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# Navigating the wildland-urban interface: Sensory pollution and infrastructure effects on mule deer behavior and connectivity

Mark A. Ditmer [a,b,*], Neil H. Carter [c], Kent R. Hersey [d], Martin Leclerc [c], George Wittemyer [b], David C. Stoner [e]

[a] USDA Forest Service Rocky Mountain Research Station, 240 West Prospect, Fort Collins, Colorado, 80526, USA
[b] Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado, 80523, USA
[c] School for Environment and Sustainability, University of Michigan, 440 Church Street, Ann Arbor, Michigan, 48109, USA
[d] Utah Division of Wildlife Resources, 1594 W. North Temple, Salt Lake City, Utah 84116, USA
[e] Department of Wildland Resources, Utah State University, 5230 Old Main Hill, Logan, Utah, 84322, USA

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ABSTRACT

Climate and land-use change are modifying the availability of food and water resources, which is driving more wildlife to the wildland-urban interface. For many wildlife populations, use of these areas still requires habitat connectivity both within the interface and/or to wildland habitats. However, navigating these areas can be difficult due to human development and sensory pollutants, such as artificial night light. Determining how these components of urbanization influence the behaviors and functional connectivity of species is important for managing wildlife within these mixed-use landscapes. Here we used a movescape approach based on graph theory to characterize functional uses of the landscape using metrics for behavior, connectivity, and space use intensity. We found that mule deer (*Odocoileus hemionus*; n = 43) functional uses of anthropogenic landscapes in the Intermountain West, USA, were dependent not only on physical barriers, terrain, and sensory factors, but also the local levels of light exposure and vegetative greenness. Remotely sensed artificial light levels had a strong influence on how mule deer used the landscape by reducing the intensity of use in the most illuminated areas given forage availability. In contrast, relatively high local light levels were associated with increased use intensity within less developed areas—highlighting the foraging tradeoffs for species using the wildland-urban interface. Corridor use was reduced in areas where road and housing density were higher, and within-corridor movement was faster when artificial light was high and vegetative greenness was low. Developing a more mechanistic understanding of how species functionally use the landscape in relation to features of urbanization can enhance conservation by delineating areas important for connectivity and foraging, while providing insights into how future development and climate change may alter movement and behavior. Spatially-explicit estimates of functional uses can directly guide management decisions to maintain species resiliency and improve land-use planning.

## Introduction

Climate change is altering the predictability and abundance of resources for wildlife species (D. A. Frank et al., 2023; Pecl et al., 2017), driving changes in species' distributions (Walther et al., 2002), ecological niches (Prugh et al., 2018), and movement patterns (Riotte-Lambert & Matthiopoulos, 2020). Vagile, synanthropic species can exploit resources where they may be artificially elevated, such as the wildland-urban interface and agricultural areas (Bateman & Fleming, 2012; Ditmer et al., 2016) typically up to some species-specific threshold of human alteration or presence (Evans et al., 2017). Use of urban or agricultural areas can provide access to caloric hotspots, which may mitigate some losses stemming from climate change, but for many species, the resources within these areas do not provide for all annual habitat requirements (Barker et al., 2019) necessitating connectivity to other areas required for other life history needs (e.g., natal care, mating; Lowry et al., 2013; McClure et al., 2005). Therefore, determining how species behave, exploit, and maintain connectivity in anthropogenic

* Corresponding author.
*E-mail address:* mark.ditmer@usda.gov (M.A. Ditmer).

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landscapes is important for wildlife conservation and land-use planning in the face of climate and land-use change.

The potential rewards of foraging within urban and agricultural areas often comes with increased risk of conflict with humans (Abrahms et al., 2023; Beckmann & Berger, 2003) and mortality (Olson et al., 2015). Movement within these landscapes not only requires wildlife to avoid direct human presence and barriers to movement (e.g., fences, roadways, buildings), they must also navigate under ambient conditions for which most did not evolve – high levels of sensory pollution (e.g., anthropogenic light, noise; Barber et al., 2010). The footprint of artificial light pollution is expanding and intensifying globally (Kyba et al., 2023), reducing dark refugia within species' ranges by altering ambient conditions to radiance levels far beyond moonlight (Ditmer, Stoner, & Carter, 2021; Gaston et al., 2014; Kyba et al., 2017). The highest radiance occurs near urban areas, but fine-scale variation in light intensity within the urban-interface can result in dark refugia within an illuminated landscape, altering how species within the urban interface move and forage (Ditmer, Stoner, Francis, et al., 2021).

The Great Basin of the American West is a large region undergoing rapid urbanization while aridification associated with climate change has already brought major changes to the availability and predictability of resources for wildlife (Seager et al., 2013; Stoner et al., 2018). This changing environment provides an ideal setting to assess how a species colonizes a novel landscape despite the high degree of human alterations and sensory pollution. Mule deer (*Odocoileus hemionus*) are a habitat generalist, common throughout the western United States, but declining abundance in some regions has brought about concerns over the impacts of aridification on forage and fragmentation from human development separating critical summer and winter ranges (Polfus & Krausman, 2012; Stoner et al., 2018). Bliss-Ketchum et al., (2016) demonstrated that high levels of artificial light reduced deer passage within wildlife overpasses, and K. M. Frank et al., (2023) found that deer generally cross roadways in the darkest sections. Ditmer, Stoner, Francis, et al., (2021) found strong influences of light pollution on both mule deer and cougar (*Puma concolor*) resource selection dependent on the light exposure level of the population – urban mule deer selected for areas of elevated light up to a point, yet still used darker areas despite greater predation risk from cougars. Mule deer inhabit the urban-wildland interface of Salt Lake City, UT, an area of growing road networks, developments, light levels, and therefore risk of human-caused mortality (K. M. Frank et al., 2023; Moore et al., 2023). These trends have challenged practitioners to develop management strategies that satisfy the often conflicting goals of species conservation and minimizing human-wildlife conflicts (Howard, 2018). Thus, going beyond avoidance and selection to consider the role of urbanization on behavior and functional connectivity of the landscape can provide a more mechanistic view to enhance management recommendations (LaPoint et al., 2015).

The movescape method (Bastille-Rousseau & Wittemyer, 2021) is an approach based on graph theory that is an effective means of identifying critical areas of habitat connectivity. The method quantifies and clusters metrics of space use intensity, movement behavior, and locational contributions to connectivity (Bastille-Rousseau et al., 2018) to characterize areas with different movement properties. These clusters characterize functional roles of locations with similar values, e.g., slow/fast corridors, foraging sites, etc. Although the movescape approach does not offer insights into habitat selection (it compares among used areas of the landscape), it does offer a means of deriving a mechanistic understating from observational data, thereby enabling us to better designate areas for habitat restoration, conservation of wildland habitats, and connectivity considerations for species that routinely move across the wildland-urban interface (Wittemyer et al., 2019).

Here, we aim to assess how natural and anthropogenic features, forage availability, and artificial light exposure influence space use patterns in mule deer, and how these factors impact the landscape functionality across a large gradient of urbanization. We used the movescape approach to classify and map functional roles, and modeled factors influencing the probability that a given location used by mule deer would be assigned to each functional role classification. We hypothesized that the level of urbanization experienced for each location within our study area may create differences in the relationships between functional roles and our candidate factors. We also tested how forage availability would interact with the intensity of light radiation on mule deer functional roles to better understand tradeoffs between associated forage access in the urban-interface, and light pollution.

## Materials and methods

### *Study area and mule deer GPS locations*

Our study area included the urban-interface of Salt Lake City, UT in the east and extended westward into far less developed areas of the Great Basin Desert, including the Stansbury and Oquirrh mountain ranges (Fig. 1). From 2012 – 2018, mule deer were net-gun captured with helicopter and fitted with GPS collars during either early winter (~November or December) or late winter (~March; see Van de Kerk et al., 2020 for details). GPS fixes were attempted either every two ($n = 31$) or three ($n=12$) hours resulting in 43 individuals used in the analysis. We only included GPS locations collected at the two- or three-hour GPS sampling interval (dropping movement steps that included missed GPS fixes) and we only included individual deer that collected a minimum of 300 successful GPS locations in our analysis. The final GPS data set included 182,578 locations with an average of 4,246 locations per individual (range: 359 – 8,060; Fig. 1).

### *Developing a movescape*

We developed a movescape (Bastille-Rousseau & Wittemyer, 2021) to determine the functional landscape roles and distinguish the environmental conditions and features associated with mule deer behavior, movement, and connectivity. Animal movement locations were converted to occupied pixels within a larger grid representing the entire landscape (Bastille-Rousseau et al., 2018). Occupied pixels were treated as nodes and the connections among them as edges. A graph theoretic approach was used to calculate an adjacency matrix which enabled calculations of metrics useful for understanding space use, connectivity, and spatial structuring.

We began by determining the median step lengths (i.e., the distance traveled from the starting GPS location to the next GPS location) of mule deer in our system to set the resolution of each pixel within the grid. We calculated the median by individual and then averaged all median values. Average median step-lengths were 122 m and 153 m dependent on whether fixes occurred every two or three hours, respectively. Pixel resolution and associated node-level metrics are robust to a degree of variability in step lengths (Bastille-Rousseau & Wittemyer, 2021), so we used the combined average of 135 m for our pixel resolution. Following the recommendations of (Bastille-Rousseau et al., 2018), we used the package 'moveNT' (Bastille-Rousseau, 2020) in program R (R Core Team, 2022) to calculate metrics representing the (1) intensity of use within each occupied pixel (weight) and (2) the number of occupied pixels each pixel is connected to (degree). See examples in Fig. 2 and **Appendix A: Fig. 2**. These metrics adequately represent core areas of use and inter-patch movements (Bastille-Rousseau et al. 2018). We used (3) betweenness centrality, defined as a count of the shortest paths through occupied pixels relative to the total number of shortest paths, as our metric of importance for connectivity, and thus to identify corridors. Finally, we quantified how mule deer moved within each pixel by calculating (4) the rates of movement (speed) and (5) the mean cosine (i.e., dot product, a measure of path tortuosity) based on movement trajectories occurring within each pixel (Bastille-Rousseau and Wittemyer, 2021). For plotting purposes, we used the mean of all the calculated metrics aside from maximum betweenness based on recommendations from Bastille-Rousseau (2020).

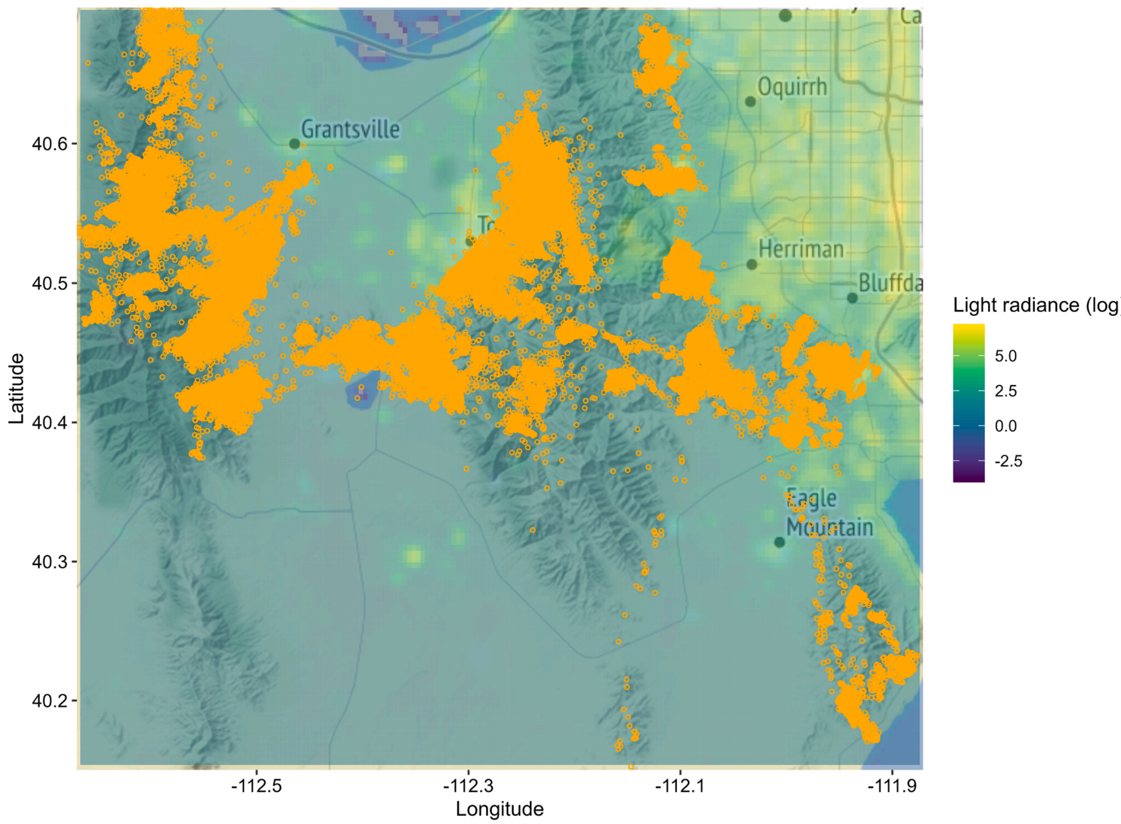


**Fig. 1.** GPS locations of mule deer within the urban-interface of Salt Lake City, UT and areas westward including the Oquirrh and Stansbury Mountains. We were interested in determining how various factors, including remotely-sensed artificial light (overlaid here), influence the movement behaviors of mule deer. A map of light radiance with satellite imagery is available in Appendix A: Fig. 1.

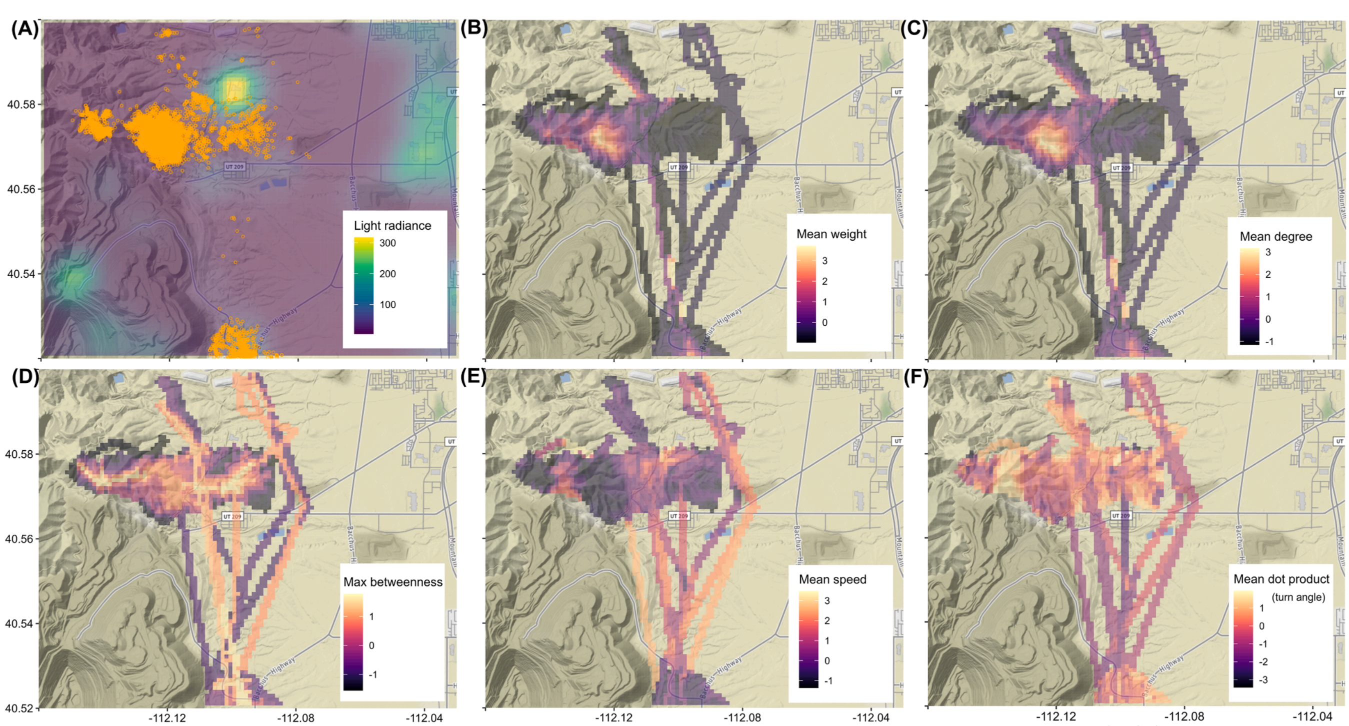


**Fig. 2.** Example showing mule deer locations and artificial light emissions near the urban-interface of Salt Lake City, Utah (**A**), along with the interpolated movement metrics representing aspects of space use intensity (mean weight (**B**), mean degree (**C**)), connectivity value (max. betweenness (**D**)), and movement trajectory characteristics (mean speed (**E**), mean dot product – i.e., turning angle (**F**)). The metrics displayed (**B-F**) are interpolated using the moveNT package in program R. Only cells with corresponding GPS locations (A) were used in the models.

Next, we clustered the five metrics from the discretized mule deer GPS locations into movement classes with a machine learning approach. The function "ind_clust" in package moveNT (Bastille-Rousseau, 2020) clustered the pixel values of the five metrics using a Gaussian mixture model with equal mean and variance for each cluster. Clustering was applied independently to each mule deer dataset and we used a Bayesian information criterion (BIC) to determine the optimal number of clusters with the maximum possible set to 8 for interpretability. A second population-level clustering approach was then applied using the "pop_clust" function in moveNT, which used the mean value of each individual deer's cluster movement class clusters to provide equal weight to all individual mule deer in the population clustering procedure (Bastille-Rousseau & Wittemyer, 2021). Based on the population-level clustering output, we assigned functional roles to describe mule deer space use and behavior (e.g., slow corridor, low use and fast and straight movements, highest use; Table 1).

*Environmental and landscape variables*

Within each occupied pixel, we calculated spatial covariates hypothesized to influence how mule deer move within the study area. We converted 30 $m^2$ NLCD (National Land Cover Dataset) 2016 data (Yang et al., 2018) for forest, herbaceous, and crop into a percentage of coverage of each class within each occupied pixel (determined based on whether the centroid of each 30 $m^2$ NLCD cell was within the 135 $m^2$ movescape analysis cell). We did not consider shrub cover because it comprised the vast majority of the landscape, and thus acts as a reference category for these three less common included land cover types. Terrain ruggedness was calculated using the R package 'spatialEco' (Evans, 2021) using the "tri" function with a 150 m scale window to approximate the movescape pixel resolution (135 $m^2$). Forage availability was represented by remotely sensed mean vegetative greenness measured by Normalized Difference Vegetation Index (NDVI) estimates during summer (May through October) months at each occupied pixel's location (MOD13A1; Didan et al., 2015).

We represented anthropogenic features using the maximum housing density based on 2010 estimates at a 100 $m^2$ resolution (National Park Service, 2010), the Euclidean distance to the nearest roadway and road density based on the USGS National Transportation Dataset (U.S. Geological Survey, 2017). Artificial light estimates were created from daily remotely sensed data collected at a 500 $m^2$ resolution (VNP46A2; Román et al., 2018). Light emissions are moonlight- and atmosphere-corrected and thus represent anthropogenic contributions to night time lights. We created a summer (May through Oct) composite of the daily values from 2012-2018 because of the expanded extent of human and light footprints during the summer months.

*Statistical analysis*

We constructed models to discern what factors influenced the probability that mule deer would use a given location with: 1) low intensity, 2) high intensity, 3) as a movement corridor, and 4) with differing movement rates within corridors (Table 2). Each model used contrasts among different groupings of the functional role clusters within a mixed-effects logistic model, such that each cluster was either assigned to the response variable as "1", "0", or was excluded from the analysis. For each model, we included pixels with a ≥ 80% classification certainty (based on variation in cluster assignment at the pixel-level), included a random intercept for each mule deer ID, and an autovariate term to account for spatial autocorrelation. The autovariate term was calculated for each model using the package 'spdep' (Bivand, 2022) using equal weighting scheme for a 6 km neighborhood. As a sensitivity analysis, we ran all of our models (described below) using a ≥95% classification certainty threshold and found very similar results. We present findings and maps from the ≥ 80% classification here because of the additional coverage within the study area.

To incorporate artificial light emissions in our models, we used a model selection process for each of the four functional models of mule deer space which included: 1) all covariates described except for artificial light – i.e., the "base" model which could be considered the null model; 2) base model and a main effect for artificial light; 3) base model and an interaction between NDVI and artificial light, 4) base model, NDVI X artificial light, and an interaction between artificial light and the easting value of each occupied cell to assess changes across the study area, and 5) base model, no artificial light, and a main effect for easting. In our study area, urbanization declines from east to west; thus, the "easting" variable was used to capture gradients associated with urbanization and other habitat variables not fully captured by our other covariates. Model fit was assessed using ΔAIC. If multiple models were within 2 AIC of the top model, we selected the most parsimonious model to report the beta coefficients and 95% confidence intervals. Prior to fitting the models, we assessed each for multicollinearity using variance

**Table 1**
Mean cluster values from unsupervised classification for five metrics of mule deer (n=43) movement located along the urban-interface and areas to the west of Salt Lake City, Utah. Summaries of both the proportion of pixels classified in each cluster, as well as the proportion of the mule deer exhibiting behavior within a given cluster classification are provided. From these cluster values, we assigned functional roles to each as described in the bottom row.

| | Cluster 1 | Cluster 2 | Cluster 3 | Cluster 4 | Cluster 5 | Cluster 6 | Cluster 7 |
|---|---|---|---|---|---|---|---|
| Weight | -0.024 | -0.425 | -0.391 | -0.497 | 0.356 | 2.159 | 1.138 |
| Degree | 0.194 | -0.520 | -0.426 | -0.665 | 0.682 | 1.915 | 0.742 |
| Betweenness | 0.913 | -0.033 | -0.350 | -0.215 | 0.168 | 0.712 | 4.374 |
| Speed | -0.191 | 1.168 | -0.103 | 1.145 | -0.380 | -0.512 | 1.396 |
| Dot product | 0.024 | -0.707 | -0.133 | 0.840 | -0.056 | -0.059 | 0.189 |
| Proportion of pixels | 0.160 | 0.102 | 0.174 | 0.120 | 0.191 | 0.150 | 0.103 |
| Proportion of individuals in cluster (n=43) | 0.721 | 0.581 | 0.884 | 0.791 | 0.860 | 0.953 | 0.628 |
| Functional role classification | slow corridor | Low use, fast and tortuous | low use slow | Low use, fast and straight | medium use | highest-use | fast corridor |

**Table 2**
Descriptions of the contrasts used among clusters (see Table 1) in logistic regression analyses modeling mule deer functional use of the study region near Salt Lake City, Utah.

| Model | Clusters included (y =1) | Clusters included (y = 0) | Excluded |
|---|---|---|---|
| Low use | Low use (Clusters 2–4) | Highest use (Clust 6) & Med-High use (Clust 5) | Slow & Fast Corridors (Clusters 1,7) |
| High use | Highest use (Clust 6) | Low use - w/ various movement characteristics (Clusters 2–4) | Medium Use (5), Slow & Fast Corridors (Clusters 1,7) |
| Corridor | Slow & Fast Corridors (Clusters 1,7) | Non-corridors (Clusters 2–6) | None |
| Corridor Behavior | Slow corridor (Cluster 1) | Fast corridor (Cluster 7) | Non-corridors (Clusters 2–6) |

inflation factors (all VIF values were < 2; Dormann et al., 2013). Continuous variables were centered and scaled to assess effect size among variables. All analyses and mapping were done in program R. Maps containing imagery were developed within the package 'ggmap' (Kahle & Wickham, 2013) and effects plots were created with package 'ggeffects' (Lüdecke, 2018).

## Results

We identified seven clusters based on mule deer movement behavior metrics (**e.g.,** Fig. 2 **& Appendix A: Fig. 2**) at the population level and assigned each a functional role (Table 1, e.g., area near Salt Lake City, UT [Fig. 3A&C] and Tooele, UT [Fig. 3B,D]). The clusters had similar proportions across the landscape (range: 0.10—0.19; Table 1). Two population-level clusters (1, 7) exhibited high values of betweenness, but with a major difference in movement speed. These two clusters were designated as "slow corridor" and "fast corridor". Metrics for weight and degree were highly correlated but the values differed greatly among the five clusters not designated as corridors resulting in classifications of "low use", "medium use", or "high use". Three of the clusters were designated as "low use" ("medium" and "high" were assigned to one each), and thus movement characteristics based on the speed of movement and dot product (tortuosity) were used to differentiate among them (Table 1). Individual mule deer most commonly displayed six of the cluster designations, with "low use, fast and tortuous" containing the lowest proportion of individual mule deer within the cluster (0.58), and high use containing the greatest proportion of individual mule deer (0.95; Table 1).

### *What factors influence high intensity of use?*

Mule deer used areas more intensively when the location had a higher NDVI value (i.e., more green vegetation), and a greater degree of terrain roughness (Table 3). Mule deer had a lower probability of using a location with high intensity when road density, percent forest and percent herbaceous were higher (Table 3). The top-supported model included interactive effects between artificial light and NDVI, and artificial light and easting (Appendix A: Table 1). In the eastern urban-interface, high use intensity locations decreased with elevated exposure to artificial light (0.15 [0.09— 0.24] from the $5^{th}$ quantile of observed light values to 0.01 [0.00— 0.02] at the $95^{th}$ quantile). Conversely, in the areas with lower light exposure in the less-illuminated western half of the study area, an increase in light levels increased the predicted high use intensity from the $5^{th}$ quantile to the $95^{th}$ from 0.10 [0.06—0.16] to 0.34 [0.21— 0.49]. Mule deer reduced high intensity use associated with the $95^{th}$ quantile of NDVI to 0.20 [0.08—0.40] when light exposure was high ($95^{th}$ quantile), compared to 0.38 [0.30—0.46] at low levels of light exposure ($5^{th}$ quantile; Fig. 4C). Given an area with low NDVI values ($5^{th}$ quantile), greater exposure to artificial light surprisingly increased the use of those locations given the expected use with low vegetative greenness (from low [$5^{th}$ quantile] 0.05 [0.04—0.07] to high light exposure [$95^{th}$ quantile] 0.29 [0.17—0.45]).

### *What factors influence low intensity of use?*

As expected, the model of low use intensity was nearly the inverse of the high intensity of use model. However, because the comparison for this model includes the medium intensity use classification (Table 2), the effect sizes were generally smaller (Table 3). Mule deer used areas less intensively when the location had a lower NDVI value (i.e., less green vegetation), a lower degree of terrain roughness, and more forest or herbaceous landcover (Table 3). Areas with higher road densities were also associated with lower use, although the effect size was relatively small. The best-supported model for low use intensity included

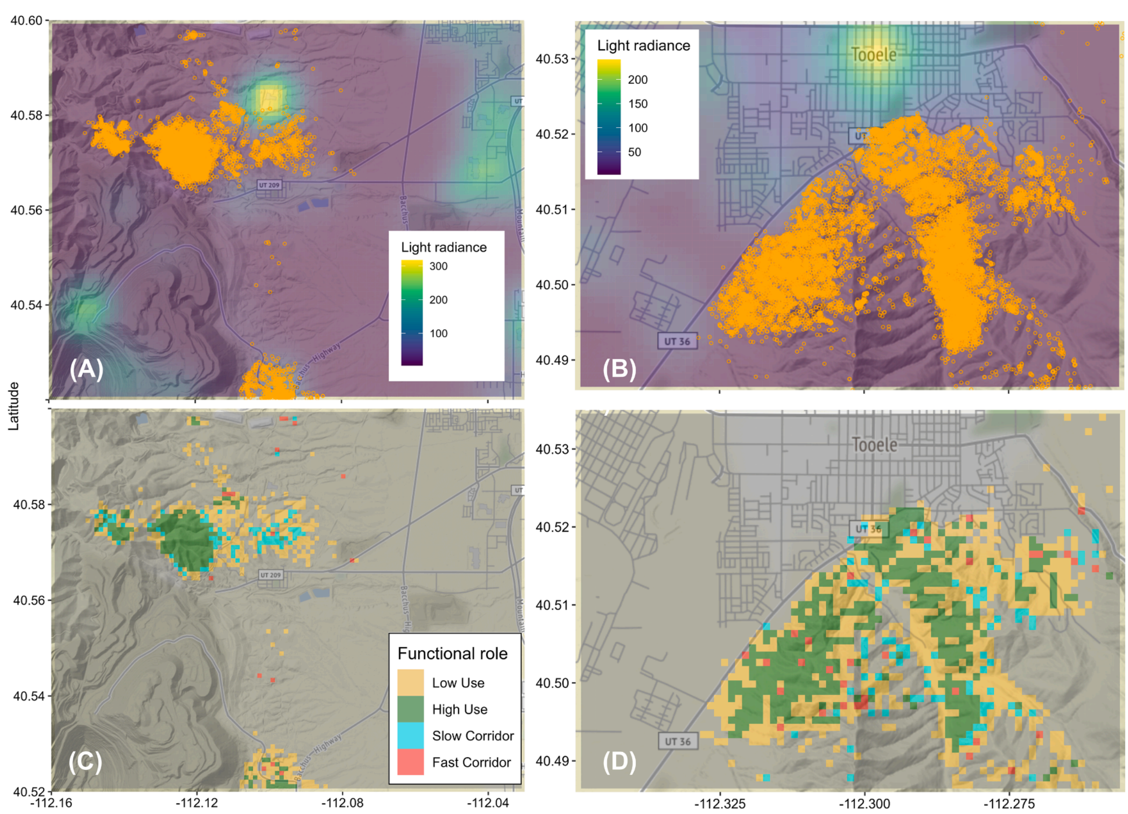


**Fig. 3.** Maps showing the GPS locations, artificial light emissions, and corresponding functional roles assigned to each area of use by mule deer within the urban-interface of Salt Lake City, UT (**A, C**), and the western portion of the study area that includes the town of Tooele, UT (**B, D**).

**Table 3**

Coefficient values and 95% confidence intervals from logistic regression models exploring factors influencing the intensity of use and movement corridors by mule deer near Salt Lake City, Utah. Behaviors were assigned using a movescape approach and model contrasts among movement behaviors are described in Table 1 and Table 2. Results with 95% confidence intervals that do not overlap zero are in bold.

| Covariates | Low Use | High Use | Corridors | Slow Corridor |
|---|---|---|---|---|
| Intercept | **1 (0.72 – 1.29)** | **-1.85 (-2.16 – -1.54)** | **-2.62 (-3.08 – -2.17)** | 1.35 (-0.12 – 2.81) |
| Artificial Light X NDVI | **0.13 (0.03 – 0.23)** | **-0.27 (-0.41 – -0.14)** | **0.17 (0.07 – 0.27)** | **—** |
| NDVI | **-0.41 (-0.47 – -0.36)** | **0.52 (0.45 – 0.6)** | **-0.34 (-0.41 – -0.26)** | **0.21 (0.03 – 0.38)** |
| Artificial Light X Easting | **0.43 (0.29 – 0.57)** | **-0.67 (-0.88 – -0.47)** | — | — |
| Easting | 0.09 (-0.11 – 0.28) | -0.09 (-0.32 – 0.15) | — | **0.96 (0.31 – 1.62)** |
| Artificial Light | **-0.16 (-0.26 – -0.05)** | **0.32 (0.17 – 0.47)** | **0.14 (0.05 – 0.24)** | — |
| Road Density | **0.08 (0.02 – 0.14)** | **-0.17 (-0.25 – -0.08)** | -0.06 (-0.13 – 0.02) | 0.06 (-0.11 – 0.24) |
| Distance to Road | -0.01 (-0.07 – 0.04) | 0.03 (-0.04 – 0.1) | -0.02 (-0.09 – 0.04) | **0.64 (0.43 – 0.85)** |
| Housing Density | 0 (-0.04 – 0.05) | -0.04 (-0.12 – 0.03) | **-0.45 (-0.77 – -0.13)** | **-0.21 (-0.42 – -0.01)** |
| Terrain Ruggedness | **-0.53 (-0.59 – -0.48)** | **0.57 (0.5 – 0.64)** | **0.16 (0.09 – 0.23)** | 0.13 (-0.07 – 0.32) |
| % Forest | **0.13 (0.08 – 0.18)** | **-0.12 (-0.18 – -0.05)** | **-0.13 (-0.2 – -0.05)** | **-0.17 (-0.33 – -0.01)** |
| % Herbaceous | **0.12 (0.07 – 0.17)** | **-0.12 (-0.19 – -0.05)** | **-0.07 (-0.12 – -0.01)** | -0.1 (-0.24 – 0.05) |
| % Agriculture | 0 (-0.05 – 0.04) | -0.03 (-0.1 – 0.03) | **0.07 (0.02 – 0.12)** | -0.03 (-0.26 – 0.21) |
| Autovariate Term | **-0.12 (-0.2 – -0.04)** | 0.03 (-0.1 – 0.16) | **-0.08 (-0.16 – -0.01)** | **0.59 (0.39 – 0.79)** |

interactions for artificial light x easting and artificial light x NDVI (**Supp. Table 1**). The influence of light on the probability of low intensity of use was dependent on its relative location within the study area. Among mule deer living within the eastern side of the study area, i. e., closer to the Salt Lake City urban-interface, an increase in light emissions across the 95% distribution of values increased the probability that a location was considered low intensity use from 0.72 [0.62–0.81] to 0.96 [0.90–0.98] (Fig. 4A; Fig. 3A,C; Fig. 5 B,C). In contrast, deer from the less urban western portion of the study area (drier, darker), (Fig. 1; Fig. 5B), had a lower probability of using an area less intensively with increasing artificial light levels (average predicted probability decreased from 0.76 [0.67—0.83] to 0.48 [0.34–0.62] using the 95% distribution in the less lit western half of the study; Fig. 5A; Fig. 4B,D; Fig. 6B,C). The interactive effects of NDVI and artificial light had a homogenizing influence of the probability of low use intensity. Although locations with higher NDVI values had a lower probability of being classified as "low use" intensity, at high light emission levels, the predicted probability increased from 0.49 [0.41— 0.57] to 0.60 [0.41—0.76] while areas with very low NDVI values decreased their probability from 0.85 [0.81—0.88] to 0.68 [0.55—0.79].

*What factors were associated with movement corridors?*

Mule deer used areas with lower housing density and lower NDVI as movement corridors (Table 3). Although less influential, mule deer corridor use was positively associated with terrain roughness and the percentage of agriculture, and negatively associated with the percentage of both forest and herbaceous landcover (Table 3). The top model of corridor use supported the interaction of artificial light and NDVI only (Appendix A: Table 1). Here, predicted corridor use decreased with increasing artificial light for areas with low NDVI (5$^{th}$ quantile light: 0.11 [0.07—0.17]; 95$^{th}$ quantile light: 0.08 [0.05—0.14]) but areas with high NDVI had a higher predicted probability of being used as a movement corridor (5$^{th}$ quantile light: 0.03 [0.02—0.04]; 95$^{th}$ quantile light: 0.11 [0.05—0.24]).

*What influences movement speeds within corridors?*

Distance to roadways had the largest influence over mule deer movement speeds within corridors (Table 3). Movement corridors further from roadways, with higher NDVI values, were associated with slower movement. Mule deer moved faster through corridors containing more forest cover and higher housing densities (Table 3). The top model

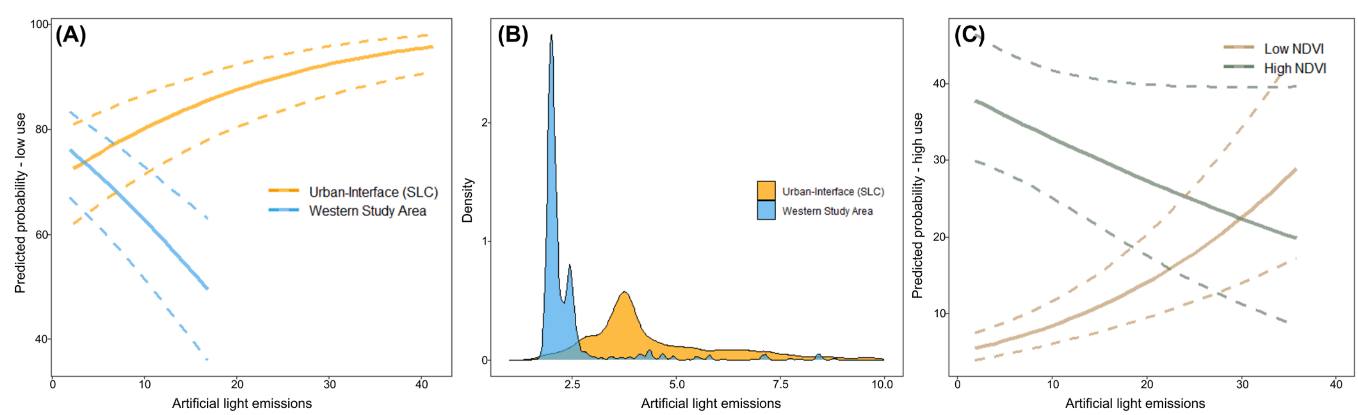


**Fig. 4.** Effects plot (A) showing the probability that a location was considered low use intensity by mule deer based on the interaction term between artificial light emissions and location within the study region. In the eastern urban-interface near Salt Lake City, UT, the probability of a pixel being considered low use intensity increases with greater light emissions. The opposite relationship occurs in the far less developed western portion of the study area where artificial light emissions are far less extensive and less bright on average (A, B). The model of high use intensity by mule deer showed a strong effect of the interaction between NDVI (vegetative greenness) and artificial light (C). The resulting predictions from the model show that areas with high NDVI, which are associated with high use intensity, have a lower probability of being classified as high use intensity with increasing levels of artificial light. The opposite effect occurred for the areas with low NDVI which had a low probability of being a classified as high use intensity. Predicted mean and 95% confidence intervals for panels (A) and (C) were predicted across the 95% distribution of observed values on the X-axes. We used the 5$^{th}$ and 95$^{th}$ quantile point values for the plotted variable. All other variables in the models for low and high use intensity were held at their mean values.

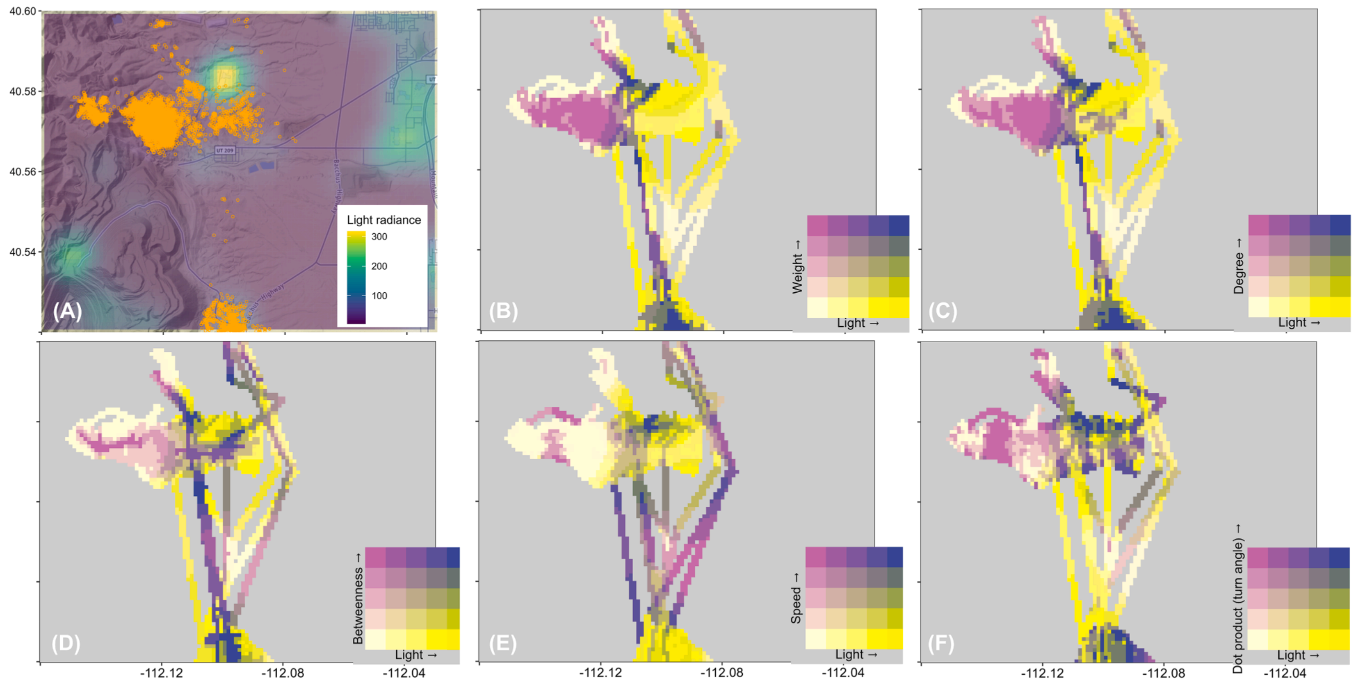


**Fig. 5.** Bivariate choropleth maps depicting the spatial overlap between artificial light emissions and movement behavior metrics of mule deer near the urban-interface of Salt Lake City, Utah. Panel (A) shows the raw GPS locations overlaid on remotely-sensed light radiance estimates and the interpolated movement metrics representing aspects of space use intensity (mean weight (B), mean degree (C)), connectivity value (max. betweenness (D)), and movement trajectory characteristics (mean speed (E), mean dot product – i.e., turning angle (F)) from the same areas as the locations shown in (A). The metrics displayed (B-F) are interpolated using the moveNT package in program R. Only cells with corresponding GPS locations (A) were used in the models.

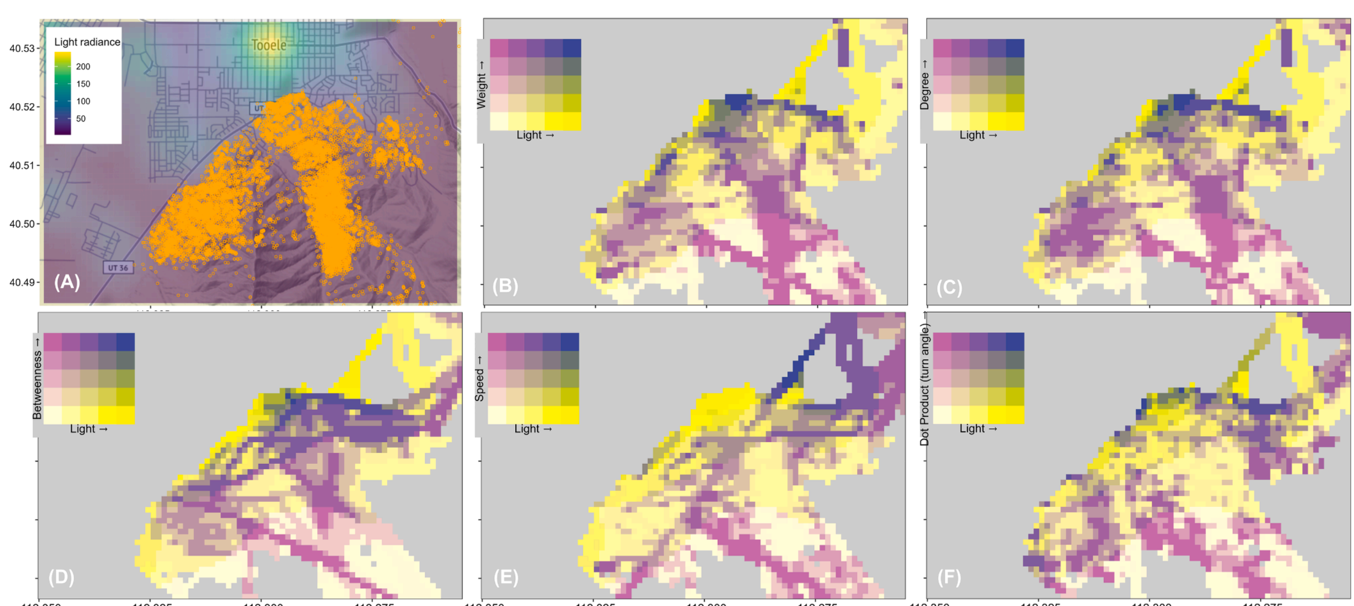


**Fig. 6.** Bivariate choropleth maps depicting the spatial overlap between artificial light emissions and movement behavior metrics of mule deer near the town of Tooele, Utah in the far western portion of the study. Panel (A) shows the raw GPS locations overlaid on remotely-sensed light radiance estimates and the interpolated movement metrics representing aspects of space use intensity (mean weight (B), mean degree (C)), connectivity value (max. betweenness (D)), and movement trajectory characteristics (mean speed (E), mean dot product – i.e., turning angle (F)) from the same area as the locations shown in (A). The metrics displayed (B-F) are interpolated using the moveNT package in program R. Only cells with corresponding GPS locations (A) were used in the models.

for corridor speed included the easting term in addition to the base model, but did not support the inclusion of artificial light as a main effect or with an interaction. Interestingly, the modeled easting term was positive but slow corridors occurred at a rate of 2.4X (slow:fast corridors = 1,293:534) more than fast corridors in the western half of the study compared with a 1.9X in east the east (slow:fast corridors = 665:348). Although slow corridors occurred less frequently in the more developed east, they were still more common than expected (based on the top model) given there are fewer areas that are far from roadways and/or contain low housing densities (Table 3).

## Discussion

As resources dwindle or become less predictable in the face of climate change, many species seek out the abundant and predictable resources in the urban-interface (Abrahms et al., 2023; Pecl et al., 2017). We demonstrated several factors that influenced mule deer functional uses of the landscape across a gradient of urbanization near Salt Lake City, Utah, USA. Artificial light levels played an important role in shaping how mule deer used the landscape, but the specific relationships between functional uses was mediated through the overall light exposure in the environment and vegetation. Decisions to seek out the resources in urban-interfaces may offer high rewards, but our findings show that not all resources are actually available, or may not be fully utilized due to both physical barriers to movement or sensory pollutants that reduce the time spent foraging. Times and places where sensory pollutants exceed tolerance for mule deer may require movement through relatively darker areas where both risk of predation and vehicle-collisions increase (Ditmer, Stoner, Francis, et al., 2021; K. M. Frank et al., 2023). The mechanistic view of mule deer movement and space use provided by the movescape method extended our understanding of how different aspects of urbanization, forage availability, and sensory pollution interact to shape use of the urban-interface beyond a typical resource selection analysis. For species such as mule deer that often seek out the resources within the urban-wildland interface, the movescape outputs, which provide spatially-explicit classifications of functional uses throughout the study area, can directly aid in management actions and conservation planning by delineating areas important for species' resiliency in a rapidly changing landscape.

The influence of artificial light levels on mule deer behavior was dependent on vegetative greenness. Mule deer movements and space use (e.g., Merkle et al., 2016; Stoner et al., 2018) as well as fitness measures (Hurley et al., 2014) have been linked with vegetative greenness, and deer in our study also responded strongly to NDVI availability by increasing their intensity of use and slowing down and foraging within corridors where NDVI was relatively high. However, as artificial light increased in areas with more green vegetation, mule deer used these areas less than they would have under natural lighting conditions. This finding raises additional questions about forage efficiency in these locations and the consequent fitness levels of urban versus wildland deer (e.g., Cleveland et al., 2012; Longshore et al., 2016). In contrast, artificial light increased the probability of higher intensity use within areas of very low NDVI levels. Ditmer, Stoner, Francis, et al., (2021) showed that deer residing in more urbanized areas used habitat patches with higher NDVI values relative to their wildland counterparts. K. M. Frank et al., (2023) also showed the importance of considering habitat in relation to artificial light levels; deer in the Salt Lake City urban-interface crossed roads in the relatively less illuminated segments, and moreover, crossings were more frequent when surrounded by preferred shrub habitat. Our findings also highlight the importance of vegetation when considering the impacts of artificial light, but they further demonstrate how the expanded footprint of artificial light can impact the utility of a resource itself by reducing the expected amount of use in a location while controlling for other aspects of urbanization.

We were surprised to find a positive association between space use intensity and artificial light levels for deer with lower artificial light exposure. On the surface, this finding appears to contradict some of our previous work. Ditmer, Stoner, Francis, et al., (2021) showed mule deer exhibit a negative functional response to artificial light levels at the movement-step scale using GPS data from some of the same deer and other study sites in the Intermountain West region (n=263). However, several differences between the studies explain the differing results between the integrated step selection function outputs of Ditmer, Stoner, Francis, et al., (2021) and those from our movescape analysis. First, our analysis used the latest release of NASA's VIIRS Black Marble data which provided estimates of artificial light at four times the spatial granularity of previously available data (500 $m^2$ vs. 1 $km^2$). Second, our study considered circadian deer movement whereas Ditmer, Stoner, Francis, et al., (2021) only modeled movements occurring during crepuscular and nocturnal periods. Here, we considered all deer movements because the movescape graph-based metrics used to assign functional roles for corridors would have contained numerous gaps in night only movement data—an important consideration when determining the applicability of a movescape approach for any study. Potentially most importantly, the movescape approach does not model use vs. availability, but instead it compared among used pixels rather than resource selection. High light levels may both reduce the intensity of use given resources considered available (e.g., higher greenness levels within the urban-interface as Ditmer, Stoner, Francis, et al., 2021 found) compared to other used locations, while also being considered "selected for" relative to available darker locations.

Our findings in combination with Ditmer, Stoner, Francis, et al., (2021) show a difficult tradeoff for mule deer within the urban-interface; illuminated areas may contain some of the best available forage because they are often irrigated or cultivated, but these locations are consequently used less intensively given the forage availability either due to the sensory pollution itself or associated human activity (i.e., fear drives reduced use of highly illuminated areas in urban areas). However, darker areas in the region further from developments and increased forage might provide respite from human activity in a more natural setting, but these areas are associated with relatively far greater predation risk from cougars (Ditmer, Stoner, Francis, et al., 2021). As such, greater use of illuminated areas in these darker, rural settings may capture a predatory shielding effect. Future work that incorporates a movescape approach to both predator and prey could further enhance our understanding of how light pollution may shape the movements and interactions of species along the urban-interface. The availability of fine resolution anthropogenic nightlight emissions provide a way of quantifying light pollution across broad spatial scales and better integrating sensory ecology with wildlife conservation (Dominoni et al., 2020), but far more work is needed to disentangle the impacts, especially in context of acclimatization to sensory pollutants and species-specific thresholds.

The large negative effects of housing density and roadways on corridor use and increased corridor speed by mule deer is unsurprising, but concerning given the rapid growth of residential sprawl throughout the Rocky Mountain West (Carlson et al., 2022; Polfus & Krausman, 2012). Artificial light levels also played a role in corridor use, whereby increased light levels interacted with low amounts of green vegetation or forage to reduce corridor use. Chambers et al., (2022) found that mule deer located far from the urban interface on the Colorado Plateau increased their movement distances and used metabolically costly pathways to avoid oil and gas developments. Similarly, the rapidly expanding footprint of urban sprawl reduced corridor use behavior resulting in use of areas with greater terrain ruggedness. Our findings also follow the general trends described by Tucker et al., (2018), who examined the movements of 57 terrestrial species and found a strong trend towards less vagility (i.e., less long distance movement as measured by GPS tags) with increasing urbanization despite resources that are often more spatially fragmented. The differences in corridor behavior between the highly urbanized eastern portion of our study area relative to the less developed west, suggests that the human footprint may not just restrict longer movements, but that movement behaviors within more urban areas are done to quickly change locations. The result is less time spent foraging within movement corridors as compared to more natural habitats. We do caution that our "slow category" designation had a far lower average weight (i.e., intensity of use) than the fast corridor category, suggesting the slow corridors were used less intensively compared to the fast movement corridors. This could be due to a variety of factors that would require additional analyses. While the movescape approach enables a unique look into wildlife behavior and landscape factors that shape the behavior, the analysis still requires interpretation of the metrics of behavior considered, and this may differ greatly from species to species (e.g., our values for "slow corridor" are different in some categories compared to the African elephants' [*Loxodonta africana*] "slow corridor" determined by Bastille-Rousseau & Wittemyer, 2021) and potentially among populations of the same species.

Our movescape outputs enabled us to discern which aspects of the human footprint most strongly impacted mule deer space use intensity (artificial light levels) and which altered corridor use (housing and roads) to connect heavily used areas of the landscape. At macro scales, many mammalian species have ranges fragmented by both human changes to the physical landscape and by sensory pollutants far above conditions species evolved under (Ditmer, Stoner, & Carter, 2021). As more wildlife seek resources within the urban-interface, understanding how the expanding human footprint impacts both the physical landscape as well as sensory conditions within remaining habitat is important for reducing potential human-wildlife conflict, maintaining or improving habitat, and ensuring functional connectivity between habitats and/or climatic refugia. Future research should consider how the functional uses of the landscape, and the underlying factors that influence those roles, relate to individual fitness along with mortality risk from both anthropogenic sources and native predators (Wittemyer et al., 2019). As species like mule deer rely more heavily on the urban-interface, at least in years with reduced resources in natural areas, developing a deeper understanding of critical areas for forage and connectivity is not only important for wildlife conservation, but also understanding movement corridors for reducing human risks and economic costs associated with wildlife-vehicle collisions (Cunningham et al., 2022; K. M. Frank et al., 2023). Areas throughout Utah and the American West at large are experiencing rapid urbanization accompanied by increased sensory pollution; integrating remotely-sensed data on forage and light pollution with our movescape models provided maps and inference to better target landscape planning and habitat improvements in this increasingly important habitat.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2023.10.002.

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