2 March 2024

RH: Wildey and Bickford 2024 • Mule Deer Habitat Selection and Density

**Near and Deer: Individual and Population Responses of Mule Deer to Human Recreation**

Eli Wildey, CSU-Pueblo, 2200 Bonforte Blvd, Pueblo, CO 81001, USA

Nate Bickford, Oregon Institute of Technology, 3201 Campus Dr, Klamath Falls, OR 97601, USA

**Correspondence:** Eli Wildey, CSU-Pueblo, 2200 Bonforte Blvd, Pueblo, CO 81001, USA. Email: [eli.wildey@gmail.com](mailto:eli.wildey@gmail.com)

**ABSTRACT** Outdoor recreation extends human influence on landscapes beyond built environments but is often thought to be compatible with wildlife conservation. Human capability as a highly efficient predator creates a strong selective force on wildlife, analogous to natural predation risk, regardless of trophic level. Behavioral responses of wildlife have been observed across taxa but linking these changes in individual behavior to population-level responses represents an important step in understanding and mitigating the impact of our everyday presence on ecosystems. Here we present results of an integrated step selection analysis (iSSA) of the habitat selection exhibited by ten mule deer (*Odocoileus hemionus*) in response to environmental and human factors and the possible impact on population density. Mule deer in our study area had differential habitat use and movement characteristics with time of day and intensity of human disturbance. Mule deer increasingly selected for forest land cover as human presence increased. Deer showed different movement responses with increasing human presence depending on the time of day. Changes to habitat selection and movement patterns have important implications for habitat management of winter range and potential costs to deer populations. Pairing our movement data with camera data, we found evidence for a low density of mule deer on our winter range compared to winter ranges across Colorado possibly caused by human recreation. Low densities of mule deer has implications for the role density-dependent effects play in modifying the impact of recreation. Our study provides critical information on the role human recreation plays in modifying the effectiveness of habitat management on deer winter ranges and possible scenarios this may scale up to impact mule deer populations.

**KEYWORDS** camera traps,Colorado, density dependence, habitat selection, human recreation, integrated step selection functions, mule deer, *Odocoileus hemionus,* time to event modeling

Humans play many roles in ecosystems locally and globally. One of the simplest but most profound impacts we have is through our presence, as our capabilities as highly efficient predators has been found to affect wildlife in many ways (Darimont et al. 2015, Larson et al. 2016). These effects are felt even when our activities are non-lethal, as is the case with recreation (Smith et al. 2021). Importantly, these impacts transcend individuals to influence populations, and communities (Larson et al. 2016). Uncovering how impacts at these different hierarchical levels are related, and when negative consequences scale up is important for mitigation, however these mechanisms are understudied (Marion et al. 2020, Wilson et al. 2020).

Protected natural areas often face a dual mandate to conserve natural resources and provide recreational opportunities, which garner public support and serve as a financial incentive for land conservation (Reed and Merelender 2008). Recent reviews have identified a need to more accurately measure the magnitude of recreation, in part to help identify thresholds at which negative effects transition to long term impacts (Larson et al. 2016, Marion et al. 2020). Determining these thresholds, and the mechanisms by which they occur, can inform the balance of needs between recreation and conservation (Marion et al. 2020, Wilson et al. 2020).

In response to human presence, animals may flee, hide or increase their vigilance behavior. These interruptions disrupt fitness-enhancing behaviors such as foraging, parental care or mating (Frid and Dill 2002). Individuals may take a more proactive response avoiding risk across the landscape by altering their spatiotemporal niche (Lesmerises et al. 2017, Ladle et al. 2019, Suraci et al. 2019). Increasing nocturnal activity (Gaynor et al. 2018, Naidoo et al. 2020, Sévêque et al. 2020), and/or changing the type of habitat selected or altogether avoiding habitat near trails (Muhly et al. 2011, Coppes et al. 2017, Ladle et al. 2019, Smith et al. 2018) have all been observed. Such changes are also reflected in decreases or increases to movement rates, depending on the species and chosen response (Tucker et al. 2018, Doherty et al. 2021).

Interruption of fitness- enhancing behaviors, alteration of spatiotemporal niche, and increased movement costs provide possible mechanisms of individual changes scaling up to populations. The relationship between impacts at the individual-level and population-level is not always straightforward, as modulators like density dependence and habitat quality can alleviate or aggravate expected effects (Tablado and Jenni 2017). Density-dependence theory predicts populations well below carrying capacity experience less competition for forage and are in better body condition, potentially mitigating the negative impacts of recreation at the individual level (Stewart et al. 2005, Bowyer et al. 2014). Improved habitat quality could allow for the compensation of energetic losses at the individual-level through more nutritious and abundant forage.

Habitat management to improve habitat quality for overwintering mule deer (*Odocoileus hemionus*) is a common practice, with research supporting the idea that winter habitat is limiting populations declining range-wide (Unsworth 1999, Bishop et al. 2009, Bergman et al. 2014, Bergman et al. 2015, Bombaci and Pejchar 2016). To alleviate some of these challenges, habitat management has focused on deer winter range with thinning of pinyon-juniper forest intended to improve winter forage (Bombaci and Pejchar 2016, Miller at al. 2019). These efforts have been shown to increase overwinter fawn survival, an important bellwether for mule deer populations although a corresponding increase in deer density was not observed (Bishop et al. 2009, Bergman et al. 2014, Bergman et al. 2015).

Research on how human recreation affects mule deer is rather limited and its interaction with habitat management has not previously been considered. Multispecies camera studies have detected temporal responses of mule deer to recreation, documenting decreases in daytime activity during times of increased human presence but not observing shifts in space use away from cameras with the highest human activity (George and Crooks 2006, Reilly et al. 2017). Return times to specific sites have also shown to be impacted, with human presence typically a more important factor in determining the timing of these recursive movements than the presence of predators or competitors (Visscher et al. 2023). Previous telemetry research determined deer increased movement rates slightly during periods of biking, hiking, and horseback riding in comparison to a control but did not observe a change in flight responses between treatment and control, suggesting deer might be responding to recreation with fine-scale changes in habitat use (Wisdom et al. 2004). This previous work demonstrates behavioral responses of mule deer to recreation, however whether these more nuanced behavioral changes are, or are not, transmitted to populations can better inform management efforts for mule deer and possibly other species showing similarly nuanced responses.

Here we examine mule deer responses to recreation on winter range in Salida, Colorado. The goal of this study was to investigate behavioral changes of mule deer to human recreation and the link to possible population level change in deer density. Our objective was to 1) identify if mule deer are which habitats they’re selecting avoiding areas near trails, or changing when they are most active in response to human presence on trails, 2) assess how these changes relate to habitat management actions, 3) obtain an index of deer density across our study area as a product of environmental factors, and 4) explore whether behavioral alterations at the individual level can amplify to changes in deer density at the population level.

**STUDY AREA**

**A map of the world

Description automatically generated**

Our study area was near Salida, Colorado, USA (approximately 38° 30´ 8" N and 106° 0´ 41" W). Salida sits in the Arkansas River Valley and is an outdoor recreation hub for a variety of outdoor activities including mountain biking, hiking, whitewater rafting, skiing and snowboarding. Elevation ranged from 2180m – 2465m. Mean annual precipitation is 282mm, mean annual minimum temperature is -1.26° C and mean annual maximum temperature is 15.98° C (Oregon State University PRISM Climate Group 2012). Land cover type varied from developed land on the edge of town to agricultural lands, grasslands, and pinyon-juniper forest in the foothills. The Methodist Mountain trail network is on Bureau of Land Management property south of Salida, Colorado. Methodist Mountain is the northern terminus of the Sangre de Cristo range which is characterized by pinyon dominant pinyon-juniper forest with cottonwood (*Populus deltoides*) growth along major washes and interspersed patches of gambel oak (*Quercus gambelii*). Habitat management has been performed for the purposes of fuel reduction, habitat management, and watershed improvement (Miller et al. 2019). This involves thinning of pinyon juniper forest on flat ground accessible to machinery. This thinned habitat appears on land cover classification layers as “shrub” habitat as opposed to surrounding “forest” habitat. The managed habitat promotes the growth of shrub species such as golden currant (*Ribes aureum*), mountain mahogany (*Cercocarpus ledifolius*), and rabbitbrush (*Ericameria spp.*). Our study area serves as a winter range for a migratory population of mule deer who migrate about 11km southwest to summer range across the San Luis Valley.

**METHODS**

**Field methods**

Six mule deer were captured using clover traps baited with corn and alfalfa, and four were free darted from a vehicle and chemically immobilized (April 2021 and November 2021 – February 2022). Capturing, handling and radio-tagging procedures were approved by the Institutional Animal Care and Use Committee at Colorado State University-Pueblo (Protocol #: 000-000A-028). Ten deer had a Cellular Tracking Technology (CTT) GPS-GSM Solar-powered CTT®-ES400 ear tag placed in their ear (Cellular Tracking Technologies, Cape May, New Jersey), with a cattle tag placed in the opposite ear. Locations were taken every 2-4hrs depending on solar charge of the batteries; for analysis purposes 4 hour location intervals were used. Nine deer total, three males and six females, and 1,354 locations were ultimately used for this analysis.

We arranged 36 cameras in a grid pattern at a spacing of ~400m for a total grid area of ~5.6km. 6 LTL Acorns LTL-5310A and 31 Bushnell Prime Low Glow Trail Cameras. Cameras were set to motion trigger and took 5 photos per trigger for Bushnell cameras and 3 pictures per trigger for Acorn cameras, with a 1-minute quiet period and a high sensitivity setting. Specific camera locations were randomized within a 100m buffer of the center of each grid cell using QGIS, following recommendations for *a priori* rules when deploying cameras for our specific analysis (Loonam et al. 2021). Microsite selection involved placing cameras along a corridor of travel established by humans or animals within 30m of randomized point. Hiking trails were used if they were present within the microsite search area for camera placement. Cameras were placed at knee height, ~5m off path of travel at a 30 degree angle to maximize exposure time of animals crossing the camera frame. Cameras were deployed from April 2022- August 2022 and checked once, approximately halfway through deployment. Trail camera photos were uploaded to Wildlife Insights for processing photos using an artificial intelligence model trained on 35+ million images (Ahumada et al. 2020). Wildlife Insights was used to filter out blank images, which can be identified 88% of the time with an error rate of less than 2% (Wildlife Insights). Photos tagged as containing an animal were reviewed for identification, while a subset of blank images was reviewed for quality assurance.

**Covariates for telemetry analysis**

Trailheads at either end of the study area were equipped with infrared trail counters from which human activity was estimated. A TRAFx trail counter (TRAFx Research Ltd., Canmore, Alberta, CA) was placed on the actual trail while a TRAFx vehicle counter (TRAFx Research Ltd.) was placed on the parking lot recording the number of cars. While this does not count the exact number of trail users from one end of the trail network, we assume it is an accurate index of human activity originating from that trailhead. Trail counters recorded the number of people per hour. We summed the number of users from each trailhead and created a rolling average of trail users from the current hour and the previous 3 hours to match our GPS fix interval. Distance to trail for each location was also included as a covariate to test for avoidance of the trail network.

We included layers of terrain ruggedness index (TRI), aspect and landcover type to model habitat selection. TRI was chosen to not only represent rugged terrain but also as a proxy for predation risk from mountain lions, a primary predator of mule deer, as has been done in other studies (Kohl et al. 2019, Smith et al. 2019). Aspect, measured in radians, was cosine transformed to represent “northness”, as deer may preferentially select warmer south-facing slopes in winter (Sawyer et al. 2006, Anderson et al. 2012, Coe et al. 2018).  Land cover classes were modeled using the most recent landcover data from the National Land Cover Database (NLCD) in 2019 (DeWitz 2021). Landcover classes were simplified into forest, shrub, herbaceous, developed and wetland land cover types. Thinned forest from habitat management was represented by the shrub land cover class from the NLCD. Land cover types associated with human development were considered as available habitat for mule deer in our analysis and not excluded, due to the presence of a resident deer population in the town of Salida indicating this habitat could be used. Wetland habitat represented riparian vegetation along a stream. Time of day for each location was classified as day, night or crepuscular using the time\_of\_day function in R package animal movement tools (Signer et al. 2019), and then used to subset data to evaluate the temporal aspect of habitat selection. All continuous variables were scaled and centered for analysis.

**Habitat selection statistical analyses**

We analyzed deer habitat selection using integrated Step Selection Analysis (iSSA) which simultaneously estimates a component modeling habitat selection free of movement constraints and a component estimating a likelihood of selection based on movement parameters in a homogeneous environment (Avgar et al. 2016). This analysis compares used steps, those taken by the animal, to available steps, calculated by combining a random step length and turn angle sampled from distributions fit to the empirical observations of step length and turn angles. The model calculates a probability of use between 0 and 1 as the response variable based on the binary used (1) and available (0) points (Fieberg et al. 2021). Used steps were paired with 20 available steps in this analysis (Avgar et al. 2016, Fieberg et al. 2021). We fit a von Mises distribution to observed turn angles and a lognormal distribution to observed step lengths as a heavy tailed distribution better fit the probability of larger step lengths.

We used a mixed Poisson regression to calculate population level estimates of habitat selection. A Poisson regression, with stratum-specific intercepts fixed at a large variance, is likelihood equivalent to the conditional logistic regression that is traditionally used in iSSA (Muff et al. 2020). But the Poisson regression allows for the incorporation of random slopes that are computationally and mathematically challenging when fit with conditional logistic regression models (Muff et al. 2020). This allowed us to account for individual responses to habitat and recreation parameters. Regression analyses were run using the R package glmmTMB (Brooks et al. 2017).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Global 2 | Global 1 | Human | Habitat | Null | Model Name |
| log step length + log step length² +  cosine turn angle | log step length + log step length² +  cosine turn angle | log step length + log step length² +  cosine turn angle | log step length + log step length² +  cosine turn angle | log step length + log step length² + cosine turn angle | Movement Parameters |
| Developed + **Forest** + Herbaceous Wetlands+ **Cosine Aspect** +  Terrain Ruggedness | Developed + **Forest** + Herbaceous Wetlands+ **Cosine Aspect** +  Terrain Ruggedness |  | Developed + **Forest** + Herbaceous Wetlands+ **Cosine Aspect** +  Terrain Ruggedness |  | Habitat Parameters |
| **Distance to**  **Trail** | **Distance to**  **Trail** | **Distance to**  **Trail** |  |  | Recreation  Parameters |
| Distance to Trail: Human Activity | Log step length : Human Activity  Log step length2: Human Activity | Distance to Trail: Human Activity |  |  | Interactions |

We included a null model that contained only attributes of movement representing how an animal would move free of selection for habitat (Table 1). Parameters included cosine-transformed turning angle, cosine-transformed turning angle squared, log step length and the squared log step length. Cosine-transformed step length allowed us to account for the tendency of movement in the same direction. Log step length and squared log step length were included to update the estimated parameters of our step length distribution (Avgar et al. 2016). Furthermore, we included interactions of these movement parameters with human activity to explore consequential changes in movement patterns (Fieberg et al. 2021).

A habitat model was fit incorporating habitat covariates land cover classes, cosine-transformed aspect, terrain ruggedness index. A recreation model was fit with main effects of, and an interaction between, rolling average of human activity and distance to trail (Table 1). Two models combining our habitat and recreation variables were fit which we refer to as our global models (Table 1). The first of which, Global 1, included interactions between movement characteristics and rolling average of human activity. We used this interaction to investigate how movement behavior changed in response to changes in human activity. The second global model, Global 2, contained an interaction between rolling average of human activity and forest habitat selection. The five models were fit on the whole dataset, data subsetted by night and data subsetted by day. Continuous variables were scaled and centered. Analysis was not done with the crepuscular time period due to a small sample size. Models were evaluated using Akaike Information Criterion (AIC) (Burnham and Anderson 2002).

To compare and visualize deer movement patterns in relation to human activity between different time periods including crepuscular times, we used a linear mixed effects regression in R package nlme (Pinhiero and Bates 2023), with a log-transformed response variable of mean movement rate (meters/hour) over each time period of each day for each individual. We tested a model with an interaction between human activity and time of day versus a model with just the main effects of human activity and time of day. Since human activity could not be incorporated at the hourly level, we used a daily measurement of human activity as an explanatory variable. Human activity measurements for movement rates at night corresponded to the previous day's value of human activity. We included a random effect for individual deer and the main effect of sex in both models. Models were checked for fit with residuals and qq plots and evaluated using Akaike Information Criterion (AICc) (Burnham and Anderson 2002).

*Covariates – Camera Analysis*

Relative human activity was measured as weekly detections of humans at camera sites. An estimate of slope at camera site and mean slope within 100 meters of camera site were derived from a digital elevation raster. Landcover classes were extracted from the National Land Cover Database for 2019 (DeWitz 2021) and simplified in the same manner as for the habitat selection portion of the study. Forest and shrub land cover was modeled as a percent land cover within three different buffer distances of camera locations — 100m, 250m, and 385m. Distance to herbaceous cover, assumed to be a proxy for high quality forage for mule deer based on our habitat selection study, was also included as a variable. Trails in the study area were digitized and trail length was measured at the grid cell scale and within 100m of camera locations. All continuous variables were scaled and centered for analysis.

*Time-to-event Camera Analysis*

Time-to-event modeling (TTE) (Moeller et al. 2018, Loonam et al. 2021) allows us to leverage movement data from mule deer telemetry, in combination with captures of our study species on trail cameras to estimate abundance (Moeller et al. 2018, Loonam et al. 2021). TTE and similar statistical approaches (space-to-event, random encounter models) sample the landscape as opposed to modeling unmarked animals and therefore do not carry the same difficult assumptions as other models to estimate unmarked populations of animals (Loonam et al. 2021a, Moeller et al. 2022). More specifically, TTE models the distribution of animals in the collective viewshed of all the cameras as a Poisson distribution and utilizes the exponential distribution to represent the amount of time it takes for a Poisson distributed event to occur (Loonam et al. 2021a). Time-to-event models have been shown to have more precise estimates than space-to-event or random encounter models (Morin et al. 2022), and estimated densities are comparable to more intensively derived density estimates (Loonam et al. 2021).

An estimate of speed is required to define the sampling period as the time it takes to cross the viewshed of a camera (Moeller et al. 2018, Loonam et al. 2021). Estimation of speed is non-trivial, as movement rate measured in discrete time is dependent on sampling rate with coarse time scales under-estimating speed and very fine time scales over-estimating speed (Noonan et al. 2019, Poulin et al. 2021). Over- and underestimating speed has been shown to cause a linear bias in density estimates from TTE models (Loonam et al. 2021a, Santini et al. 2022). To solve this, we calculated speed using continuous time movement modeling which has shown to be robust to variable sampling rates (Noonan et al. 2019), while also calculating movement rate from more frequent (<1hr) locations, estimating density from both movement rates. Viewshed area was estimated as 45m², based on ex situ measurements of camera detection area used in other TTE modeling applications (Loonam et al. 2021). Other measures of trail camera viewshed area include a total viewshed area of 87m² area with detection reduced to 22-65m² depending on direction of animal movement in a controlled test (Apps and McNutt 2018), and 106m² used in similar space-to-event modeling (Ausband et al. 2022). To account for uncertainty in camera viewshed we estimated density at three different measurements of viewshed area, sampling camera viewsheds from a normal distribution centered around 45m², 65m², and 80m², all with a standard deviation of 5m².

A time frame from April 14, 2022- May 15, 2022 was chosen for an overall density estimate for the study area. This timeframe was chosen to match the timing of our habitat selection study and deer habitation on our winter range. To separately investigate heterogeneous density among cameras, the entire deployment period (April 2022-August 2022) was used to maximize data available for estimation of density at individual cameras. When the assumption of a closed population is violated, TTE models estimate average abundance across the duration of the survey (Loonam et al. 2021). Following the recommendations of Moeller et al. 2019, fewer number of sampling periods per occasion were used for modeling density at individual cameras, accounting for animals in the immediate vicinity of the camera (Moeller et al. 2018). Heterogeneous density was modeled at individual cameras using generalized linear models with a gamma distribution and identity link function. Given the small sample size, environmental (slope and land cover at different scales, distance to herbaceous cover) and human factors (trail density at different scales and relative human activity at the camera) were tested individually before combining the environmental layers that best predicted the data, as measured by ΔAIC, with human factors.  Models were checked to ensure assumptions were met and evaluated using Akaike Information Criterion for small sample sizes (AICc) (Burnham and Anderson 2002).

**RESULTS**

**A graph with black lines and white text

Description automatically generated**

**Pooled iSSF model**

The best fit model for the pooled dataset was the global model containing an interaction between forest land cover and rolling average of human activity (“Global 2” model, Table 1). Due to a large difference in ΔAIC and model weight, we proceeded with inference from this model. The beta estimates for the effects of all covariates can be seen in Figure 2. The interaction for forest land cover and rolling average of human activity was found to have a strong, positive effect on selection, meaning as the rolling average of human activity increased, selection for forest habitat as compared to shrub habitat increased. Herbaceous and wetland landcover types also have a strong positive effect on selection in relation to shrub habitat. There is a weak, positive effect of forest habitat on selection. Lastly there is a strong, negative effect of distance to trail on selection implying selection for areas closer to trail.

A screenshot of a graph

Description automatically generated

**Day iSSF model**

The global model including interactions between human activity and movement characteristics was the best fit model for the day dataset (Table 2). In terms of habitat selection, we found a weak, negative effect of herbaceous land cover on selection, while we see a weak, positive effect for forest land cover on selection (Figure 3). Suggesting a minor avoidance of herbaceous land cover and selection for forest land cover during the day. There is a significant, positive effect of wetland land cover, meaning wetland habitat along a riparian corridor was preferred during the day (Figure 3).

We also see significant interactive effects with movement characteristics. Interactions between log step length and human activity and squared log step length x rolling average were significant. Using the beta coefficients from our model we can update our step length distribution to facilitate interpretation of this interaction on movement behavior. Doing so produces Figure 4 illustrating that as human activity increases the step length distribution changes and deer are move less.

A graph of a step

Description automatically generated

*A graph of steps

Description automatically generated*

**Night iSSF model**

For our nighttime model set, the global model with an interaction between movement characteristics and human activity once again was the best fit model similar to the day dataset (Table 3). There was a strong, positive effect of herbaceous land cover type on selection), indicating deer selected for herbaceous land cover at night. There was also a significant interaction between human activity and log step length (Figure 3). Similar to our day iSSF model, we can update our step length distribution with the beta coefficients from our interaction terms to ease interpretation. This indicates a greater likelihood of longer step lengths with increasing human activity at night implicating deer move more at night with increases in human activity (Figure 5), albeit this is a smaller effect when compared to the step length distribution for the daytime analysis.

*A graph with black lines and white text

Description automatically generated*

**TTE modeling**

Data was sufficient to estimate densities at 21 individual cameras. Four models had a ΔAICc < 2 (Table 4) and were model averaged to get final parameter estimates. All four models contained either trail density at a grid cell scale, or relative human activity. The full model average resulted in no strong effect of any of the covariates and camera-level density (Figure 10). The intercept, or average density at cameras, was 0.613 deer/km², trail density at the camera grid level had a non-significant, negative effect; relative human activity had a non-significant, negative effect and slope had a weak, non-significant, negative effect.

A diagram of a graph

Description automatically generated with medium confidence

**DISCUSSION**

**Deer habitat selection and movement patterns**

With both our pooled dataset and separate day/night datasets, the models that best explained the data incorporated anthropogenic and habitat factors. Our model for the pooled dataset indicated a change in habitat use with increasing human activity, as indicated by a significant interaction between rolling average of human activity and forest habitat in reference to shrub habitat. The shrub habitat, increasingly avoided by deer with human activity, is indicative of areas where forest management has been implemented for fuel reduction and habitat management (Miller et al. 2019). This involves mastication of pinyon and juniper trees in areas flat enough for heavy machinery, resulting in thinned, open savannah-like habitat. A loss of foraging opportunities could result from this shift in habitat preference, with the shrub habitat providing a greater abundance and diversity of browse for mule deer (Bombaci et al. 2016, Miller et al. 2019). Habitat management of winter range for mule deer may be rendered less effective with increasing human recreation as potentially important cover habitat is removed and productive foraging habitat is perceived to be riskier. Thoughtful consideration of the goals of pinyon-juniper management may be needed to balance the needs of wildlife management along with other benefits of this practice (Miller et al. 2019). However, compromise may exist in the patch size and arrangement of treatments. Short et al. 1977 examined deer use across different thinning treatments finding that small patch cuttings (≤0.5km) were used more often by deer and that the arrangement of treatment patches near undisturbed woodland was important for use. Further examination of this question could help resolve equivocal results on the utility of pinyon-juniper habitat management to mule deer population health.

This change in habitat preference as a result of human presence has also been observed in other wildlife species (Cristescu et al. 2013, Smith et al. 2019). Competing mesocarnivore species in high use open spaces, showed greater habitat overlap between a generalist carnivore – coyote – and more specialized carnivores, gray fox and bobcat, than low use open spaces (Smith et al. 2018). Grizzly bears showed changes in selection for resting sites depending on level of human activity (Cristescu et al. 2013). This pattern suggests niche compression due to human activity (Gilbert et al. 2022) could be at play on our study area, if deer are facing competition from other herbivores, such as elk, simultaneously altering habitat selection in response to human presence. Further research of competition with other ungulate/herbivore species from niche compression could reveal an indirect pathway impacting mule deer, or competing ungulate species, initiated by increased human presence. Greater intraspecies competition could also result from increased human presence as well if individual deer are seeking a similar solution to human presence.

Mule deer also show divergent responses to increasing human activity depending on the time of day. During the day, deer moved less in response to increasing human activity while at night and during dawn/dusk they moved more. Changes to activity patterns of mule deer, and specifically reducing daytime activity, have been found in camera studies looking at deer response to human activity on trail networks (George and Crooks 2006, Reilly et al. 2017, Nix et al. 2018, Lewis et al. 2021). The only other telemetry study examining this question found slightly increased hourly movement rates for deer when looking at activity patterns during four recreation activities in comparison to a control and suggested, as we found, that deer might be seeking different habitat in response to high human activity (Wisdom et al. 2004). On a global scale, human footprint has been shown to reduce terrestrial mammal movements and increase wildlife nocturnality (Gaynor et al. 2018, Tucker et al. 2018), while a different review found that human disturbance changed animal movement across taxa, with disturbance caused by human activities like recreation causing a greater effect than habitat modification (Doherty et al. 2021).

There was a negative effect of distance to trail on deer habitat selection, indicating selection for areas near trails and no indirect loss of habitat caused by human recreation. This is also reflected in camera work indicating no spatial avoidance with an increase of human activity on trail networks (George and Crooks 2006, Reilly et al. 2017, Lewis et al. 2021). Previous telemetry work similarly did not find avoidance of trail by mule deer unlike elk (Wisdom et al. 2004), indicating the possibility that elk could be more sensitive to human presence. However, indirect loss of habitat has been found for mule deer on winter range in response to natural gas drilling (Sawyer et al. 2006). Distance to trail was modeled as a linear response in my model set. It is possible the relationship between habitat selection and distance to trail is more complex, resulting in selection for an intermediate distance from trail. A lack of spatial avoidance may not be a reliable indicator for a lack of effect either, as suitable, alternative habitat may not exist or be accessible (Gill et al. 2001). Deer are already constrained by snow and human development on winter range, possibly limiting alternative, suitable habitat. Many of the individual deer in this study also utilized habitats where farther from trail meant closer to humans, such as developed land cover, actively managed and fallow agriculture fields, and riparian habitat. The trail network could in fact allow deer to balance foraging risk tradeoff by offering a less risky habitat in comparison to open fields to utilize during the day for refuge. Deer could also prefer similar biophysical characteristics we use for trails that we did not consider in this model, coincidentally causing this preference for areas near trails. Deer could also be habituated to the repeated stimuli of recreation showing decreased responses in terms of avoidance, as ungulate populations in areas of high human presence have shown weaker flight responses (Stankowich 2008)

Potential foraging habitat, represented by wetland and herbaceous land cover, did have a positive effect on selection, with these land cover types creating a strong enough draw to overcome proximity to human development dependent on time of day. It is important to remember that habitat selection parameters should be interpreted as relative intensity of use, meaning that all other factors being held equal deer will choose wetland or herbaceous cover over forest landcover (Fieberg et al. 2021). In reality, herbaceous and wetland habitat is an order of magnitude rarer in availability than shrub or forest habitat. Selection does not indicate where an animal is likely to be found most of the time, but where it selects for with all other variables held constant and different habitat being equally available (Fieberg et al. 2021). Taken this way, we can interpret deer as being choosy about what habitat they are in when they are far from the trail and balancing their risk of foraging closer to developed habitat when far from trail by utilizing these habitats during times of human inactivity. The potential non-linearity of selection in response to distance from trail could also resolve the seemingly contradictory conclusions from distance to trail and selection of herbaceous and wetland habitat. Utilization of wetland and herbaceous habitat during different times of day, analyzed in our separate day/night datasets further clarify how deer balance selection based on time of day associated with differing behaviors and human activity.

During the day deer selected for wetland habitat, while at night we see selection for herbaceous habitat. Importantly, herbaceous landcover covariates seem to be time dependent, with a weak, negative effect for selection during the day but positive effect of selection at night. Contrasting habitat selection estimates based on time of day suggests a spatiotemporal strategy to balance needs for cover and foraging, with deer preferring habitats offering more cover during the day and habitats associated with better forage at night. This indicates the ability of mule deer to spatiotemporally avoid risk in an important habitat type more closely associated with humans, akin to balancing forage-risk tradeoffs with natural predators active during different times of the day such as wolves and mountain lions (Kohl et al. 2019, Smith et al. 2019).

**Measurement of recreation**

Human recreation involves both human presence and human infrastructure. While both can have an impact on wildlife, infrastructure is often measured and serves as a proxy for recreation with only 6.7% of studies remotely monitoring recreation activity (Larson et al. 2016). Human activity is also commonly measured as a binary with high and low use areas, but this may not put a specific number to human activity or track changes over a continuum of activity (Larson et al. 2016). Use of infrared trail counters for tracking human presence fulfills the need for better measurements of human activity needed in recreation research (Marion et al. 2020). Trail counters provide a valuable metric down to the hour, and measure trends over longer periods of time than was needed for this study, making it possible to monitor long term recreation trends. Trail counter data provides a useful tool for managers looking to manage trail traffic and detect thresholds at which human presence might become significantly more damaging (Monz et al. 2013, Larson et al. 2016). Our research using both measures of human activity (trail counter data) and infrastructure data (distance to trail) disentangles the two components human recreation brings, isolating the effects of changes in human presence while accounting for infrastructure associated with recreation.

**Deer density estimates**

Time to event modeling is part of a relatively new set of models still under development, with separate simulation studies finding an overestimation (Santini et al. 2022) or an underestimation (Moeller et al. 2018) of density, depending on the animal movement model used in simulations. Uncertainty and bias in estimates can also be introduced when assumptions of the model are not met, and we follow recommendations in consideration of these violations (Gilbert et al. 2021). Previous research into TTE models indicated they are robust to some assumptions but suffer decreased accuracy and bias when movement rate was poorly estimated, when cameras are placed non randomly with respect to habitat, and with inaccurate measurements of camera viewshed area (Moeller et al. 2018, Loonam et al. 2021, Santini et al. 2022, Moeller et al. 2023). However, previous studies found TTE models to have comparable estimates of density to more established methods (Moeller et al. 2018, Loonam et al. 2021a). At the landscape level, cameras were placed systematically, and were then placed randomly within grid cells, while trails were targeted within proximity of randomized locations. Cameras were placed randomly at 2 of 3 scales, and followed recommendations of *a priori* rules for camera deployment (Loonam et al. 2021). Cameras placed randomly at microsite scales could be impractical with camera viewsheds potentially being obstructed and censored from analysis (Loonam et al. 2021). We would expect our non-random placement of cameras along travel corridors, would increase detection rate and would once again bias estimates high (Loonam et al. 2021).

Furthermore, while our model average results were non-significant, our top models of density estimates at individual cameras repeatedly contained human activity and trail density. With these factors explaining the data better than any other included covariates; suggesting trail density, and relative human activity may play a role in decreases in density.

Nevertheless, the notion of anthropogenic caused habitat degradation, loss or avoidance has been suggested as a mechanism limiting carrying capacity, supporting the evidence of our individual camera density modeling (Forrester and Wittmer 2013, Johnson et al. 2017). Unfortunately, the scope of these competing hypotheses is beyond the capabilities of our study but the possibilities to expand beyond the framework of our study to answer these questions will be discussed later.

**Conclusions and future study**

While mule deer density can possibly provide numerical feedback indicating the severity of recreation impacts, recruitment or fawn survival could provide an earlier indication of a decline in population health for mule deer (Monteith et al. 2014). Earlier detection of deleterious effects through physiological and energetic mechanisms are important to understand to enable earlier action and detect thresholds where impacts move beyond behavioral changes. It is possible with accelerometer data to construct a landscape to understand energetic costs associated with human disturbance as has been done with mountain lions in California (Nickel et al. 2019).

Mule deer have shown a capability of adapting to human disturbance in increasingly urbanized areas as illustrated by resident populations of deer being those closest to human development (Robb et al. 2019). Our population demonstrates that deer who summer in comparatively natural habitats can still depend on increasingly urbanized winter ranges. Mule deer migration is culturally transmitted and declines in ungulate migration have been associated with increasing human development, possibly due to constraints to movement caused by anthropogenic barriers or availability of preferred forage within human environments (Bolger et al. 2008, Robb et al. 2019). Increasing human presence on winter ranges could contribute to a loss of migratory individuals by amplifying fear effects to impact populations or the desensitization of deer to human presence, either way resulting in losses of migratory deer. Simultaneous influences of human development and recreation must be considered, these two different aspects of humanity have differing effects, but synergy between them could amplify the problem. Barriers and potential loss of foraging habitat near town through conversion to higher intensities of human development could act in concert with increasing trail presence to further constrain deer between deep snow at higher elevation, human development, human presence on trail, and natural predators. Loss of migratory movements can eliminate typical dual-range migrants or other variations in migration, such as multi-range migrants or partial migrants, decreasing diversity in migration behavior and limiting available strategies to adapt to a changing world (van de Kerk et al. 2021). The outcome of these changes to mule deer winter range and potential consequences to migratory behavior requires more study.

Most research examining mule deer responses to recreational activity has looked at immediate behavioral responses, such as probability of fleeing and fleeing distance (Taylor and Knight 2003) or used camera traps to examine activity patterns and occupancy patterns (George and Crooks 2006, Muhly et al. 2011, Reilly et al. 2017, Nix et al. 2018, Lewis et al. 2021) with only one other study using telemetry data (Wisdom et al. 2004). This was surprising given that cervids are the most studied group of wildlife in terms of recreation research (Marion et al. 2020). Our study provides important, detailed examination of deer habitat selection and movement considering multiple strategies mule deer may use to cope with human presence. Changes in the selection of managed habitat, increased movement costs, and loss of foraging opportunities may broaden impacts of human presence from individuals to populations of migratory deer increasingly constrained on their winter range. Additionally, we observed evidence for possible population level consequences from recreation in the form of reduced deer density in relation to documented estimates on other winter ranges.

Further study could build on our research using TTE modeling as a less intensive and invasive method for estimating density (Moeller et al. 2018, Loonam et al. 2021), while following further development of TTE study design (Moeller et al. 2023). Maximizing data derived from collared individuals including survival, reproduction and nutritional condition can help identify nutritional carrying capacity, revealing the role recreation plays in the limitation of wildlife species and other density-independent impacts recreation might have at the population level. With density estimations not being particularly sensitive and having high variability from year to year collecting this supplemental data will provide support for the mechanisms we propose may be important in this population (Bergman et al. 2015). Our work represents a snapshot in time with low density possibly caused by a variety of reasons that we were not able to distinguish. Longer term study following the trends of recreation over time can resolve this uncertainty present in our study design. There is still a lot we don’t know about the severity of recreation impacts, as the magnitude can be modulated by other factors such as density dependence outlined above. Understanding the behavioral pathways leading to population ramifications and ecological changes will help us determine when we should strive to mitigate behavioral changes caused by recreation and when changes may be less impactful, in order to better direct conservation efforts (Wilson et al. 2020).

**MANAGEMENT IMPLICATIONS**

While resident urban deer demonstrate the ability to adapt to human environments, resident deer are more closely associated with human development (Robb et al. 2019). Shifts in the balance of migratory and resident individuals towards residents have been documented (Hebblewhite and Merrill 2000, Middleton et al. 2013), portending poor outcomes for migratory portions of deer populations. A review of flight responses of ungulates found a robust yet weak effect of habituation at higher levels of recreation (Stankowich 2008). Reduced response to human presence may be a good outcome for deer allowing them to maintain normal behaviors, although this desensitization may lead to increased human-wildlife conflict (Thompson and Henderson 1998), increased disease prevalence (Farnsworth et al. 2005) and loss of migratory behavior (Robb et al. 2013). Similar research into energy development did not find habituation by mule deer with respect to decreased avoidance of well pads, also observing a concomitant decline in the population over 15 years of development (Sawyer et al. 2017). However responses may differ between these two disturbance types, as the most active phase of natural gas development includes noise and artificial light beyond heavy traffic volumes and human activity (Northrup et al. 2021). Unlike energy development which experiences a predictable rise and fall of disturbance over the course of development peaking with drilling and extraction (Northrup et al. 2021), the story of development for recreation is often one of escalating disturbance, with this shifting baseline requiring continuous adaptation. Indeed, more trail development is planned for our study area. Many wildlife management agencies have implemented seasonal closures of deer winter ranges to improve winter condition of mule deer through decreased disturbance. Part of our study area has an unlocked gate across the trail with signage requesting trail users avoid the trail from December 1st to April 15th. Seasonal closures have similarly been suggested to improve elk reproductive success during calving season (Phillips and Alldredge 2000, Shively et al. 2005). Efforts to mitigate disturbance on mule deer have the ancillary benefit of providing protection for species more sensitive to human disturbance.

Off-trail recreation is also an unaccounted for presence on the study area with hikers accompanied by off leash dogs being regular enough to establish several social trails through otherwise trail-less control areas. Quantifying the magnitude of this problem and limiting its extent may be important as mule deer have shown stronger avoidance responses to both off trail recreationists (Miller et al. 2001, Taylor and Knight 2003), and humans accompanied by dogs (Miller et al. 2001, Lenth et al. 2008).

The results of our habitat selection analysis and observation suggest herbaceous and riparian wetlands land cover provide an important foraging habitat for mule deer, providing a partially human-derived benefit that counteracts the negative impacts of recreation. Preventing the transition of this type of landcover to higher intensity development may be important for continuing to subsidize resources for this deer herd, as has been argued for the conservation of other species (Guitierrez-Gonzalez et al. 2015, Kreye and Pienaar 2015), although this may cause a clash with future housing needs (Wondra 2022).

The size and arrangement of thinned pinyon-juniper could contribute to mitigation with greater cover afforded by unmanaged habitat close to better forage in shrub habitat (Short et al. 1977). Current treatment areas already conform to suggested patch sizes for treatment potentially providing this mitigation. However more formal testing of patch size and arrangement should be conducted to investigate this idea to better inform future habitat management efforts.

Finally, the most effective form of mitigation may be education of recreationists. Taylor and Knight 2003 assessed visitor perceptions along with research into ungulate flight behavior, finding that ~50% of recreationists did not believe recreation was impacting wildlife. Recreationists believed they could approach wildlife closer than observed flight distances without causing harm and that other recreation types are responsible for major disturbance (Taylor and Knight 2003). Research on visitor perception of wildlife impacts was difficult to find, indicating a need for future research. Increasing awareness about potential negative consequences of recreation on wildlife could foster more responsible stewardship and perhaps hold the greatest potential in mitigating our impact, facilitating experiences that inspire us to conserve wildlife.

Snow and climate at high elevation constrains available habitat forcing migration to winter ranges where snow depths can increase movement costs and obscure nutritionally limited forage (Northrup et al. 2021). Winter range is under additional threat from human development, as humans often seeking similar biophysical traits in habitat to wildlife (Leu et al. 2008, Johnson et al. 2017). Mule deer winter range in Colorado has experienced greater residential and energy development than summer range correlating with declines in recruitment (Farnsworth et al. 2005).

**ACKNOWLEDGMENTS**

Thanks to S. Bundick, H. Westacott, R. Heule, F. Mack-Carlo, E. Landi, E. Norton, C. Weissburg, B. LaMont, D.McNitt, M. Rustand, K. Marshall, C. Ramos, F. Sandmeier

**ETHICS STATEMENT**

Capturing, handling and marking procedures were approved by the Institutional Animal Care and Use Committee (IACUC) at Colorado State University Pueblo (Protocol #: 000-000A-028) .

**REFERENCES**

Alberti, M., J. M. Marzluff, E. Shulenberger, G. Bradley, C. Ryan, and C. Zumbrunnen. 2008. Integrating humans into ecology: Opportunities and challenges for studying urban ecosystems. BioScience 53:143–158.

Anderson, E. D., R. A. Long, M. Paul Atwood, J. G. Kie, T. R. Thomas, P. Zager, and R. Terry Bowyer. 2012. Winter resource selection by female mule deer *Odocoileus* *hemionus*: functional response to spatio-temporal changes in habitat. Wildlife Biology 18:153–163.

Ausband, D. E., P. M. Lukacs, M. Hurley, S. Roberts, K. Strickfaden, and A. K. Moeller. 2022. Estimating wolf abundance from cameras. Ecosphere 13:e3933.

Avgar, T., J. R. Potts, M. A. Lewis, and M. S. Boyce. 2016. Integrated step selection analysis: bridging the gap between resource selection and animal movement. Methods in Ecology and Evolution 7:619–630.

Avgar, T., G. S. Betini, and J. M. Fryxell. 2020. Habitat selection patterns are density dependent under the ideal free distribution. Journal of Animal Ecology 89:2777–2787.

Bauer, S., and B. J. Hoye. 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. Science 344:1242552.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letters, 3:620–623.

Bergman, E. J., C. J. Bishop, D. J. Freddy, G. C. White, and P. F. Doherty. 2014. Habitat management influences overwinter survival of mule deer fawns in Colorado. Journal of Wildlife Management 78:448–455.

Bergman, E. J., P. F. Doherty, G. C. White, and D. J. Freddy. 2015. Habitat and herbivore density: response of mule deer to habitat management. Journal of Wildlife Management 79:60–68.

Bishop, C. J., White, G. C., Freddy, D. J., Watkins, B. E., and Stephenson, T. R. 2009. Effect of enhanced nutrition on mule deer population rate of change. Wildlife Monographs, 172:1–28.

Bolger, D. T., Newmark, W. D., Morrison, T. A., and Doak, D. F. 2008. The need for integrative approaches to understand and conserve migratory ungulates. Ecology Letters 11:63–77.

Bombaci, S., and L. Pejchar. 2016. Consequences of pinyon and juniper woodland reduction for wildlife in North America. Forest Ecology and Management 365:34–50.

Bowker, J.M., and A. Askew. 2012. U.S. outdoor recreation participation projections to 2060. In: Cordell, H. K. ed. 2012. Outdoor Recreation Trends and Futures: A technical document supporting the Forest Service 2010 Resources Planning Act Assessment. Gen. Tech. Rep. SRS-150. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 105-124.

Bowyer, T. R., V. C. Bleich, K. M. Stewart, J. C. Whiting, and K. L. Monteith. 2014. Density dependence in ungulates: a review of causes, and concepts with some clarifications. California Fish and Game. 100:550-572.

Brooks, M.E., K. Kristensen , K. J. van Benthem, A. Magnusson , C.W. Berg, A. Nielsen, H.J. Skaug, M. Maechler, B.M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9:378–400.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information‐theoretic approach. Second edition. Springer, New York, New York, USA.

Ciuti, S., J. M. Northrup, T. B. Muhly, S. Simi, M. Musiani, J. A. Pitt, and M. S. Boyce. 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. PLOS ONE 7:e50611.

Coe, P. K., D. A. Clark, R. M. Nielson, S. C. Gregory, J. B. Cupples, M. J. Hedrick, B. K. Johnson, and D. H. Jackson. 2018. Multiscale models of habitat use by mule deer in winter. Journal of Wildlife Management 82:1285–1299.

Coppes, J., J. Ehrlacher, D. Thiel, R. Suchant, and V. Braunisch. 2017. Outdoor recreation causes effective habitat reduction in capercaillie *Tetrao urogallus*: a major threat for geographically restricted populations. Journal of Avian Biology 48:1583–1594.

Crawford, D. A., L. M. Conner, M. Clinchy, L. Y. Zanette, and M. J. Cherry. 2022. Prey tells, large herbivores fear the human ‘super predator.’ Oecologia 198:91–98.

Cristescu, B., G. B. Stenhouse, and M. S. Boyce. 2013. Perception of human-derived risk influences choice at top of the food chain. PLOS ONE 8:e82738.

Darimont, C. T., C. H. Fox, H. M. Bryan, and T. E. Reimchen. 2015. The unique ecology of human predators. Science 349:858–860.

Dewitz, J., and U.S. Geological Survey. 2021. National Land Cover Database (NLCD) 2019 Products (ver. 2.0, June 2021): U.S. Geological Survey data release, <https://doi.org/10.5066/P9KZCM54>.

Doherty, T.S., Hays, G.C. and Driscoll, D.A. 2021. Human disturbance causes widespread disruption of animal movement. Nature Ecology and Evolution 5:513–519.

Dorresteijn, I., J. Schultner, D. G. Nimmo, J. Fischer, J. Hanspach, T. Kuemmerle, L. Kehoe, and E. G. Ritchie. 2015. Incorporating anthropogenic effects into trophic ecology: predator - prey interactions in a human-dominated landscape. Proceedings of the Royal Society B: Biological Sciences 282:20151602.

Dzialak, M. R., S. M. Harju, R. G. Osborn, J. J. Wondzell, L. D. Hayden-Wing, J. B. Winstead, and S. L. Webb. 2011. Prioritizing conservation of ungulate calving resources in multiple-use landscapes. PLOS ONE 6:e14597.

Farnsworth, M. L., L. L. Wolfe, N. T. Hobbs, K. P. Burnham, E. S. Williams, D. M. Theobald, M. M. Conner, and M. W. Miller. 2005. Human land use influences chronic wasting disease prevalence in mule deer. Ecological Applications 15:119–126.

Fieberg, J., J. Signer, B. Smith, and T. Avgar. 2021. A ‘How to’ guide for interpreting parameters in habitat-selection analyses. Journal of Animal Ecology 90:1027–1043.

Forrester, T. D., and H. U. Wittmer. 2013. A review of the population dynamics of mule deer and black-tailed deer *Odocoileus hemionus* in North America. Mammal Review 43:292–308.

Freddy, D. J., W. M. Bronaugh, and M. C. Fowler. 1986. Responses of mule deer to disturbance by persons afoot and snowmobiles. Wildlife Society Bulletin 14:63–68.

Frid, Alejandro, and Dill, L. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:11.

Gaynor, K. M., C. E. Hojnowski, N. H. Carter, and J. S. Brashares. 2018. The influence of human disturbance on wildlife nocturnality. Science 360:1232–1235.

Gilbert, N. A., J. D. J. Clare, J. L. Stenglein, and B. Zuckerberg. 2021. Abundance estimation of unmarked animals based on camera-trap data. Conservation Biology 35:88–100.

Gilbert, N. A., J. L. Stenglein, J. N. Pauli, and B. Zuckerberg. 2022. Human disturbance compresses the spatiotemporal niche. Proceedings of the National Academy of Sciences 119:e2206339119.

Gill, J. A., K. Norris, and W. J. Sutherland. 2001. Why behavioral responses may not reflect the population consequences of human disturbance. Biological Conservation 97:265-268.

Gutiérrez-González, C. E., M. A. Gómez-Ramírez, C. A. López-González, and P. F. Doherty. 2015. Are private reserves effective for jaguar conservation?. PLOS ONE 10:e0137541.

Hebblewhite, M., and Merrill, E. H. 2011. Demographic balancing of migrant and resident elk in a partially migratory population through forage-predation tradeoffs. Oikos 120: 1860–1870.

Hurley, M. A., J. W. Unsworth, P. Zager, M. Hebblewhite, E. O. Garton, D. M. Montgomery, J. R. Skalski, and C. L. Maycock. 2011. Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. Wildlife Monographs 178:1–33.

Johnson, H. E., J. R. Sushinsky, A. Holland, E. J. Bergman, T. Balzer, J. Garner, and S. E. Reed. 2017. Increases in residential and energy development are associated with reductions in recruitment for a large ungulate. Global Change Biology 23:578–591.

Kays, R., A.W. Parsons, M.C. Baker, E.L. Kalies, T. Forrester, R. Costello, C.T. Rota, J.J. Millspaugh and W.J. McShea. 2017. Does hunting or hiking affect wildlife communities in protected areas?. Journal of Applied Ecology 54:242-252.

Kohl, M. T., T. K. Ruth, M. C. Metz, D. R. Stahler, D. W. Smith, P. J. White, and D. R. MacNulty. 2019. Do prey select for vacant hunting domains to minimize a multi-predator threat?. Ecology Letters 22:1724–1733.

Kreye, M. M., and E. F. Pienaar. 2015. A critical review of efforts to protect Florida panther habitat on private lands. Land Use Policy 48:428–436.

Ladle, A., T. Avgar, M. Wheatley, G. B. Stenhouse, S. E. Nielsen, and M. S. Boyce. 2019. Grizzly bear response to spatio-temporal variability in human recreational activity. Journal of Applied Ecology 56:375–386.

Larson, C. L., S. E. Reed, A. M. Merenlender, and K. R. Crooks. 2016. Effects of recreation on animals revealed as widespread through a global systematic review. PLOS ONE 11:e0167259.

Larson, C. L., S. E. Reed, A. M. Merenlender, and K. R. Crooks. 2019. A meta‐analysis of recreation effects on vertebrate species richness and abundance. Conservation Science and Practice 1:e93.

Laundre, J., Hernández, L., and W. Ripple. 2010. The landscape of fear: ecological implications of being afraid. The Open Ecology Journal. 3:1-7.

Leighton, P. A., Horrocks, J. A., & Kramer, D. L. 2010. Conservation and the scarecrow effect: can human activity benefit threatened species by displacing predators?. Biological Conservation 143: 2156–2163.

Lenth, B. E., R. L. Knight, and M. E. Brennan. 2008. The effects of dogs on wildlife communities. Natural Areas Journal 28:218–227.

Lesmerises, F., Johnson, C. J., & St-Laurent, M. H. 2017. Refuge or predation risk? Alternate ways to perceive hiker disturbance based on maternal state of female caribou. Ecology and Evolution 7:845–854.

Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the west: A large-scale analysis of anthropogenic impacts. Ecological Applications 18:1119–1139.

Loonam, K. E., D. E. Ausband, P. M. Lukacs, M. S. Mitchell, and H. S. Robinson. 2021. Estimating abundance of an unmarked, low-density species using cameras. Journal of Wildlife Management 85:87–96.

Loonam, K. E., P. M. Lukacs, D. E. Ausband, M. S. Mitchell, and H. S. Robinson. 2021a. Assessing the robustness of time-to-event models for estimating unmarked wildlife abundance using remote cameras. Ecological Applications 0:e02388.

Mallord, J. W., P. M. Dolman, A. Brown, and W. J. Sutherland. 2007. Quantifying density dependence in a bird population using human disturbance. Oecologia 153:49–56.

Marion, S., A. Davies, U. Demšar, R. J. Irvine, P. A. Stephens, and J. Long. 2020. A systematic review of methods for studying the impacts of outdoor recreation on terrestrial wildlife. Global Ecology and Conservation 22: e00917.

McGarigal, K., H. Y. Wan, K. A. Zeller, B. C. Timm, and S. A. Cushman. 2016. Multi-scale habitat selection modeling: a review and outlook. Landscape Ecology 31:1161–1175.

McMurry, S., A. K. Moeller, J. Goerz, and H. S. Robinson. 2023. Using space to event modeling to estimate density of multiple species in northeastern Washington. Wildlife Society Bulletin 47:e1390.

Merrill, E., J. Killeen, J. Pettit, M. Trottier, H. Martin, J. Berg, H. Bohm, S. Eggeman, and M. Hebblewhite. 2020. Density-dependent foraging behaviors on sympatric winter ranges in a partially migratory elk population. Frontiers in Ecology and Evolution 8:269.

Middleton, A. D., M.J. Kauffman, D.E. McWhirter, J.G. Cook, R.C. Cook, A. A. Nelson, M. D. Jimenez, and R. W. Klaver. 2013. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. Ecology 94: 1245–1256.

Miller, R. F., J. C. Chambers, L. Evers, C. J. Williams, K. A. Snyder, B. A. Roundy, and F. B. Pierson. 2019. The ecology, history, ecohydrology, and management of pinyon and juniper woodlands in the great basin and northern Colorado plateau of the western United States. US Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Miller, S., R. Knight, and C. Miller. 2001. Wildlife responses to pedestrians and dogs. Wildlife Society Bulletin 29:124–132.

Moeller A.K., P.M. Lukacs, J.S. Horne. 2018. Three novel methods to estimate abundance of unmarked animals using remote cameras. Ecosphere 9:e02331.

Moeller, A. K., and P. M. Lukacs. 2022. spaceNtime: an R package for estimating abundance of unmarked animals using camera-trap photographs. Mammalian Biology 102:581–590.

Moeller, A. K., S. J. Waller, N. J. DeCesare, M. C. Chitwood, and P. M. Lukacs. 2023. Best practices to account for capture probability and viewable area in camera-based abundance estimation. Remote Sensing in Ecology and Conservation 9:152–164.

Moll, R. J., A. K. Killion, M. W. Hayward, and R. A. Montgomery. 2021. A framework for the Eltonian niche of humans. BioScience 71:928–941.

Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, J. G. Kie, and R. T. Bowyer. 2014. Life-history characteristics of mule deer: effects of nutrition in a variable environment. Wildlife Monographs 1–62.

Monz, C. A., C. M. Pickering, and W. L. Hadwen. 2013. Recent advances in recreation ecology and the implications of different relationships between recreation use and ecological impacts. Frontiers in Ecology and the Environment 11:441–446.

Moraga, A. D., A. E. Martin, and L. Fahrig. 2019. The scale of effect of landscape context varies with the species’ response variable measured. Landscape Ecology 34:703–715.

Morin, D. J., J. Boulanger, R. Bischof, D. C. Lee, D. Ngoprasert, A. K. Fuller, B. McLellan, R. Steinmetz, S. Sharma, D. Garshelis, A. Gopalaswamy, M. A. Nawaz, and U. Karanth. 2022. Comparison of methods for estimating density and population trends for low-density Asian bears. Global Ecology and Conservation 35:e02058.

Muhly, T. B., C. Semeniuk, A. Massolo, L. Hickman, and M. Musiani. 2011. Human activity helps prey win the predator-prey space race. PLOS ONE 6:e17050.

Murray, B. D., C. R. Webster, and J. K. Bump. 2013. Broadening the ecological context of ungulate-ecosystem interactions: the importance of space, seasonality, and nitrogen. Ecology 94:1317–1326.

Naidoo, R., and A. C. Burton. 2020. Relative effects of recreational activities on a temperate terrestrial wildlife assemblage. Conservation Science and Practice 2:e271.

Nickel, B. A., J. P. Suraci, M. L. Allen, and C. C. Wilmers. 2020. Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. Biological Conservation 241:108383.

Nickel, B. A., J. P. Suraci, A. C. Nisi, and C. C. Wilmers. 2021. Energetics and fear of humans constrain the spatial ecology of pumas. PNAS 118:e2004592118.

Noonan, M. J., C. H. Fleming, T. S. Akre, J. Drescher-Lehman, E. Gurarie, R. Kays, and J. M. Calabrese. 2019. The fast and the spurious: scale-free estimation of speed and distance traveled from animal tracking data. Movement Ecology 7:35.

Northrup, J. M., C. R. Anderson, B. D. Gerber, and G. Wittemyer. 2021. Behavioral and demographic responses of mule deer to energy development on winter range. Wildlife Monographs 208:1–37.

Oregon State University PRISM Climate Group. 2012. http://prism. oregonstate.edu. Accessed 8 March 2024.

Pinheiro J, Bates D, R Core Team. 2023. nlme: Linear and nonlinear mixed effects models. R package version 3.1-162.

Phillips, G. E., and A. W. Alldredge. 2000. Reproductive success of elk following disturbance by humans during calving season. The Journal of Wildlife Management 64:521–530.

Price, M. V., E. H. Strombom, and D. T. Blumstein. 2014. Human activity affects the perception of risk by mule deer. Current Zoology 60:693–699.

Reed, S. E., and A. M. Merenlender. 2008. Quiet, Nonconsumptive Recreation Reduces Protected Area Effectiveness. Conservation Letters 1:146–154.

Robb, B., Q. Huang, J. O. Sexton, D. Stoner, and P. Leimgruber. 2019. Environmental differences between migratory and resident ungulates — predicting movement strategies in Rocky Mountain mule deer (*Odocoileus hemionus*). Remote Sensing 11:1980.

Romme, W. H., C. D. Allen, J. D. Bailey, W. L. Baker, B. T. Bestelmeyer, P. M. Brown, K. S. Eisenhart, M. L. Floyd, D. W. Huffman, B. F. Jacobs, R. F. Miller, E. H. Muldavin, T. W. Swetnam, R. J. Tausch, and P. J. Weisberg. 2009. Historical and modern disturbance regimes, stand structures, and landscape dynamics in piñon-juniper vegetation of the western United States. Rangeland Ecology and Management 62:203–222.

Rosenzweig, M. L. 1981. A Theory of Habitat Selection. Ecology 62:327–335.

Santini, G., M. Abolaffio, F. Ossi, B. Franzetti, F. Cagnacci, and S. Focardi. 2022. Population assessment without individual identification using camera-traps: a comparison of four methods. Basic and Applied Ecology 61:68–81.

Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70:396–403.

Sawyer, H., N. M. Korfanta, R. M. Nielson, K. L. Monteith, and D. Strickland. 2017. Mule deer and energy development—long-term trends of habituation and abundance. Global Change Biology 23:4521–4529.

Schmitz, O. J., J. H. Grabowski, B. L. Peckarsky, E. L. Preisser, G. C. Trussel, and J. R. Vonesh. 2008. From individuals to ecosystem function: toward an integration of evolutionary and ecosystem ecology. Ecology 89:2436–2445.

Sévêque, A., L. K. Gentle, J. V. López-Bao, R. W. Yarnell, and A. Uzal. 2020. Human disturbance has contrasting effects on niche partitioning within carnivore communities. Biological Reviews 2020:000-000.

Shively, K. J., W. A. Alldredge, and G. E. Phillips. 2005. Elk reproductive response to removal of calving season disturbance by humans. Journal of Wildlife Management 69:1073–1080.

Short, H. L., W. Evans, and E. L. Boeker. 1977. The use of natural and modified pinyon pine-juniper woodlands by deer and elk. The Journal of Wildlife Management 41:543-559.

Signer J, Fieberg J, Avgar T. 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecology and Evolution 9: 880–890.

Smith, B. J., D.R. MacNulty, D. R. Stahler, D. W. Smith, and T. Avgar. 2023. Density-dependent habitat selection alters drivers of population distribution in northern Yellowstone elk. Ecology Letters 26:245–256.

Smith, J. A., A. C. Thomas, T. Levi, Y. Wang, and C. C. Wilmers. 2018. Human activity reduces niche partitioning among three widespread mesocarnivores. Oikos 00:1-12.

Smith, J. A., E. Donadio, J. N. Pauli, M. J. Sheriff, and A. D. Middleton. 2019. Integrating temporal refugia into landscapes of fear: prey exploit predator downtimes to forage in risky places. Oecologia 189:883–890.

Smith, J. A., K. M. Gaynor, J. P. Suraci, and K. M. Gaynor. 2021. Mismatch between risk and response may amplify lethal and non-lethal effects of humans on wild animal populations. Frontiers in Ecology and Evolution 9:604973.

Stankowich, T. 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biological Conservation 141:2159–2173.

Stewart, K. M., R. T. Bowyer, B. L. Dick, B. K. Johnson, and J. G. Kie. 2005. Density-dependent effects on physical condition and reproduction in North American elk: An experimental test. Oecologia 143:85–93.

Suraci, J. P., M. Clinchy, L. Y. Zanette, and C. C. Wilmers. 2019. Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. Ecology Letters 22:1578–1586.

Sutton, N. M. and J.E. Heske. 2017. Effects of human state park visitation rates on escape behavior of white-tailed deer. Human–Wildlife Interactions 11:86-98.

Tablado, Z., and L. Jenni. 2017. Determinants of uncertainty in wildlife responses to human disturbance. Biological Reviews 92:216–233.

Taylor, A. R., and R. L. Knight. 2003. Wildlife responses to recreation and associated visitor perceptions. Ecological Applications 13:951–963.

Thompson, M. J., and R. E. Henderson. 1998. Elk habituation as a credibility challenge for wildlife professionals. Wildlife Society Bulletin. 26:477-483.

Tucker, M. A., K. Böhning-Gaese, W. F. Fagan, J. M. Fryxell, B. Van Moorter, S. C. Alberts, A. H. Ali, A. M. Allen, N. Attias, T. Avgar, H. Bartlam-brooks, B. Bayarbaatar, J. L. Belant, A. Bertassoni, D. Beyer, L. Bidner, F. M. Van Beest, S. Blake, N. Blaum, C. Bracis, D. Brown, P. J. N. De Bruyn, F. Cagnacci, D. Diefenbach, I. Douglas-Hamilton, J. Fennessy, C. Fichtel, W. Fiedler, C. Fischer, I. Fischhoff, C. H. Fleming, A. T. Ford, S. A. Fritz, B. Gehr, J. R. Goheen, E. Gurarie, M. Hebblewhite, M. Heurich, A. J. M. Hewison, C. Hof, E. Hurme, L. A. Isbell, R. Janssen, F. Jeltsch, P. Kaczensky, A. Kane, P. M. Kappeler, M. Kauffman, R. Kays, D. Kimuyu, F. Koch, B. Kranstauber, S. Lapoint, J. Mattisson, E. P. Medici, U. Mellone, E. Merrill, T. A. Morrison, S. L. Díaz-Muñoz, A. Mysterud, D. Nandintsetseg, R. Nathan, A. Niamir, J. Odden, R. B. O. Hara, L. G. R. Oliveira-santos, K. A. Olson, B. D. Patterson, R. C. De Paula, L. Pedrotti, B. Reineking, and M. Rimmler. 2018. Moving in the Anthropocene: global reductions in terrestrial mammalian movements. Science 359:466–469.

Unsworth, J. W., D. F. Pac, G. C. White, and R. M. Bartmann. 2016. Mule deer survival in Colorado, Idaho, and Montana. The Journal of Wildlife Management. 63:315–326.

Verdolin, J. L. 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. Behavioral Ecology and Sociobiology 60:457–464.

Visscher, D. R., P. D. Walker, M. Flowers, C. Kemna, J. Pattison, and B. Kushnerick. 2023. Human impact on deer use is greater than predators and competitors in a multiuse recreation area. Animal Behaviour 197:61–69.

van de Kerk, M., R.T. Larsen, D. D. Olson, K. R. Hersey, and B. R. McMillan. 2021. Variation in movement patterns of mule deer: have we oversimplified migration?. Movement Ecology, 9:44.

White, G. C., and R. M. Bartmann. 1998. Effect of density reduction on overwinter survival of free-ranging mule deer fawns. The Journal of Wildlife Management 62:214–225.

Wilson, M. W., A. D. Ridlon, K. M. Gaynor, S. D. Gaines, A. C. Stier, and B. S. Halpern. 2020. Ecological impacts of human-induced animal behaviour change. Ecology Letters 23:1522–1536.

Wisdom, M. J., A. A. Ager, H. K. Preisler, N. J. Cimon, B. K. Johnson. 2004. Effects of off-road recreation on mule deer and elk. Pages 531-550 *in* Transactions of the 69th North American Wildlife and Natural Resources Conference. Pacific Northwest Research Station, Corvallis, Oregon, USA.

Wondra, J. 2022. Scope of the Chaffee county local housing crisis made crystal clear: 1105 more units needed by 2027. Ark Valley Voice. 1 August 2022.

Yovovich, V., M. Thomsen, and C. C. Wilmers. 2021. Pumas’ fear of humans precipitates changes in plant architecture. Ecosphere 12:e03309.

Figure Captions

Figure 1: Study area overlaid with the Methodist mountain trail network, telemetry locations for 9 deer from 2021-2022, randomized camera locations and associated grid cells, and land ownership. Inset map depicts location of study area within Colorado.

Figure 2: Coefficient estimates of covariates from the top ranked model of deer habitat selection for the pooled dataset analysis. Habitat covariates include land cover types: developed, forest, herbaceous and wetland as well as terrain ruggedness index (TRI) and cosine aspect. Distance to trail and rolling average of human activity are the human covariates. This model includes interactions between rolling average of human activity and forest land cover selection.  Asterisks (\*) represent estimates where confidence intervals did not overlap zero.

Figure 3: Coefficient estimates of covariates for the top-ranked model of deer habitat selection for both the day and night dataset analyses. Habitat covariates include landcover types: developed, forest, herbaceous and wetland as well as terrain ruggedness index (TRI) and cosine-transformed aspect. Distance to trail and human activity measured at the interval of locations (Rolling Average=RA) are the human covariates. These models include interactions between human activity metrics and movement characteristics.  Asterisks (\*) represent estimates where confidence intervals did not overlap zero. Estimates for the day step selection analysis are represented in orange and estimates for the night step selection analyses are represented in blue.

Figure 4: Update step length distributions for the day step selection analysis, modeled as a lognormal distribution, incorporating the interaction between rolling average of human activity and step length parameters. Rolling average of human activity is modeled at three levels with the corresponding change in probability density function represented by orange (low human activity), blue (medium human activity), and green (high human activity). As human activity increases the probability of smaller steps increases.

Figure 5: Update step length distributions for the night step selection analysis, modeled as a lognormal distribution, incorporating the interaction between rolling average of human activity and step length parameters. Rolling average of human activity is modeled at three levels with the corresponding change in probability density function represented by orange (low human activity), blue (medium human activity), and green (high human activity). As human activity increases the probability of smaller steps increases.

Figure 6: Coefficient estimates for the top ranked model of diel movement rate of deer. Covariates include human activity measured as the daily average, time of day including day and night, sex, and an interaction between human activity and time of day factors. Asterisks (\*) represent estimates where confidence intervals did not overlap zero.

Figure 7: The effect of time of day and human activity, measured at a daily temporal scale, on movement rate of mule deer, measured in meters per hour. Increasing human activity results in an increase in movement rate during dawn/dusk and night, while resulting in a decrease in movement during the day.

Figure 8: Density estimates for the study area based on varying estimates of the camera viewshed area parameter.

Figure 9: Density estimates for the study area based on varying estimates of the deer movement rate (speed) parameter.

Figure 10: Coefficient estimates from the full model average of top ranked models explaining deer density estimates at individual cameras

Tables

Table 1: Model Selection table for full mule deer (*Odocoileus hemionus*) dataset modeled with an integrated step selection function. Global 2 model represents a model with an interaction between forest land cover and rolling average of human activity, global represents a model with interaction between movement characteristics (log step length, log step length squared) and rolling average of human activity.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Model Selection** | | | | | | | |
| **Models** | **K** | **AICc** | **Δ AICc** | **Likelihood** | **AICc Wt** | **LL** | **Cum. Wt** |
| Global 2 | 15 | 29,598.62 | 0 | 1 | 0.97 | −14,784.30 | 0.97 |
| Global | 16 | 29,605.44 | 6.82 | 0.03 | 0.03 | −14,786.71 | 1 |
| Habitat | 12 | 29,612.01 | 13.39 | 0 | 0 | −14,794.00 | 1 |
| Human | 7 | 29,634.41 | 35.79 | 0 | 0 | −14,810.20 | 1 |
| Control | 4 | 29,643.26 | 44.64 | 0 | 0 | −14,817.63 | 1 |
|  |  |  |  |  |  |  |  |

Table 2: Model selection table for the diurnal subset of telemetry data for mule deer (*Odocoileus hemionus*) modeled with an integrated step selection function. Global 2 model represents a model with an interaction between forest land cover and rolling average of human activity, and the  global model contains an interaction between movement characteristics (log step length, log step length squared) and rolling average of human activity.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Model Selection- Day** | | | | | | | |
| **Models** | **K** | **AICc** | **Δ AICc** | **Likelihood** | **AICc Wt** | **LL** | **Cum. Wt** |
| global | 16 | 13,609.83 | 0 | 1 | 1 | −6,788.89 | 1 |
| global2 | 15 | 13,676.19 | 66.37 | 0 | 0 | −6,823.08 | 1 |
| habitat | 12 | 13,695.43 | 85.61 | 0 | 0 | −6,835.71 | 1 |
| human | 7 | 13,709.38 | 99.55 | 0 | 0 | −6,847.69 | 1 |
| control | 4 | 13,746.63 | 136.8 | 0 | 0 | −6,869.31 | 1 |

Table 3: Model selection table for the nocturnal subset of telemetry data for mule deer (*Odocoileus hemionus*) modeled with an integrated step selection function. Global 2 model represents a model with an interaction between forest land cover and rolling average of human activity, the global model contains an interaction between movement characteristics (log step length, log step length squared) and rolling average of human activity.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Models** | **K** | **AICc** | **Δ AICc** | **Likelihood** | **AICc Wt** | **LL** | **Cum. Wt** |
| global | 16 | 12,427.25 | 0 | 1 | 1 | −6,197.60 | 1 |
| human | 7 | 12,444.06 | 16.82 | 0 | 0 | −6,215.03 | 1 |
| global2 | 16 | 12,449.57 | 22.32 | 0 | 0 | −6,208.76 | 1 |
| habitat | 12 | 12,459.93 | 32.68 | 0 | 0 | −6,217.95 | 1 |
| control | 4 | 12,464.49 | 37.24 | 0 | 0 | −6,228.24 | 1 |

Table 4: Model selection results for the generalized linear models of mule deer (*Odocoileus hemionus*) density estimate at individual cameras. Model evaluation is based on Akaike’s Information Criterion for small sample sizes (AICc). The total number of parameters is represented by K. The scale at which the covariate was assessed is in parantheses such as in Shrub (100m) and Trail Density (Grid), which represents the scale of the camera grid.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Model** | **K** | **AICc** | **Δ AICc** | **Likelihood** | **AICc Wt** | **LL** | **Cum. Wt** |
| Trail Density (Grid) | 3 | 65 | 0 | 1 | 0.25 | −28.80 | 0.25 |
| Human Activity | 3 | 65.22 | 0.22 | 0.9 | 0.23 | −28.90 | 0.48 |
| Human Activity + Slope | 4 | 66.42 | 1.41 | 0.49 | 0.13 | −27.96 | 0.61 |
| Human Activity + Trail Density (Grid) | 4 | 66.76 | 1.76 | 0.42 | 0.11 | −28.13 | 0.71 |
| Shrub (100m) + Human Activity | 4 | 67.09 | 2.09 | 0.35 | 0.09 | −28.30 | 0.8 |
| Trail Density (Grid) + Slope | 4 | 67.76 | 2.75 | 0.25 | 0.06 | −28.63 | 0.87 |
| Trail Density (Grid) + Human Activity + Slope | 5 | 69.01 | 4 | 0.14 | 0.03 | −27.50 | 0.9 |
| Distance to Herbaceous | 3 | 69.17 | 4.17 | 0.12 | 0.03 | −30.88 | 0.93 |
| Slope (100m) | 3 | 69.21 | 4.2 | 0.12 | 0.03 | −30.90 | 0.96 |
| Trail Density (Grid) \* Human Activity | 5 | 70.21 | 5.21 | 0.07 | 0.02 | −28.11 | 0.98 |
| Trail Density (Grid) + Human Activity + Distance to Herbaceous | 5 | 70.23 | 5.23 | 0.07 | 0.02 | −28.12 | 1 |