**Methods GLMM movement rate regression**

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).

**Methods- Camera Stuff**

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 – 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).

**Movement rate regression**

The model including an interaction between daily human activity and diel period was the best fit model. Daily human activity had a strong, positive effect on movement rates, and deer movement rate was smaller at night compared to crepuscular times of day, while daytime movement did not differ significantly from crepuscular time periods (Figure 6). Male deer had higher movement rates and the effect of human activity interacting with time of day was significantly negative for both day and night in comparison to crepuscular times of day (Figure 6). Figure 7 shows the effect of this interaction, with deer increasing their movement rate most during crepuscular periods of the day in response to human activity and also showing increases in movement rate during the night in response to human activity. Meanwhile we see a decrease in deer movement in response to human activity during the day (Figure 7).

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A graph of a person's activity

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Overall deer density estimates on the study area dependent on camera viewshed estimates were 4.21 deer/km² for a viewshed area of 45m², 3.42 deer/km² for a viewshed area of 65m² and 2.87 deer/km² for a viewshed area of 80m² (Figure 8). As parameters estimates for camera viewshed area increased, density estimates for mule deer decreased.

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Overall deer density estimates dependent on movement rate estimates for mule deer were 13.91 deer/km² at a movement rate of 41 meters/hr, 4.61 deer/km² at a movement rate of 106 meters/hr and 1.80 deer/km² at a movement rate of 208 meters/hr (Figure 9). The movement rate of 208 meters/hr was estimated from an average movement rate of continuous time movement models fit to the movement data of 9 deer. As deer movement rate increased, estimates of deer density decreased.

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We attempted to account for uncertainty in movement rate using two estimates of movement rate from discrete movement data, including intervals between locations less than 2 hrs (41 meters/hr), less than 1 hr (106 meters/hr) and using a continuous time movement model robust to the resolution of location data (208 meters/hr) (Noonan et al. 2019). With density estimates decreasing with movement speed, we suspect, if anything, a positive bias in density (Loonam et al. 2021a, Santini et al. 2022).

We attempted to account for uncertainty surrounding camera viewshed area estimates by including density estimates at three different parameter values, finding a decrease in density estimates with an increase in camera viewshed area. Given our conservative estimate of camera viewshed area, we again suspect this may overestimate deer density, while other studies have similarly used a single value to represent viewshed area across all cameras (Moeller et al. 2018, Loonam et al. 2021, Ausband et al. 2022, McMurry et al. 2023). Considering our attempts to account for uncertainty in estimates in our area and movement rate parameters, previous findings indicating comparable estimates of TTE models to other estimates of density, and the violation of all these assumptions more likely leading to overestimation of density, we feel confident in our density estimates reflecting a low density of mule deer on our study area in comparison to other winter ranges.

Density of mule deer on our study area was estimated using time to event modeling resulting in estimates of 1.8-13 deer/km² depending on different estimates of camera viewshed area and movement rates. We focused our density estimates in pinyon-juniper habitat as we were most interested in the density of deer this predominant winter range habitat type could support and this is where recreation took place. Density estimates for other winter ranges in Colorado include estimates ranging from 4-14 deer/km² to 20-84 deer/km² across the Uncompahgre Plateau (Bergman et al. 2015). Earlier mule deer density estimates from the same range were <2 to >30 deer/km², with chosen study sites having densities that varied between 31-59 deer/km² regularly reaching 85 deer/km² (Bishop et al. 2009). Elsewhere in Colorado, mule deer density estimates on a winter range impacted by natural gas development were ~6-14 deer/km² (Northrup et al. 2021), while earlier estimates on the same range were ~40-80 deer/km² before natural and intended reductions brought densities down to ~20 deer/km² (White and Bartmann 1998). By comparison, our estimate of mule deer density is on the low end for reported densities in comparison with other winter ranges comprised of pinyon-juniper habitat, and in line with estimates of deer densities on winter range with high intensities of energy development (Northrup et al. 2021).

While our density estimate is low compared to values from other winter ranges, this is not necessarily a reflection of human disturbance. Low densities could simply reflect timing of surveys, our density estimate took place in late spring (April-May) immediately prior to deer migrating to summer range, with deer less constrained by snow during this time of year and therefore potentially less concentrated than if surveys had been conducted earlier in winter. Additionally, lower density could be an artifact of past conditions or events that reduced density, as well as a product of limitation on summer range, although as previously discussed mule deer in Colorado are thought to be limited by winter habitat (Bishop et al. 2009, Bergman et al. 2015, Northrup et al. 2021). Lower density could also be due to poor habitat quality regardless of human activity potentially limiting nutritional carrying capacity of the range (Northrup et al. 2021).

**Density dependent impacts**

Regardless of the cause, low densities raise questions about density dependence, which can modulate the impact of recreation (Tablado and Jenni 2017). For large-bodied, long-lived species like mule deer, whose life history is characterized by small litter sizes, multiple reproductive efforts, and high adult survival rates, density-dependence plays a critical role in population dynamics (Bowyer et al. 2014, Bergman et al. 2015). Increasing competition for resources at higher densities leads to worsening nutritional condition causing decreases in reproduction and survival metrics contributing to lower population growth rates (Bowyer et al. 2014, Monteith et al. 2014). With lower densities of mule deer, improved nutritional condition and reproductive rates of adult females, in addition to improved survival rates of juveniles could counteract some of the negative behavioral consequences of human recreation. While this has not been shown in ungulates, reduced densities of woodlarks in highly disturbed sites exhibited density dependent responses of larger chick masses, higher post-fledgling survival, and lower rates of starvation related nestling mortality compared with high bird density, less disturbed sites (Mallord et al. 2007). However, recreation is often associated with habitat degradation (Tablado and Jenni 2017), providing a possible mechanism for reductions in carrying capacity of disturbed landscapes to lower densities (Bergman et al. 2015). Additionally, human disturbance during calving season has been shown to impact reproductive rates of elk, indicating the timing of disturbance could cause a density-independent effect on wildlife, although elk density was not considered in these studies (Phillips and Aldredge 2000, Shively et al. 2005). Determining the impacts of recreation at the population level within the context of density dependence population dynamics will be important to understanding whether recreation simply impacts density, resulting in a smaller population with improved vital rates, or if recreation might additionally lower carrying capacity resulting in lower density populations with poor nutrition and vital rates. Measuring nutritional carrying capacity (Montieth et al. 2014) as a component in future study designs provides a pathway to answer these questions.

Density dependence has also been theorized to change habitat selection (Rosenzweig 1981, Avgar et al. 2020). While rarely investigated in wild populations of large mammals, changes in habitat selection have been documented, although with contrasting results (Merrill et al. 2020, Smith et al. 2023). The specific change in habitat selection is dictated by how resources are coupled in space, with habitat providing forage often attracting predators as well, creating a forage-risk tradeoff (Verdolin 2006). Under scenarios with low densities and decreased competition for food resources, mule deer may be able to meet foraging requirements while prioritizing safer habitat. Under these circumstances the selective force of avoiding predation is greater than that to acquire better food, while the per capita predation rate is also higher with less conspecifics around (Lehtonen and Jaatinen 2016, Visscher et al. 2016). Higher densities increase competition for lower quality forage in safer habitats and the consequences of a poor diet become more severe, changing the calculus and leading to an increased selection for forage. This relationship between density and habitat selection was documented with elk wintering in Yellowstone National Park (Smith et al. 2023). Other research into density dependent habitat selection and the tradeoff between forage and risk in elk found a higher selection for forage and safety at low densities. The speculation being that human activity was providing a refugia from wolf predation allowing elk to select safe habitat with quality forage (Merrill et al. 2020). Assumed low density on our study area could indicate deer are able to use safe habitat while meeting forage requirements akin to Smith et al. 2023 or deer could be the beneficiary of humanity as a refuge from natural predation while exploiting high quality forage, which has been described in previous studies (Berger 2007, Leighton et al. 2010, Lesmerises et al. 2017). However, this is still a new area of inquiry with uncertainty about how these relationships might translate across species, ecosystems, and different levels of human activity, but density dependent habitat selection should be considered when developing recommendations to mitigate impacts of recreation.

**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.

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**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.

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.

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).

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

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).

**Conclusions and future study**

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.

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.

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.

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).

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).

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).

**Rearrange this:**

**Conclusions and future study**

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). The population included in this study 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 either through consequences of behavioral avoidance or the desensitization of deer to human presence, both 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, decreasing diversity in migration behavior and limiting available strategies to adapt to a changing world (van de Kerk et al. 2021).

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 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 winter range habitat, increased movement costs, and loss of foraging opportunities may broaden impacts of human presence from individuals to populations of migratory deer increasingly constrained by human development on their winter range (Farnsworth et al. 2005).

**MANAGEMENT IMPLICATIONS**

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). 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 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).

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.