**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).