Functional attributes of ungulate migration: landscape features facilitate movement and access to forage

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Abstract. Long-distance migration by terrestrial mammals is a phenomenon critical to the persistence of populations, but such migrations are declining globally because of over-harvest, habitat loss, and movement barriers. Increasingly, there is a need to improve existing routes, mitigate route segments affected by anthropogenic disturbance, and in some instances, determine whether alternative routes are available. Using a hypothesis-driven approach, we identified landscape features associated with the primary functional attributes, stopovers and movement corridors, of spring migratory routes for mule deer in two study areas using resource selection functions. Patterns of selection for landscape attributes of movement corridors and stopovers mostly were similar; however, landscape features associated with movement corridors aligned better with areas that facilitated movement, whereas selection of stopovers was consistent with sites offering early access to spring forage. For movement corridors, deer selected for dry sites, low elevation, and low anthropogenic disturbance. For stopovers, deer selected for dry sites, with consistently early green-up across years, south-southwesterly aspects, low elevation, and low anthropogenic disturbance. Stopovers and movement corridors of a migratory route presumably promote different functions, but for a terrestrial migrant, patterns of habitat selection indicate that the same general habitat attributes may facilitate both movement and foraging in spring. Our findings emphasize the roles of topographical wetness, vegetation phenology, and anthropogenic disturbance in shaping use of the landscape during migration for this large herbivore. Avoiding human disturbance and tracking ephemeral forage resources appear to be a consistent pattern during migration, which reinforces the notion that movement during migration has a nutritional underpinning and disturbance potentially alters the net benefits of migration.

Key words: anthropogenic disturbance; connectivity; habitat selection; mule deer; Odocoileus hemionus; stopover; Wyoming

INTRODUCTION

Seasonal, preemptive movement sometimes across hundreds of kilometers by entire populations of animals between distinct ranges that are typically unused at other times of year defines the awe-inspiring phenomenon of migration (Dingle and Drake 2007). Migration facilitates access to seasonally abundant resources and allows animals to avoid severe weather conditions, fulfill habitat or resource needs of critical life stages, and in some instances, reduce risk of predation (McCullough 1985, Fryxell and Sinclair 1988, Alerstam et al. 2003). Although migration is a critical life-history strategy that presumably evolved because of the fitness benefits it conferred to migrants (Fryxell et al. 1988), migrations occurring worldwide and across taxa ranging from birds to fish to large mammals are in steep decline (Caudill et al. 2007, Bolger et al. 2008, Bowlin et al. 2010, Milner-Gulland et al. 2011). Of particular concern are long-distance, terrestrial migrations that are being disrupted and in some instances severed by roads, fencing, energy development, dams, and other anthropogenic features that may subsequently lead to population declines (Berger 2004, Harris et al. 2009, Sawyer et al. 2013, 2016). The great distances traversed by some species create a problem for conservation because migratory routes often intersect competing land uses and geopolitical boundaries (Bull et al. 2013). The complexities with conserving migratory populations emphasize the need to better understand the ecology of this phenomenon to improve existing migratory routes, mitigate or offset impacts to route segments, and in some instances, restore previously lost routes (Milner-Gulland et al. 2011).

In temperate regions, migration among large herbivores is typified by movement to summer ranges at high elevation in spring following the leading edge of advancing plant phenology, with return movements to low-elevation winter ranges that are prompted by winter weather in autumn (Monteith et al. 2011, Sawyer and Kauffman 2011, Bischof et al. 2012, Jones et al. 2014, Aikens et al. 2017). Therefore, twice each year animals must navigate through a complex and potentially risky landscape to successfully reach their destinations (Nicholson et al. 1997, Lendrum et al. 2012, Sawyer et al. 2012, Seidler et al. 2015). Construction of impermeable barriers along a migratory route can result in the loss of connectivity and benefits obtained from seasonal ranges, which can lead to population collapse (Whyte and Joubert 1988, Benshahar 1993).
The primary function of a migratory route, to provide the connection between two seasonal ranges, is obvious; however, migratory routes themselves have functional attributes that yield important benefits beyond simple connectivity (Sawyer et al. 2013). For example, some route segments are used primarily for movement (i.e., movement corridors), whereas in other route segments, forward movement slows to remain in sync with vegetation phenology as those areas (i.e., stopover sites) are used for extending foraging bouts (Sawyer and Kauffman 2011). Other functional attributes such as parturition areas or security habitat exist for some migrations, but movement corridors and stopovers are common among ungulates that migrate long distances (>50 km; White et al. 2010, Monteith et al. 2011, Sawyer and Kauffman 2011, Blum et al. 2015). Previous research has revealed that mule deer synchronize their initiation (Monteith et al. 2011, Lendrum et al. 2013) and movement (Sawyer and Kauffman 2011, Aikens et al. 2017) during migration to correspond with plant phenology, which allows individuals to exploit young, protein-rich plants that are highly digestible (Albon and Langvatn 1992, Lendrum et al. 2014, Merkle et al. 2016).

Encroachment of anthropogenic features onto migratory routes may not sever the connectivity between seasonal ranges, but may reduce the functionality and thus, the benefits of the route itself. For example, disturbance associated with energy development caused mule deer to increase their rate of movement during migration, which disconnected their timing of arrival on summer range from plant phenology (Lendrum et al. 2012, 2013). Indeed, a better understanding of the functional attributes of migratory routes and what landscape features dictate where they occur where they do is warranted (Sawyer et al. 2013), especially because migration by large herbivores often occurs along traditional routes with high fidelity both within and between seasons and years among individuals (McCullough 1985, Sweanor and Sandegren 1988, Sawyer et al. 2009b, Sawyer and Kauffman 2011).

Our goal was to identify landscape features associated with the primary functional attributes (i.e., stopovers and movement corridors) of spring migratory routes for mule deer. Understanding landscape features of stopovers and movement corridors may help identify habitat manipulations or treatments that could improve existing routes, mitigate for route segments that have lost functionality caused by human disturbance, and potentially restore routes in areas currently inaccessible or unused by migrants.

We used GPS data from two populations of migratory mule deer in western Wyoming, USA, and the Atlantic Rim in southwestern Wyoming, USA (Fig. 1). The study areas provided the opportunity to compare and contrast patterns of habitat selection for functional attributes of migratory routes in two different systems. The Upper Green River Basin included both low-lying areas of sagebrush–steppe habitat as well as mountainous conifer forests. The low-lying areas were characterized by sagebrush and upland species intermixed with a network of energy development on winter range (Sawyer et al. 2009a). Mountainous areas were dominated by conifer forests with forb and shrub understories. Land ownership in the region was mostly (71%) administered via the federal government either by the Bureau of Land Management or the United States Forest Service, whereas 2% was managed by the state of Wyoming and 27% was privately owned. Average elevation throughout the study area was 2,310 m (range 1,739–3,391 m). Detailed descriptions of the vegetation and land-use characteristics of the study areas were provided in Sawyer et al. (2006, 2009a).

Similar to the upper Green River Basin, the Atlantic Rim area was characterized by winter ranges dominated by sagebrush, intermixed with other mixed-mountain shrub and some Utah juniper (Juniperus osteosperma). Elevations ranged from 1,920 m to 2,530 m. The population migrated to summer ranges dominated by aspen (Populus tremuloides) and mixed shrubs, including chokecherry (Prunus virginiana), serviceberry (Amelanchier alnifolia), and bitterbrush (Purshia tridenta). Animals were exposed to low to moderate levels of natural gas wells along their migratory route. Detailed descriptions of the vegetation and land-use characteristics of the study areas were provided in Sawyer et al. (2009b, 2013). Average gain in elevation between winter and summer ranges was greater for the Upper Green study area (~610 m) compared with the Atlantic Rim (~325 m).

**Methods**

Our dataset comprised GPS locations from 42 adult female mule deer that were captured in December during 2003, and 2007–2012 on a winter range in the upper Green River Basin of western Wyoming, USA, as part of a different study (Sawyer et al. 2006, 2009a). In addition, we used data from 47 adult female deer that had been captured and equipped with
GPS collars during 2005–2006 as part of a different study on two distinct winter ranges, locally known as Dad and Wild Horse in the Atlantic Rim area, southern Wyoming, USA (Sawyer et al. 2009b, 2013). We fitted deer with store-on-board GPS radio collars (TGW 3500; Telonics, Mesa, Arizona, USA) programmed to collect one location every 2.0 or 2.5 h for 1–2 yr. In our analysis, we included deer that migrated between distinct winter and summer ranges because our primary interest was in developing predictive models for migratory corridors and stopovers. We excluded autumn migration because deer in this region have high overlap (62% overlap in seasonal stopovers) in their seasonal routes (Sawyer and Kauffman 2011), thereby making a parallel analysis for autumn migration largely redundant. Therefore, our dataset comprised data for 45 spring migrations from 42 deer in the upper Green River Basin and 60 spring migrations from 47 deer in the Atlantic Rim.

**Resource selection**

We followed the approach of Sawyer et al. (2009b) to identify migratory routes and stopover sites. We delineated start and end dates of spring migration based on inspection of net squared displacement (Bunnefeld et al. 2011), defined the start and end of migratory routes as locations occurring outside a minimum convex polygon generated from winter and summer range locations, and used the sequence of GPS locations that composed the time between those periods including the 24-h period before and following migration (Sawyer et al. 2009b). We first used the Brownian bridge movement model (BBMM; Horne et al. 2007) to estimate utilization distributions (UD) for each migratory route from GPS-collared deer. The BBMM estimates the probability of use along a migratory route based on time-specific location data; the probability of being in an area is conditioned on the start and end locations, the time elapsed between locations, and the rate of movement (Horne et al. 2007). Therefore, the UD from the BBMM accounts for uncertainty associated with the actual movement path of an individual. Following the delineation of migratory routes using BBMM, we separated stopovers and corridors to allow modeling of the primary functional attributes of a migratory route (Sawyer et al. 2013).

We classified stopover sites as the highest 12% of the values in the UD for each migratory route, which reflected segments of a route where animals ceased forward movement (Sawyer et al. 2009b), and presumably was associated with acquisition of high-quality forage at those sites (Sawyer and Kauffman 2011). Although numerous GPS locations occurred within stopovers, we considered the entire area of the polygon from an individual stopover as our sampling unit rather than the individual locations because collectively, they composed a

![Fig. 1. Location of study areas in the (A) Upper Green River Basin and (B) Atlantic Rim of Wyoming, USA, with 22 representative migratory routes of adult female mule deer connecting winter to summer ranges displayed as an example, with movement corridors and stopovers as delineated by our analyses.](image-url)
single stopover. Stopovers derived in this manner became the data points used for the stopover analysis.

Next, we sought to characterize the movement corridors used by animals to connect stopover sites along a migratory route; however, few GPS locations actually occur in corridors because deer spend 95% of their time in stopovers when migrating (Sawyer and Kauffman 2011). Consequently, modeling resource selection during migration without distinguishing between movement corridors and stopovers would essentially constitute a model for stopovers. Therefore, to model movement corridors, we first clipped out stopovers from the UD of the migratory route, removing all GPS locations that fell within the stopovers, and replaced them with a single point in the center of each stopover. This provided a means to retain the connection between corridor locations after stopover locations were removed so as not to bias sampling based on an aggregation of stopover points. Based on the resulting GPS locations that included a single location at the center of each stopover and all locations within movement corridors, we estimated a UD using the BBMM that represented the probability for the movement corridor of each animal. We then excluded areas overlapping stopovers and cast 100 points within each corridor in a random, but probabilistic manner based on the relative probability of use estimated by the UD that we rescaled (0–100) and separated into categories (0–20, 20–40, and so forth). These points represented the used locations in our corridor models. By using this approach we were able to overcome the limitation of too few GPS locations being located along movement corridors (typically <20 per individual) for meaningful analysis. Our probabilistic approach to defining movement corridors may create some bias associated with confidence around parameter estimates; however, it does account for the uncertainty in the actual movement path traversed by individuals.

We defined extent for available resource units as the entire study area that encompassed a minimum convex polygon placed around all migratory routes and buffered by 2.5 km. At the spatial scale of the study area, available units reflected the entire area that may have logically been traversed by migrating animals within the population because it encompassed all known migratory routes between known winter and summer ranges with an additional arbitrary buffer. We paired each observed stopover with 10 random stopovers and each migration corridor location to 10 random locations within the defined study area. We chose 10 random locations per used because those points provided a relatively uniform distribution across our study area. We generated random stopovers by placing circles with areas equal to that of each used stopover.

**Landscape variables**

To measure resource availability, we extracted habitat covariates based on spatial data layers available from public sources. We extracted all predictor variables as a mean value for each stopover sample with the exception of landcover data, which we assigned landcover class to each stopover based on the cover type that composed the majority of the polygon. Previous research has identified a number of landscape variables that are important contributors to deer migration including elevation, slope, aspect, terrain ruggedness, anthropogenic disturbance, vegetation type, and plant phenology (Sawyer and Kauffman 2011, Lendrum et al. 2012). We obtained a digital elevation model (DEM) at a resolution of 30 m and used the DEM to derive other metrics associated with landscape structure (DEM available online).\(^6\)

We transformed elevation so that a 1-unit change in elevation represented 100 m. We used ArcGIS Spatial Analyst Tools (Environmental Systems Research Institute, Redlands, California, USA) to derive values of slope (%). We derived a measure of surface curvature relative to surrounding cells within 250 m to index convex (large positive values) vs. concave (large negative values) surfaces that would reflect the relative differences between ridgelines and canyon bottoms, respectively (Bolstad and Lillesand 1992, McNab 1993, Cushman et al. 2010). We calculated a metric of wetness, known as compound topographic index (CTI), which is a function of the slope and upstream contributing source area per unit width orthogonal to the flow direction (Gessler et al. 1995). We also derived a continuous measure of aspect (TRASP) based on a transformation of circular aspect to assign a value of zero to land oriented in a north-northeast direction (reflecting the coolest and wettest orientation), and a value of 10 for the warmer and dryer south-southwesterly aspects (Roberts and Cooper 1989).

Rather than use a distance to nearest well pad or road as a metric of anthropogenic disturbance, we extracted a measure of disturbance that reflected the relative degree of disturbance at each site that range from 0 (no disturbance) to 100 (highly disturbed) from an updated version of a previously published layer (Copeland et al. 2007). We initially calculated a vector ruggedness measure (VRM; Sappington et al. 2007), but did not include it in our modeling efforts because it was highly correlated with CTI (\(|r| > 0.62\)) and slope (\(|r| > 0.94\)).

We obtained vegetation types using the 2006 National Land Cover Dataset (NLCD), which contained 15 habitat classes within the study area at a resolution of 30 m (Fry et al. 2011). We reclassified the NLCD data into three categorical habitats based on their functional similarities throughout our study area: (1) sagebrush scrub, (2) grassland, and (3) forest. Classes of barren land, herbaceous grassland, and shrubland were combined to create sagebrush scrub. We combined riparian, pasture, perennial crops (which was mostly alfalfa and grass hay farming), wooded wetlands, and several classes of development into pasture because they were typically located in proximity to each other and exhibited similar characteristics. All forest categories were combined to form a single forest class. Although we initially included development as a separate land cover type, models failed to converge because zero used locations were located within that cover type. For the analysis of stopovers, we included the dominant cover type that composed each stopover, because in most instances a single cover type represented most if not all of the stopover.

Migrating herbivores commonly follow the leading edge of the phenological wave that occurs across elevational gradients in spring (Monteith et al. 2011, Sawyer and Kauffman 2011, Lendrum et al. 2013); however, inter-annual

\(^6\)\text{http://datagateway.nrcs.usda.gov/}
fidelity to migratory routes and stopover sites indicate that there may be key aspects associated with plant phenology at those locations compared with other areas (Sawyer and Kauffman 2011). We derived spatially explicit metrics of plant phenology that characterized spring during a 10-yr period (2001–2011), because we were interested in describing specific phenological characteristics for each location on the landscape that may dictate why migratory routes occur where they do instead of linking phenology with timing of migration, which has been demonstrated in other work (Monteith et al. 2011, Sawyer and Kauffman 2011, Lendrum et al. 2013). We used the satellite-derived, normalized difference vegetation index (NDVI) to reflect plant phenology (Pettorelli et al. 2005). We obtained NDVI data during 2000–2011 from the moderate resolution imaging spectroradiometer (MODIS) at 250-m² resolution (NASA Land Processes Distributed Active Archive Center 2012, https://lpdaac.usgs.gov/). We constructed NDVI time series, based on 8-d composite images, for each pixel within our study area for each year, which we then fitted with a double-logistic curve (Beck et al. 2006, Hird and McDermid 2009) to allow the extraction of three seasonal metrics in program TIMESAT (Jönsson and Eklundh 2004). We calculated date of onset of spring to reflect the start of the green-up and availability of quality forage (Pettorelli et al. 2005). We estimated the rapidity of the rate of green-up in spring based on the rate of increase in NDVI derived from the slope of the fitted double-logistic curve, which reflected how quickly green-up in spring occurred (Pettorelli et al. 2005). We also derived a metric of the level of annual primary productivity by calculating integrated-NDVI, which is the sum of positive NDVI values between start of spring and end of growing season (Pettorelli et al. 2005).

### Data analysis

We estimated RSFs separately for each study area and for movement corridors and stopovers using conditional logistic regression (Boyle 2006, Lendrum et al. 2012), resulting in a total of four modeling efforts. We considered each mule deer as a stratified variable to account for variation among individuals; therefore, logistic models were conditioned on each individual (Long et al. 2009a). Before modeling, we screened predictor variables (Table 1) for collinearity ($|r| < 0.60$) using a correlation matrix. For both stopovers and movement corridors in both study areas, timing of green-up was correlated (all $r > 0.67$) with elevation. Timing of spring is delayed at higher elevation because of cooler temperatures, greater snow accumulation, and delayed snowmelt, but is also what allows migratory herbivores to follow emergent growth in spring as they migrate to high-elevation ranges for summer (Sawyer and Kauffman 2011). Consequently, the actual timing of green-up at a location is less important to a migrating animal as is the relative timing of green-up compared with locations surrounding it at similar elevations (sensu Sawyer and Kauffman 2011). Therefore, to provide a measure of the start of spring that accounted for elevation, we extracted the residuals of a linear regression between elevation and start of spring separately for each study area (Upper Green: corridors $r^2 = 0.41$, $P < 0.001$, $y = -73.36 + 7.78x$; stopovers $r^2 = 0.35$, $P < 0.001$, $y = -63.6 + 7.4x$). Consequently, a 1-unit change in our time of spring metric corresponded to a 1-d change in timing of spring, independent of elevation.

For the stopover models, slope and CTI (wetness index) were highly correlated ($|r| > 0.82$); we chose to retain CTI because we expected forage production in early spring to be

### Table 1. Variables included in the resource selection functions (RSF) of migration by adult female mule deer in the Upper Green River Basin and Atlantic Rim, Wyoming, USA, 2003–2012.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Attributes</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Land cover</td>
<td>land cover type</td>
<td>sagebrush, forest, cropland</td>
<td>National Land Cover Dataset (Fry et al. 2011)</td>
</tr>
<tr>
<td>Elevation</td>
<td>height above sea level</td>
<td>height in meters divided by 100 (1 unit change reflects 100 m) degrees</td>
<td>digital elevation model (<a href="http://datagateway.nrcs.usda.gov/">http://datagateway.nrcs.usda.gov/</a>) derived from digital elevation model</td>
</tr>
<tr>
<td>Slope</td>
<td>steepness of a cell</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Surface curvature</td>
<td>concavity and convexity</td>
<td>index reflecting degree of concavity or convexity</td>
<td>derived from digital elevation model</td>
</tr>
<tr>
<td>Compound topographic index</td>
<td>wetness index</td>
<td>combination of slope and upstream contributing area</td>
<td>derived from digital elevation model</td>
</tr>
<tr>
<td>Aspect</td>
<td>TRASP; radiation index</td>
<td>continuous measure of aspect with zero reflecting north-northeast direction and one reflecting south-southwesterly aspects</td>
<td>derived from digital elevation model</td>
</tr>
<tr>
<td>Anthropogenic disturbance</td>
<td>relative degree of disturbance</td>
<td>metric associated with proximity and degree of human disturbance</td>
<td>Copeland et al. (2007)</td>
</tr>
<tr>
<td>Date of spring</td>
<td>day of the year of onset of green-up</td>
<td>date when NDVI exceeded 10% of baseline in spring</td>
<td>Pettorelli et al. (2005)</td>
</tr>
<tr>
<td>Rate of increase in NDVI</td>
<td>rapidity of green-up in spring</td>
<td>slope of the fitted double-logistic curve</td>
<td>Pettorelli et al. (2005)</td>
</tr>
<tr>
<td>Integrated-NDVI</td>
<td>overall productivity and biomass</td>
<td>sum of positive values of NDVI from base value over the growing season</td>
<td>Pettorelli et al. (2005)</td>
</tr>
<tr>
<td>Date of spring/elevation</td>
<td>date of spring relative to elevation</td>
<td>residuals of a regression between elevation and start of spring</td>
<td></td>
</tr>
</tbody>
</table>

Note: NDVI, normalized difference vegetation index.
affected more so by wetness (i.e., CTI) than by slope. Our elevationally corrected index to timing of spring green-up was correlated positively with rate of spring green-up (all \( r > 0.67 \)) and positively correlated with integrated-NDVI (all \( r > 0.64 \)) for both stopovers and movement corridors. Therefore, date of onset of spring corrected for elevation was already explaining much of the variation in spring plant phenology: sites with an earlier spring exhibited a slower rate of green-up and produced less biomass. We chose to retain our index to timing of spring, rather than other phenological metrics, because we expected spring migration to be more closely associated with sites that exhibited early spring green-up, which would allow animals to depart winter range and arrive to summer range following the leading edge of spring green-up (sensu Sawyer and Kauffman 2011). No other predictor variables were correlated (all \( |r| < 0.60 \)) and thus remained within our set of predictor variables.

We used an information theoretic approach to model selection by calculating Akaike’s Information Criterion adjusted for small sample size (AICc), \( \Delta \text{AIC}_c \), and Akaike weights \( (w_i) \) for each model (Burnham and Anderson 2002). Before proceeding with model selection, we evaluated potential interaction terms between predictor variables by including them in the global model and determining if the 95% CI of their parameter estimate overlapped zero and if their inclusion improved model fit (reduced \( \text{AIC}_c \) by \( >2 \) units). Since our predictor variables represented our hypotheses and predictions, instead of a specific combination of those variables to formulate model sets, we evaluated all possible combinations of predictor variables for each analysis. Modeling all possible combinations of predictor variables in such instances is subject to less bias and is repeatable (Arnold 2010, Doherty et al. 2010). We ranked models based on \( \text{AIC}_c \), and considered models within 2 AIC units of the top-supported model as being potentially competitive. We screened those potentially competitive models for uninformative parameters based on whether they contained one additional parameter, but had essentially the same log-likelihood (Arnold 2010); such models were considered noncompetitive (Burnham and Anderson 2002, Arnold 2010). To simplify interpretation, we converted parameter estimates to odds ratios by exponentiation; we considered odds ratios with 95% CI that contained 1 as being not significant and those that did not overlap 1 to be significant. In addition to reporting odds ratios of the top model, we standardized predictor variables so that estimates of coefficients could be interpreted as the relative magnitude of the effect of each variable on the response variable. We used \( k \)-folds cross validation (Boyce et al. 2003, Anderson et al. 2005, Long et al. 2009b) to assess the predictive strength of our resource-selection function for both study areas for stopovers and movement corridors.

**Results**

We first evaluated interaction terms between main effects using the global model for each analysis; however, none of the interaction terms we considered resulted in an improvement in model fit (reduction in \( \text{AIC}_c > 2 \)). Therefore, we included only additive effects of predictor variables in subsequent model evaluation. Cross-validation analyses indicated satisfactory fit for resource-selection functions for both populations for movement corridors and stopovers based on positive slopes of regression lines, and high coefficients of determination (Table 2). Results from all possible combinations of predictor variables indicated that overall, patterns in selection for land-cover types in movement corridors and stopovers were similar. With one exception, female mule deer selected sagebrush-dominated communities for stopovers and movement corridors during spring migration over forested and grassland cover types (odds ratios for most habitat types \(<1.0\); Fig. 2). For stopovers in the Atlantic Rim, nearly every used stopover occurred in sagebrush-dominated habitat, which precluded an estimate of selection for this habitat type (Fig. 2).

**Movement corridors**

At the spatial scale of the study area, we initially considered three models as supported by the data for explaining patterns of selection for movement corridors of migrating

<table>
<thead>
<tr>
<th>Study area and model</th>
<th>S</th>
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<th></th>
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</thead>
<tbody>
<tr>
<td>Slope</td>
<td>0.049</td>
<td>0.56</td>
<td>0.91</td>
</tr>
<tr>
<td>Stopover</td>
<td>0.006</td>
<td>0.32</td>
<td>0.57</td>
</tr>
<tr>
<td>Atlantic Rim</td>
<td>0.005</td>
<td>0.72</td>
<td>1.0</td>
</tr>
<tr>
<td>Stopover</td>
<td>0.29</td>
<td>0.31</td>
<td>0.96</td>
</tr>
</tbody>
</table>

**Table 2. Results of cross-validation for resource-selection functions of movement corridors and stopovers for spring migrations of adult female mule deer, Upper Green River Basin \( (n = 45) \) and Atlantic Rim \( (n = 60) \), Wyoming, USA, 2003–2012.**

![Fig. 2. Odds ratios (±95% CI) for cover types forest and croplands (i.e., riparian and irrigated hay) obtained from resource-selection functions for movement corridors and stopovers of spring migratory routes for adult female mule deer during 2003–2012 in the Upper Green River Basin \( (n = 45) \) and 2005–2006 in the Atlantic Rim \( (n = 60) \) of Wyoming, USA. Odds ratios represent the percent change \( (1 = no \ change) \) in odds of use by mule deer for each cover type relative to sagebrush steppe. There was no estimate for stopovers in the Atlantic Rim because all used areas occurred within sagebrush steppe.](image-url)
mule deer in the Upper Green; however, the second- and third-ranked models contained either the elimination (time of spring) or addition of a single variable (aspect), with little improvement in log likelihood compared with the top model (Table 3). Therefore, we eliminated those models from consideration, which resulted in our top model containing anthropogenic disturbance, CTI, elevation, slope, time of spring, curvature, and landcover. In contrast, the global model was the most supported model in the Atlantic Rim and comprised 100% of the weight of evidence (Table 3).

Patterns of resource selection by mule deer for movement corridors were relatively similar between study areas. In both areas, deer selected areas with low anthropogenic disturbance, low wetness (low CTI), low elevation, and concavity (Fig. 3A). The primary differences between the two areas were slope and aspect. Deer in the Upper Green did not exhibit selection relative to aspect; however, deer in the Atlantic Rim selected for south-southwesterly aspects in movement corridors. For slope and timing of spring, deer in the two regions exhibited opposing patterns of selection, with selection for steep slope with delayed timing of spring in the Atlantic Rim and gradual slope and early timing of spring in the Upper Green.

Based on standardized selection coefficients, variables with the greatest influence on patterns of selection for movement corridors were anthropogenic disturbance, elevation, CTI, slope, and timing of spring, even though patterns of selection for slope and timing of spring were opposing between the two regions (Fig. 3B). With every 1-unit increase in anthropogenic disturbance, odds of selection decreased by 1.5% in the Upper Green and 2.9% in the Atlantic Rim. For every 100-m decrease in elevation, odds of selection increased >11% in both areas. Odds of selection for movement corridors increased by >9% in both areas for every 1-unit decrease in wetness (CTI). For every 1% decrease in slope, odds of selection in the Upper Green increased by 3.6%, whereas odds of selection decreased by 6% in the Atlantic Rim. With every 1 d that spring occurred earlier (after correcting for elevation), odds of selection increased by 4% in the Upper Green but decreased by 30% in the Atlantic Rim (Fig. 3A).

**Stopovers**

For stopovers, our global models, which included anthropogenic disturbance, wetness (CTI), elevation, time of spring green-up, landcover, curvature, and aspect, were the top models and possessed >50% of the supporting weight of evidence at both the Upper Green and Atlantic Rim study areas (Table 4). Therefore, we considered our global models for interpretation of landscape features associated with

<table>
<thead>
<tr>
<th>Model</th>
<th>AntDist</th>
<th>CTI</th>
<th>Elev</th>
<th>Slope</th>
<th>Spring</th>
<th>Landcover</th>
<th>Curve</th>
<th>Aspect</th>
<th>K</th>
<th>Log likelihood</th>
<th>AICc</th>
<th>ΔAICc_1</th>
<th>wi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper Green</td>
<td>1</td>
<td>X</td>
<td>X</td>
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**Notes:** Models were evaluated based on Akaike’s Information Criterion adjusted for small sample size (AICc), ΔAICc, and log likelihood; we also provide the number of parameters (K) for each model. Covariates included relative degree of anthropogenic disturbance (AntDist), an index of wetness (CTI), elevation (Elev), slope, timing of spring green-up corrected for elevation (Spring), landcover, landscape curvature (Curve), and a continuous measure of aspect (Aspect). An X in a cell indicates that the covariate was used in the model.
stopover habitat. Overall, selection of stopovers was similar between study areas and associated with areas of low anthropogenic disturbance, low wetness, low elevation, early spring green-up, and south-southwesterly aspects (Fig. 3). The only inconsistent pattern of selection was towards convexity (positive curvature) in the Upper Green and concavity (negative curvature) in the Atlantic Rim.

Based on standardized selection coefficients, selection for dry sites (low CTI) was by far the most influential landscape feature, followed by time of spring, and elevation (Fig. 3B). With every 1-unit decrease in CTI (i.e., wetness), odds of selection increased by 62% in the Upper Green and by 79% in the Atlantic Rim (Fig. 3A). Deer selected for stopover sites at low elevation, with a 26.7% increase in odds of selection in the Upper Green and an 11% increase in odds of selection in the Atlantic Rim for every 100-m decrease in elevation. For every 1 d that spring occurred earlier, odds of selection increased by 3–5% depending upon the area (Fig. 3A).

Although deer selected for dry sites with early spring green-up for both movement corridors and stopovers, site wetness and time of spring green-up were far more influential for selection of stopovers than movement corridors. Nevertheless, deer exhibited similar avoidance of anthropogenic disturbance for stopovers and movement corridors (Fig. 3).

**DISCUSSION**

Migration, and the resulting occupancy of summer and winter ranges, has long been known to play key roles in the dynamics of ungulate populations (Fryxell et al. 1988), whereas ranges traversed during migration were traditionally viewed as a minor component in the life of a migratory animal because of their ephemeral use when compared with other seasonal ranges. Nonetheless, comprehensive and complementary research in recent years has called to attention the importance of connectivity between seasonal ranges to sustain viable populations of migratory ungulates, a conservation challenge that is dependent upon a firm understanding of the landscape components associated with functional attributes of migratory routes. Migratory routes not only function to transport individuals from one seasonal range to another (i.e., movement corridors), but also to prolong access to foods that are potentially more diverse or at a prime phenological state compared with that available on an often impoverished winter range or a summer range exposed to inclement weather (Monteith et al. 2011, Sawyer et al. 2013, 2016). We evaluated separately, the landscape features associated with movement corridors and stopovers, which are thought to be key functional attributes of migratory routes in mule deer that migrate long distances (Sawyer et al. 2013). Although patterns of selection for landscape attributes for movement corridors and stopovers were similar, in support of our hypothesis, landscape features associated with movement corridors aligned better with areas that facilitated movement, whereas selection of stopovers aligned with sites that facilitated foraging.

Migrating deer in our study area consistently selected for sagebrush-steppe habitat over other habitats such as crop-land and forest (Fig. 2). Although sagebrush habitat composed the largest component (78.2% Upper Green; 52.1% Atlantic Rim) of available habitat in the area, sagebrush habitat was still selected over any other habitat type. When considered along with results from other research (Welch and Wagstaff 1992, Kucera 1997, deVos et al. 2003, Sawyer et al. 2006, Stewart et al. 2010, Anderson et al. 2012, Lendrum et al. 2012), selection for sagebrush habitat emphasizes the importance to mule deer as a source of forage and likely cover on both winter range and during migration, at least in this system. Nevertheless, shifts in ecological dimensions that animals chose during or upon completion of migration may differ across regions or migratory tactic (Peters et al. 2017). Deer may select agricultural lands where forbs and grain crops become available in early spring (Garrott et al. 1987, Stewart et al. 2010, Anderson et al. 2012); however, such selection is not consistent among populations; agricultural lands were avoided by deer in western Wyoming (this study) and northwest Colorado (Lendrum et al. 2012). Although it is unclear why selection for agricultural crops is not ubiquitous, the relatively high elevations in our study sites preclude the production of grain crops and alfalfa that are heavily utilized by deer in regions with longer growing seasons. Additionally, fidelity to long-established routes away from low-elevation areas, where most agriculture and anthropogenic disturbance exist, may further reduce their use by migratory deer. Anthropogenic disturbance in agricultural areas may shift selection to habitats that offer greater obstruction or concealment, such as juniper woodlands (Lendrum et al. 2012), but doing so may come at a cost to forage availability (Bergman et al. 2014).

Avoidance of anthropogenic disturbance is common among most large herbivores (Wasser et al. 2011, Webb et al. 2011, Beckmann et al. 2012) and is particularly well documented in mule deer (Sawyer et al. 2006, 2009a, 2017, Lendrum et al. 2012, Blum et al. 2015). We expected selection of
stopovers to be more sensitive to disturbance than migratory corridors, because forward movement ceases within stopovers and deer generally spend more time in stopovers than they do in movement corridors (Sawyer and Kauffman 2011). In contrast to our prediction, avoidance of anthropogenic disturbance was evident and similar in magnitude among both movement corridors and stopovers (Fig. 3). Similarly during spring migration, mule deer migrating through natural gas fields in Colorado, USA, increased rate of movement and consequently, failed to maintain synchrony with advancing plant phenology because of delayed departure from winter range and premature arrival to summer range (Lendrum et al. 2013). With high levels of disturbance (e.g., road density 1.1 km/km²; well pad densities 1.5 km/km²), deer may detour from established routes, while increasing rate of movement and reducing use of stopovers (Sawyer et al. 2013). Avoidance of anthropogenic disturbance for both movement corridors and stopovers during migration provides further evidence of the sensitivity of mule deer to anthropogenic features on the landscape and emphasizes that such factors must be considered carefully in conservation planning because although connectivity may be maintained, functionality may be compromised.

Movement corridors are characterized by areas where deer move quickly, and based on standardized selection coefficients, the key landscape features associated consistently with these areas were slope, elevation, and degree of wetness. Dry locations at low elevation with less snow accumulation all would facilitate long-distance movement in spring, as opposed to wet areas where snowmelt is delayed (Petorelli et al. 2011). Snow is a driving force behind the seasonal distribution of migratory ungulates in temperate climates (Monteith et al. 2011, Geremia et al. 2014), and locomotion through deep snow can come at a greater energetic cost than moving upslope (Parker et al. 1984). We expected deer to choose gradual slopes to facilitate ease of movement during migration, which was supported by selection of gradual slopes in the Upper Green and as shown in other studies (Ager et al. 2003, Lendrum et al. 2012). Nonetheless, deer in the Atlantic Rim region selected for steep slopes, which presumably should have increased locomotive costs. It is possible that such energetic costs are mitigated by the relatively low amounts of snowfall, short migration distances (20–50 km), and limited range in elevation in the Atlantic Rim area. In general, however, upslope travel increases energy expenditures and thus, navigating a complex landscape by avoiding rugged and steep topography would reduce energy demands associated with locomotion (Parker et al. 1984).

Stopovers are areas of high-quality forage along a migratory route that allow animals to move in synchrony with advances in plant phenology and maximize forage intake rather than speed while migrating (Sawyer and Kauffman 2011). In support of the hypothesis that stopovers would be associated with landscape features offering high-quality forage in spring, standardized selection coefficients indicated that selection for stopovers was driven primarily by the wetness of a site, with strong selection for dry sites (Fig. 3). Selection for dry locations would not only provide snow-free areas for movement and foraging, but also would yield areas with early access to emergent forage in spring. Indeed, selection of stopovers was associated with locations on the landscape that did not necessarily green-up early in any one particular year, but on average across 10 yr exhibited earlier green-up than other available sites (Fig. 3). Temperate ungulates often migrate along gradients in plant phenology created by elevation and topography (Sawyer and Kauffman 2011, Merkle et al. 2016, Aikens et al. 2017) and as our results indicate the resulting patterns of snow accumulation and snowmelt in spring. Doing so yields access to forage plants early in development that are highly digestible and high in protein (Albon and Langvatn 1992, Hebblewhite et al. 2008), thereby enhancing replacement of fat and protein losses incurred over winter (Monteith et al. 2013). Consequently, migratory ungulates follow nutritious forage across the landscape by both synchronizing their timing of departure from a foraging patch and subsequent arrival to the next patch in accordance with vegetation phenology, a pattern that is evident temporally (Sawyer and Kauffman 2011, Aikens et al. 2017) and spatially (Fig. 3). Such synchronized movements are in accordance with optimal foraging theory in that relocation to a different foraging patch (i.e., stopover) occurs when the quality of the current stopover becomes equal to or less value than that of another (Charnov 1976), change in relative value of the current stopover likely being more a function of phenological shifts than of resource depletion.

Although some large terrestrial herbivores do not use stopovers on their migrations and do not remain in synchrony with a wave of vegetation green-up (Bischof et al. 2012, Lendrum et al. 2013), stopovers appear to be especially common in large herbivores that migrate long distances (>50 km; White et al. 2010, Monteith et al. 2011, Sawyer and Kauffman 2011, Sawyer et al. 2013, Blum et al. 2015, Skarin et al. 2015), which may underscore their importance in sustaining long-distance migrations. Selection for migratory corridors was linked poorly with emerging forage associated with spring green-up, and in the instance of the Atlantic Rim study area, it was associated with sites with delayed vegetation phenology (Fig. 3). In contrast, selection for stopovers in both study sites was associated with dry locations on south-southwesterly slopes with early green-up and low anthropogenic disturbance, which supports the hypothesis that stopovers are critical locations on a migratory route that facilitate refueling and energy gain. Indeed, mule deer in western Wyoming, USA, spent >95% of their time in stopovers during migration, and timing of occupancy of each stopover closely tracks that of plant phenology (Sawyer and Kauffman 2011).

Selection for slope and spring green-up in movement corridors differed between our two study populations, and in other populations, patterns of selection during migration are not ubiquitous (Garrott et al. 1987, Nicholson et al. 1997, Lendrum et al. 2012). Selection for elevation, aspect, agricultural lands, and slope, in particular, varies across populations, and in some instances, selection for stage of plant phenology may vary across species and populations (Merkle et al. 2016). Interannual variability in plant phenology may cause nuanced differences in habitat selection across years or even species, especially if the foundation for selection of their migratory route is determined by memory and fidelity (Sawyer and Kauffman 2011, Bracis and Mueller 2017). With
strong fidelity to seasonal ranges and migratory routes (Sawyer and Kauffman 2011), habitat selection associated with plant phenology and associated landscape features reflects a long-term mean of vegetation phenology as opposed to timing of movement, which is an annual decision (Monteith et al. 2011, Jones et al. 2014, Aikens et al. 2017). Moreover, variable patterns of selection of some landscape features indicate that over time, selective processes have had localized influences (Kaitala et al. 1993). Nevertheless, we observed strong avoidance of human disturbance and selection of foraging areas associated with stopovers with early spring green-up (Fig. 3), a pattern consistent across multiple species of temperate ungulates (Lendrum et al. 2012, Poor et al. 2012, Blum et al. 2015, Merkle et al. 2016, Paton et al. 2017), which reinforces the notion that movement during migration has a nutritional underpinning and disturbance potentially alters the net benefits of migration. Indeed, barriers to migration or alterations to routes that force detours (Sawyer et al. 2013, Seidler et al. 2015) may displace animals onto wetter habitat with delayed spring green up, thereby hampering forward movement and forage gain.

Nomadic or migratory movements that vary by season or year create difficulties for conservation planning and understanding seasonal movements (Singh and Milner-Gulland 2011, Runge et al. 2014); however, the strong fidelity to seasonal ranges and migratory routes displayed by most temperate ungulates (Berger 2004, White et al. 2010, Sawyer and Kauffman 2011) offers a valuable opportunity to delineate and target areas for conservation (Sawyer et al. 2009b). The strong link between fitness and nutritional condition in temperate ungulates underscores the importance of migratory tactics that enhance nutritional gain (Monteith et al. 2014, 2018). Therefore, it is critical for migrating animals to not only have access to stopovers where snow recedes and green-up occurs predictably early, but also to have readily traversable pathways that connect them. Maintaining connectivity between seasonal ranges as well as the functionality of migratory routes is now a critical focus of conservation (Berger 2004, Berger and Cain 2014, Copeland et al. 2014, Berger et al. 2014). One of the greatest shortcomings of effective conservation has been a fragmented understanding of migration (Bolger et al. 2008), of which has been improved by recent works focused on the impetus (Monteith et al. 2011, Lendrum et al. 2013, Singh and Ericsson 2014, Merkle et al. 2016, Aikens et al. 2017) and population-level consequences (Hebblewhite and Merrill 2009, Middleton et al. 2013, Monteith et al. 2014, White et al. 2014) of migration. Understanding the evolutionary underpinnings of migration and its effects on population dynamics is critical, but more pressing is the need to effectively manage and conserve migratory populations in an increasingly altered landscape (reviewed by Bolger et al. 2008). Therefore, identifying migratory routes and the landscape attributes associated with them are keys to mitigating, enhancing, and protecting the migratory habitat needed to sustain ungulate populations.

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Literature Cited


[Acknowledgments continued]


Data Availability

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.j4r13dc