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Colorado

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Thesis

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Effects of outdoor recreation on ungulate behavior in the Gunnison Basin, Colorado

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Abstract:

Maintaining opportunities for outdoor recreation while balancing sustainable use of natural resources presents a challenge for natural resources managers in the face of rapidly increasing recreational use. Outdoor recreation provides health and well-being benefits to humans and is often perceived as having neutral ecological impacts on wildlife and the environment. Human recreation, however, disrupts many aspects of wildlife ecology by triggering trade-offs between avoidance of perceived risk and spending time in other fitness-enhancing activities such as foraging. In the presence of human recreation, ungulates could spend more time in vigilant behavior, which could lead to lowered fitness in the long term. We deployed wildlife cameras to explore how recreation volume, the type of recreation, and the distance from trails influenced the probability of vigilance in ungulates. Mule deer (*Odocoileus hemionus*) and Rocky Mountain elk (*Cervus canadensis*) vigilance was highly dependent on recreation volume, distance to the trail, and environmental variables. Ungulate species increased vigilance as recreational volume increased. Environmental factors potentially alleviated recreation impacts in certain circumstances however the level of recreation use facilitated higher levels of vigilance in ungulates. The use of wildlife cameras to collect human recreation and wildlife behavior data

should be further explored for use in wildlife studies. Additional study in compounding direct and indirect factors of recreation is needed to more fully understand recreational influences on ungulate vigilance.

Introduction

Natural resources managers face a challenging task of balancing opportunities for outdoor recreation and sustaining natural resources, especially as recreational use rapidly increases throughout the western United States. In Colorado, 92% of residents participate in outdoor recreation at least once a week, along with 84.7 million annual visitors who come to Colorado for its abundant recreation opportunities (SCORP 2019). According to the 2019 Statewide Comprehensive Outdoor Recreation Plan (SCORP), outdoor recreationists spent \$62.5 billion in 2017 in Colorado, representing an 81% increase from 2014 (CPW 2019). The increase in revenues generated by the outdoor recreation industry benefits Colorado's economy. Increased interest and pursuit of outdoor recreation since World War II has led United States government agencies to invest in more recreation facilities and shift natural resource management focus to recreation (Hendee 1969). The rapid increase in recreation demand stems from the growing human population, increased access to more remote areas, and an increase in urbanization and technologies that push people to look for opportunities to recreate further into previously untouched areas (Knetsch 1963). In addition to economic remunerations to communities, recreation provides significant health and well-being benefits to individuals and society (Marzano et al. 2012) and is generally assumed to have little negative impact on wildlife; however, a recent review showed that in 59% of studies, human recreation had a negative effect on wildlife (Larson et al. 2016, Taylor and Knight 2003). The ecological impacts of outdoor recreation on wildlife and the environment can be perceived as a threat to the integrity of those

ecosystems in which they occur (Marzano et al. 2012, O'Brien 2005). As the number of recreationists increases, so do the number of trails and infrastructure that fragment natural areas and thus reduce the functionality and connectivity of wildlife habitats (Miller et al. 1998).

The presence of humans can instill fear in wildlife, similar to the way a predator elicits fear, which may lead to a variety of non-consumptive effects, including behavioral changes in wildlife (Graynor et al. 2018, Hernandez et al. 2005). While predators affect prey by direct mortality of individuals, they also trigger antipredator responses such as vigilance, avoidance, and defensive actions (Waser et al. 2014). Human initiated disturbance creates behavioral trade-offs for wildlife between avoiding perceived risk or engaging in other fitness-enhancing activities such as foraging (Frid and Dill 2002). Recreation on multi-use trails can have pronounced impacts on wildlife individuals, populations, and communities by changing behaviors, reducing fitness, and altering interactions between wildlife and their habitat as well as between species (Ciuti et al. 2012). Whereas the presence of natural predators can cause stress due to the fear of predation, continual human presence can prompt chronic stress in ungulates that may not differentiate between human hunters and recreationists (Theuerkauf et al. 2008). Human activities can influence how animals assess the risk of predation and disturbances by recreation (Price et al. 2014). The presence of both predators and humans can disrupt normal activity patterns and can induce high levels of stress in wildlife, which lowers their ability to cope with environmental stressors (Sheriff et al. 2011). Wildlife may exhibit higher vigilance in the presence of human disturbances which may result in decreased foraging or other behaviors that ultimately reduces reproduction and/or survival (Ciuti et al. 2012, Knight et al. 1995).

The impact of disturbance on ungulates manifests in diverse ways ranging from direct mortality from hunting or vehicle collisions to indirect disturbances associated with recreational activities

(Dertien et al. 2021). Phillips and Alldredge (2000) observed a decline in Rocky Mountain elk (*Cervus canadensis nelsoni*) calf production as a response to increased levels of disturbance by backcountry hiking during the calving season. Disturbances during sensitive phenological stages, such as elk calving season, exacerbate the vulnerability of elk and potentially result in decreased reproductive success and fitness (Phillips et al. 2000, Shively et al. 2005). Results from multiple studies in the Starkey Experimental Forest suggest that elk show a variable and measurable behavioral response to disturbances from ATVs, mountain bikers, hikers, and horseback riders (Preisler et al. 2013, Wisdom et al. 2004). Elk distribution shifted away from motorized roadways seasonally, across many areas of the western United States (Rowland et al. 2000). Mule deer (*Odocoileus hemionus*), unlike elk, showed little measurable response to disturbance treatments within the Starkey experiments (Wisdom et al. 2004). While mule deer may not spatially avoid roads, they could experience high stress and be spending more time in vigilant behaviors, which can cause reduced foraging time and lead to lowered fitness in the long term (Bedjer et al. 2009, Taylor and Knight 2003).

Vigilance behavior refers to an animal's examination of its surroundings (Beauchamp 2015), and is an essential aspect of animal behavior in the context of three core principles: external danger (e.g. predation), environmental resources (e.g. access to food and safe resting habitat), and intraspecific communication (e.g. communication cues for reproduction and danger) (Dimond and Lazerus 1974). Mule deer show distinct vigilance responses depending on the nature of the threat. When confronted by a coyote, mule deer more likely altered their habitat use, bunched together, or directly attacked the predator (Lingle and Wilson 2001). In contrast, when a human approached, mule deer fled the area or bunched together to face the disturbance (Lingle and Wilson 2001). Vigilance in elk primarily takes the form of an alert state in which elk scan for

predators using a head-up posture to bring the sensory organs to a position that increases detection range (Proudman et al. 2020, Childress et al. 2003).

Colorado, USA, supports one of the largest elk herds in the world with approximately 280,000 animals, along with a mule deer population of approximately 430,000 animals (CPW 2020). Elk and mule deer hunting provides significant funding to Colorado Parks and Wildlife, the agency tasked with the conservation of wildlife species in the state. The Gunnison basin in southcentral Colorado supports approximately 15,000-20,000 elk and 15,000-25,000 mule deer (CPW 2020). Disturbances from human activities may be a factor in ungulate survival, reproduction, and overall behavior. Ungulates could be expending energetic reserves to stay alert in disturbed areas, which lowers their time foraging and preparing themselves for winter conditions (cold temperatures, deep snow, and limited food availability) in this high mountain basin.

More time spent in vigilant behavioral states can be detrimental to ungulate time management by reducing foraging activity that would otherwise provide fitness benefits for individuals (Proudman et al. 2020, Childress et al. 2003). Our study focused on examining effects of outdoor recreation on vigilance behavior in elk and mule deer during summer and fall in the Gunnison basin, Colorado. Using wildlife cameras in a paired sampling design (on-trail vs. off-trail), we studied the behavioral responses of ungulates to the volume of outdoor recreation, type of trail use (motorized vs. non-motorized), and distance from a trail. We tested multiple hypotheses regarding ungulate vigilance relative to recreation characteristics and environmental variables (Table 1).

Table 1. Elk and mule deer vigilance hypotheses for all combinations of recreational and environmental independent variables.

Hypothesis	
H₀	Vigilance is random with respect to recreation volume, distance to trail, and environmental covariates.
H₁	Vigilance is dependent on recreation volume at a given site.
H₂	Vigilance is dependent on the Euclidean distance to trail at a given site.
H₃	Vigilance is dependent on the environmental covariates at a given site.
H₄	Vigilance is dependent on the recreation volume and the Euclidean distance to trail at a given site.
H₅	Vigilance is dependent on recreation volume and environmental covariates at a given site.
H₆	Vigilance is dependent on recreation volume, Euclidean distance to trail, and environmental covariates at a given site.
H₇	Vigilance is dependent on recreation volume but is mediated by the Euclidean distance to trail at a given site.
H₈	Vigilance is dependent on recreation volume but is mediated by the environmental covariates at a given site.
H₉	Vigilance is dependent on the Euclidean distance to trail and the environmental covariates at a given site.

Methods

Study Area

This study occurred in the Upper Gunnison River basin in southwestern Colorado (Figure 1).

Study area boundaries were originally created using the extent of collared ungulate locations from an ongoing Colorado Parks and Wildlife study (2009 – 2021). Over 80% of the land within the study area was comprised of and managed by the United States Forest Service (USFS), National Park Service (NPS), and Bureau of Land Management (BLM).

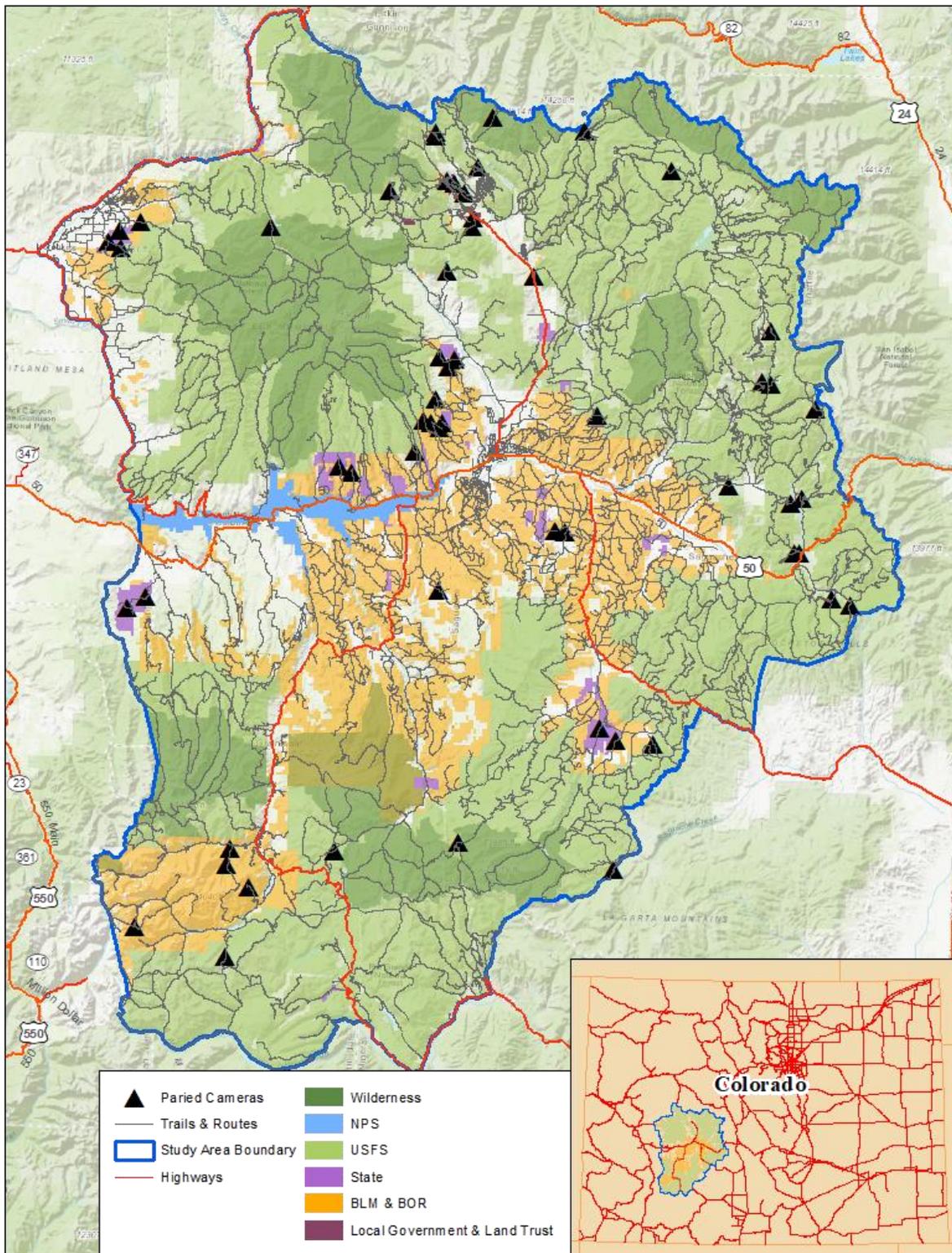


Figure 1. The Gunnison basin in southcentral Colorado showing land ownership, study area boundaries, major highways, trails, and the approximate locations of 59 paired cameras.

The Gunnison basin has a large network of recreational trails that fall predominantly on these public lands. Permission to place cameras could not be obtained from BLM or USFS without various stipulations (i.e., trailhead signage) that had the potential to draw negative attention to the cameras' locations and influence the collection of recreational data. Therefore, camera locations were restricted to segments of public land trails where permission could be obtained (i.e., local government land, Colorado state land, and privately-owned land), which together comprised 18% of the overall study area.

Habitat Selection and Site Selection

We defined a trail in this study as any designated route excluding paved roads. A set of potential trail segments to be sampled were chosen based on overlapping a comprehensive recreation trail layer intersecting any lands where permission was potentially attainable to place on-trail cameras (i.e., private lands, State of Colorado lands, local government lands) without signage stipulations. All trails within were assigned a route type strata to help identify the predominant type of recreational use (gravel-maintained roads, dirt vehicle/OHV trails, single-track motorized trails, single-track mechanized trails, single-track non-mechanized trails). Within each strata, an on-trail candidate population of potential camera locations was generated along the trail lines at 30 m spacing. Potential points were reviewed in randomized order to ultimately choose one on-trail camera location for any given potential trail segment (trail segments were defined as a continuous route between intersection nodes). Potential on-trail points appearing close (<500 m) to an adjacent trail were filtered out to minimize the effect of neighboring trails. If no alternative was available >500 m from an adjacent route, the matched off-trail sampling location (as described below) was limited in the Euclidean distance-to-trail strata options. Potential on-trail

points without sufficient vegetation available to camouflage the camera (i.e., short vegetation or rock fields) were also removed from consideration.

A candidate set of off-trail sample points, spaced on a 30 m grid, was generated within a 3,000 m radius of the on-trail camera location. Each candidate point was assigned an Euclidean distance-to-trail strata (in 100 m increments) radiating away from the selected on-trail segment. Euclidean distances of other nearby recreation routes were extracted to each point, to allow candidate off-trail points to be culled if the adjacent trail segment's Euclidean distance was less than that of the selected trail segment. Thus, not all Euclidean strata were available to be sampled at each on/off-trail pairing. For each pairing, the Euclidean strata intended to be sampled was randomly assigned. These Euclidean strata ensured that a relatively wide range of off-trail distances were sampled evenly (~5 sites per 100 m distance band).

Fourteen landscape variables known to potentially influence ungulate distribution were extracted to each on-trail point and each candidate off-trail point (within the 3000 m buffer) using electronic raster grids. These included: percent canopy cover (USFS LANDFIRE), presence of conifer vegetation (LANDFIRE), distance to forest edge (LANDFIRE), housing density (500 m moving focus search window), distance to nearest man-made structure (Gunnison county parcel data), distance to perennial stream, distance to intermittent stream, distance to nearest highway, elevation (10 m DEM - USGS), and various topographic metrics generated from the DEM including topographic position index, terrain ruggedness index (TRI), southern aspect difference, eastern aspect difference, and slope (Table A1). Each landscape variable received an equal weight to ensure all landscape variables were assessed for each point, except for canopy cover, which received double weight to account for ungulates' preferences towards certain high or low levels of canopy cover (Coe et al. 2018). For each location, the percent difference between the

variables of the candidate off-trail and the on-trail point was calculated. An integer ranking was then assigned based on this percent difference, with ties resolved with random ordering. The mean integer rankings were calculated across all 14 landscape variables to develop a final similarity index relative to the on-trail cameras' landscape attributes. This similarity index was generated for points within each Euclidean distance-to-trail strata intended to be sampled for a paired camera coupling. Starting at the most similarly ranked candidate point, the point's general vicinity was visually examined in GIS using high resolution imagery to verify that on-trail and off-trail cameras appeared in similar micro-habitats (due to potentially erroneous electronic landscape attribute grids). This visual scan also ensured that permission could be obtained to place the camera by checking landownership boundaries. Off-trail cameras were restricted to lands of cooperating private landowners, State of Colorado lands, and non-wilderness federal lands >100 m away from trails. If any potential issues arose in the visual scanning of micro-habitats and landowner permission, the off-trail point was culled and the point with the next highest similarity ranking was scanned. Each pairing of on-trail and off-trail cameras received a unique group ID.

On-trail and Paired Off-trail Cameras

We deployed 118 wildlife cameras starting on 24 June 2020 and retrieved all cameras by 4 December 2020. The study used two brands of cameras, Reconyx (model PC800) and multiple models of Browning (models consisted of BTC-5HDPX, BTC-5HDP, and BTC-6HDE). All cameras were programmed and labeled with the study purpose along with researcher's contact information. We programmed cameras to take a photo at every trigger, with a one second delay between triggers. We attempted to keep programming similar across brands and models however there were some slight differences due to discrepancies in available programming settings.

Each camera within a paired group, on-trail and paired off-trail, were deployed on the same day to ensure both cameras were in the field for the same time interval. Cameras were temporarily attached to trees using straps or onto customized rebar mounting posts when suitable trees were not present (Figure 2). The predominant direction that the cameras faced had a mean aspect of 135° in reference to a northeast aspect (Table A1). The observed range of all the environmental covariates and covariate definitions can be found in Table A1. Off-trail cameras were deployed as close to the generated sampling point as possible and placed randomly with respect to ungulate movement and signs (i.e., trails, scat, beds, clearings).



Figure 2. Tree set up of a Reconyx on-trail camera (left) and a sagebrush post set up of a Browning on-trail camera (right).

Cameras were checked mid-study (late August – September) to ensure the camera was still functioning and to conduct general maintenance. We originally deployed 59 on-trail cameras with 59 paired off-trail cameras. The final data encompassed photos from 57 on-trail cameras, which was the total number not stolen after the study period ended, and 60 off-trail cameras, that included one new off-trail location to accommodate a site relocation after a theft. SD cards were replaced at each maintenance visit and batteries were replaced if the camera had collected over 20,000 photos. Any camera that was tampered with was repaired or moved slightly to a new

location in the same general area to avoid further conflict. The paired sites of stolen cameras remained in the field to collect data until the end of the study. We imported images from the retrieved SD cards into a customized database.

Database Set Up and Classification

We used the Colorado Parks and Wildlife Photo Warehouse database to classify wildlife camera photos (Ivan and Newkirk 2016). Site locations, visit dates, and a “species” list for expected camera triggering sources were customized for our study. Photos were classified by the type of recreation and the number of individuals. A “new party” designation for human recreators ensured that consecutive photos of unique recreators were only counted once (see process description below).

Each unique recreator was classified as one of the following: on-foot non-mechanized (hikers and runners), mechanized (mountain bikes), on and off leash dogs, quad bikes (ATVs), side-by sides (UTV), motorcycles, and motorized vehicles. For side-by sides and motorized vehicles, the number of occupants were not classified, and each vehicle was counted as a single recreator. Environmental factors such as vegetation, atmosphere (i.e., clouds or sun glare), dust, and false trigger (i.e., camera malfunction triggers) were also included in the “species” list as possible classification options to aid with filtering photo records. Animal species included any species that were encountered within the study area. Two observers scanned photos individually to identify what triggered the camera and thus populate the “species” list. To check for observer consistency, a sample of photos were classified by both observers to ensure classifications were consistent. Photos of recreators were deleted after all classification data were collected to protect recreator privacy.

Photo classification occurred in two phases. In the first round we assessed every photo captured by the cameras and identified the three categories of camera photos, including recreation (employing the new party designation process), animal species, and environmental triggers. For each photo that included recreators or animals, we also quantified the number of individuals in the photo. Once all the photos were classified, elk and mule deer were queried from the database and separated into respective species sets. In round two, we classified behavior using the “in field” observation methods pioneered by Lingle and Wilson (2001) and Childress and Lung (2003). Lingle and Wilson (2001) defined alert behavior in mule deer as orienting towards the disturbance and displaying alert postures such as head erect, erect neck, and ears angled upward facing the source of disturbance. Other anti-predator behaviors included tail flagging, escape gaits, or simply moving away into a different area (Lingle and Wilson 2001). Childress and Lung (2003) observed elk in multiple behavioral states including: feeding, scanning, travelling, and resting. Feeding was defined as standing or walking slowly with the head below shoulder level, whereas scanning involved standing with the head at or above shoulder level (Childress and Lung 2003). Traveling was defined broadly as walking, trotting, or running with the head below the level of the shoulder (Childress and Lung 2003). Resting was any behavior while lying on the ground (Childress and Lung 2003). Observable ungulate characteristics for this study were created by combining the comparable characteristics from the two template studies into seven larger behavior categories used for both elk and mule deer (Table 2). For each photo, each individual ungulate in a photo was classified into a behavior category along with the number of individuals displaying that behavior. Given cameras were programmed to collect photos every second an ungulate group triggered the camera, each photo was recognized as a one-second instantaneous sample of the ungulate group’s behavioral time budget, while occupying the

camera’s field-of-view. While the behavior was classified for each individual in a given photo frame, no attempt was made to track unique individual identities across a series of consecutive photo frames, nor was it possible to in most cases given the lack of unique markings or body features.

Table 2. Observable animal characteristics and the corresponding behavior category within the database used to quantify elk and mule deer behaviors relative to human recreation in the Gunnison basin, Colorado in 2020.

Observable Characteristics	Behavior Classification
Head up above shoulder line/ears up and forward/fixed gaze	Alert
Head up above shoulder line/ears up different directions/head scanning	
Head up above shoulder line	
Head high/tail high/running	Fleeing
Head high/running	
Running short distance in frame	
Running out of frame	
Head level with shoulder line/ears level/walking	Walking
Head level with shoulder line/ears forward/tail up/walking	
Head down below shoulder line/standing/eating	Foraging
Head down below shoulder line/walking	
Laying down/head up (ruminating)	Resting
Laying down/head down (sleeping)	
Interaction between two or more individuals (i.e., young nursing, kicking, sparring between males)	Interacting
Sniffing/biting/nudging/rubbing on camera directly	Camera Interaction

Outdoor Recreation and Behavior Processing

A chronological succession of photos represented a single individual or group of the same party passing the camera. Input files from the master database were imported into program 'R', where the new party designation was used to condense recreation data from multiple photos for one recreation user passing in front of the camera into one non-inflated count of the individual or party that triggered the camera. We used the new party designation to differentiate unique individuals or groups (e.g. parties).

At the daily and study period temporal scales, we summed counts (volume) of recreation traffic occurrences (by motorized and non-motorized) for each calendar day, for each camera. Further, we classified ungulate behavior into vigilant and normal (non-vigilant behavior) categories.

Behavior was represented as counts of behavioral displays for each individual in the captured photos and then summarized into the daily and study period time scales. We also grouped observations by active (open) deer or elk hunting seasons, holidays, and a binary variable for pre- or post- Labor Day. Daily scale data were summarized into the study period scale values (R package: 'dplyr'). This collapsed all daily level data into a single record for each site, and thus had the same fields attributing vigilance behavior, human recreation traffic volume, and site level landscape variables. The daily and study period scales were separated by species resulting in a total of four ungulate behavior datasets (elk daily data, elk study period data, mule deer daily data, and mule deer study period data).

Ungulate Behavior Modelling

We analyzed ungulate behavior in relation to recreation and habitat variables at the daily and study period time scales for deer and elk using a binomial response variable under a logistic regression framework. We used generalized linear mixed effects models to test nine hypotheses

(Table 1) examining ungulate behavior as a function of recreation volume, motorized and non-motorized recreation volume, the distance the camera site was to the recreation trail, and the environmental habitat variables (Table A1). Recreation and habitat variables were included in the global model to assess the most parsimonious variables to be used in smaller candidate models for each hypothesis. Various model combinations of variables were tested to ensure every variable was examined for influence on vigilance behavior for both species at the daily and study period scale. A random intercept and/or random slope term were included in every model output. The random intercept was designated as the Location Name of the site, specific to on- and off-trail sites, and the random slope grouping term (if present) was Group ID which identified paired on- and off-trail site. At the daily period scale, the Location Name was assigned as the random grouping term to account for serially autocorrelated measures derived from consecutive daily records. At the study period scale, only GroupID could be assigned as the grouping term, as count information was collapsed across days. The random slope term varied depended on variables within the model and was always designated with a continuous variable. The model.select function (AICcmodavg package) was used to generate AIC tables. Delta AICc and AICc weights were used to identify the most parsimonious model with respect to the influence of recreation volume, distance to trail, recreation type, and environmental variables on vigilance behavior.

Results

Of the 118 wildlife cameras deployed at unique sites, 117 provided useable photo data. We collected 582,063 photos in total from all of the cameras during the field season. A total of 134,008 trail users of all types (73,733 motorized and 60,275 non-motorized) were observed on the sampled trails. We obtained 54,481 records of ungulate behavior, where each record accounts

for one individual ungulate where behavior was classified in a photo, across all sites and throughout the study period.

Over 75% of mule deer and elk behaviors were non-vigilant, normal behaviors (walking, foraging, interacting, and resting), whereas less than 25% of the time ungulates showed vigilant behaviors (fleeing and alert) (Table 3). Based on relative proportions, vigilance behavior was lowest at distances further away from trails and higher at sites where the distance decreased to the trail (Table 4). Ungulate vigilance and recreation use occurrences were higher within the 0-25% canopy cover habitats (Table 5).

Table 3. Percent of displayed behaviors, combined percent of vigilant behavior (fleeing, alert), percent of normal behavior (foraging, walking, resting, interacting), and total count of behaviors documented by trail cameras for elk and mule deer at the study period time scale across all camera sampling sites.

Behavior Category	Observed Behavior	Elk	Mule Deer
Normal	Walking	34.2%	44.6%
	Foraging	42.8%	29.3%
	Resting	1.8%	1.8%
	Interaction among individuals	1.0%	0.2%
Sub-total normal behavior		79.8% (n=18,722)	75.9% (n=23,543)
Vigilant	Fleeing	2.5%	2.5%
	Alert	16.1%	20.3%
Sub-total vigilant behavior		18.6% (n=4,364)	22.8% (n=7,072)
	Camera Interaction	1.00	1.2%
	Unknown Behavior	0.7%	0.1%
Total		100%	100%
Sample size (n)	Total behavior occurrences	23,462	31,019

Table 4. Photo sample size of elk vigilance, mule deer vigilance, and recreation events relation to the distance a camera was from a recreational trail. The number of sites within each distance range is also reported.

Distance to trail	Elk vigilance	Mule deer vigilance	# of on-trail sites	# of off-trail sites
0-20 m	1,397	2,645	57	1
0-500 m	921	3,183	0	29
500-1000 m	1,793	877	0	21
Over 1000 m	261	368	0	9

Table 5. Photo sample size of elk vigilance, mule deer vigilance, and recreation events in relation to canopy cover. The number of sites within each canopy cover category is also reported. None of the study sites had over 75% canopy cover.

Canopy cover	Elk vigilance (n)	Mule deer vigilance (n)	# of recreation events	# of on-trail sites	# of off-trail sites
0-25%	2,195	2,865	52,398	26	25
25-50%	1,322	1,635	41,944	19	20
50-75%	847	2,575	39,666	12	15

Outdoor Recreation

We documented the presence of trail use by human recreators at every on-trail site. Non-motorized recreation comprised 45.2%, whereas motorized recreation accounted for 54.8% of outdoor recreation volume over the duration of the study and across all study sites. Recreational trail volume was significantly higher on weekends than on weekdays throughout the study period ($F = 133.1, p = <2e-16$). Recreation occurrences gradually decreased from the peak around calendar day 200 (in mid-July) through the fall (Figure 4).

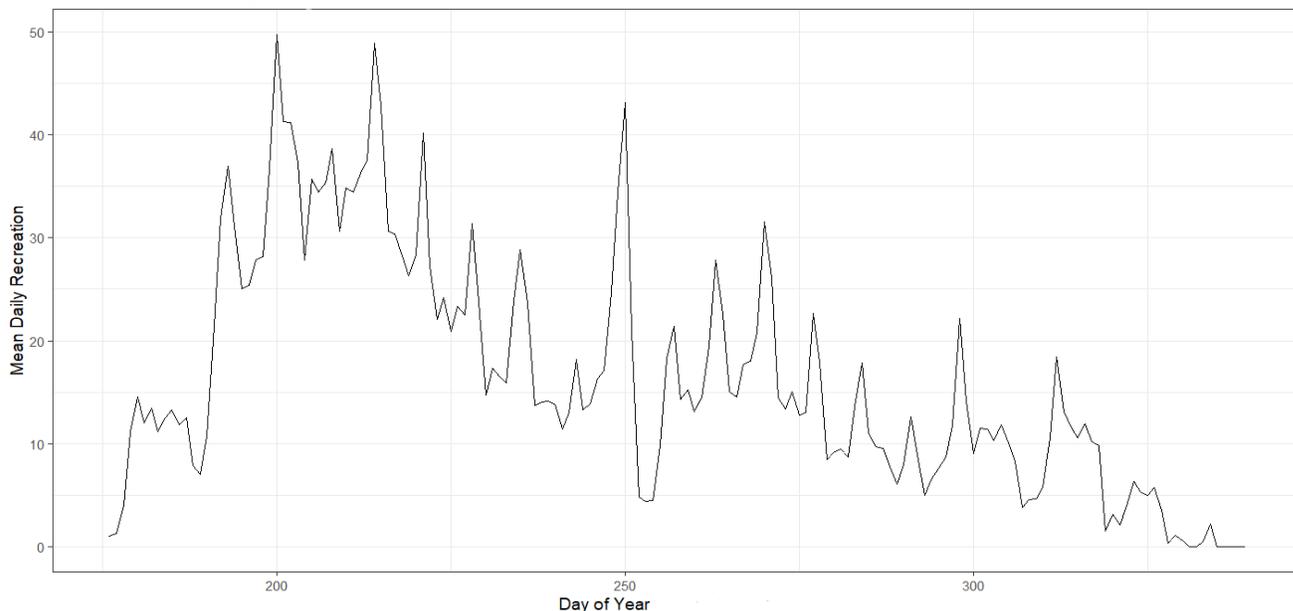


Figure 4. Mean of all recreation use types at a daily scale across the study area and throughout the study duration for on-trail camera triggers only. Labor Day is Day 251. Note the peaks of high weekend recreation volume use across the study period.

We classified 21,940 photos of elk behavior and 19,599 photos of mule deer behavior near motorized trails, of which 4,211 elk photos and 4,484 mule deer photos were classified as vigilant behavior. Of the 1,146 photos of elk behavior and 11,016 photos of mule deer behavior near non-motorized trails, 143 elk photos and 2,588 mule deer photos were classified as vigilant behavior (Table 6). Elk and mule deer had higher behavior occurrences near motorized trails than non-motorized trails, likely a result from larger proportions of cameras being placed on motorized trails

Table 6. Photo sample size in relation to motorized or non-motorized trail designation.

	Elk vigilant (n)	Elk normal (n)	Mule deer vigilant (n)	Mule deer normal (n)
Motorized trails	4,211	17,729	4,484	15,115
Non-motorized trails	153	993	2,588	8,428
Total occurrences	4,364	18,722	7,072	23,543

Elk

We obtained 10,220 photos of elk at 67 of the 118 camera deployment sites. At the daily scale we obtained 370 records of elk behavior where each record accounts for one day of data combined from all the camera sites.

The top model that explained elk vigilance at the daily time scale supported hypothesis H₇ (Table 1) in which recreation volume influenced elk behavior but was mediated by distance to trail. This model held 100% of the AICc weight (Table 7). In this top model, recreation volume was best described by separating non-motorized volumes ($\beta = 3.98$) which interacted with distance to trail ($\beta = -1.06$), and motorized recreation volume ($\beta = -0.96$). Summary of model structure and variables can be found in the appendices (Table A2). Volume of non-motorized recreation was associated with increased elk vigilance at a mean distance from trail of 573 m or greater (Figure 5). As daily recreation numbers increased above 20 daily non-motorized recreators at sites over 573 m away from the trail, the model predicted elk would display vigilance behavior 100% of the time. Vigilance behavior in elk remained steady as the daily recreation volume increased for camera location sites that were under the mean of 573 m from the trail (Figure 5).

Table 7. Top models associated with each hypothesis test for elk at the daily time scale. Hypotheses are described in Table 1.

	Log Likelihood	K	Delta AIC	AICc Weight
H₇	-1481.86	5	0.000	1.00
H₁	-1582.83	5	197.7	1.13E-43
H₄	-1582.33	6	198.8	6.56E-44
H₈	-1659.40	7	355.0	7.87E-78
H₅	-1759.21	7	554.7	3.52E-121
H₆	-1758.72	8	555.8	2.01E-121
H₉	-1758.95	8	556.2	1.59E-121
H₃	-1888.64	4	807.3	4.89E-176
H₀	-1916.17	1	856.2	1.16E-186
H₂	-1915.68	2	857.3	6.91E-187

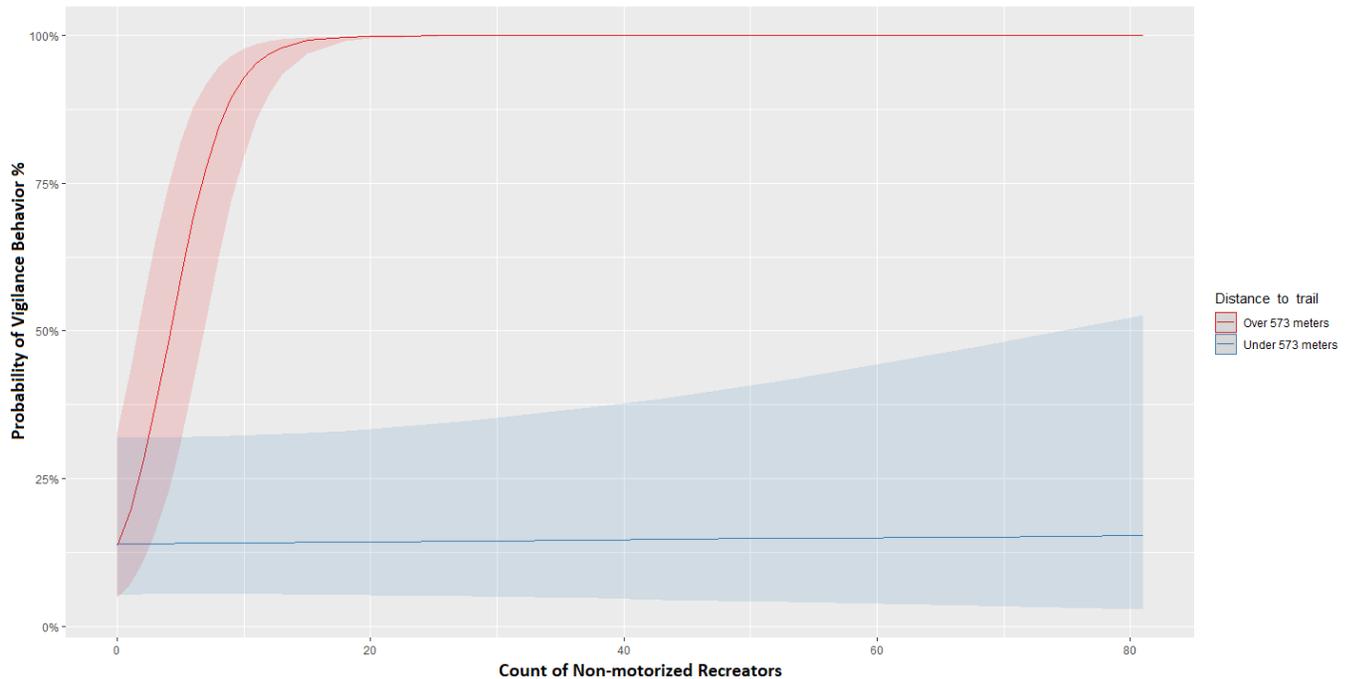


Figure 5. Probability of elk vigilance behavior out of the total sampled individuals (Y-axis) in relation to the daily volume of non-motorized recreators (X-axis) depending on whether the camera location was over or under the mean distance of 573 m from the trail, during summer and fall 2020 in the Gunnison Basin, Colorado.

At the study period time scale for elk, we recorded elk photos at 68 of the 118 camera sites. Each record represented the proportion of vigilance across the study period at a given site. The top model that explained elk vigilance at the study period time scale supported hypothesis H₆, held 100% of the AICc weight, and included motorized recreation volume ($\beta=0.46$) interacting with distance to trail ($\beta=-0.22$, interaction $\beta=-1.04$) and environmental variables (Table 8). Variables in the top model included aspect ($\beta=0.42$), TRI ($\beta=0.22$), distance to perennial stream ($\beta=0.31$), housing density within 500 m ($\beta=-0.06$), and slope ($\beta=-0.10$) (Table A3). Elk vigilance increased as motorized recreation increased for sites that were under 600 m away from the trail. Alternatively, for sites further than 600 m from the trail elk vigilance decreased (Figure 6).

Table 8. Top models associated with each hypothesis explaining time spent by elk in vigilant behaviors at the study period time scale. Hypotheses are described in Table 1.

	Log Likelihood	K	Delta AIC	AICc Weight
H₆	-281.39	9	0.000	1.00
H₉	-308.51	7	0.532	4.55E-10
H₈	-304.64	10	0.747	3.49E-10
H₅	-310.70	8	7.035	1.35E-11
H₃	-313.32	6	7.041	1.35E-11
H₂	-332.23	2	35.36	9.54E-18
H₇	-330.01	4	35.51	8.85E-18
H₄	-331.79	3	36.73	4.81E-18
H₀	-358.32	1	85.35	1.33E-28
H₁	-357.35	2	85.61	1.17E-28

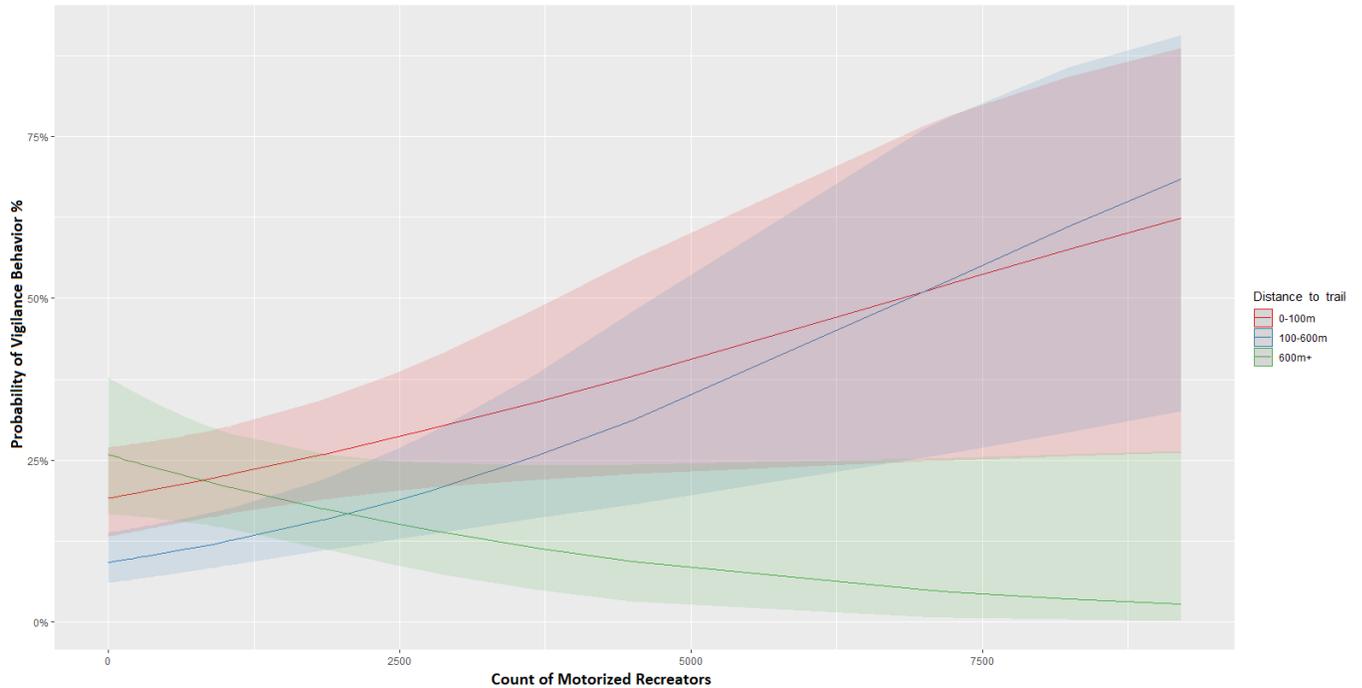


Figure 6. Probability of elk vigilance (Y-axis) behavior in relation to motorized recreation and the Euclidean distance to trail (X-axis) at the study period scale in the Gunnison Basin, Colorado in 2020.

Mule Deer

We obtained 22,436 photos of mule deer at 108 of the 118 camera deployment sites. At the daily scale, we obtained 1,721 records of mule deer behavior where each record accounts for one day of data combined from all camera sites.

The top model for deer at the daily time scale supported hypothesis H₈ that linked vigilance to non-motorized recreation volume (93% AICc weight) (Table 9). The top model also contained non-motorized recreation interacting with TRI ($\beta = -0.27908$) and hunting season ($\beta = -0.19548$) (Table A4), which resulted in a mixed vigilance response by mule deer depending on lower (increased vigilance) or higher terrain ruggedness (decreased vigilance) (Figure 7). Deer vigilance was relatively flat when assessed with the variable containing all recreation types (motorized and non-motorized) combined.

Table 9. Top models associated with each hypothesis test to explain time spent by mule deer in vigilant behaviors at the daily time scale. Hypotheses are described in Table 1.

	Log Likelihood	K	Delta AIC	AICc Weight
H₈	-4208.13	2	0.000	0.9314
H₅	-4213.13	3	5.949	0.0475
H₆	-4212.94	5	7.582	0.0210
H₁	-4233.40	4	42.46	5.60e-10
H₄	-4233.18	5	44.02	2.56e-10
H₇	-4231.42	4	44.55	1.97e10
H₉	-4234.00	7	47.69	4.10e-11
H₃	-4250.38	7	74.40	6.50e-17
H₀	-4265.93	1	101.48	8.54e-23
H₂	-4272.35	2	120.35	6.82e-27

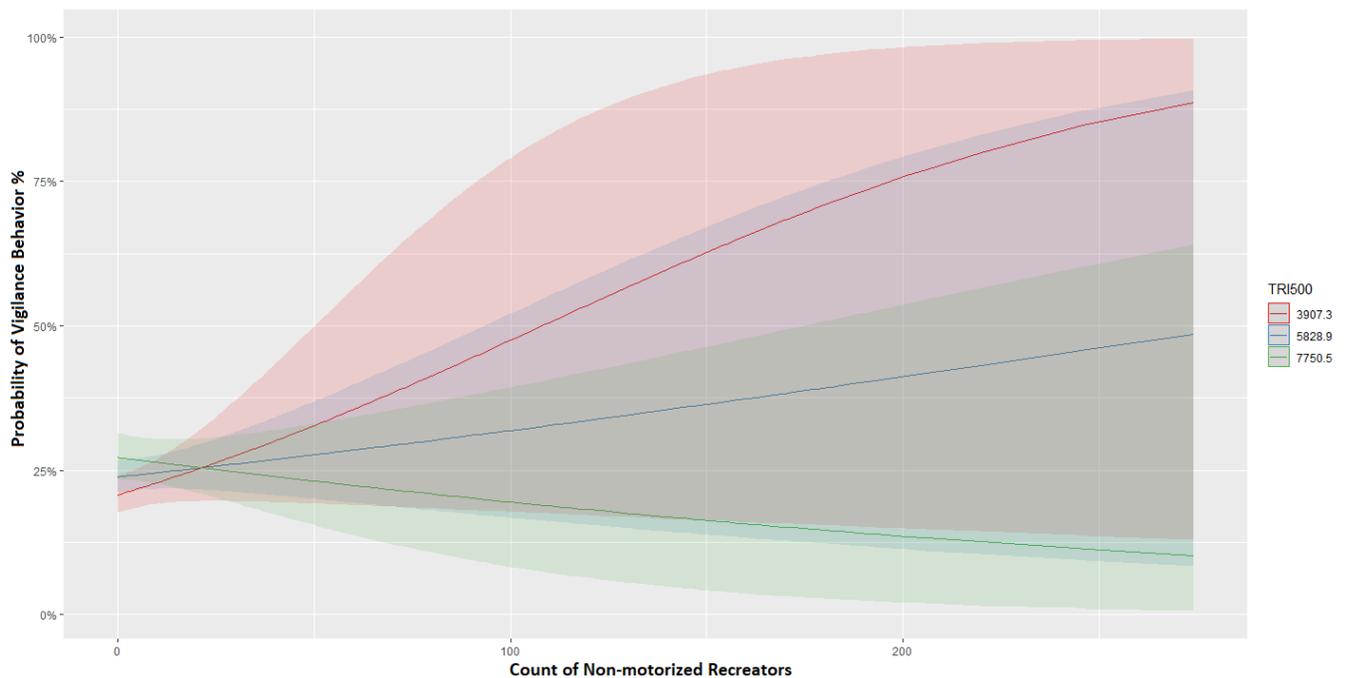


Figure 7. Probability of mule deer vigilance (Y-axis) behavior in relation to the daily volume of non-motorized recreation (X-axis) depending on the terrain ruggedness (flattest terrain, moderate terrain, and most rugged terrain) of a site at the daily time scale in the Gunnison Basin, Colorado in 2020.

At the study period time scale for mule deer, we recorded photos at 109 of the 118 sites. Each record represented the proportion of vigilance across the study period at a given site. The top model for mule deer vigilance at the study period time scale also supported hypothesis H₈ with deer vigilance influenced by recreation volume interacting with environmental variables. The hypothesis accounted for 100% of AICc weight (Table 10). In the top model, deer vigilance was related to motorized recreation volume ($\beta = 0.13$), distance to forest edge ($\beta = 0.06$), aspect ($\beta = -0.02$), and terrain ruggedness index interacting with non-motorized recreation volume ($\beta = -0.3373$) (Table A5). Increased mule deer vigilance showed an association with increased motorized recreation volume at the study period scale depending on the level of terrain ruggedness (Figure 8), whereas increased non-motorized recreation volume was associated with a general decrease in mule deer vigilance.

Table 10. Top models associated with each hypothesis explaining time spent by mule deer in vigilant behaviors at the study period time scale. Hypotheses are described in Table 1.

	Log Likelihood	K	Delta AIC	AICc Weight
H₈	-512.06	7	0.00	1.00
H₆	-548.19	5	67.62	2.07e-15
H₉	-549.50	4	68.02	1.69e-15
H₇	-555.89	4	80.79	2.85e-18
H₃	-561.70	4	92.41	8.56e-21
H₂	-563.88	2	92.42	8.52e-21
H₅	-560.76	5	92.76	7.17e-21
H₄	-563.33	3	93.48	5.02e-21
H₀	-577.76	1	118.07	2.29e-26
H₁	-577.57	2	119.79	9.71e-27

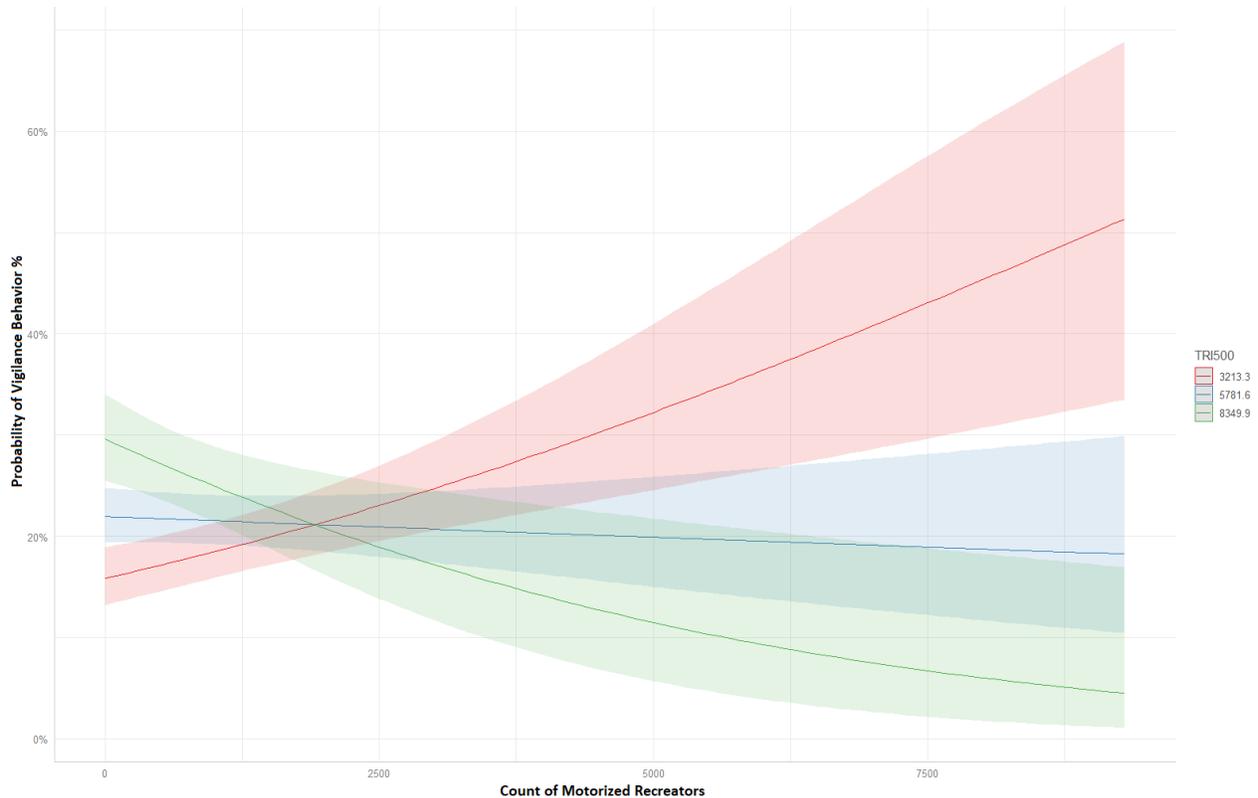


Figure 8. Probability of mule deer vigilance behavior (Y-axis) in relation to the volume of motorized recreation (X-axis) depending on the camera site location’s terrain ruggedness index (TRI) within 500 m of the site, at the study period time scale in the Gunnison Basin, Colorado in 2020.

Discussion

The presence of trails and humans within sensitive wildlife habitats can cause ungulates high levels of stress that results in long periods of displayed vigilance behavior (Sheriff et al. 2011). Higher levels of stress can also lead to lower survival and reproductive rates (Ciuti et al. 2012, Phillips et al. 2000, Shively et al. 2005, Knight et al. 1995). Ungulate vigilance in our study depended on multiple factors including: species, time scale (e.g., daily vs. study period), camera site locations, volume of recreation, type of recreation (e.g., motorized or non-motorized), distance to trail, and numerous environmental covariates. Our data suggests that ungulate vigilance responses to human trail use is complex, context dependent, and highly dependent on multiple factors.

At the daily time scale, elk showed an increased level of vigilance behavior with an increase in non-motorized recreation volume depending on if the site location was over or under the mean distance to trail of 573 m. At closer distances elk vigilance stayed consistent as non-motorized recreation increased, alternatively, at further distances vigilance in elk increased. Vigilance in elk at the daily time period was counter intuitive with respect to the interaction of Euclidean distance and traffic volume. However, habituation by elk at close distances to trails could help explain these results. The presence of elk nearby human disturbance could suggest habituation to human presence and thus an association with lower vigilance behavior (White et al. 1998). Conversely, elk further from trails could be less habituated and more sensitive to human disturbance and experience higher levels of stress causing an association with higher vigilance regardless of being further from the recreation trail. At the study period time scale, lower elk vigilance was associated with an increase in distance to trail and higher vigilance was associated with a decrease in distance to trail. While elk may be conversely affected by recreation at the two-time scales in our study, at the longer temporal scale, distance from trail played an important role in decreased levels of vigilance behavior. Evidence suggests that throughout the Western United States elk demonstrate avoidance of travel routes including roads and trails (Rowland et al. 2000). This shift away from trails could represent a behavioral response by elk to an increased amount of recreation volume on trails (Rowland et al. 2000). Within our study, elk occurrences were limited compared to mule deer and the small sample size could contribute to the non-intuitive variation observed in increased vigilance behavior at higher recreation volumes and at locations relatively further from trails. Habituation by elk closer to trails could influence the occurrences of vigilance behavior within our study, however further study into habituation would be needed to determine the full effects in addition to the site's environmental characteristics.

Vigilance in mule deer varied suggesting vigilance behavior was highly dependent on location specific site characteristics. At the daily and study period scales mule deer vigilance increased with the increase in recreation volume (motorized or non-motorized volume depending on temporal scale) at sites with lower terrain ruggedness (i.e., flatter), while mule deer showed decreased vigilance with increases in recreation volume at sites with relatively more rugged terrain. Thus, in our study, ruggedness of terrain appears to be a mediator of deer's behavioral response to non-motorized recreation. Higher levels of mule deer vigilance were associated with lower levels of terrain ruggedness, and therefore, deer potentially benefit if they occupy more secluded and rugged terrain. At the study period temporal scale, results reflected the daily temporal scale with increased vigilance behavior by mule deer being associated with an increase in motorized recreation use but was mediated by terrain ruggedness. The highly variable behavior probabilities across our analysis for mule deer at the daily and study period scales could be an indicator of their ability to adjust to fluctuations in human use and presence so long as there is favorable habitat (Lingle and Wilson 2001). Northrup et al. (2021) suggest mule deer may adjust to higher densities of human influence provided there was sufficient vegetation and topographic cover within the area. In our study, increased terrain ruggedness was associated with decreased mule deer vigilance at each time scale and provides support that topographic cover influences mule deer behavior. Mule deer behavior observed in our study suggests a need for further examination into the direct and indirect influence of recreation and habitat characteristics to better understand impacts on vigilance behavior (Erb et al. 2012).

At the daily time scale, vigilance behavior was strongly associated with increased recreational use, particularly non-motorized recreational use for both elk and mule deer. Alternatively, at the study period time scale, increased vigilance was associated with increased motorized recreation

volume. Recreation volume influenced increased levels of vigilance in both species, however, variables such as distance to trail and terrain ruggedness seem to alleviate some of the negative influence at each temporal scale. These results are important from the standpoint of designing trail networks for the future. Lower elk vigilance levels can be maintained when further distance from trails are available. This is important for trail management strategies in terms of trail realignments and restricting new trail development from occurring in large intact blocks of habitat. Mule deer analysis determined that the ruggedness of the terrain mediates the influence of increased recreation volume. This can be important to trail network design for the future to ensure mule deer and elk have ample distance from trails and within a variety of terrain ruggedness landscapes to allow wildlife to reduce their levels of stress and vigilance behavior.

The Gunnison basin experienced an extreme snow event (25-30 cm accumulation) just after Labor Day 2020 (day 251 of the year) and the weather event likely influenced levels of recreational use on the days leading up to and after the holiday weekend. Our study used Labor Day as a marker for recreational use change from predominantly summer use to hunting based recreational use. While the marker was arbitrary it helped to signify a change of seasons for both humans and ungulates on the landscape. Elk had higher probability of vigilance in the summer recreational periods, alternatively, mule deer had higher probability of vigilance after Labor Day in the hunting recreational period. While mule deer had higher probability of being vigilant outside of designated hunting dates within the fall, elk had higher vigilance probabilities during designated hunting season dates. On average elk had higher hunter harvest rates for the 2020 season as compared to mule deer (CPW 2020). Higher harvest rates of elk could be a factor influencing higher vigilance in elk during the designated hunting seasons.

The use of wildlife cameras was highly pertinent to the specific data collection of this study and provided an opportunity to assess behavior in a novel method. Wildlife cameras allowed for data to be collected on types of recreational use and traffic volume, species, gender, animal behavior, and number of ungulates present at a given time. However, four on-trail, four off-trail cameras, and one SD card were stolen during the study. Only one camera was stolen before any photo data were retrieved. Cameras were labeled with researcher contact; however, we did not receive any complaints from the public regarding cameras. The cameras were largely unknown to the public and we had high success in collecting human recreational use information and wildlife observations using these techniques. Unlike studies reliant on telemetry data that only show locations of a sample of animals and provide primarily location information, our study was able to provide spatial attributes, animal group numbers, and quantify unique vigilance behaviors non-invasively, from the view-point of a sample of landscape locations. While telemetry or similar study methods can show wildlife usage near trails, routine telemetry methods cannot quantify animal's behaviors without the addition of on-board bio-loggers (camera collars, accelerometers on their ear, necks, and tails). Traditional field-based behavior studies often perform real time observation of animal behavior by placing observers at a sample of locations in the field for extended time to watch wildlife (Lark and Slade 2008, Lung and Childress 2007, Childress and Lung 2003, Lingle and Wilson 2001). In our study, we employed wildlife cameras for the collection of behavior data without the risk of disturbance from observers and collected these data at large spatial and temporal scales. However, a limitation to the camera-based method is the interpretation of behavior based off a single frame of data which could over generalize the time animals spend in a given behavior. To accommodate the generalizations of behavior based

off a single frame, cameras could also be deployed to capture video and photo data to compare the time spent in the observed behavior.

Management Implications

Understanding animal vigilance responses to human disturbances can help natural resource agencies better plan trails and manage existing trails in ways that can help minimize stress on wildlife. For example, management could consider limiting the use of motorized vehicles in sensitive fawning/calving summer and migration ranges to reduce disturbances from human presence (Rodgers et al. 2021). With the relatively unknown effects of the Covid-19 pandemic on the summer recreation in 2020, further study into vigilance behavior and outdoor recreation will be needed to make informed future management recommendations after multiple study seasons to acquire a baseline of recreation quantity and type. Future studies would benefit from implementing wildlife camera methodology to address the relationships between wildlife disturbance and human recreation.

These results support management strategies including clustering trails or implementing new trail design methods given the increasing demands for trails and recreational access to public and sometimes private lands. While Euclidean distance was not always the primary driver in our four analyses, this study shows that animals can spend more time in a vigilant state as trail traffic volume increases. While public land managers may not always be able to control recreation traffic volumes, the proximity of trails to sensitive habitats can be controlled through thoughtful trail placement. More information is needed to assess the potential and realized impacts of trails and trail use on wildlife and wild lands and to manage resources sustainably in the context of burgeoning trail advocacy (Dertien et al. 2021). Information from this study and similar studies could aid management agencies in future decisions for wildlife and trail management.

Our study showed that elk benefit from areas with increased distances from trails. Clustering trails reduces the overall trail footprint on the landscape and allows for more trail-less, undisturbed area between existing trails to be available as wildlife refuge. Refuges can provide safe areas from recreational and other environmental influences on animals that use them by reducing stress and providing safe areas for fitness building behaviors (Andersson et al. 2010). Management agencies looking to create new trails to satisfy recreational demand can do so by creating trails nearby existing trails so as to not impede further into wildlife lands.

Sensitive and biologically important wildlife habitats can be identified by wildlife managers so that future trail development does not infringe on wildlife. Winter habitats and summer offspring production habitats are vital to ungulate survival. Critical migration corridors that are impeded by trails have the potential to disturb animal movement patterns that ultimately reduce survival by fragmenting their habitats (Miller et al. 1998). Trail planners and wildlife managers can work cooperatively to help manage trail systems that consider sensitive and biologically important habitats. Agencies can benefit from continual studies that examine recreation, wildlife abundance, wildlife movement, and wildlife behaviors throughout a large geographic environment.

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APPENDICES

Table A1. Range of recorded site values for recreation and habitat variables for the entire study area through the study period.

	Definition	Min	Median	Max
Recreation volume (count)	Combination of motorized and non-motorized recreation volume	0	1,139	10,299
Motorized recreation volume (count)	Cars/trucks/vehicles, side by sides, ATV's, dirt bikes, snowmobiles	0	415	9207
Non-motorized recreation volume (count)	Hiking, mountain bikes, on/off leash dogs, skiing	0	110	10,299
Elevation (Elev, feet)	Vertical distance above sea level	6,127	9,292	12,769
Slope (Degrees)	Measured incline or decline of the ground surface in a North to South or East to West direction	2.86	32.64	68.14
Terrain Ruggedness Index (TRI)	Variability in elevation and slope	1,225	5,673	14,838
Topographic Position Index (TPI)	Comparison of elevation in a Digital Elevation Model to the mean elevation of a neighboring cell	-242	-9	124
Distance to perennial stream (PERN, meters)	Distance to a stream or river which has constant water throughout the year	0	430	5451
Distance to intermittent stream (INT, meters)	Distance to a stream or river which has water at certain periods of the year or in certain conditions	0	281	1,812
Euclidean distance to trail (Euc, meters)	Distance between two points, calculated in GIS to produce a raster of distances from trails	0	14.14	1,810.43
Distance to forest edge (DFE, meters)	Distance to the forest edge, whether inside or outside of the forest. Best analyzed in conjunction with canopy cover	0	42.42	547.44
Housing density within 500 meters (HD)	Number of dwellings within 500 meters of the site location	0	0	12.73
Structure Kernel Density (SKD)	Number of structures (including restroom facilities, parking lots, etc.) within 500 meters of the site location	3	76	1,870
Percent canopy cover (CanCov) (%)	Percent of forest floor covered by vertical projections (i.e. trees and shrubs)	0	35	68
Aspect, 45° reference (ASP)	Compass bearing pertaining to the camera direction based on a 45° Northeast reference	0°	93°	180°

Table A2. Modifying recreation variables and distance from trail variables for 5 out of 23 models of the top performing hypothesis (H7: from Table 1) for elk at the daily scale. Mean distance to trail (DtT) is used as a partitioned set of the Euclidean distance to trail. Variables within the parentheses represent the variable used for a random slope and random grouping variables.

	Model Variables	Log Likelihood	K	Delta AIC	AICc weight
H7	DtT*Nonmotorized + Motorized + (Motorized, LocationID)	-1444.74	5	0.000	1.00
H7	Euc*Nonmotorized + Motorized (Motorized, LocationID)	-1481.86	5	74.24	7.56E-17
H7	Euc*Motorized + Nonmotorized + (Nonmotorized, LocationID)	-1534.93	5	180.3	6.74E-40
H7	DtT*Motorized + Nonmotorized + (Nonmotorized, LocationID)	-1552.18	5	214.8	2.18E-47
H7	Euc*Nonmotorized + Motorized + (Nonmotorized, LocationID)	-1579.35	5	269.2	3.46E-59

Table A3. Modifying distance from trail and environmental variables for 10 out of 62 models of the top performing hypothesis (H6: from Table 1) for elk at the study period time scale. Mean distance to trail (DtT) is used as a partitioned set of the Euclidean distance to trail. Variable within the parentheses represent the random grouping variable.

	Model Variables	Log Likelihood	K	Delta AIC	AICc weight
H₆	DtT*Motorized + HD + ASP + Slope + TRI + PERN + (GroupID)	-281.39	8	0.000	1.00
H₆	EUC + TRI + ASP + Slope + PERN + HD + Motorized + Nonmotorized + (GroupID)	-306.18	9	43.77	3.13E-10
H₆	EUC + TRI + ASP + Slope + PERN + Rec + Elev + HD+ (GroupID)	-306.18	9	43.77	3.13E-10
H₆	EUC + TRI + ASP + Slope + PERN + Recreation + HD+ (GroupID)	-307.63	8	43.92	2.91E-10
H₆	EUC + TRI + ASP + Slope + PERN + Elev + HD + Motorized + Nonmotorized+ (GroupID)	-304.90	10	44.05	2.72E-10
H₆	EUC + TRI + ASP + Recreation + Elev + HD + (GroupID)	-309.25	7	44.49	2.18E-10
H₆	EUC + TRI + ASP + Slope + PERN + Motorized + Nonmotorized+ (GroupID)	-307.92	8	44.50	2.18E-10
H₆	EUC + TRI + ASP + PERN + Recreation + Elev + HD+ (GroupID)	-307.98	8	44.61	2.06E-10
H₆	EUC + TRI + ASP + PERN + Elev + HD + Motorized + Nonmotorized+ (GroupID)	-306.68	9	44.77	1.90E-10
H₆	EUC + TRI + ASP + Slope + PERN + Recreation + (GroupID)	-309.44	7	44.86	1.81E-10

Table A4. Recreation predictor variables for the top performing hypothesis (H8: from Table 1) for mule deer at the daily scale used in model selection. Variables within the parentheses represent the random intercept variable used for the model.

	Model Variables	Log Likelihood	K	Delta AIC	AICc Weight
H8	TRI*Nonmotorized + Hunting*Nonmotorized (Recreation, LocationID)	-4208.13	2	0.000	1.000
H8	Hunting*Nonmotorized + Hunting*Motorized + TRI + (Nonmotorized, LocationID)	-4248.82	3	77.3243	1.62E-17
H8	Hunting*Motorized + TRI + CanCov + Nonmotorized+ (Nonmotorized, LocationID)	-4247.86	3	77.43628	1.53E-17
H8	Hunting*Motorized + Nonmotorized + Slope + (Nonmotorized, LocationID)	-4248.95	1	77.5901	1.42E-17
H8	Hunting*Recreation + TRI+ (Recreation, LocationID)	-4250.02	2	77.71504	1.33E-17
H8	Motorized + Hunting*Nonmotorized + TRI+ (Nonmotorized, LocationID)	-4249.12	2	77.92337	1.20E-17
H8	TRI + Hunting*Recreation + CanCov+ (Recreation, LocationID)	-4249.13	3	77.9493	1.18E-17
H8	Hunting*Recreation + Slope+ (Recreation, LocationID)	-4250.22	3	78.11473	1.09E-17

Table A5. Modifying recreation variables and environmental variables for 10 out of 37 models of the top performing hypothesis (H8: from Table 1) for mule deer at the study period time scale. Variable within the parentheses represent the random grouping variable.

	Model Variables	Log Likelihood	K	Delta AIC	AICc weight
H8	DFE + TRI + ASP*Motorized + Nonmotorized+ (GroupID)	-512.068	7	0	1.00
H8	ASP*Nonmotorized + Motorized+ (GroupID)	-522.212	5	15.67066	0.000395
H8	DFE + TRI + ASP*Recreation+ (GroupID)	-530.752	6	35.03571	2.47E-08
H8	ASP*Recreation+ (GroupID)	-539.988	4	48.98279	2.31E-11
H8	TRI + DFE + PERN*Motorized + Nonmotorized+ (GroupID)	-549.708	7	75.27919	4.50E-17
H8	TRI + Slope*Motorized + Nonmotorized+ (GroupID)	-552.577	6	78.68668	8.19E-18
H8	TRI + Slope*Motorized + Nonmotorized + DFE+ (GroupID)	-551.54	7	78.94233	7.21E-18
H8	Recreation*TRI+ (GroupID)	-555.69	4	80.38543	3.50E-18
H8	Recreation*TRI+DFE+ (GroupID)	-554.937	5	81.12045	2.43E-18
H8	Recreation*PERN + TRI + DFE+ (GroupID)	-554.702	6	82.93588	9.78E-19