Surf's Up: Green Wave Surfing Resilience to Anthropogenic Disturbance in Wyoming Mule Deer during Spring Migrations

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ABSTRACT

Seasonal ungulate migrations are a global phenomenon, yet they are increasingly threatened by human development. Understanding how disturbance alters ungulate behavior and location selection during migrations is critical to identifying effective conservation strategies to preserve migrations and their benefits. I examined the resiliency of green wave surfing during spring migrations of Wyoming mule deer to human disturbance along their migration corridors. I analyzed the GPS locations of collared mule deer during their spring migrations in Wyoming and modeled green wave surfing success on the instantaneous rate of green-up. I applied a step selection function to determine resource selection near two major forms of disturbance along their migration corridors: roads and buildings. I fit a multivariate autoregressive model to estimate the impact of proximity to disturbance on green wave surfing success. I used a generalized additive model on an individual's resource selection and impact values. At the population-level, deer significantly avoided roads. Proximity to neither roads nor buildings was associated with significant decreases in green wave surfing success. Though mule deer behaviorally respond to human development via avoidance, this response is not connected with a subsequent drop in green wave surfing ability. In conclusion, green wave surfing by mule deer during spring migrations appears to be resilient to human disturbance.

KEYWORDS

Odocoileus hemionus, green wave hypothesis, human disturbance, step selection function, MAR covariates

INTRODUCTION

Ungulate migrations are a global phenomenon accounting for some of the largest animal movements around the world. While there is a huge diversity of characteristics and underlying drivers across species, these migrations have substantial impacts on population dynamics and are essential to population condition and survival. Whole ungulate populations, or a significant proportion of a population, migrate between distinct seasonal home ranges, residing in higher elevations or latitudes in the summer and lower elevations or latitudes in the winter. Migratory individuals experience reduced predation risk, less snow, and greater access to suitable vegetation compared to resident individuals (Hebblewhite and Merrill 2009). These migrations have significant ecological implications for ecosystems and other species. Due to the large biomass passing through ecosystems at regular intervals, their grazing and defecation alter grassland processes and presence provides prey sources to diverse predators (Bauer and Hoye 2014). However, migrations are threatened globally by habitat destruction, human development, exploitation, climate change, noise and light pollution, and a host of other anthropogenic hazards (Wilcove 2008). These threats can alter the migration corridor or destination or the environmental cues essential for the timing of migrations (Hurlbert and Liang 2012). Despite these challenges, hundreds of ungulate populations still migrate each year.

Ungulate feeding strategy is influential in determining the timing and pace of their migrations. Ungulates are selective browsers, as described by the forage maturation hypothesis, whereby they consume new-growth vegetation with a balance between sufficient biomass to sustain their energy needs and high enough quality to be easily digestible (Fryxell 1991, Hebblewhite et al. 2008). During the spring migration period, this optimal forage is available at staggered intervals across the landscape. As winter snow melts and temperatures rise, vegetation enters a growing period, with distinct peak or high growth that progresses across the landscape. These distinct peaks are known as the green wave and are dynamic within a season and across years. These peaks are reflected in the Normalized Difference Vegetation Index (NDVI), a measure of the greenness of the landscape, and its rate of change, or instantaneous rate of green-up (IRG) (Figure 1). When vegetation is experiencing its fastest growth, i.e. its highest IRG value, during this season, the vegetation has the balance of mass and quality that ungulates select for. The Green Wave Hypothesis states individuals "surf" or follow this green wave by spatially and temporally tracking the leading edge of the wave across a landscape during migrations (Drent 1978). While the Green Wave Hypothesis originated for waterfowl migrations, it is now applied to ungulate migrations (Merkle et al. 2016, Aitkens et al. 2017). Being able to access the optimal forage throughout their migration period gives individuals a fitness advantage, leading to higher fat levels, which are important for survival in the following season, as well as pregnancy success in females (Middleton et al. 2018). While green wave surfing during migrations has been observed in multiple ungulate populations, the fine-scale mechanisms of green wave surfing and which factors may impact surfing success are not well known.

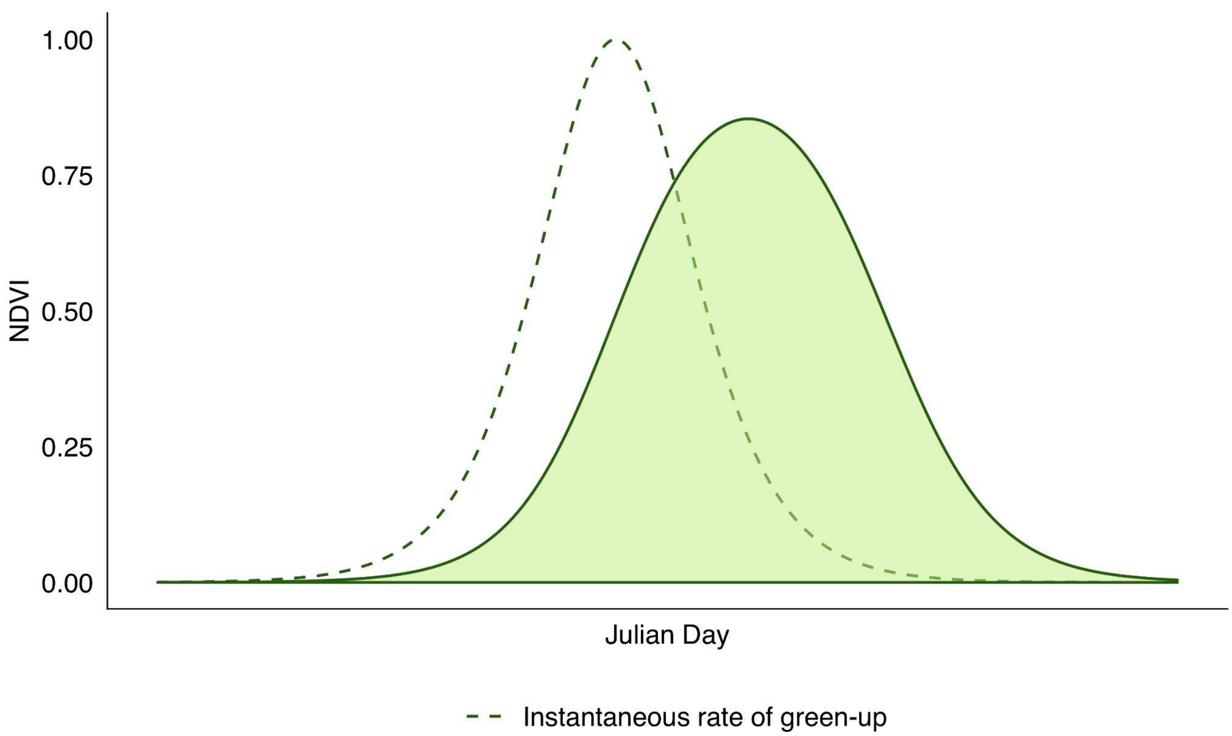

Figure 1. Instantaneous rate of green-up (IRG) curve derived from the Normalized Difference Vegetation Index (NDVI) curve. IRG values are calculated from the rate of change of the NDVI at the same moment in time. Successfully surfing means experiencing peak IRG of 1.

While attempting to surf green waves during migrations, ungulates have to navigate barriers throughout their migration corridors. Some of these barriers may be natural, such as large rivers or barren areas. More recently, even rural herds are facing increasing encroachment by human development and activity (Kauffman et al. 2020). Construction and infrastructure along migration corridors reduce available habitat with suitable forage, limiting browsing opportunities for migrating ungulates. Impassable barriers block regular routes, which individuals demonstrate high fidelity to, suspending the migration before individuals reach the final seasonal range or forcing huge detours around the barrier (Xu et al. 2019). Semi-permeable barriers temporarily prevent forward progress, prompting hesitations and extra time spent attempting to cross successfully (Xu et al. 2021). Disturbance is associated with patterns of avoidance and limited eventual habitation (Rost and Baily 1979, Sawyer et al. 2017, Sawyer et al. 2020). These disruptions are explained by the “landscape of fear” where individuals avoid areas associated with high risks (Laundré et al. 2010). It is understood that human activity and development impact ungulate migrations, but exactly how and to what extent these barriers may impact green wave surfing is unknown. Green wave surfing is a deliberate behavior as individuals manage their location and speed for access to optimal forage. If disturbance provokes a behavioral response, this could affect the ability of individuals to select ideal locations or time their movement. These disruptions could reduce the ability of individuals to successfully surf the green wave during their spring migrations.

The purpose of this study is to assess the resiliency of ungulate green wave surfing to human Disturbance along migration corridors. For a Wyoming population of mule deer, I investigated 1) whether individuals exhibited a behavioral response in proximity to Disturbance, 2) whether proximity to Disturbance caused a decline in green wave surfing success, and 3) whether the strength of an individual’s behavior was correlated to the severity of the surfing decline for that individual. I expected some degree of avoidance in response to disturbance leading to a surfing disruption, indicating low green wave surfing resilience to Disturbance during migrations.

METHODS

Study site

Northwestern Wyoming is a semi-arid ecosystem in the Rocky Mountain region of the western United States (Figure 2). There are two herds of Rocky Mountain mule deer (*Odocoileus hemionus hemionus*) in the area, known as the Clarks Fork and Upper Shoshane herds. There are other large migratory mule deer herds, as well as migratory populations of elk, moose, bison, and bighorn sheep throughout the study site. Their winter seasonal ranges are just to the east of Cody and are characterized by sagebrush steppe basins, lower elevations (~5,000 ft), cold temperatures (17 - 37.6 ℉), and little rainfall (0 - 0.14 inches) or snow (0 - 0.3 inches) (US Geological Survey 1999, National Oceanic and Atmospheric Administration 2006). Their summer seasonal ranges are inside Yellowstone and Grand Teton National Parks in higher elevation forests (~8,000 ft), cool temperatures (46.6 - 64.5 ℉), little rainfall (0 - 0.19 inches), and no snow (US Geological Survey 1999, National Oceanic and Atmospheric Administration 2006). To access both seasonal ranges, individuals migrate across the Absaroka Range.

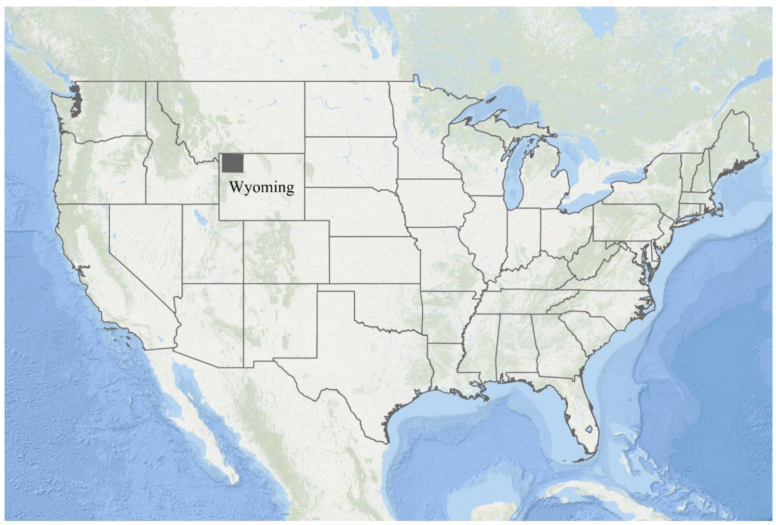

Figure 2. Study site in Wyoming, USA. The black square represents the nine million hectare study site in northwestern Wyoming. It is approximately 300 kilometers wide between the north border of Wyoming and Grand Teton National Park, and approximately 300 kilometers long between the west border of Wyoming and Cody.

Data collection and processing

Individual deer location data was provided by the Wyoming Cooperative Fish and Wildlife Research Unit at the University of Wyoming. They captured 28 adult female mule deer in March 2016 near Cody, Wyoming using a net gun fired from a helicopter. Each individual was fitted with a Global Positioning System (GPS) collar (Advanced Telemetry Systems, Iridium, Isanti, Minnesota, USA) that was programmed to collect locations every two hours between March and August 2016. To determine the migration period of each individual, I calculated net squared displacement, or the distance between an individual's initial GPS location and each subsequent location, with *migrateR* R package (R Development Core Team 2006, Spitz 2017). I then fit those values to a movement behavior model, as described in Bunnefeld et al. (2011), and identified the start and end dates of their migration period. Dispersal behavior is detected when they leave their seasonal range to begin their migration, as a sudden increase in distance from the initial point is followed by subsequently larger distances.

I identified roads and buildings as common forms of anthropogenic disturbance present in the study site. Roads, such as US-14E and WY-120E, and buildings from the outskirts of Cody and Wapiti, are both common forms of human activity development, but represent semi-permeable and impassable barriers, respectively. For the locations of buildings, I used a building density shapefile provided by the Middleton Lab (A. Middleton, unpublished data). For the locations of roads, I used a shapefile of primary and secondary roads in 2015 in Wyoming (US Census Bureau 2015).

Calculating metrics of green wave surfing

To quantify the forage landscape, I used the Normalized Difference Vegetation Index (NDVI), which is a measure of the greenness of a landscape. I used the *MODIStsp* R package to download NDVI data from the NASA servers (R Development Core Team 2006, Busetto and Ranghette 2016). I used the MOD09GQ Version 6 product of the Terra Moderate Resolution Imaging Spectroradiometer (MODIS) surface reflectance and quality bits at 250-m spatial resolution with daily temporal resolution from 2015 and 2016 (Vermote 2015). The NDVI values are calculated automatically by the package by dividing the difference between near-infrared and visible radiation over the sum of the near-infrared and visible radiation.

To quantify green wave surfing, I fit a double logistic curve to the time series of the NDVI values, using the methods described by Bischof et al. (2012), with the *irg* R package (R Development Core Team 2006, Robitaille 2019). This created a time series of daily instantaneous rate of green-up (IRG) values at each pixel throughout the study site. I matched these IRG values to individual GPS locations based on their GPS location each day. The time series of the IRG values for an individual represents the rate of growth they experienced at each location and, therefore, their surfing success throughout their migration.

Modeling resource selection in response to disturbance

To detect whether individuals exhibited a behavioral response in proximity to disturbance, I fit a step selection function (SSF). SSFs estimate resource selection of an individual using conditional logistic regression to estimate the probability of an individual selecting a location based on associated environmental characteristics (Thurfjell et al. 2014). The model generates random steps, or straight line movements, between the observed GPS locations by drawing step lengths from a gamma distribution and turn angles from a uniform circular distribution. It then calculates the probability of an individual selecting a location with specific environmental characteristics based on the frequency of used steps to available steps with the same characteristics.

I fit a SSF to the GPS locations, grouped by individual, using the *amt* R package (R Development Core Team 2006, Signer et al. 2019). I used disturbance as the SSF environmental characteristics at the end of each step. From the original shapefiles for each disturbance type, I created a raster where each cell's value is the distance from that cell to the nearest feature of each disturbance type, presented as a negative number. Fitting the model produced beta values, or selection coefficients, which represent the strength of selection for or against environmental characteristics, and robust standard errors for each individual. A negative selection coefficient indicates an individual is selecting locations with greater distances to disturbance, i.e. selecting steps away from disturbance, revealing avoidance.

Assessing the effect of disturbance proximity on surfing success

To whether proximity to disturbance caused a decline in green wave surfing success, I applied a multivariate autoregressive model (MAR). The MAR model identifies underlying trends in data given stochasticity and estimates effects of covariate data. It is used for interpreting, evaluating, and forecasting time series data. It is described with the following equation

[1] $x_t = Bx_{t-1} + U + Cc_t + w_t$, where $w_t \sim MVN(0,Q)$

where *X* is a matrix of each individual's IRG surfing scores at subsequent time steps. *B* is a matrix describing the interaction between individuals, set in this case to exclude any density dependence or interactions between individuals. *U* is the overall trend of each individual, but is void here based on the assumption that each individual is actively surfing the green wave and therefore should have a stationary trend of IRG = 1. *C* is a matrix that manages the covariate effects of the disturbance, or the change in *X*, with changing values of *c*. *c* is a matrix of covariate data. *w* describes white noise from the multivariate normal distribution of *Q,* the stochastic variation that is shared among all individuals.

I fit the MAR model to the individual IRG scores using the *MARSS* R package (R Development Core Team 2006, Holmes et al. 2012). I edited the *C* matrix so each individual is affected by each form of disturbance differently than other individuals to the same disturbance type. For the *c* matrix data, I used the distance from the individual's location at that time step to the nearest form disturbance, with values extracted from the rasters used in the SSF. After the model converged, I bootstrapped it (n = 1000 times) to obtain maximum likelihood estimates and 95% confidence intervals for the covariate effect parameters. A negative covariate effect value indicates an individual experiences lower IRG values when they are in closer proximity to disturbance.

Determining relationship between behavior and barrier effects

To determine whether the strength of an individual's behavior was correlated to the severity of the surfing decline for that individual, I fit a generalized additive model (GAM). The GAM modeling technique estimates smooth nonlinear relationships between the predictor and dependent variables. It is described with the equation of smooth functions

[2] $$g(E(Y)) = \alpha + s_1(x_1) + \ldots + s_p(x_p)$$

where Y is the dependent variable to predict, E(Y) is the expected value, g(Y) is the function that links the expected and predictor x_1 values. The terms $s_p(x_p)$ represent smoothed and nonparametric functions. I fit a GAM with the *mgcv* R package (R Development Core Team 2006, Wood 2011). I used the individual selection coefficients from the SSF as the predictor values and the individual covariate effects from the MAR model as the dependent variable, with a separate model for each type of disturbance. This produced a formula model, the effect of a predictor variable with significance and variance explained.

RESULTS

Migrations and green wave surfing

The GPS location data of the 28 female mule deer consisted of more than 4600 unique locations. Net squared displacement revealed individual deer migrations ranged from five to 25 days long during April and June. One individual was excluded from analysis as an outlier due to its migration period lasting 61 days, nearly three times as long as the next longest migration. There are 61 major roads and more than 490,000 buildings present in the study site (Figure 3).

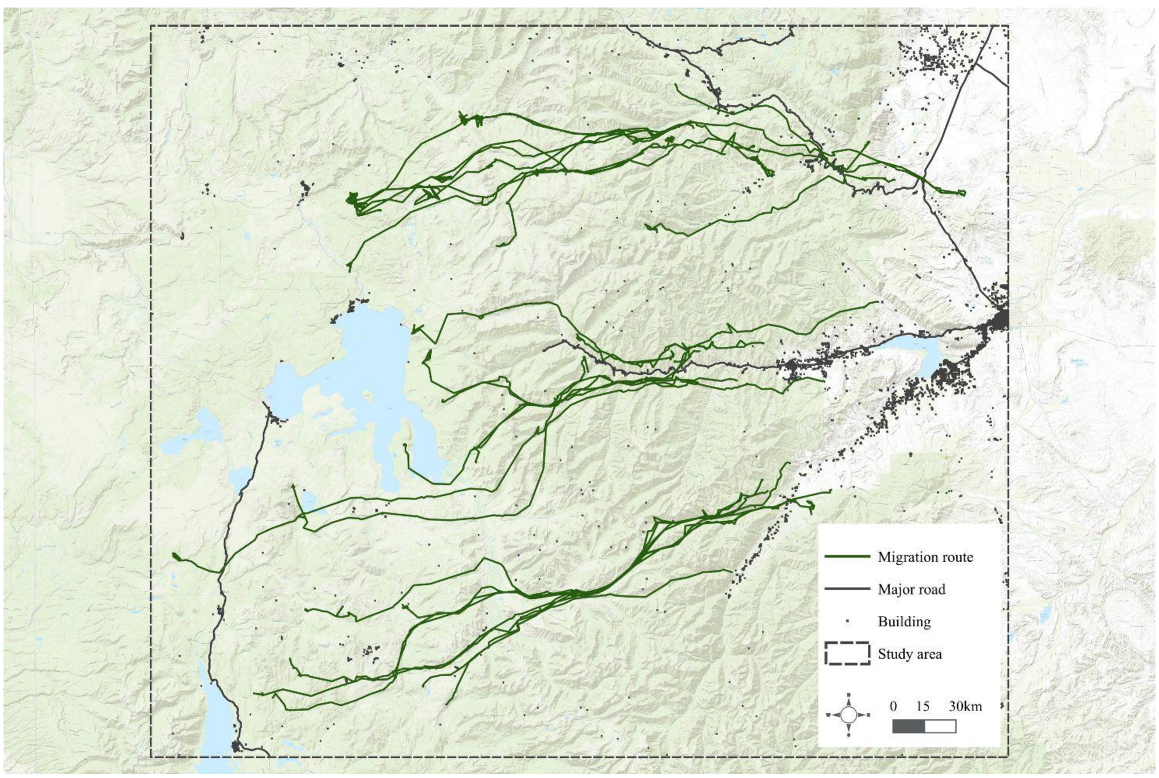

Figure 3. Migration routes of individuals and anthropogenic disturbance as roads and buildings.

The Instantaneous Rate of Green-Up (IRG) values of individuals ranged from near zero to one, with only about 6% of the values equaling the 'perfect surfer' score of one (Figure 4). Even though each individual had high variation in their IRG values, individuals still experienced very high IRG scores overall (mean = 0.9433497, SD = 0.08113616).

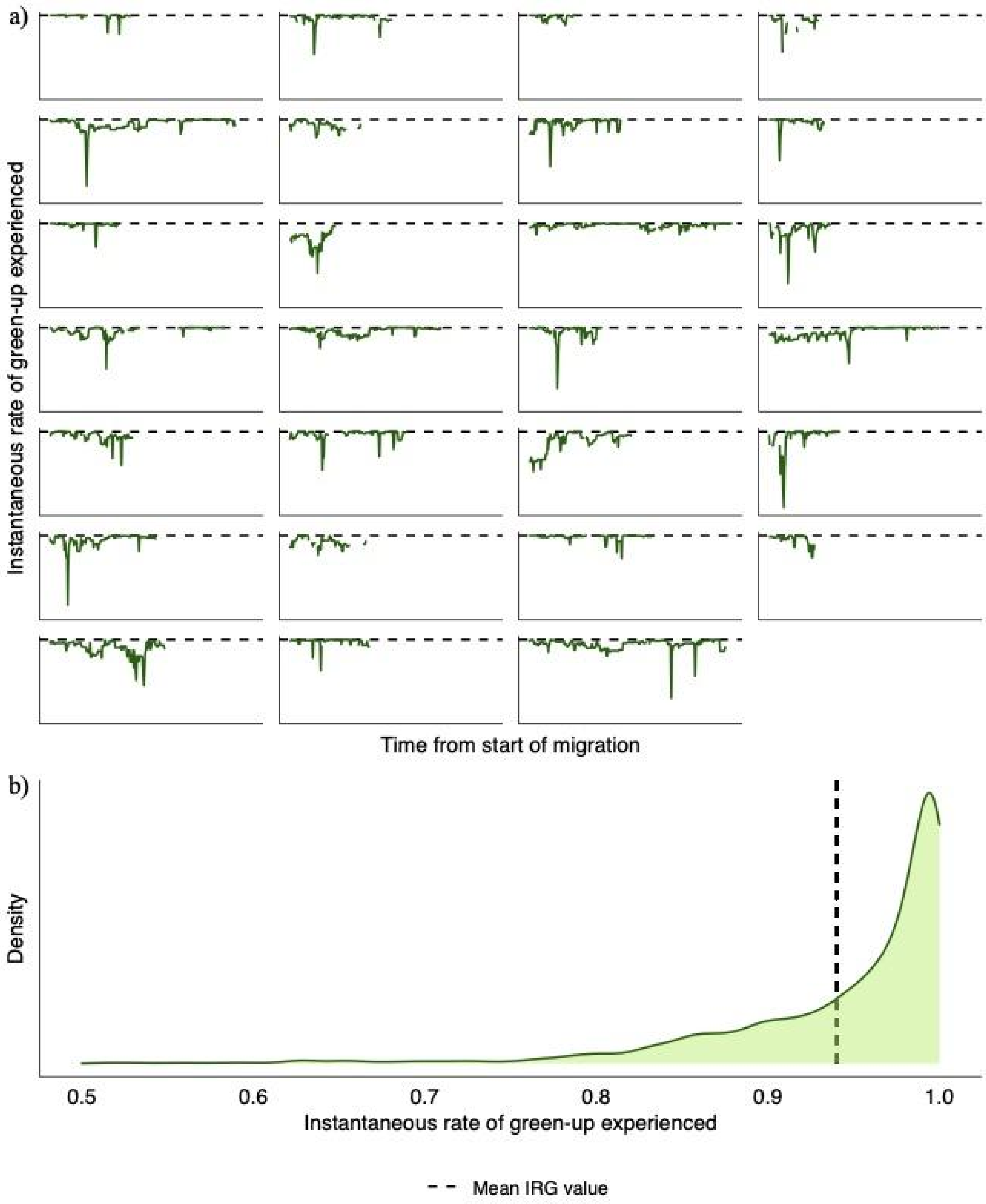

Figure 4. Metrics of green wave surfing success. (a) IRG values of individuals experienced every two hours since the start of their migration periods. The x-axis spans 25 days but the line of each individual stops at the day and time of their last GPS location.. (b) Histogram of all the IRG values experienced during the full spring migration period with mean value of 0.94.

Habitat selection in response to disturbance proximity

Mule deer individuals exhibited avoidance behavior to disturbance by selecting locations away from roads. Population averages of the selection coefficients from the step selection function were negative for both roads (β = -1.61) and buildings (β = 0.02), but selection was only statistically significant for roads (p = 0.05) (Table 1). Negative selection coefficients from the step selection function indicate individuals selected steps with greater distances to disturbance, i.e. they are avoiding disturbance. Selection coefficients varied greatly by individuals, with some selecting towards instead of away from disturbance, and only some individual coefficients were significant (Figure 5). Of the 27 individuals, 17 individuals avoided roads, though only three had significant coefficients. No individuals significantly selected for roads. 14 individuals avoided buildings. One individual significantly selected for and one significantly avoided buildings. Despite these differences, individuals did not respond significantly differently to roads than buildings (p = 0.3483, Wilcoxon signed rank test). To an extent, these results support my expectations that individuals would avoid anthropogenic disturbance.

Table 1. Population-level selection coefficients. Population averages and standard errors are calculated from individual selection coefficients, or β values, from the SSF with respect to distance to the nearest disturbance. Selection coefficients and standard errors are reported at 10,000 times their original values. (*) denotes selection coefficients that are significantly at the p =0.05 level from a one-sample Wilcoxon signed rank test.

Barrier	**β**	**SE**	**p**
Buildings	0.01805	0.47700	0.5619
Roads	-1.60892*	0.76558	0.0491

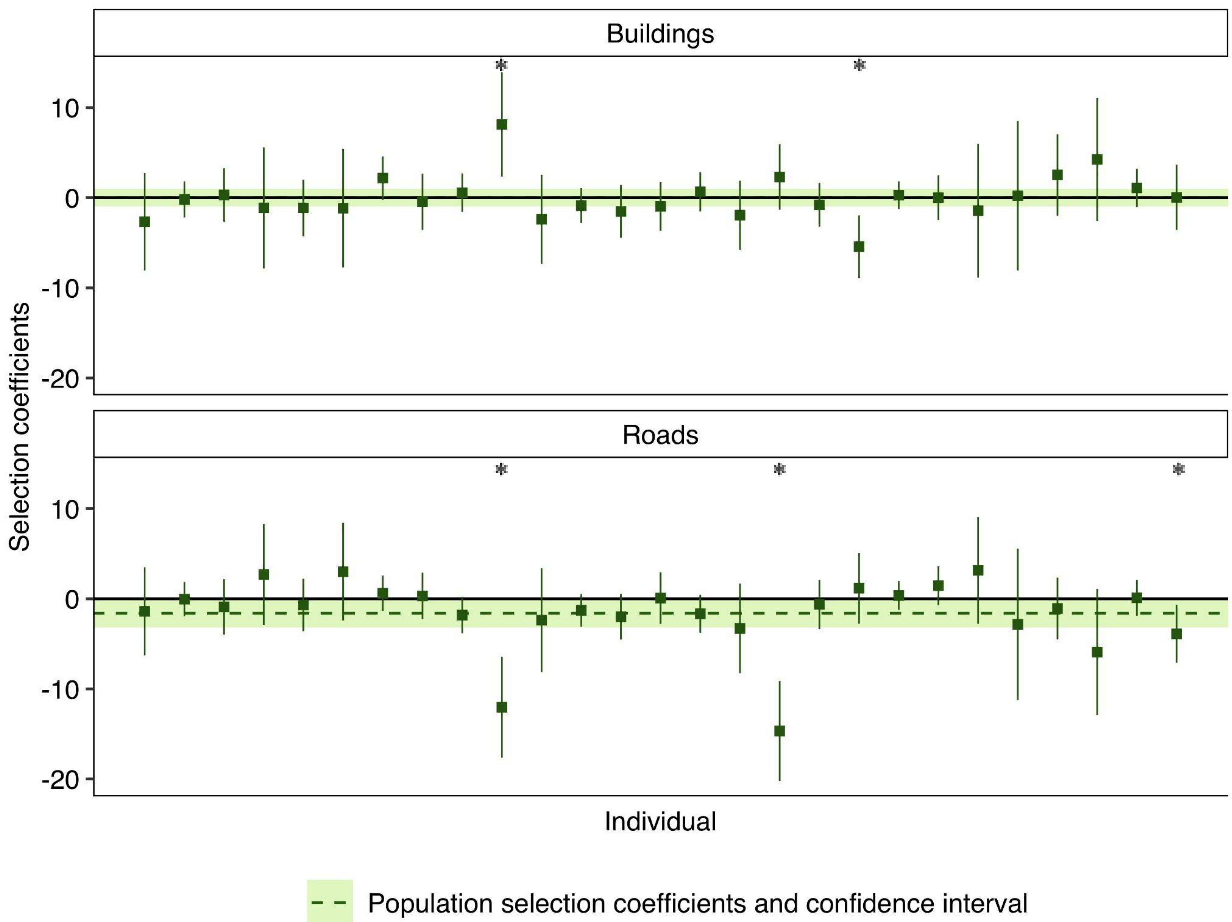

Figure 5. Individual selection coefficients and 95% confidence intervals from the SSF. Selection coefficients and confidence intervals are shown at 10,000 times their original values. An individual selects steps with greater distances to disturbance when their selection coefficient is below the x-axis. Statistically significant selection coefficients are noted with an asterisk.

Disturbance proximity covariate effects on IRG values

Increasing proximity to disturbance did not cause a decline in the green wave surfing success of individuals. Population-level averages of the individuals covariate effects were negative for buildings (C = -0.004) but positive for roads (C = 0.001), but neither were statistically significant (Table 2). The MAR model estimates negative covariate effects when individuals experience lower IRG values as they become closer to a disturbance. Covariate effects at the individual level varied, but none were significant (Figure 6). Despite these differences, surfing success was not impacted significantly differently to roads than buildings (p

= 0.9341, Wilcoxon signed rank test). These results do not support my expectation that proximity to disturbance would reduce green wave surfing success. Instead, surfing success is not significantly affected when individuals encounter disturbance.

Table 2. Population-level covariate effects. Population averages and standard errors are calculated from individual covariate effects, or *C* parameters, from the MAR models with respect to distance to the nearest disturbance. Covariate effects and standard errors are reported at 10,000 times their original values. Neither covariate effect is significant at the p =0.05 level from a one-sample Wilcoxon signed rank test.

Barrier	***C***	**SE**	**p**
Buildings	-0.00390	0.00522	0.8593
Roads	0.00044	0.00140	0.9341

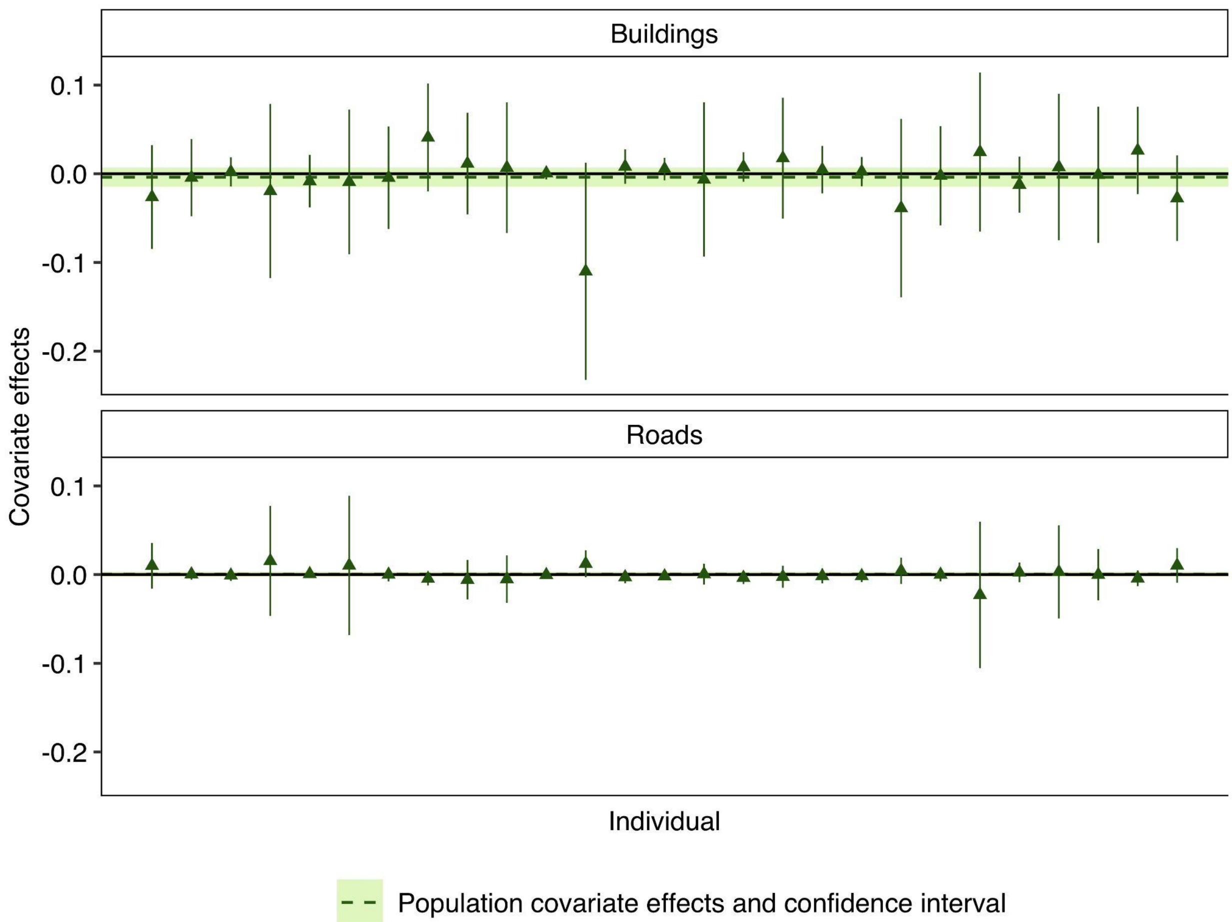

Figure 6. Individual covariate effects and 95% confidence intervals from the MAR model. Covariates and confidence intervals are shown at 10,000 times their original values. When closer to a disturbance, an individual's IRG values significantly decline when their covariate effect is below the x-axis. There are no statistically significant covariate effects.

Smoothed relationship between behavior and effect

The strength of an individual's behavior was not correlated to the severity of the surfing decline for that individual. The GAM revealed no significant association between an individual's selection coefficients and covariate effects for roads ($p = 0.57$, $R^2 = -0.03$) or buildings ($p = 0.707$, $R^2 = -0.03$). I expected large, negative selection coefficients to be associated with large, negative covariate effects, such that the stronger the avoidance behavior, the larger the decline in surfing success when near disturbance. This is not supported by the GAM results. Instead, these results indicate that even though some mule deer individuals avoid roads and buildings along their migration routes, their selection of locations away from disturbance does not result in them browsing vegetation below peak green-up.

DISCUSSION

This study investigated how resilient green wave surfing is to human disturbance during spring migrations. It assessed behavioral responses and declines in surfing success in response to proximity to disturbance, and if there was an association between an individual's behavior and the decline it experienced. Mule deer individuals are behaviorally impacted by anthropogenic development and encroachment into their migrations corridors, but resilient enough to be able to maintain their green wave surfing ability. In their resource selection, mule deer avoided roads, but despite this, proximity to roads did not reduce their surfing success. Overall these results indicate green wave surfing in mule deer is resilient to anthropogenic disturbance throughout their spring migrations.

Migrations and green wave surfing

There was high variation in migration route, distance, and length among individuals, along with separate summer and winter seasonal ranges among herds. This variation means individuals had inherently different exposure to disturbance during their migrations. Each individual passed by a different number of buildings and roads along their migrations. However, a more nuanced reality is that each individual experienced a unique composition of human development and activity. Each major road could have different widths and traffic activity. The buildings were present at different densities and likely had varying degrees of human presence, smaller surrounding roads, and traffic activity. In addition to typical individuality among migrations, this variation suggests the behavioral responses to and surfing success impacts of disturbance should vary by individuals.

Despite high variation in migration lengths and routes, mule deer individuals experienced high IRG values and can therefore be assumed to be actively surfing the green wave. Multiple studies have found strong evidence in support of the Green Wave Hypothesis in mule deer populations, making it reasonable to assume this population of mule deer are as well (Merkle et al. 2016, Aikens et al. 2017, Aikens et al. 2020). This means they are actively managing their timing and locations to follow these green waves of forage. Therefore, their migration corridors are important habitat for forage consumption, as well as routes between their summer and winter ranges.

Habitat selection in response to barrier proximity

The resource selection analysis revealed mule deer individuals actively responded to and avoided roads. This was expected as behaviorally mediated responses to anthropogenic infrastructure have been observed before, including against fences (Xu et al. 2021), energy development (Sawyer et al. 2017, Dwinnell et al. 2019), and highways (Coe et al. 2015). Despite the observed avoidance of roads in this study and additional forms of disturbance in other studies, in this study buildings did not significantly induce a change in resource selection.

This avoidance of roads is likely due to the associated risk outweighing the forage quality. The term “landscape of fear” describes how resource use and behavior of prey is largely controlled by perceived risk of predation, and is an additional method of control beyond predation mortality (Laundré et al. 2010). This concept is also applicable to the substantial impacts human activity and development have on wildlife behavior (Ciuti et al. 2012). Major roads along the migration corridors likely have high traffic activity and noise. Older and more experienced mule deer may associate roads with injury or death. In this area of rural Wyoming, the level of human activity, and therefore potential risk, associated with buildings may be less so, explaining the lack of avoidance.

An alternative, possibly more likely, explanation is that forage availability may explain the lack of significant selection against buildings. When resources are abundant, mule deer will select locations based on perceived safety rather than based on forage availability. However, when resources are scarce, mule deer will select locations to optimize their forage intake, despite any perceived risk, including of human development and activity (Hayward et al. 2015, Sawyer et al. 2017). Buildings may be perceived as a smaller risk than roads so mule deer will not avoid them if forage is scarce. Mule deer could select against buildings, and even more strongly against roads, if high quality forage was abundant enough elsewhere.

It is also necessary to note resource selection is not the only behavioral response that mule deer may exhibit near disturbance. Though mule deer did not actively select away from buildings, they still may have responded to buildings, and roads, in other ways. Mule deer have been found to travel faster through areas with human development, using stopover habitat for shorter amounts of time (Sawyer et al. 2012, Wyckoff et al. 2018). Additionally, when in proximity to disturbance, mule deer may become more vigilant (Dwinnell et al. 2019). It is likely mule deer will alter their behavior before diverging from their migration routes, especially considering they exhibit high fidelity to migration routes even with changing landscapes and significant disturbance (Merkle et al. 2022).

Disturbance proximity covariate effects on IRG values

The time series analysis revealed increasing proximity to roads and buildings did not reduce an individual's surfing success. This is inconsistent with previous studies where human development, and subsequent avoidance by mule deer, results in limited forage quality (Dwinnell et al. 2019) and habitat loss in seasonal ranges (Sawyer et al. 2017). Furthermore, roads and buildings represent high levels of human development, and the likely conversion of forage to infrastructure or barren land. Therefore, I expected both forms of disturbance to disrupt green wave surfing, which is not supported by these results. Mule deer may be experiencing less forage or disrupted surfing in areas closest to disturbance, however it may not be detectable with the spatial and temporal resolution of the two hour tracking period and daily NDVI resolution. This would mean the disruption is so minor that mule deer are able to easily recover, and therefore not a significant impact.

Behavioral effect on green wave surfing

Despite avoidance against roads, proximity to roads did not influence the surfing success of mule deer. Given there was no significant selection against buildings, it was expected that proximity to buildings would have no impact, as mule deer did not avoid them and should have been able to still browse ideal forage. In accordance with the Behaviorally Mediated Forage-Loss Hypothesis (Dwinnell 2019), I expected the avoidance of roads to result in reduced surfing ability. If individuals attempted to avoid roads, their ideal location selection or timing would be compromised, disrupting their green wave surfing. However, roads do not have this impact. As previously mentioned, mule deer have been found to speed up when near development. So instead of stalling deer, roads may spur them on so they're able to continue surfing to match the green wave. However, this may reduce, or prevent, stopovers, which would limit forage intake. In that case, roads would reduce the overall benefit of migrations via stopovers rather than green wave surfing. Nonetheless, mule deer green wave surfing is resilient to behavioral response to disturbance.

Limitations

This study has advanced our understanding of green wave surfing resilience and the impact of anthropogenic disturbance. However, mule deer migrations are a repeating occurrence whose successful completion twice a year helps to sustain mule deer populations (Fryxell and Sinclair 1988). These results are drawn from a single spring migration for one population and may not be generalizable to a greater variety of conditions. Specifically, this study was not able to assess whether successful green wave surfing despite disturbance varies by year. When forage is scarce during spring or in the previous winter, mule deer may tolerate the perceived risk of anthropogenic disturbance more to access necessary vegetation, but experience greater stress.

There could be a confounding variable not accounted for in this study. The analysis is completed under the assumption that the distribution of forage near roads and buildings does not differ from the distribution of forage further away. However, human development generally reduces the available forage and results in the direct habitat loss of the surrounding area (Dwinnell et al. 2019). Therefore, mule deer may avoid areas near disturbance due to lack of forage more than perceived risk. In this situation, areas near roads and buildings suffered the removal of forage that would have been part of the green wave. While this distinction between forage availability and perceived risk isn't incorporated in the step selection function or selection coefficients, the insignificant covariate effects from the multivariate autoregressive model still signify a resiliency of green wave surfing to disturbance. Even so, incorporating forage availability into the behavioral response analysis would make these results more robust and lead to a more well-rounded understanding of the relationship between disturbance and green wave surfing.

Future directions

Roads and buildings are certainly not the only form of disturbance migrating ungulates encounter. Mule deer exist in large populations throughout western United States with an abundance of disturbance throughout both their seasonal ranges and migration corridors. Other forms of human development and activity should be included in the analysis, for example fences, railroads, and oil fields. Variation within the same type of disturbance should also be considered. The level of activity, i.e. light, noise, or traffic, and how migration-friendly the infrastructure is, such as modified fences and roads with wildlife crossing, could all have unique impacts on mule deer behavior when in proximity to disturbance and subsequently may have distinct effects on green wavy surfing.

Additionally, disturbance density should be included in the analysis alongside proximity to disturbance. Higher density could deter individuals from remaining in a location for too long or limit available steps with desirable distances from a disturbance. This would likely produce insignificant selection coefficients despite altering individual behavior. In that case, investigating effects on turn angle and step length within the step selection function would reveal those behavior responses not detected by only examining selection coefficients.

There could be large-scale and long-term effects of disturbance in addition to localized step selection adaptations. Though this study measured resource selection by step location, mule deer also exhibit avoidance behavior at larger scales. Development can have long-term effects where mule deer alter their home ranges to avoid areas of development. This has been extensively documented in oil fields during construction and in production (Sawyer et al. 2017). A similar situation could occur where, as disturbance increases along with avoidance behavior, each migration deviates slightly more from the ideal or original migration route. Eventually the impact is realized as a significantly different corridor, removing mule deer from the optimal path for green wave surfing. This would be explained as avoidance via routes rather than steps.

Broader Implications

While mule deer and their green wave surfing ability seem to be resilient to anthropogenic disturbance, we should still take steps to limit human encroachment and development into their critical migration corridors. These results demonstrate mule deer and their ability to surf green waves are affected by, but resilient, to human development and activity. Despite this resiliency, green wave surfing is an essential component of migrations and contributes to overall population well-being and we should take steps to limit stress and disturbance due to human causes. While these results are encouraging, it's important to remember green wave surfing is just one aspect of ungulate migrations. Disturbance can impact mule deer populations and their migrations in a variety of ways. Mule deer green wave surfing during migrations may be resilient but we should still take steps to limit our impact on these declining populations and migrations essential to their survival.

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