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**Mule Deer Habitat Selection on Managed Winter Range in Response to Recreation**

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**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 and these changes can scale up to impact populations. Mule deer (*Odocoileus hemionus*) abundance has generally declined throughout their range and winter range condition has been implicated as a limiting factor resulting in significant habitat management. Here we present results of an integrated step selection analysis (iSSA) of the habitat selection of mule deer on winter range in response to environmental and human factors. The strongest models included a combination of human and environmental factors. Mule deer in our study area exhibited distinct patterns of habitat use and movement that varied with both time of day and the level of human recreation activity. Mule deer increasingly selected for forest land cover over shrub land cover as human presence increased. Importantly, shrub cover on our study area represented thinned pinyon-juniper forest managed, in part, for mule deer winter range. Deer showed different movement responses with increasing human presence depending on the time of day, with increased movement at night and reduced movement during the day. Changes in selection of favored foraging habitat and increased movement costs have the potential for ramifications at the population level as well as decreasing the effectiveness of tools available to managers.

**KEYWORDS** Colorado, habitat selection, human recreation, integrated step selection functions, mule deer, *Odocoileus hemionus,* winter range

Humans play many ecological 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 human 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 informing effective management, however these mechanisms, especially as they scale, 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 adopt proactive strategies to reduce risk across the landscape by shifting their spatiotemporal behavior (Lesmerises et al. 2017; Ladle et al. 2019; Suraci et al. 2019). This can include increasing nocturnal activity (Gaynor et al. 2018; Naidoo et al. 2020; Sévêque et al. 2020), altering habitat selection, or avoiding areas near recreational trails altogether (Muhly et al. 2011; Coppes et al. 2017; Ladle et al. 2019; Smith et al. 2018). These behavioral adjustments are often accompanied by changes in movement rates—either increases or decreases—depending on the species and the specific strategy employed (Tucker et al. 2018; Doherty et al. 2021).

Disruption of fitness-enhancing behaviors, shifts in spatiotemporal niche, and increased energetic costs associated with movement represent potential mechanisms by which individual-level responses to disturbance can scale up to influence population dynamics. However, 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 in the intermountain West 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). The effect of these efforts in Colorado increased 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). Human presence is also an important factor in delaying return times to camera sites, and was found to be more influential 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). While previous research has documented behavioral responses of mule deer to recreational activity, it remains unclear whether these subtle behavioral shifts translate into population-level effects. Understanding this connection is critical for informing effective management strategies for mule deer and potentially other species exhibiting similarly nuanced responses to human disturbance.

In this study we examine mule deer responses to recreation on managed 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 changing their temporal or spatial use of habitat 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**

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Our study area is located on Bureau of Land Management south of Salida, Colorado, USA (approximately 38° 30´ 8" N and 106° 0´ 41" W) and is centered on the Methodist Mountain trail network. Salida sits in the Arkansas River Valley and is an outdoor recreation hub for a variety of outdoor activities including mountain biking and hiking, and serves as winter range for migratory and resident mule deer populations. Elevation ranges 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 varies 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 comprised of several trails tailored to mountain biking and extending from the valley floor into higher elevation habitat managed by the US Forest Service. 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 within the study area has been implemented with multiple objectives in mind, including fuel reduction, enhancement of wildlife habitat, and watershed restoration. (Miller et al. 2019). This involves thinning of pinyon juniper forest on flat ground accessible to machinery. Importantly, this thinned habitat appears on land cover classification layers as “shrub” habitat as opposed to surrounding “forest” habitat (Figure 1). 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 across about 11km southwest to summer range outside the Arkansas river valley.

**METHODS**

**Field methods**

Ten total mule deer were captured. 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.

**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). This analysis was conducted on the full dataset as well as a reduced separate day and night datasets to identify differential responses depending on time of day. The inclusion of human activity as an interaction term with habitat and movement covariates prevented the inclusion of time of day as an additional interaction term (Table 1).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| 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, log step length and the squared log step length. Cosine-transformed turning angle 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 the 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).

**Covariates for analysis**

Two trailheads at either end of the study area were equipped with infrared trail counters from which human activity was estimated. On one trailhead a TRAFx trail counter (TRAFx Research Ltd., Canmore, Alberta, CA) was placed on the actual trail while at the other trailhead 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. We summed the number of users from each trailhead, recorded as number of people per hour, to obtain a rolling average of trail users from the current hour and the previous 3 hours to match our GPS fix interval of 4 hours. Distance to trail from each location was calculated as Euclidean distance from the nearest trail feature using the sf package in R and included as a covariate to test for avoidance of the trail network (Pebesma 2018).

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.

**RESULTS**

196 people a day on average over time period when collared deer were on winter range.

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**Pooled iSSF model**

The best fit model for the pooled dataset was the global model containing movement covariates, habitat covariates, human covariates and 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 (0.19, 0.04 — 0.35), meaning as human activity increased, selection for forest habitat as compared to shrub habitat increased. Herbaceous (0.44, 0.1 — 0.79) and wetland (0.71, 0.31 — 1.11) landcover types also have a strong positive effect on selection in relation to shrub habitat. There is a weak, positive effect of forest habitat (0.28, -0.02 — 0.59) on selection. Lastly there is a strong, negative effect of distance to trail (-0.25, -0.47 — -0.04) on selection implying selection for areas closer to trail.

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**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 (-0.64, -1.37 — 0.08) on selection, while we see a weak, positive effect for forest land cover (0.33, -0.03 — 0.68) 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 (0.86, 0.28 —1.45), 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 (-0.51, -0.64 — -0.37) and squared log step length x rolling average (-0.1, -0.17 — -0.03) 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.

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**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(0.63, 0.13 — 1.11), indicating deer selected for herbaceous land cover at night. There was also a significant interaction between human activity and log step length (1.5, 0.9 — 2.09) (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.

**DISCUSSION**

**Deer habitat selection and movement patterns**

Deer habitat selection and movement patterns in our study were best explained by a combination of anthropogenic influences and environmental habitat characteristics. Deer increased their use of forest habitat compared to shrub habitat in response to increasing human activity. The shrub habitat, as indicated by land cover, matched areas where management of pinyon-juniper forest has been implemented for fuel reduction and habitat management, resulting in thinned, open savannah-like habitat useful for mule deer forage (Miller et al. 2019). A loss of foraging opportunities could result from this shift in habitat preference, with 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 secure forest habitat is removed and productive foraging habitat is perceived to be riskier. Careful consideration of the objectives behind pinyon-juniper management is essential to ensure that wildlife conservation goals are balanced with other intended outcomes of the practice, such as wildfire risk reduction (Miller et al. 2019). Compromise may exist in the patch size and arrangement of treatments. Short et al. (1977) investigated deer use across various thinning treatments and found that small patch cuttings (≤0.5 km²) were more frequently utilized by deer. Their findings also highlighted the importance of treatment patch arrangement, noting that proximity to undisturbed woodland significantly influenced deer use. Further investigation into this question could help clarify the mixed findings regarding the effectiveness of pinyon-juniper habitat management on mule deer population health. Similar shifts in habitat use due to human recreational activity have also been documented in other wildlife species (Cristescu et al. 2013; Smith et al. 2019). This likely reflects a behavioral adaptation: during the day, when deer are bedded down in refuge, remaining still is the safest strategy unless they are directly threatened. At night, however, when they are foraging in more exposed areas, it is safer to move away from potential predators.

Mule deer showed 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 they moved more. This likely reflects a behavioral adaptation: during the day, when deer are bedded down in refuge, remaining still is the safest strategy unless they are directly threatened. At night, however, when they are foraging in more exposed areas, it is safer to move away from potential predators. Changes to activity patterns of mule deer, and specifically reduced 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).

Deer selected for areas near trails and thus experienced no indirect loss of habitat caused by human recreation. This is supported by trail camera research on mule deer 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 (Wisdom et al. 2004). Preference for areas near trails could also indicate deer are selecting for similar biophysical characteristics we seek in trails that were not considered in our modeling. 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). Alternatively, a lack of spatial avoidance may not be a reliable indicator for a lack, however, 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 utilized habitats where being farther from trail put them closer to human-associated land cover, such as developed areas, and actively managed and fallow agriculture fields. The trail network may be perceived as safer daytime refuge than more open habitat closer to highly developed human landscapes.

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 often categorized dichotomously into high- and low-use areas; however, this classification is relative to each study site, making it challenging to develop standardized guidelines for assessing recreational impacts or to compare results across different studies (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 long periods of time, 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.

However, off-trail recreation is an unaccounted for component of human 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).

Deer selected for potential foraging habitat, represented by wetland and herbaceous land cover. On our study area wetland and herbaceous land cover was found in the valley downslope of the forest and shrub-covered foothills. Forage in these land cover types create a strong enough draw to overcome proximity to human development dependent on time of day. Herbaceous and wetland habitat are an order of magnitude rarer in availability than shrub or forest habitat. Selection does not indicate where an animal is most frequently found, but rather reflects the relative preference for certain habitats when all other variables are held constant and all habitat types are equally available (Fieberg et al. 2021). Interpreted this way, deer appear selective about habitat use when far from trails, favoring safer areas and minimizing risk. When closer to developed habitats, they seem to balance the risk of foraging by utilizing these areas during periods of low human activity. Our separate day and night datasets further illustrate this behavior, showing how deer adjust their use of wetland and herbaceous habitats based on time of day, likely in response to both behavioral needs and patterns of human presence.

During the day, deer selected for wetland habitat, while at night they selected for herbaceous habitat. The variation in herbaceous habitat selection between day and night suggests that deer employ a spatiotemporal strategy to balance their needs for cover and foraging. During the day, they tend to prefer habitats that offer greater cover, while at night, they shift toward areas that provide better foraging opportunities.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).

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 and a reduction in flight responses to higher levels of recreation (Stankowich 2008, Robb et al. 2019). The population in this study demonstrates that deer who summer in comparatively natural habitats can still depend on increasingly urbanized winter ranges. More trail development is planned for our study area illustrating that the story of development for recreation is often one of escalating disturbance, with this shifting baseline requiring continuous adaptation. 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). Increasing human presence on winter ranges could contribute to a loss of migratory individuals either through consequences of behavioral avoidance or the desensitization of deer to human presence, both resulting in losses of migratory deer. 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). Loss of migratory movements can eliminate typical dual-range migrants or other variations in migration, decreasing diversity in migration behavior and limiting available strategies to adapt to a changing world (van de Kerk et al. 2021).

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). Measures aimed at reducing disturbance to mule deer can also offer ancillary benefits by protecting other species that are even more sensitive to human activity.

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). 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.

**MANAGEMENT IMPLICATIONS**

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**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) .

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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.

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| --- | --- | --- | --- | --- | --- | --- | --- |
| **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.

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| --- | --- | --- | --- | --- | --- | --- | --- |
| **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 |