odocoileus hemionus*) and forage quality, as indexed by spatiotemporal patterns of fecal nitrogen and remotely sensed greenness of vegetation (Normalized Difference Vegetation Index; NDVI) in spring 2010 in the Piceance Basin of northwestern Colorado, USA. NDVI increased throughout spring, and was affected primarily by snow depth when snow was present, and temperature when snow was absent. Fecal nitrogen was lowest when deer were on winter range before migration, increased rapidly to an asymptote during migration, and remained relatively high when deer reached summer range. Values of fecal nitrogen corresponded with increasing NDVI during migration. Spring migration for mule deer provided a way for these large mammals to increase access to a high-quality diet, which was evident in patterns of NDVI and fecal nitrogen. Moreover, these deer "jumped" rather than "surfed" the green wave by arriving on summer range well before peak productivity of forage occurred. This rapid migration may aid in securing resources and seclusion from others on summer range in preparation for parturition, and to minimize detrimental factors such as predation, and malnutrition during migration.

Introduction

Many ungulates exhibit cyclical movements by migrating along traditional routes between seasonal ranges, often associated with plant phenology and weather (Bischof et al., 2012; Fryxell and Holt, 2013; Monteith et al., 2011; Mysterud et al., 2001; Sawyer and Kauffman, 2011). Several hypotheses have been forwarded to explain why herbivores migrate, including differences in forage quality, variation in climate, reduced competition from density-dependent effects, and escape from predation (Fryxell and Sinclair, 1988; Middleton et al., 2013). By migrating, herbivores can follow seasonal changes in food quality, phenology, or availability, allowing access to critical resources that differ by location and season (Albon and Langvatn, 1992; Nicholson et al., 1997). Increases in spring temperatures, however, may result in an earlier onset of plant growth, with a potentially shorter duration of growth, resulting in reduced spatial heterogeneity and thereby, forage quality (Post et al., 2008). Furthermore, migratory behavior may be influenced by human disturbances (Berger, 2004; Harris et al. 2009; Lendrum et al., 2012, 2013; Sawyer et al. 2013). Such environmental alterations (i.e., changing plant phenology, habitat loss, increasing disturbance) may reduce benefits thought to be conferred by seasonal migration. Migratory herbivores may make behavioral adjustments to cope with such changes and remain in synchrony with peak forage availability across the landscape, thereby minimizing potentially negative effects on reproductive success (Monteith et al., 2011; Post et al., 2008). Spring migration is of utmost importance to ungulates living in temperate and arctic regions, because the arrival of migrants on summer range closely coincides with the timing of parturition (Eastland et al., 1989; Rachlow and Bowyer, 1991), and rising energetic demands of late gestation and lactation (Forbes, 1986).

The distribution, abundance, and quality of vegetation may exert strong influences on the distribution and population dynamics of

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large herbivores (Hebblewhite et al., 2008; Pettorelli et al., 2011; Pierce et al., 2012). Fecal indices often are employed to reflect forage quality at fine spatial and temporal scales (Blanchard et al., 2003; Hodgman and Bowyer, 1986; Hodgman et al., 1996; Leslie et al., 1989, 2008). Relating forage quality to the population ecology of large herbivores at the landscape level, however, is more difficult. Satellite-derived metrics, especially the Normalized Difference Vegetation Index (NDVI), which is an index to primary productivity of plants, have been used with increasing frequency in ecological studies (Bischof et al. 2012; Hebblewhite et al., 2008; Monteith et al. 2011; Pettorelli et al., 2011; Ryan et al., 2012). Indeed, those fecal and satellite-derived indices recently have been combined to assess diet quality for a large herbivore (Hamel et al., 2009). We examine relationships between forage quality during spring migration as indexed by fecal nitrogen, satellite-derived NDVI, and patterns of movement for mule deer (*Odocoileus hemionus*) in northwest Colorado, USA, to better understand how forage quality determines the timing and type of movements exhibited by mule deer during migration.

The "green-wave" hypothesis, originally proposed for avian taxa (Owen, 1980), postulates that herbivores follow phenological gradients, thereby optimizing access to high-quality forage for prolonged periods. The notion of herbivores following the green wave subsequently has been applied to ungulates, and recast as the "forage-maturation" hypothesis (Fryxell et al., 2004; Hebblewhite et al. 2008), and now incorporates the concept of stopover ecology (Monteith et al., 2011; Sawyer and Kauffman, 2011; Sawyer et al., 2013), wherein animals pause during migration in "holding areas" to await the green-up of forage along the migratory path.

Plant quality declines with maturation and senescence, and intake rates are reduced by herbivores at low levels of plant biomass. Ungulates are predicted to select for intermediate forage biomass, where high digestibility and intake rates intersect, thereby enhancing energy intake, especially for concentrate selectors such as mule deer (Kie et al., 2003). Whether ungulates accomplish such movements by "surfing" (i.e., following phenological gradients) or "jumping" (i.e., migrating ahead of green up) the green wave to enhance forage acquisition has been a topic of considerable interest, because of the need to better understand factors that underpin migration in large herbivores (Bischof et al., 2012).

We hypothesized that mule deer would follow spatiotemporal patterns of emerging vegetation during spring migration, thereby accessing higher-quality forage as they migrated from winter to summer range. We predicted that forage quality would improve as temperatures warmed and snow melted, resulting in increased levels of NDVI, and corresponding increases in diet quality as indexed by fecal nitrogen. NDVI has been used previously to assess green-up of plants by migrating mule deer (Lendrum et al., 2012, 2013; Monteith et al., 2011). Not all plants, however, are suitable forage for deer. By combining indices of vegetation greenness (NDVI), and diet quality (fecal nitrogen), we were then able to test for influences of forage quality on movement patterns of a large, migratory ungulate, and determine whether mule deer surfed or jumped the green wave.

Material and methods

Study area

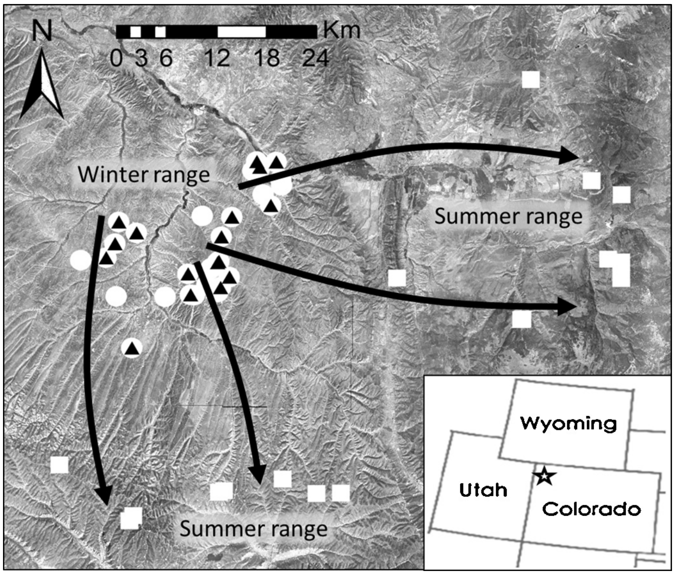

Fig. 1. The Piceance Basin, northwestern Colorado, USA, showing approximate migration routes of adult female mule deer for each of the four subpopulations (dotted, short dash, long dash, and solid arrow). Locations of fecal pellet collections from 6 May to 8 June 2010: winter range collections prior to departure (white circles), fresh samples collected at initiation of spring migration (black triangles), and summer range collections upon arrival of deer (white squares).

The Piceance Basin is a topographically diverse region located in northwest Colorado, USA (39.909736° N, 108.163605° W) that supports one of the largest migratory populations of mule deer in North America, previously estimated at 21,000–27,000 animals (White and Lubow, 2002). The area also includes one of the largest natural-gas reserves in North America, with varying levels of development that migratory mule deer must navigate (Lendrum et al., 2012, 2013). Four adjacent subpopulations of mule deer wintered in the Piceance Basin. Individuals in those subpopulations subsequently migrated to two distinct summer ranges (Lendrum et al., 2012; Fig. 1); all deer on our study area were migratory (i.e., used distinct winter and summer ranges). One subpopulation experienced "low development" which contained no development on either winter or summer range; however, the transition between those ranges included increased levels of human activity from vehicle traffic and housing infrastructure because of proximity to the town of Meeker, Colorado (Lendrum et al. 2012, 2013). The second subpopulation was exposed to "medium-low development" which exhibited a low density of active well pads on winter range ($\leq$0.05 pads/km^2) and along migration paths (0.17 pads/km^2), and no active well pads on summer range, although deer crossed one major highway with scattered ranch holdings along their migration path. The third subpopulation navigated "medium-high development" exhibited by moderate development on winter range (0.37 pads/km^2), and throughout the transition range (1.54 pads/km^2), with a decreased density of development on summer range as deer spread across the landscape (0.06 pads/km^2). The fourth subpopulation was considered "high-development area" and had the highest level of natural-gas development activity on winter range (0.70 pads/km^2), and along migration corridors (1.99 pads/km^2), with low levels of development on summer range (0.04 pads/km^2; Lendrum et al. 2012).

Primary winter range for mule deer was between 1675 and 2285 m in elevation, and summer range varied from 2000 to 2800 m. Winter range in the Basin was a relatively open, mixed pinion pine (*Pinus edulis*)-Utah juniper (*Juniperus osteosperma*) woodland, and the sagebrush (*Artemisia* spp.)-steppe community. Dominant vegetation communities on summer range varied, with Gambel's oak (*Quercus gambelii*)-mountain shrub complex at lower elevations, transitioning to quaking aspen (*Populus* tremuloides)-Douglas-fir (*Pseudotsuga menziesii*) forest, and Engelmann spruce (*Picea engelmannii*)-subalpine fir (*Abies lasiocarpa*) forest at higher elevations (Garrott et al., 1987). Lendrum et al. (2012) provide a more detailed description of this area.

The climate of the region was characterized by warm, dry summers (28° C mean high) and cold winters (−12° C mean low), with most of the annual moisture coming from spring snow melt (Western Regional Climate Center, 1893–2010). The Piceance Basin contained several large herbivores in addition to mule deer including North American elk (*Cervus elaphus*) and wild horses (*Equus caballus*), which occurred on winter and summer range, and moose (*Alces alces*), which were uncommon on summer range. This area also was inhabited by a variety of predators on winter and summer ranges, including coyotes (*Canis latrans*), mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), and black bears (*Ursus americanus*).

Animal capture and sampling of movements

During March 2010, we net-gunned 100 adult (≥1.5 years old) female mule deer from a helicopter, a method that provided a safe and humane way to capture ungulates (Krausman et al. 1985); only 3.9% of deer succumbed to capture myopathy. We fit individual females with store-on-board GPS collars (G2110D; Advanced Telemetry Systems, Isanti, Minnesota, USA), from which we gathered data on all remaining deer on timing and paths of migration. Those collars were programed to obtain one fix every 5 h during spring migration. All 3D fixes or fixes with a horizontal dilution of precision <10 were retained (90% of fixes <20-m accuracy; D'Eon and Serrouya, 2005). All collars were equipped with mortality sensors (i.e., increased pulse rate following 4–8 h of inactivity)—80.7% of deer survived during the period of migration. Those collars also had timed drop-off mechanisms scheduled to release during April of the year following deployment. All aspects of animal handling were approved by an Institutional Animal Care and Use Committee at Idaho State University (protocol # 6700410), and followed methods adopted by the American Society of Mammalogists for research on wild mammals (Sikes et al., 2011). These methods have been used successfully to study migration in subpopulations of mule deer in the Piceance Basin (Lendrum et al., 2012, 2013).

Spring migration

Following Lendrum et al. (2013), we used Hawth's Analysis Tools in ArcGIS 9.3 (ESRI, Redlands, California, USA) to derive 95% kernel-density estimates of seasonal ranges for each individual. We determined the initiation of spring migration based on the day a particular deer left winter range on a trajectory path (i.e., three successive locations leading away from winter range); arrival on summer range was determined as the first location inside the summer home range for that same deer (Garrott et al. 1987). We then calculated the distance and rate of travel (distance/days to complete migration) between winter and summer range along the migratory path using the Distance Between Points Tool in Hawth's Analysis Tools. We also calculated elevation of summer range for each deer as the average elevation of all locations within their summer range.

Plant phenology

We used the Normalized Difference Vegetation Index (NDVI) as an indicator of primary productivity to monitor greenness of vegetation (Hebblewhite et al., 2008; Pettorelli et al., 2011), and potential associations with dietary quality (Ryan et al., 2012). We derived 7-day composites of NDVI corrected for atmospheric contamination from MODIS (moderate-resolution imaging spectroradiometry; ftp://emodisftp.cr.usgs.gov/eMODIS/CONUS/historical/TERRA/), with a 250-m^2 spatial resolution. We then assigned values of NDVI that corresponded with GPS locations of individual mule deer on a weekly time step for winter and summer range. Once an individual departed from winter range, the locations of that individual during the last week on winter range were used to estimate phenological patterns for winter range for the remainder of the monitoring interval. Similarly, locations from the first week on summer range were used to extract values of NDVI prior to migration to summer range for each deer. We then calculated a weekly change in NDVI as the average value of all individuals, first across locations for an individual and then among individuals, treating winter and summer range separately. We then subtracted that value of NDVI from the NDVI value of the previous week. NDVI can perform poorly in predicting green up when substantial amounts of coniferous overstory are present (Chen et al., 2004); however, in our study areas, stands of conifers were isolated primarily to north-facing drainages or exhibited patchy distributions. In addition to NDVI, we obtained data on average daily temperature (°C) from a weather station located within winter range (Western Regional Climate Center 2008–2010). We also obtained data on snow depth from a SNOTEL weather station located near summer range (2865 m), which served as an index to snow depth.

Fecal samples

During 6 May–8 June 2010, we surveyed for fecal pellets by visiting known wintering grounds and locating mule deer, either visually or by radio-telemetry, which resulted in the collection of 340 fecal samples. We first focused our efforts on winter range, and then as deer began to depart, we attempted to move with deer, collecting feces along their migratory paths; however, because of the rapid migration exhibited by this population (median = 4 days, *this study*), we were only able to collect fresh samples at the time of departure. We were, however, able to collect fresh samples during the average duration of the migratory period because of the staggered departure time exhibited by deer in the Piceance Basin, and therefore, we used fresh samples as an indication of forage quality during the rapid migration period. Once deer arrived on summer range, we then began fecal collections there. We collected 20 composites of samples <2 weeks old on winter range, 20 individual samples of fresh pellets (Jenks et al., 1989) during the time of departure from winter range, and 12 composites of fresh samples on summer range. We obtained composite samples by combining five individual pellets from each of 10 pellet groups following the methods of Hebblewhite et al. (2008). Samples collected during departure from winter range were analyzed individually because of a decreased sample size (Jenks et al., 1989). We searched areas until we failed to locate fecal pellets of sufficient freshness (sensu Jenks et al., 1990).

Fecal samples were analyzed at Wildlife Habitat and Nutrition Laboratory at Washington State University (Pullman, Washington, USA) for fecal nitrogen of neutral detergent fiber (N-NDF). Total nitrogen levels in feces are composed of undigested plant nitrogen and metabolic nitrogen (Barboza et al., 2009). We chose N-NDF as an index of forage quality resulting from undigested plant nitrogen, because the NDF rinse eliminated metabolic nitrogen from samples, which is influenced by microbial digestion of forages, nitrogen recycled in saliva, and cells from the digestive systems of animals (Barboza et al., 2009). Consequently, N-NDF provides the most direct measure of plant nitrogen in fecal samples (P.S. Barboza, University of Alaska Fairbanks, personal communication). The remaining N in feces reflects values of N in plants that were not digested, not values that deer were unable to digest. For instance, Monteith et al. (2014) reported that lactating females were able to assimilate greater amounts of N-NDF than non-lactating females or males, indicating that some N following the NDF rinse is still available to deer. Exposure of feces to weather and insects does not compromise retention of nitrogen for 2–3 weeks post defecation

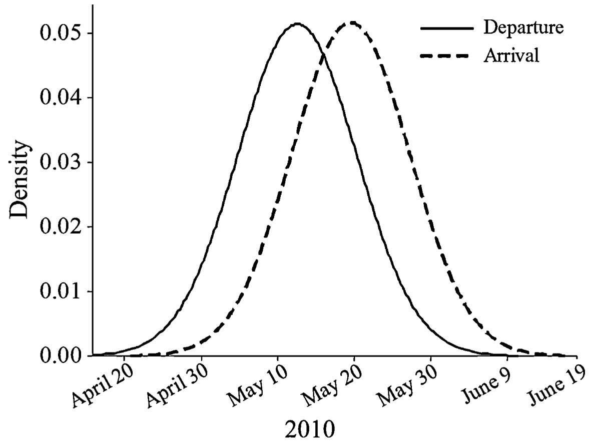

Fig. 2. Histogram of departure and arrival dates of spring migration, 2010, by adult female mule deer in the Piceance Basin, Colorado, USA. *Y* axis represents the density of mule deer as they departed or arrived; $n = 92$, mean (±*SD*) day of departure and arrival was 12 May (±7.7 days) and 19 May (±7.7 days), respectively.

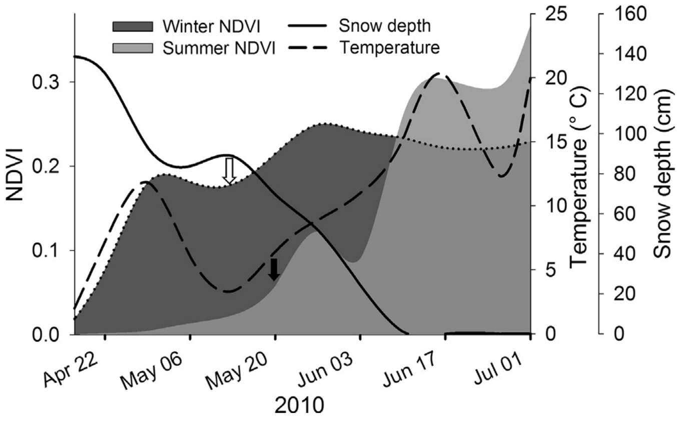

Fig. 3. Weekly change of the Normalized Difference Vegetation Index (NDVI) on winter and summer range of mule deer, mean weekly temperature, and mean weekly snow depth during spring 2010 in the Piceance Basin, Colorado, USA. Arrows represent mean departure of deer (white arrow) and arrival date (black arrow) from winter to summer range, respectively. The dotted line indicates winter NDVI.

(Jenks et al., 1990), which was not an issue because of the short duration of our study.

Statistical analyses

We used residual and sequential regression (Graham, 2003; Monteith et al., 2013a) to evaluate effects of mean weekly snow depth and temperature, which were highly correlated ($r > 0.80$), on NDVI of winter and summer range. Consequently, we regressed mean weekly temperature against snow depth, and extracted the residuals from that analysis, which yielded a metric that was independent of the snow-depth, and represented the unique contribution of temperature (Graham, 2003; Monteith et al., 2013a). We then included the residuals from that analysis in a multiple regression with snow depth and NDVI. This approach allowed us to determine whether the pattern observed in NDVI was more influenced by snow depth or temperature.

We compared levels of N-NDF (dependent variable) across the three sample periods (predictor variable) using one-way analysis of variance (*ANOVA*), and conducted pairwise Bonferroni comparisons among time periods to maintain an experiment-wise error using Minitab 16.1.0 (College City, Pennsylvania, USA). We adopted an $\alpha = 0.05$. In addition, we examined the relationship between N-NDF and the time period over which samples were collected at time of departure with a sigmoidal nonlinear regression (Neter et al., 1996). Lastly, we calculated a Spearman's rank correlation (r_s), which makes no assumptions concerning line shape, to examine N-NDF for fresh fecal samples and the corresponding date of their collection. Two of the fresh samples were extreme outliers with nonsensical values, and were removed from analyses.

Results

Spring migration for individual mule deer was rapid ($n = 92$, median = 4 days, interquartile range = 5 days; Fig. 2) and highly synchronous among three of the four study areas; deer migrating through the least developed landscape took approximately 2.5 times as long (*ANOVA*, $F_{3,91} = 5.90$, $P = 0.001$). Despite different rates of travel among subpopulations, there was no statistical difference in the mean day of arrival ($F_{3,91} = 2.61$, $P = 0.06$). Mean (±*SD*) day of departure and arrival was 12 May (±7.7 days) and 19 May (±7.7 days) 2010, respectively (Fig. 2). Radio-collared females first departed winter range on 19 April and the last deer arrived on summer range on 14 June 2010. Mean distance migrated by individual deer between winter and summer range was 46.1 km (95% CI = 40.8–51.4 km).

Changes in NDVI corresponded with changes in local patterns of weather, including mean temperature and snow depth (Fig. 3). The first initial peak in NDVI occurred during the week of 29 April on winter range; NDVI first peaked on summer range 4 weeks later, during the week of 26 May (Fig. 3).

Residual and sequential regression, with priority assigned to snow depth, indicated that snow depth was the primary factor influencing NDVI values on both winter and summer ranges ($r^2_{\text{adj}} = 0.61$, $F_{2,9} = 9.57$, $P = 0.008$; and $r^2_{\text{adj}} = 0.81$, $F_{2,9} = 24.14$, $P < 0.001$, respectively). Residuals representing temperature were not significant in predicting values of NDVI on either winter or summer ranges ($P = 0.67$; $P = 0.21$, respectively). A strong correlation occurred, however, between temperature and snow depth ($r > 0.80$). In a post hoc analysis, we assigned priority to temperature, which then indicated that temperature was the primary variable influencing NDVI values on both winter and summer ranges ($P = 0.002$; $P = 0.001$, respectively). NDVI increased throughout spring, and was affected primarily by snow depth when snow was present and temperature when snow was absent.

Mean (±*SE*) fecal nitrogen of neutral detergent fiber (N-NDF) varied among periods (*ANOVA*, $F_{2,48} = 6.63$, $P = 0.003$). N-NDF was similar between fresh samples collected during migration ($\bar{X} = 0.69 \pm 0.16\%$), and composite samples collected from summer range ($\bar{X} = 0.67 \pm 0.11\%$; sequential Bonferroni comparison for migration *vs.* summer $P = 0.81$). Samples collected at initial green up during the migration period and on summer range, however, had higher N-NDF than composite samples collected on winter range ($\bar{X} = 0.54 \pm 0.11\%$; sequential Bonferroni comparison, winter *vs.* migration $P = 0.003$, winter *vs.* summer $P = 0.04$; Fig. 4). Furthermore, fresh fecal samples increased in N-NDF over the 2-week collection period ($r^2 = 0.47$, $F_{1,16} = 6.05$, $P = 0.01$; Fig. 4). Additionally, the Spearman rank correlation comparing N-NDF of fresh fecal samples with their corresponding date of collection during migration indicated a significant, positive correlation ($r_s = 0.53$, $P = 0.05$).

Discussion

Migrating mule deer increased their access to a diet higher in nitrogen by following spatiotemporal changes in emerging vegetation, while likely reducing density-dependent consequences from deer concentrated winter range, than if deer had remained sedentary. This pattern was apparent in values of NDVI and fecal nitrogen. Mule deer inhabiting the Piceance Basin initiated spring migration

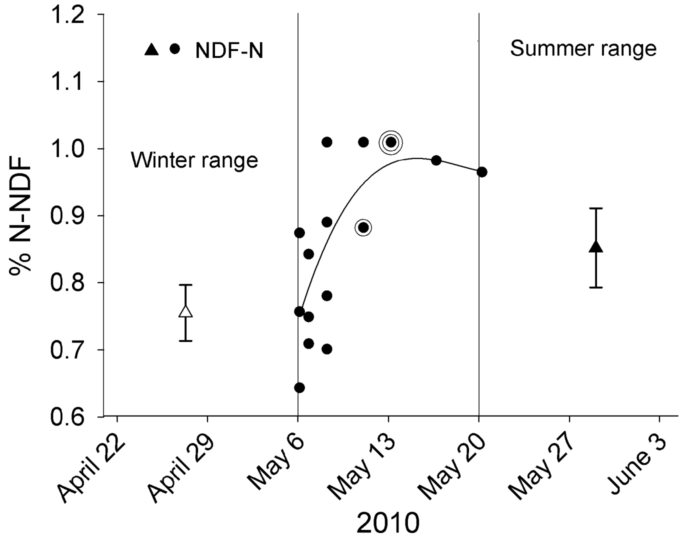

Fig. 4. Fecal nitrogen on neutral detergent fiber (N-NDF) of mule deer from winter range (white triangle) and summer range (black triangle) composites (error bars = 95% *CI*), and fresh samples collected at the time of departure from winter range during the mean migration period (black circles, rings around symbols represent multiple samples), of spring 2010 in the Piceance Basin, Colorado, USA. The regression line provides a visual comparison between NDF-N values of fresh samples sample dates.

with increasing green up on winter range. Those deer exhibited increased values of fecal nitrogen during migration, which corresponded with increases in NDVI. Mule deer in this region did not use stopovers or holding areas (mean step length = 1.3 km, mean direction traveled = −0.08°; Lendrum et al., 2012), as is common for mule deer in some other systems (95% of time during 3 week migration spent in stopovers; Sawyer and Kauffman, 2011), and arrived on summer range prior to optimum forage conditions, as indicated by NDVI and fecal nitrogen (Figs. 3 and 4). Nevertheless, premature arrival on summer range likely was still a favorable movement pattern to that of remaining on winter range, because diet quality typically is higher on summer than winter range (Monteith et al. 2013b). The positive relationship between fecal nitrogen and NDVI combined with the greater initial and continued increase of NDVI on summer range associated with new plant growth suggested that higher-quality forage occurred on summer compared with that on winter range, which was past initial green up (Fig. 3).

By following spatiotemporal patterns in new plant growth *via* migration between seasonal ranges, migratory ungulates are predicted to enhance rates of energy intake (Fryxell et al., 2004). For large herbivores, the onset of spring migration may be initiated by a combination of rising temperatures, decreasing snow cover, and the emergence of new vegetation (Garrott et al., 1987; Monteith et al., 2011). Values of NDVI on summer range gradually increased approximately 3 weeks later when compared to winter range, because snow depths on summer range took longer to ablate than elsewhere. By late spring and into early summer, values of NDVI increased rapidly on summer range while simultaneously decreasing on winter range (Fig. 3), resulting in a pattern of vegetation change conducive to migration.

All mule deer in our population were migratory, so we were unable to simultaneously collect fecal samples on winter and summer range for a direct comparison of diet quality. Moreover, we were only able to collect fresh fecal samples at the time of departure on winter range rather than along migration routes, because of the rapid migration exhibited by mule deer in this study; however, we did collect fresh samples throughout the average duration of the migratory period, which we believe provided a reliable index to conditions along migratory paths. Course forages consumed during winter have slow rates of passage (Barboza et al., 2009), and several days of fecal deposition along the migratory path would have been from food consumed on winter range. Moreover, the relationship between fecal nitrogen and NDVI indicates that fecal samples we collected were indexing a change in plant phenology. The number of samples collected during the migration period was sufficient for studying deer diets for a particular season (Anthony and Smith, 1974), although an increased sample size may have provided greater precision to our data. Furthermore, if collections of fecal pellets had continued farther into summer N-NDF values likely would have continued to increase as values of NDVI did so; however, we ceased collecting prior to parturition to reduce the likelihood of decreased nitrogen levels in feces of lactating females (Monteith et al., 2014). As reproductive females remodel their digestive tracts to support the high costs of lactation, they become more efficient at extracting nitrogen from forage (Barboza and Bowyer, 2000).

Levels of fecal nitrogen of neutral detergent fiber (N-NDF), which reflect nitrogen available in plants, were lowest in samples collected from mule deer on winter range prior to migration (Fig. 4). As the migration began, N-NDF levels increased rapidly to a high level, which coincided with the average day of departure (Fig. 4) and then tapered off as deer first arrived on summer range (Fig. 3). This observed pattern likely was because summer range occurred at higher elevation where accumulated snow still persisted. Sawyer and Kauffman (2011) noted that mule deer used stopovers during migration as a way to use areas of high forage quality, which allowed individuals to migrate in conjunction with patterns of plant phenology. Mule deer in the Piceance Basin migrated within 1 week without using stopovers, compared with the 3-week migration by mule deer with frequent use of stopovers observed by Sawyer and Kauffman (2011). Though the duration of migration was different between systems, distances traveled and elevation changes were similar. The rapid increase in N-NDF and NDVI during migration led us to postulate that deer initiated migration to coincide with green up to first improve their physiological condition (Garrott et al., 1987; Monteith et al., 2011), and then "jumped" the green wave and arrived on summer range prior to peak forage conditions (sensu Bischof et al., 2012). Mean date of arrival occurred before a substantial increase in NDVI had begun (Fig. 3), which was reflected by slightly lower N-NDF values on summer range than during migration (Fig. 4). The positive association between NDVI and fecal nitrogen, and NDVI responding to changes in snow depth, indicate that the NDVI reflected changes in phenological patterns not just of plants in general, but for those plants that constituted deer forage. How patterns of climatic warming or variability might affect the propensity of deer to jump the green wave requires further research.

One possible explanation for the pattern of migration we observed in mule deer may be to accommodate the needs of females associated with pregnancy (≥95% pregnancy rate occurred in this population; Anderson and Bishop, 2011). Little variation existed between individual females in their timing of migration to summer range. Pregnant females have increased energetic costs (Barboza and Bowyer 2000), yet reduced space available for consumption of forage during gestation, because peritoneal space may be limited during late fetal development (Forbes, 1986). Therefore, we expected pregnant females to focus on the highest-quality vegetation available prior to parturition. A rapid migration to summer range may provide pregnant females with a mechanism to arrive on birthing areas prior to parturition, locate critical resources, and seek seclusion from others (Monteith et al., 2007), give birth, and then reconnect with the green wave in time for increased nutrient demands associated with lactation (Bowyer et al., 2000).

Alternatively, migrants that "jump" between seasonal ranges may be less susceptible to detrimental factors such as predation, malnutrition, and exposure while migrating (Bischof et al. 2012). Nicholson et al. (1997) noted that migratory mule deer were more vulnerable to predation than those that remained sedentary; prolonging migration presumably could increase risk of predation. Ungulates have been observed making altitudinal shifts preceding green up, in preparation for parturition, ostensibly to reduce predation risk (Barten et al., 2001; Fiesta-Bianchet, 1988). Previous research (Lendrum et al. 2012; Sawyer et al. 2013) indicated that mule deer increase their rate of movement when migrating through disturbed landscapes, which may also account for the "jumping" behavior we observed.

Although we only have 1 year of data, our study provides evidence that migrating ungulates follow patterns of plant phenology, detectable by changes in fecal nitrogen and NDVI, and that some migratory populations may "jump" rather than "surf" the green wave. Mule deer migrations in the Piceance Basin exhibit some interannual variation in mean dates of migration, but timing of movements still was driven, in part, by snow and temperature (Lendrum et al., 2013). More research will be required to determine the degree to which migratory ungulates vary patterns of surfing or jumping the green wave. Mule deer migration routes can vary in length from relatively short (10 km; Nicholson et al., 1997) to some of the longest (240 km; Sawyer et al. 2014) migratory paths in the contiguous United States, however, these migrations are still far shorter than some of vast migration routes by ungulates in Africa (400 km, Wildebeest *Connochaetes taurinus*; Murray 1995) and the Arctic (1515 km, Caribou *Rangifer tarandus;* Fancy et al. 1988). How well surfing or jumping the green wave will apply to all long-distance migrators remains to be determined.

Conclusions

Migration strategies of ungulates are plastic and individuals may alter migration behaviors to respond to physiological demands, climatic and phenological changes, predation risk, and anthropogenic disturbances to the environment (Lendrum et al., 2012, 2013; Monteith et al., 2011; Mysterud et al., 2001; Nicholson et al., 1997). In temperate regions, such as the Intermountain West, ungulates commonly migrate between low elevations in winter to higher elevations in spring and summer, which provides release from a restricted food supply and access to newly available forage (Fryxell and Sinclair, 1988; Garrott et al., 1987; Hebblewhite et al., 2008; Monteith et al., 2011). Indeed, migrating from low-elevation winter range to high-elevation summer range provided mule deer with a means to effectively prolong conditions of high-quality forage, which was evident in NDVI and fecal-nitrogen values associated with migratory events, and help to explain this life-history characteristic. Those patterns support the hypothesis that it is favorable for mule deer to migrate during spring by tracking spatiotemporal patterns of emerging vegetation, thereby accessing high-quality forage as they migrated from winter to summer range. Mule deer use stopovers as a way to follow these spatiotemporal patterns, but more evidence is mounting that there also may be advantages to jumping the green wave. These two behaviors need not be mutually exclusive, however, and there may be advantages to each migration strategy, or by using a combination of the two. Sorting among effects of local weather conditions, climate change, forage quality, predation, population dynamics, life-history characteristics, and anthropogenic disturbances on patterns of migration is a daunting task. The ultimate currency for understanding such effects is genetic fitness, which can be difficult to measure in a long-lived and vagile large mammal, but holds a fruitful area for future research.

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