CORRIDORS FOR COEXISTENCE: EVALUATING SPATIOTEMPORAL IMPACTS OF LIVESTOCK ON WILDLIFE COMMUNITY DYNAMICS

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ABSTRACT

Livestock depredation by carnivores is a globally pervasive and detrimental interaction that leads to economic loss and retaliatory killings. Livestock trailed annually on US Rangelands impact wildlife communities- competing with ungulate herbivores for forage, disrupting predator-prey dynamics, and shifting community structures. In order to promote coexistence in these human-wildlife systems, a better understanding of how these processes interact is needed. However, studies on the topic fail to fully capture both the spatial and temporal signals of moving livestock herds.

In this study I investigated the effects of sheep grazing on a wildlife community in the Big Wood River Valley, Idaho. I developed a grazing covariate that was temporally informed; and used a scaffolded modeling technique of single- and multi-species occupancy models to evaluate the effects of grazing and environmental factors on spatiotemporal processes of wildlife.

Using an array of remote-triggered cameras, I sampled wildlife occurrence of focal carnivores including gray wolves (*Canis lupus*), American black bear (*Ursus americanus*), coyote (*Canis latrans*), and mountain lions (*Puma concolor*), along with ungulate herbivores mule deer (*Odocoileus hemonius*), elk (*Cervus canadensis*), and moose (*Alces americanus*). I evaluated processes of detection and occupancy using a single-species model for each species, two 2-species models including wolves and elk and wolves and coyotes, and a 5-species community model including bears, coyotes, mule deer, elk, and wolves.

I found that the detection of bears, wolves, and mule deer was positively related in activity to grazing and 16-day NDVI (changing greenness), while the detection of elk was negatively related to grazing and 16-day NDVI. These results suggest a divergence in community makeup as sheep move into an area- increasing predator activity and shifting prey community structure.

Furthermore, this work shows that including a temporally informed grazing covariate into a multi-species modeling structure can effectively predict changes in wildlife community activity when livestock are present. These findings have important insights for livestock and wildlife management as the livestock-carnivore human-wildlife system grows more prevalent and pertinent.

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LIST OF ABBREVIATIONS

USDA	United States Department of Agriculture
USFS	United States Forest Service
BSU	Boise State University
NDVI	Normalized Difference Vegetation Index
U.S./USA	United States/United States of America
NASS	National Agricultural Statistics Service
APHIS	Animal and Plant Health Inspection Service
BLM	Bureau of Land Management
C	Celsius
NOAA	National Oceanic and Atmospheric Administration
GB	Gigabyte
SD	Secure Digital
AOI	Annual Operating Instructions
UTM	Universal Transverse Mercator
NAD83	North American Datum of 1983
TRI	Terrain Ruggedness Index
TPI	Topographical Positioning Index
MODIS	Moderate Resolution Imaging Spectroradiometer
AICc	Akaike Information Criterion (corrected)
CI	Confidence Interval

INTRODUCTION

Spaces shared by human and wildlife populations are expanding (Ma et al. 2020; Belote et al. 2020). Conservation efforts are enabling some wildlife populations to recover and reoccupy areas settled by humans (Madhusudan 2004; Oakleaf et al. 2006; Campos-Silva et al. 2017), while in other cases human populations continue to encroach into wildlife habitats (Lamprey & Reid 2004; Venter et al. 2016; Lark et al. 2020). Finding ways for humans and wildlife to coexist is thus increasingly important. A key challenge to coexistence, however, is the high likelihood of negative interactions between humans and wildlife in shared landscapes (Morehouse & Boyce 2017; Crespin & Simonetti 2019; Lamb et al. 2020). One of the most globally pervasive and negative wildlife-human interactions is between livestock and large carnivores (Treves et al. 2004; Miller et al. 2016; Expósito-Granados et al. 2019). Livestock depredations can negatively impact human livelihoods, diminish support for carnivore conservation, and provoke retaliatory killings (Chen et al. 2016; Page-Nicholson et al. 2017). Furthermore, livestock activities in wildlife habitats alter ecosystem dynamics (Wilkinson et al. 2020; Rottstock et al. 2020). A better understanding of how domestic livestock, wild prey, and carnivores interact in shared landscapes can generate important insights for conserving wildlife and reducing the impacts of livestock and wildlife on each other.

Rangelands in the United States are an important setting in which to study these complex interactions (Hanley et al. 2018). U.S. rangelands are used by ranchers for livestock rearing and grazing, and are also inhabited by a suite of carnivores, such as the gray wolf (*Canis lupus*), mountain lion (*Puma concolor*), and grizzly bear (*Ursus arctos horribilis*). An estimated 35% (~2.9 million km^2) of the land in the contiguous U.S. is classified as rangeland, 66% (~1.9 million km^2) of which lies in the western states (Robinson et al. 2019). Pressure from carnivore activity causes ranchers to suffer yearly costs, totaling $119 million in 2010-2011 (NASS 2010; NASS 2011). These losses are dealt both directly through loss of stock and indirectly through a decrease in the value of surviving stock raised under increased stress (Laporte et al. 2010; Steele et al. 2013). This impact in turn motivates government agencies and rangeland users to lethally remove the individual carnivores responsible (Bradley et al. 2015; DeCesare et al. 2018). Between 2018 and 2019, the U.S. Department of Agriculture reportedly “lethally removed” 659 wolves, 675 mountain lions, and 2 grizzlies (APHIS 2018, 2019). These numbers do not include any retaliations carried out by other agencies such as the Department of the Interior, nor individuals acting outside of government parameters. Retaliatory killings such as these can hinder conservation efforts for threatened carnivore species (Treves & Karanth 2003; Page-Nicholson et al. 2017; Ontiri et al. 2019).

The impacts livestock exert on wildlife communities in U.S. rangelands are substantial as well, affecting wildlife composition, trophic interactions, and potentially ecosystem services (Alkemade et al. 2013; Eldridge & Delgado-Baquerizo 2017). Livestock compete with wild herbivores for space and food (Augustine & Springer 2013; Fynn et al. 2016). For example, one study found that the diets of elk (*Cervus canadensis*), mule deer (*Odocoileus hemonius*), domestic sheep (*Ovis aries*) and cattle (*Bos taurus*) have high overlap in forb forage in spring and summer seasons, when peak livestock grazing occurs (Beck & Peek 2005). Livestock can also change habitat use patterns of wild carnivores, resulting in increased activity near livestock changes in hunting behavior, and shifts in evaluation of the landscape of fear (Blaum et al. 2010; du Toit et al. 2017; Wilkinson et al. 2020). One study showed that areas reserved for livestock grazing affected spatial niche partitioning of 10 of 12 carnivore species (Schuette et al. 2013). The displacement of wildlife in time and space by livestock therefore alters both ecosystem functioning (e.g., nutrient cycling, habitat structure, and biodiversity) and predator-prey dynamics by shifting where and when wild prey are at most risk of predation by wild carnivores (Zimmerman & Neuenschwander 1984; Fleischer 1994; Prins 2000).

In addition, these ecosystems are often used by humans independent of livestock grazing. Public rangelands are also used for recreation, including hiking, vehicle use (motorized and non-motorized), horseback riding, and hunting (Sala et al. 2017; Favretto et al. 2017). These lands therefore comprise one interaction laid on top of another and interwoven with an ongoing suite of interactions between wildlife species, their environment, and human use. As these systems operate with many interacting foci (wildlife, humans, environment) and at varying spatial and temporal scales, the need then is to incorporate spatiotemporal variance into analyses of interacting wildlife species and human use.

Occupancy modeling is a powerful and increasingly common approach to understanding carnivore-herbivore-livestock systems. Occupancy models combine imperfect wildlife occurrence data and environmental attributes to predict the likelihood of wildlife occupancy in a given system. Past work has focused on evaluating spatial distributions of key species and identifying areas of concern for management and conservation, including depredation probability of livestock by canids in India (Srivathsa et al. 2019), population densities of tigers under differing livestock use intensities in India (Karanth et al. 2011), and the effects of grazing densities on wolf occupancy in the western United States (Ausband et al. 2014). However, aggregated, accessible, and accurate data of livestock movement are often scarce and are rarely integrated into occupancy studies of large carnivores and their prey. Previous work has relied on representations of livestock presence that are spatially variable but temporally static (Soofi et al. 2018; Karimov et al. 2018). In these projects, the temporal variability of livestock presence in rangeland systems is averaged into a season-long spatial accounting, resulting in the loss of any insight into how the movements of livestock affect wildlife activity.

This lack of livestock presence data can limit models' ability to provide insight into how wildlife interact with their environment. Not fully accounting for grazing introduces bias in model interpretation. When a model does not account for a key covariate of the system, signals in wildlife activity may be misattributed to other spatial and temporal covariates, such as vegetation, land cover type, or human presence, leading to a misunderstanding of the system and subsequent misallocation of management or conservation resources (Wilkinson et al. 2020; Devarajan et al. 2020). Creating a grazing covariate that adequately captures livestock movements is therefore needed for accurate interpretations of human-wildlife models in rangeland systems.

The objective of this work was to evaluate the spatial and temporal impacts of livestock on wildlife communities, sourced from three questions:

1. How does the presence of livestock impact spatial and temporal processes of wildlife?
2. How do wildlife species in a livestock-carnivore system interact with their environment?
3. How does the presence of livestock influence wildlife interspecific dynamics?

In order to answer these questions I conducted this study in a carnivore-livestock system in central Idaho, USA. I chose this system because it contains ongoing annual grazing of domestic sheep and a large community of wildlife, including focal species that interact directly with the livestock. These included predators – American black bear (*Ursus americanus)*, coyote (*Canis latrans*), mountain lion, and gray wolf – and competing herbivores – mule deer, elk, and moose (*Alces americanus*). I employed a series of single- and multi-species occupancy models to examine the spatial and temporal relationships of these species to livestock grazing, environmental factors, and interspecific dynamics at varying levels of model complexity. I sampled wildlife occurrence, estimated fine-scale livestock presence, and collected environmental covariates of elevation, terrain, vegetation, streams, and temperature, combined with human use, to describe spatial and temporal processes of wildlife. I then used a hypothesis-driven approach to identify candidate models to test in single- and multi-species structures.

I used a hypothetical framework to explain the interactions of wildlife species with livestock, their environment, and other species in this livestock-carnivore system. My general hypothesis is that the presence of livestock will alter the spatial and temporal activities of wildlife, and those changes will vary by species. That is, the responses of wildlife to their environment and other wildlife species will be different in the presence of livestock than when they are absent.

As occupancy modeling provides both spatial and temporal inference, I was able to make predictions for both of these processes in the focal wildlife species. I expected wildlife species to be more likely to occur in areas with ecological characteristics they prefer and have been previously documented to select. Specifically, I expected herbivore species to have increased presence in areas with valuable forage as indicated by vegetative cover. Elk have been shown to prefer more open areas that occur on southern and western facing slopes (Beck et al. 2013); therefore I expected to see elk have increased presence in areas of low tree cover and southern and western aspects. Bears and wolves have been shown to select denser areas of vegetation, bears selecting areas of dense tree stands and undergrowth (Fecske et al. 2002; Brodeur et al. 2008) and wolves selecting areas of highly varied scrub with low conifer density (Milakovic et al. 2011). I therefore expected that bears and wolves would have increased presence in densely vegetated areas as signified by high tree and shrub cover, respectively, and higher NDVI. Temporally, I expected to see deviations from these spatial patterns when livestock were present. As predators of livestock, I expected carnivore species to have higher likelihoods of presence when livestock were present (Nelson et al. 2012). I expected herbivore species to have lower likelihoods of presence when livestock were present, either due to directly avoiding increased predation pressure from an increased presence of carnivore species (Creel et al. 2005), or avoiding forage competition from livestock grazing (Beck & Peek 2005).

The results of this analysis will help us better understand the effects of sheep on the wildlife communities they move through. This project better accounts for the cross-scale interactions among livestock, wild herbivores, and carnivores in shared landscapes that are becoming more common worldwide.

METHODS

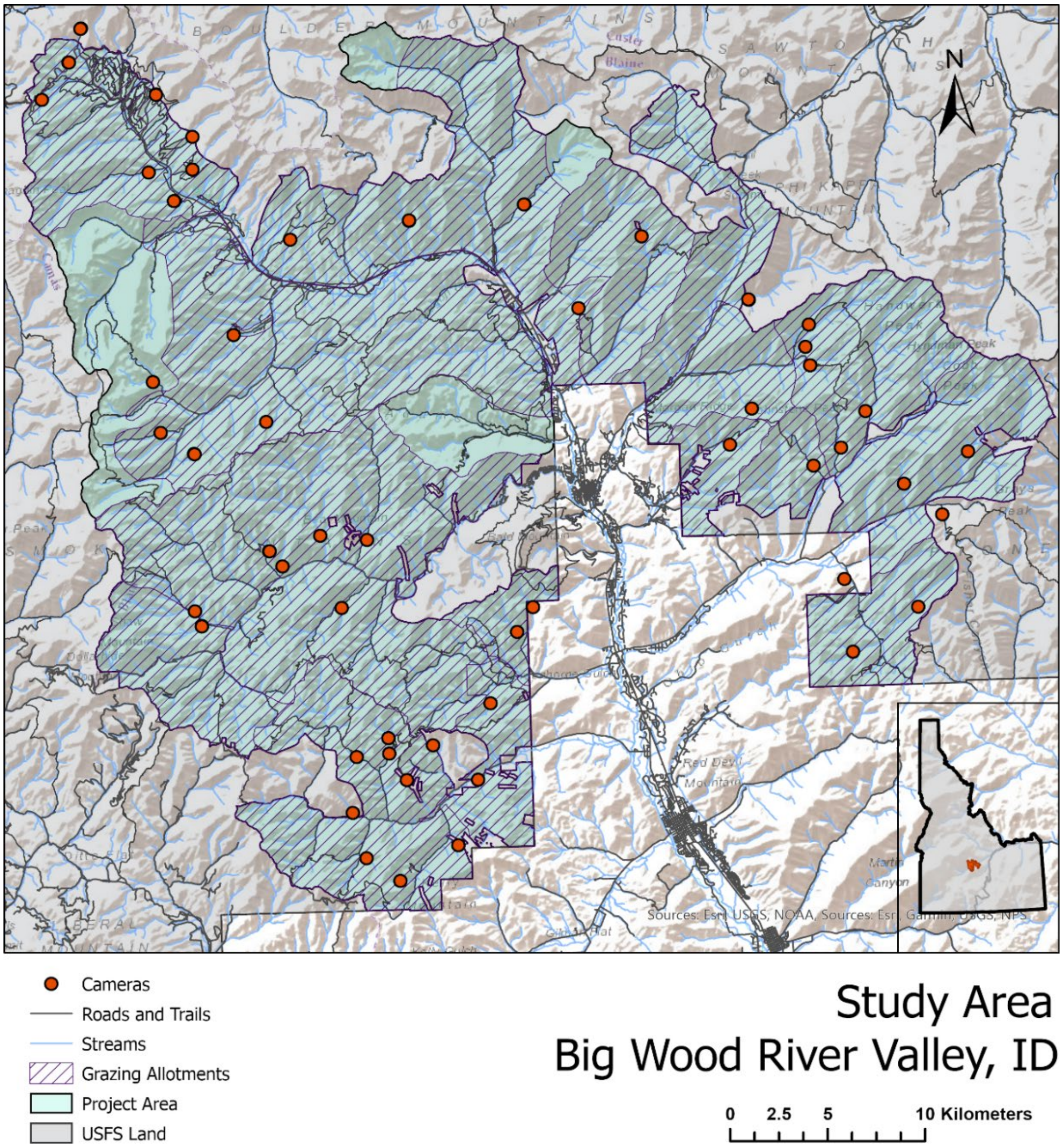
Study Area

The project study area was located in the Big Wood River watershed in central Idaho USA, encompassing nine US Forest Service grazing allotments (Map 1). Grazing allotments are well-defined spaces on the landscape, approved and allocated for limited use by livestock. Grazing usually occurs in the summer and early fall months when temperatures are amenable, snow cover low, and available forage high. Five sheep operators use allotments in the Wood River Valley every year during the summer and fall, trailing and grazing approximately 9,000-12,000 sheep (Ketchum Ranger District 2019).

The study area is 1161 km^2 in size, bounded by 43.905 N, 43.485 S, -114.067 E, and -114.719 W. The US Forest Service (USFS) manages most of the land in and near the study area, with the Bureau of Land Management (BLM) managing some areas in the south. Idaho State Highway 75 follows the river and valley floor, and passes through two towns, Ketchum (pop. ~2800) and Hailey (pop. ~8500) (United States Census Bureau 2020). Recreation, including hiking, mountain-biking, and hunting, is common in the study area.

The topography is dominated by mountains and hills that form many drainages feeding into a large valley floor. Elevation ranges from 1515 m.a.s.l. to 3570 m.a.s.l. Land-cover is predominantly montane conifer forest with Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and ponderosa pine (*Pinus ponderosa*). Near drainage floors, riparian areas are covered by willow (*Salix* spp.). Areas dominated by sagebrush (*Artemisia tridentata*) or aspen (*Populus tremuloides*) are also prevalent.

Wildlife occurrence was sampled in 2018 and 2019 during the sheep grazing season that runs roughly from May – October. During these sampling periods, temperatures ranged from -14ºC to 37ºC (mean average daily temperature 11.4ºC), and total mean precipitation for these study periods was 99.9 cm (NOAA 2020).



Map 1 Map of the Study Area 2018-2019

Data Collection

Wildlife Occurrence

Wildlife cameras are a reliable and well-tested method of sampling wildlife populations, allowing for long observation periods that aid in the detection of species that have large home ranges and high motility through them (Silver et al. 2004; Burton et al. 2015; Keim et al. 2019). To observe spatial and temporal patterns of wildlife activity, I deployed a suite of infrared-triggered wildlife cameras across the study area between July 7 – November 4, 2018 and May 25 – October 27, 2019. In 2018, I deployed 44 cameras for a total of 2704 camera days (or trap nights). In 2019, I deployed 49 cameras for a total 5900 camera days. Camera models included Bushnell TrophyCam Aggressor and Browning Strike Force Pro, powered by AA batteries (Energizer Lithium where available) and loaded with 16-32GB SD cards. I secured cameras to trees by camouflage-painted bear boxes and cable locks.

I chose camera locations to sample areas where sheep were predicted to be present during the coming grazing season. The topography of the study area encouraged the use of drainages (characterized by a stream or gulch bounded by slopes on either side) as potential areas of deployment. I examined each of these drainages in the field for a viable deployment site. Locations of interest for camera placements were decided based on signs of wildlife activity (e.g. tracks, scat, or other sign), opportune spatial and topographical locations (e.g. near game trails, saddles between drainages, and distant from roads), and areas of good visibility. I placed cameras at least 1 km apart, and they averaged 2.69 km apart.

I deployed cameras on trees or large stumps approximately 1 m from the ground and 1 – 5 m from a location of interest. I used walk tests and in-situ photo examinations to ensure that the location of interest was in frame and would be triggered by medium and large wildlife (i.e. focal species).

I revisited cameras periodically to fix issues such as dead batteries, full SD cards, or tilted/damaged cameras. Any observations from a period of time that a camera was inoperable were discarded. If I found a camera to be tilted away from the location of interest, I decided it was inoperable during that period of time.

I downloaded images from cameras, organized them, examined them twice for the presence of wildlife, and identified any wildlife species in the image. Positive detection images were examined a third time for confirmation of species identification. I processed these images using the camtrapR (v.2.0.3) package (Niedballa et al. 2016) in R (v.4.0.3) (R Core Team 2020) to create tables of detection events. Independent detection events for a species have been defined by three criteria: consecutive images of different individuals, consecutive images of unknown individuals determined by an arbitrary time-interval, and non-consecutive images of unknown individuals (Van Berkel 2014). I determined detection events as independent if the previous detection of the species occurred more than two minutes prior. I decided on this time interval based on examination of mule deer detections, since they were the species most frequently captured by the cameras. This revealed that detections more than 2 minutes apart tended to capture different individual deer. For less common species, these intervals were of less concern, as detections were often days or weeks apart, and undoubtedly independent.

The observation period for modeling was one week, in which if a species was detected once during one week, it was determined as present for that week. I then created detection histories from these data, in which presence and absence data were recorded for each species, camera, and observation, forming an RxJ matrix in which R is the number of camera deployments and J is the number of observations. I used one week as the time interval for observations in modeling in order to match the temporal resolution of the sheep presence data, which were available on a weekly basis. Therefore, each species had a detection history with R = 88 cameras and J = 23 weeks.

Sheep Grazing

Several sources of data were collected and synthesized to form a spatiotemporal grazing history for each year. These included camera detections, geo-located depredation events, and US Forest Service (USFS) Records (Map 2).

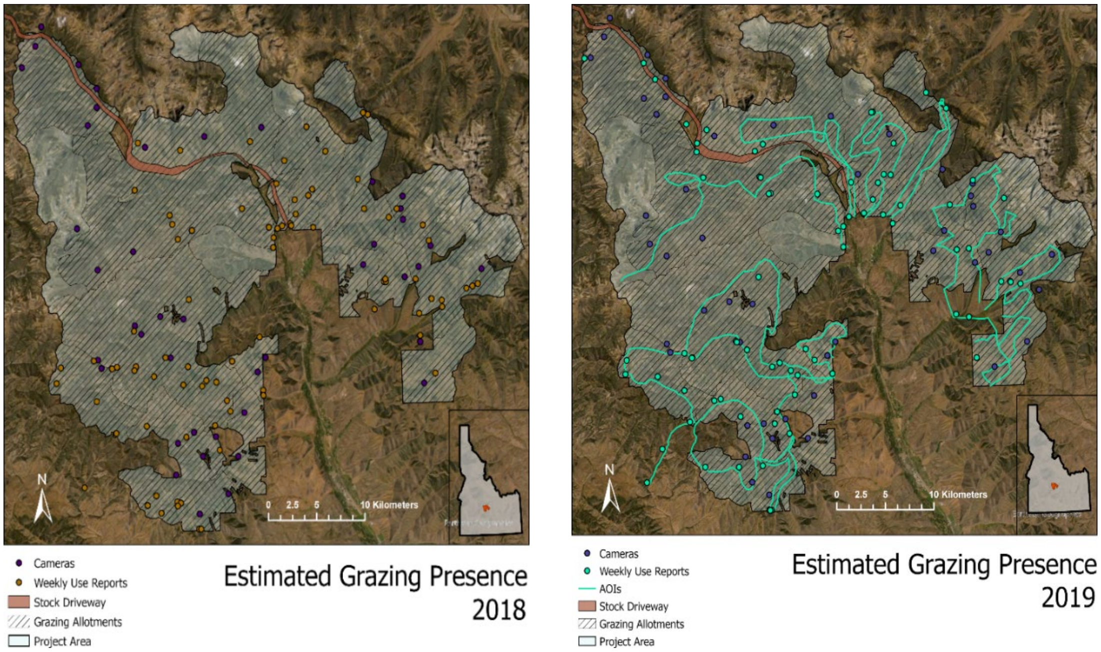
Some sheep bands were detected on the wildlife cameras. In addition, personnel from a local nonprofit group, the Wood River Wolf Project, investigated reported sheep depredation events and provided locations and known dates of these depredations, from which it was known that sheep were present.

Publicly available grazing records for each year were collected from the USFS's Ketchum Ranger District and Sawtooth National Recreation Area websites ("Sawtooth National Forest - Land & Resources Management" n.d.) and offices. Two sources were available: Annual Operating Instructions (AOIs) and weekly Actual Use Reports.

AOIs are contracts each sheep operator makes with the USFS every year for the coming grazing season, usually filed in April or May. These include expected areas of use, routes, and a basic timeline the operator will follow when trailing sheep throughout the grazing season. The AOIs use qualitative descriptions of known places in the study area, and deadline dates by which to pass through, stay, or reach those places. Most of these AOIs were filed with an accompanying map that depicted the agreed-upon route for each sheep band. These routes were digitized by georeferencing the images of the maps (PDF format) in ArcGIS Pro (*ArcGIS Pro 2.6.0* 2020), using roads and trails from USFS shapefiles as reference points. AOIs allow for changes to this planned route and schedule based on unforeseen circumstances such as weather, delays of shipping sheep to designated sites, and depredation events. Therefore, in some cases the actual sheep routes deviated from the expectations laid out in the AOIs. In all cases these AOI data were estimates of where sheep would be, both spatially and temporally.

Weekly Actual Use Reports are brief, qualitative descriptions filed by USFS offices based on reports of sheep activity for each sheep band currently on USFS land. These were examined in ArcGIS Pro alongside basemap satellite imagery, USFS grazing allotment boundaries, roads and trails, streams, and elevation contours in order to estimate sheep locations for each band in each weekly report.

Due to the coarseness of the grazing presence data from AOIs and Actual Use Reports, the grazing history was limited to a spatial resolution of HUC12 drainages from the watershed boundary dataset (U.S. Geological Survey et al. 2013) and a temporal resolution of 1 week. HUC12 drainages (hereafter drainages) in the study area varied in size (n = 22, mean = 73.8 km^2, sd = 30.1 km^2), and each contained 0 to 8 cameras (of the three drainages with 0 cameras, only one was grazed).



Map 2 Maps of collected data on sheep presence in the 2018 and 2019 grazing seasons.

These sheep location data were synthesized to form the grazing history for each season. For each week of each study season, every drainage was evaluated to determine whether there was grazing activity in that drainage, based on the available sheep presence datasets. If at least one day of grazing was estimated, then the drainage was considered to have grazing activity on it for that week. If there were data for a band crossing from one drainage into another during the course of a week, both drainages were considered to have grazing activity on them for that week. Finally, the estimated presence of sheep for each drainage for each week was used to create a by-camera, per-week grazing history for each season. This grazing history was then entered into a spatiotemporal table much like the detection history for each wildlife species, with a value of presence or absence of sheep recorded for each camera area for each week.

Environmental Covariates

A series of environmental covariates were chosen to help evaluate their effect on the spatiotemporal distribution of wildlife. These included abiotic and biotic factors, such as topography, weather, vegetation, and human activity. All spatial data for these covariates were projected to UTM Zone 11N with the NAD83 datum and resampled to 250 m spatial resolution to match the resolution of the coarsest dataset. Values for each covariate at each camera's location were extracted from the 250 m pixel in which it lay. All calculations were carried out using the raster (v.3.4-5) package in R (Hijmans 2020).

Elevation and Terrain - Elevation data from a 1 arc-second (~30 m) digital elevation model (U.S. Geological Survey 2019) were used to create covariates of slope, aspect, and three indices of topographic variation: roughness, terrain ruggedness index (TRI), and topographic position index (TPI) using the terrain function from the raster package in R (Horn 1981; Wilson et al. 2007). TRI was chosen as the covariate to represent terrain variability due to its low covariance with all other spatial covariates included in the models.

Vegetation Cover and Production - The normalized difference vegetation index (NDVI) and land cover data were used as indicators of vegetation type and production. NDVI is a commonly used, remotely sensed metric of vegetation production and greenness (Pettorelli et al. 2005). NDVI was obtained from the MODIS (MODerate resolution Imaging Spectroradiometer) program's MOD13Q1v006 product, which provides NDVI data collected at 16-day intervals and at a 250 m pixel resolution (Didan 2015). These data were used to calculate the mean of each camera's NDVI during the study period each year. The NDVI for each camera during every week of the study period was used as a temporally varying indicator of plant productivity across the growing season. If four or more days of a given week lay within the 16-day period for a given NDVI image, that image was used to supply NDVI values for that week.

Vegetation cover data were obtained from the Rangeland Analysis Program (Maestas et al. 2020; Allred et al. 2021). The cover data are yearly percent cover estimates at 30 m resolution derived from BLM Assessment, Inventory, and Monitoring datasets, the National Resources Conservation Service's National Resources Inventory, and the Landsat satellite record. Three vegetation cover types were selected as covariates: percent tree cover, percent shrub cover, and percent annual forb and grass cover. These specific vegetation types were chosen to minimize correlation among all the cover types (correlation tests used spearman's ranked test with a threshold of $\rho = 0.7$). Other cover types not chosen were percent perennial forb and grass cover and percent bare ground. Site means from 2018 and 2019 were used for these data.

Streams - The distance from each camera to the nearest stream was calculated using a perennial streams vector layer (Rea & Skinner 2009).

Temperature - Mean daily temperatures were sourced from NOAA monitoring stations in the study area (NOAA 2020). The nearest NOAA station to each camera was used to supply temperature data for that camera. The mean daily temperature for each week was calculated for each camera. Temperature and 16-day NDVI were not correlated strongly ($\rho = -0.147$). Weekly mean temperatures also tended to show a clearer seasonal signal than the 16-day NDVI data (Figure 1), suggesting that these variables were not giving redundant information about the way the environment changed across the study period each year.

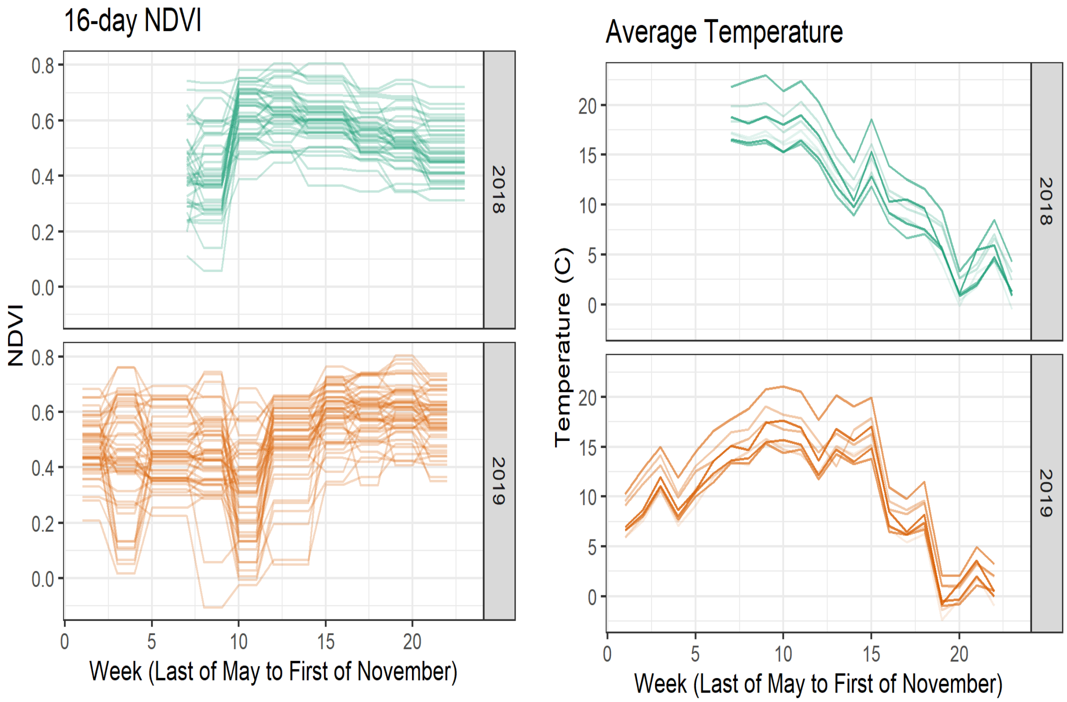


Figure 1 **Comparative plots of spatiotemporal 16-day NDVI and Temperature data**

Human Presence - Human presence was determined by camera detections. Two covariates were created from these data. The first, the average weekly number of humans for each camera across each study season, represents the magnitude of human recreation presence at each camera site. The second, the presence or absence of humans at each camera each week, was spatially and temporally informed, and accounted for the weekly fluctuation in human presence. For these covariates, the type of recreation was not categorized. Of the types of recreation detected (hiking, hunting, mountain biking, horseback riding, and motor vehicle use), hunting represented over 80% of detections, and overall human detections strongly trended with dates of hunting seasons in the study area. Hunting was determined based on the presence of a hunting weapon (bow/rifle) in the image. Therefore the human covariates are considered to be inclusive of all human activity but strongly represent the presence of hunting on the landscape.

All environmental covariates were tested for collinearity before being included in further analyses. Each had a variance inflation factor of less than 1.2, indicating low collinearity, and were thus included in the occupancy models. I found NDVI to covary strongly with tree cover (spearman $\rho = 0.698$), tree cover to covary with both grass/forb ($\rho = -0.456$) and shrub ($\rho = -0.483$) cover, and slope to covary with TRI ($\rho = 0.570$). Any possible candidate models pairing these were therefore discarded.

Data Analysis

I used both single-species and multi-species occupancy models to examine the effects of grazing and other environmental covariates on wildlife activity. This was done in an approach of building complexity and understanding of both individual species processes and interspecies relationships and interactions. I first ran single-species models for each of the seven focal species (American black bear, coyote, mule deer, elk, mountain lion, moose, and gray wolf), because they are straightforward to interpret and provide insight on the patterns by which grazing influences the occupancy of wildlife species, independent of their interactions with other species. Next, I ran two-species models that examine predator-prey and species competition dynamics. Specifically, I evaluated elk-wolf and coyote-wolf interactions, because of the apex role that wolves play in the ecosystem and their contribution to livestock depredation in the system. Finally, I ran a community (five-species) model to better capture the inter- and intra-trophic relationships that occur in a multi-species system. All analyses were carried out in RStudio (v.1.3.1093) (RStudio Team 2020).

Single-Species Occupancy Modeling

The single-species models are zero-inflated binomial models included in the unmarked (v.1.01) package of R (MacKenzie et al. 2005; Royle & Dorazio 2008; Fiske & Chandler 2011). Probabilities of both occupancy and detection are modelled as Bernoulli distributions. The true occupancy state of a species at camera i (z_i) is modelled as the occupancy probability of that species at that camera (ψ_i). The detection or non-detection of the species at camera i during week j (y_{ij}), given the true occupancy state (z_i), is modelled as the probability of detecting that species at camera i during observation j (p_{ij}), modified by the true occupancy state (z_{ij}). This can be summarized by occupancy being modelled as:

$z_i \sim Bernoulli(\psi_i)$

and the detection process as:

$y_{ij} \mid z_i \sim Bernoulli(z_i p_{ij})$

Species detections (y) at cameras i and weeks j (y_{ij}) can be used to estimate both a likelihood of detecting that species for each camera and week (p_{ij}) and a likelihood of that species occupying the area for each camera (ψ_i). Parameters ψ_i and p_{ij} are both evaluated on the logit-link scale.

Occupancy Process - Occupancy is spatially explicit, with the probability of occupancy being evaluated for each camera through the entire study period (2018 and 2019). Occupancy probability is interpreted as estimated use of a species by a given area, irrespective of the time or length of observation. A site with a high occupancy probability for a given species represents a likely area for that species to inhabit.

Detection Process - Detection is both spatially and temporally informed, with each unique spatiotemporal observation (i.e. one week at one camera) being used to model what governs detection of a species in the study system. Therefore in this project, detection was considered to be a metric not only of likelihood of detecting a species but also the intensity of that species' activity. For any given probability of occupancy at a camera site, a higher detection probability during a given week is interpreted as a higher rate of activity during that week.

Multi-Species Occupancy Modeling

Multi-species occupancy modeling is a recent and rapidly expanding methodological approach that leverages the shared occurrence data of multiple species in a community of interest to better inform, estimate, and predict processes of detection and occupancy (Devarajan et al. 2020). The inclusion of multiple species allows for better and more direct estimates of richness, species interactions, and community dynamics than single-species models (Zipkin et al. 2010; Sauer et al. 2013; Rota et al. 2016; Marescot et al. 2020). Until now, however, fine-scale spatiotemporal data on livestock have not been integrated into multi-species occupancy analyses of the space use and interactions of wild herbivores and carnivores.

The multi-species occupancy model used in this project is from the unmarked package in R (Rota et al. 2016). It allows for differing occupancy states for each species included in the model. The true occupancy state for a camera i (z_i) is thus a vector (Z_i) of occupancy states of the length of the number of species included (s). The possible combinations of occupancy states is a vector of length 2^s. Therefore, the occupancy probability parameter (Ψ_i) is also a vector of occupancy probabilities of length 2^s.

Detection at a given camera and week (y_{ij}) is a vector of length s in which each detection probability for each species (p_{sij}) is estimated. In both the occupancy and detection processes, parameters are described by a multivariate Bernoulli distribution. In the multi-species model, the occupancy process is modelled as:

$$Z_i \sim MVB(\Psi_i)$$

and the detection process as:

$$y_{ij} | Z_i \sim MVB(Z_i\, p_{sij})$$

Detection probability, parameter p_{sij}, is estimated for every species. Occupancy probability, parameter Ψ_i, is estimated for every natural parameter (i.e., the possible combination of occupancy states for all considered species). Therefore not only can occupancy be estimated for every species individually, it can also be estimated for specific species combinations (e.g. wolf and elk or wolf and coyote). Both Ψ_i and p_{sij} are evaluated on the logit-link scale.

Modeling Framework

Single-Species Structure

I evaluated each species with a single-species occupancy model. While these single-species models lack the full scope of the system, they were important as a starting place to build the context afforded by the multi-species models. They served as an early diagnostic tool for identifying signals to which individual species responded, thereby facilitating the construction of ecologically coherent, multi-species assemblages.

Two-Species Structure: Predation and Competition Models

I evaluated two two-species interactions. I evaluated elk and wolves as an example of a predator-prey dynamic and coyote and wolves as a predator-competition dynamic. Wolf predation on elk can powerfully influence an ecosystem (Fortin et al. 2005). Wolves and coyotes are interference competitors, especially at kill-sites of ungulate herbivores (Merkle et al. 2009), as observed on camera at a sheep depredation site during the study. I included these predation and competition models in order to examine how sheep presence might affect the dynamics of these interactions.

Five-Species Structure: Community Model

Finally, I ran a community occupancy model that included five species: American black bear, coyote, mule deer, elk, and wolf. Although multispecies models can be considered as more realistic representations of the system of interactions, they are difficult to converge and their outputs are less easy to interpret, a problem that is extenuated by the number of species considered. Mountain lions and moose had the lowest detection rates by far of the seven focal species and a tendency toward occurring in different habitats, as observed in the single-species models, and therefore I did not include them in the final community model.

Candidate Model Framework

I created a list of candidate models to evaluate the relationship of wildlife activity to the grazing patterns of sheep and the environmental context of the study system. I used a hypothesis-driven approach to develop candidate models comprising different combinations of covariates that were likely to affect the detection and occupancy processes. Based on these covariate combinations, I ran a total of 686 candidate models (14 detection × 49 occupancy).

Detection Process Candidates

The covariates for the detection process were grazing, 16-day NDVI, temperature, human presence, and year of study. From these covariates I derived 14 candidate models to describe the detection process (Table 1). These were grouped into three basic types of models: null (no covariates), global (all covariates), and alternative (subsets of covariates), along with a control model with year as the only covariate. I included year in all other models as an assumption that detection of a given species will vary inter-annually based on population and environmental changes not captured by the other covariates.

I examined each environmental covariate (16-day NDVI, temperature, and human presence) individually and with and without grazing. I paired 16-day NDVI and temperature together in one model (Environmental Seasonality) to evaluate seasonal change including biotic and abiotic factors.

Table 1 **Candidate models used in the detection process of modeling**

Description	**Model**	**Interpretation**
Null	~1	Detection probability does not vary with time, the landscape, nor other species.
Global	~grazing + NDVI + temp + human + year	All considered covariates affect or influence detection probability.
Year Control	~year	Detection probability only varies by year of study.
Alternative Global (without Grazing)	~NDVI + temp + human + year	All considered covariates except grazing affect detection probability.
NDVI	~NDVI + year	Grazing does not affect detection probability, but change in greenness does.
Temperature	~temp + year	Grazing does not affect detection probability, but change in temperature does.
Human Presence	~human + year	Grazing does not affect detection probability, but human presence does.
Environmental Seasonality	~NDVI + temperature + year	Grazing does not affect detection probability, but the change in environment over a season does.
Grazing Only	~grazing	Grazing is the most explanatory covariate for detection probability, regardless of year.

Description	**Model**	**Interpretation**
Grazing	~grazing + year	Detection probability is only affected by grazing and year
Grazing and NDVI	~grazing + NDVI + year	Grazing affects detection probability, along with the change in greenness.
Grazing and Temperature	~grazing + temp + year	Grazing affects detection probability, along with change in temperature.
Grazing and Human Presence	~grazing + human + year	Grazing affects detection probability, along with change in the presence of humans.
Grazing and Environmental Seasonality	~grazing + NDVI + temperature + year	Grazing affects detection probability, along with the change in environment over a season.

Occupancy Process Candidates

The covariates for the occupancy process were NDVI (season mean), percent tree cover, percent annual grass and forb cover, percent shrub cover, distance to nearest stream, elevation, slope, aspect, terrain ruggedness index (TRI), and human use (average weekly humans). These are all site covariates and do not vary within a year for any one camera.

From these covariates I derived 49 candidate models to explore the different contexts of the spatial environment that might affect wildlife space use and behaviors (Table 2). I evaluated three basic models (null, global, and year control) along with 23 additional models that test combinations of the biological and physical that I considered relevant to the study system and the species involved. I then evaluated these 23 models again with the human use covariate added to test effects of the intensity of human use on wildlife activity.

The alternation of forested and non-forested slopes, usually opposite each other in a given drainage, is a pervasive environmental context in the study area. North-facing slopes are most often characterized by being forested, south-facing slopes the opposite. The presence of forested habitat is known to be attractive to wildlife occupancy, especially predator species (Long et al. 2011; Rich et al. 2013), and the duality of forest and non-forest (open shrubland and grassland) is important both to ungulate herbivore grazing and sheep grazing (Beck & Peek 2005; Papachristou et al. 2005; Rutter 2006). To capture these dynamics, I tested models that included elevation and aspect with cover of different plant functional types (tree, annual grass/forb, shrub) and NDVI. I included models testing either NDVI or plant functional group cover as covariates for vegetation, to evaluate whether production (NDVI) or structure (tree, grass/forb, and shrub cover) drive wildlife responses to vegetation in this system.

Table 2 Candidate models used in the occupancy process of modeling.

Description	**Model**	**Interpretation**
Null	~1	Occupancy probability does not vary with the landscape, across years, or with other species.
Global	~ndvi + tree + forb + shrub + elevation + aspect + slope + TRI + human + year	All considered covariates affect or influence occupancy probability.
Year Control	~year	Occupancy probability only varies by the year of study
NDVI	~NDVI + year	Greenness directly affects occupancy probability.
Tree Cover	~trees + year	The proportion of tree cover directly affects occupancy probability.
Distance to Stream	~stream + year	The distance to water directly affects occupancy probability.
Forb and Shrub Cover	~forb + shrub + year	The proportion of non-tree cover directly affects occupancy probability
Tree Cover and Distance to Stream	~trees + stream + year	The proportion of tree cover and distance to water affects occupancy probability
NDVI and Distance to Stream	~NDVI + stream + year	Vegetation greenness and distance to water affects occupancy probability

Description	**Model**	**Interpretation**
Forb and Shrub Cover and Distance to Stream	~forb + shrub + stream + year	The proportion of non-tree cover and distance to water affects occupancy probability.
Elevation	~elevation + year	Elevation directly affects occupancy probability.
TRI	~TRI + year	Terrain ruggedness directly affects occupancy probability
Aspect	~aspect + year	The aspect directly affects occupancy probability
Slope	~slope + year	The degree of slope directly affects occupancy probability
Aspect and Slope	~aspect + slope + year	The aspect and degree of slope affect occupancy probability.
Elevation and TRI	~elevation + TRI + year	Elevation and the ruggedness of terrain affect occupancy probability.
Elevation, Aspect, and Slope	~elevation + aspect + slope + year	Elevation and the aspect and degree of slope affect occupancy probability.
Elevation and NDVI	~elevation + NDVI + year	Vegetation greenness and elevation affect occupancy probability.
Elevation and Tree cover	~elevation + trees + year	Tree cover and elevation affect occupancy probability.

Description	**Model**	**Interpretation**
Elevation and Non-tree cover	~elevation + forb + shrub + year	Non-tree cover and elevation affect occupancy probability.
NDVI and Aspect	~NDVI + aspect + year	Vegetation greenness and aspect affect occupancy probability.
Tree cover and Aspect	~trees + aspect + year	Tree cover and aspect affect occupancy probability.
Non-tree cover and Aspect	~forb + shrub + aspect + year	Non-tree cover and aspect affect occupancy probability.
Elevation, NDVI, and Aspect	~elevation + NDVI + aspect + year	Elevation, vegetation greenness, and aspect affect occupancy probability.
Elevation, Tree cover, and Aspect	~elevation + trees + aspect + year	Elevation, tree cover, and aspect affect occupancy probability.
Elevation, non-tree cover, and Aspect	~elevation + forb + shrub + aspect + year	Elevation, non-tree cover, and aspect affect occupancy probability.

Model Selection and Averaging

For each model structure (seven single-species models, predation model, competition model, and community model), I collected and evaluated all model runs across candidate models using AICc. I used the package AICcmodavg (v.2.3-1) in R to compute AICc tables and model averaging (Mazerolle 2020). I compiled the top ranked model and all models with a ΔAICc below 2. I then averaged the top ranked models using the shrink method from AICcmodavg. I averaged each model parameter individually, and held the estimate and variance at 0 for models without the parameter. This method is favored for averaging models when each parameter is not included in all models averaged (Lukacs et al. 2010).

RESULTS

Wildlife Data

A total of 285,065 images were taken over the 2018 and 2019 study periods (2018: 58,747, 2019: 226,318). After visual sorting, I determined 48,625 images to contain wildlife, livestock, or human activity (2018: 11,533, 2019: 37,092), which constituted 7,218 independent detection events (2018: 2,098, 2019: 5,120; Table 3, Figure 2). 27 species of wildlife were detected.

Table 3 Summary of independent detections of wildlife. 'Small mammals' aggregates mustelids, lagomorphs, and rodents. Human detections include project personnel.

Species	**Total Independent Detections**	**2018 Detections**	**2019 Detections**
Mule deer	2,631	566	2,065
Elk	694	120	574
Coyote	219	52	167
American black bear	193	35	158
Moose	88	17	71
Gray wolf	134	3	131
Mountain lion	27	10	17
Red fox	401	197	204
Bobcat	7	5	2
Small mammal	1,876	635	1,241
Wolverine	1	1	0
Human	678	337	341

Species	Total Independent Detections	2018 Detections	2019 Detections
Sheep	132	85	47
Dog	101	28	73
Horse	6	4	2

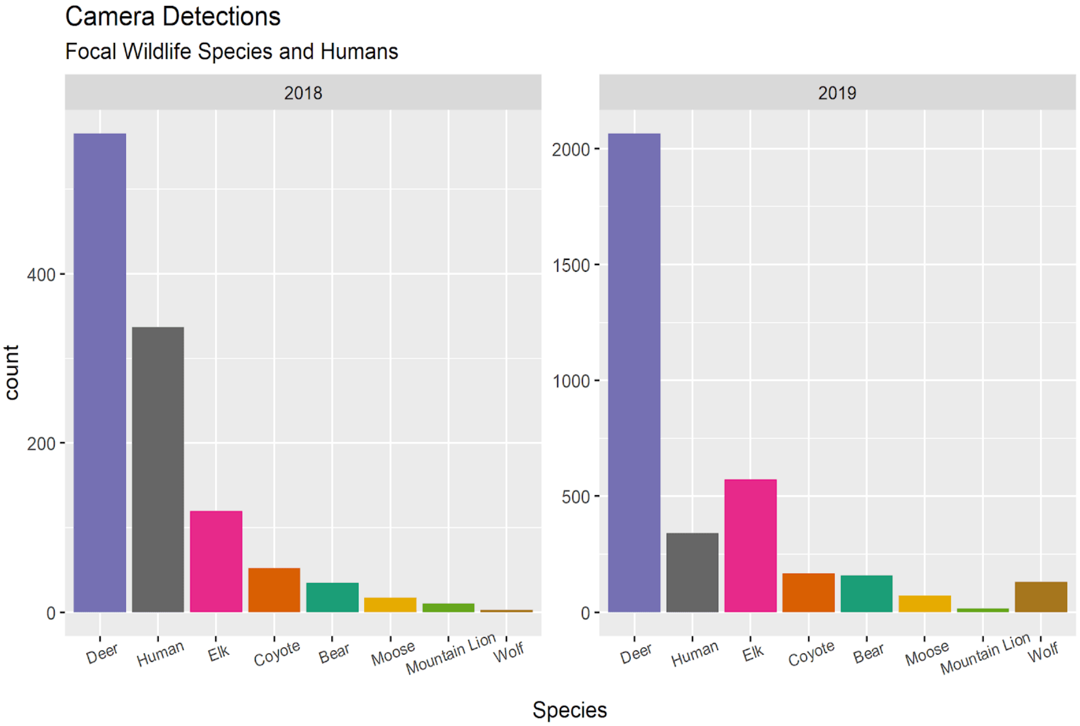


Figure 2 **Summary of independent detections of focal wildlife species and humans from camera deployment in the Big Wood River Valley, Idaho.**

Single-Species Models

In the detection process, grazing and 16-day NDVI were strong predictors of detection for most species, except for mountain lions and moose (Table 4a, Figure.5, for complete tables of all models see Appendix). Temperature was a significant predictor of detection for deer and elk, and human presence only appeared as a significant, negative predictor for elk. Almost all of the covariates in the occupancy process were insignificant in the averaged models (Tables 4b-4c). The exceptions were aspect and year for elk. Overall the occupancy process was not predictive for these 7 species.

Grazing was a significant predictor for mule deer and wolves, who responded positively to sheep presence (Table 4a, Figure 3). Bear had a positive response and elk a negative response to sheep grazing, though these were not statistically significant, suggesting the model was lacking data to provide inference. Coyotes and mountain lions had a near-zero and insignificant response to sheep presence, suggesting that their activity is not affected by grazing. For moose, grazing was not retained in the top-ranking models, suggesting that moose do not substantially interact with grazing. This describes a system in which wolves and mule deer increase in detection probability when sheep are present in the local drainage.

Table 4a Detection parameter estimates for single-species models with 95% CI. All estimates are shrunk averages from the top-ranked models (ΔAICc < 2) for each species. Parameters that were not included in the top-ranked models of a species' detection process are marked with (--). Significant results are marked in bold.

Species	**Intercept**	**Grazing**	**16-day NDVI**	**Temperature**	**Human Presence**	**Year**
Bear	-1.870 [-2.34, -1.39]	0.300 [-0.210, 0.810]	**0.290** [0.090, 0.490]	--	--	-0.230 [-0.720, 0.260]
Coyote	-1.640 [-1.860, -1.420]	0.030 [-0.200, 0.270]	--	--	--	--
Mule Deer	-0.120 [-0.340, 0.110]	**0.570** [0.290, 0.840]	-0.090 [-0.230, 0.040]	**0.140** [0.030, 0.260]	--	**0.490** [0.230, 0.750]
Elk	-0.920 [-1.300, -0.540]	-0.100 [-0.420, 0.220]	**-0.220** [-0.370, -0.070]	**-0.180** [-0.330, -0.040]	**-0.430** [-0.800, -0.060]	-0.100 [-0.480, 0.290]
Moose	-2.949 [-3.529, -2.368]	--	--	--	--	0.681 [-0.004, 1.366]
Mountain Lion	-3.450 [-4.160, -2.740]	0.010 [-0.280, 0.300]	--	0.130 [-0.330, 0.580]	0.030 [-0.270, 0.320]	0.130 [-0.760, 1.030]
Wolf	-3.980 [-5.970, -1.980]	**0.910** [0.050, 1.770]	0.530 [-0.300, 1.370]	--	--	0.280 [-1.490, 2.040]

Table 4b Occupancy (biotic) parameter estimates for single-species models with 95% CI. All estimates are shrunk averages from the top-ranked models (ΔAICc < 2) for each species. Parameters that were not included in the top-ranked models of a species' occupancy process are marked with (--). Significant results are marked in bold.

Species	**Intercept**	**NDVI**	**Trees**	**Forbs and Grasses**	**Shrubs**	**Stream**
Bear	-124.2 [-460.6, 212.3]	-131.6 [-484.4, 221.3]	--	--	--	72.9 [-120.1, 265.8]
Coyote	0.710 [0.080,1.330]	--	--	--	--	--
Mule Deer	3.59 [0.960, 6.220]	-0.080 [-0.840 ,0.680]	--	--	--	--
Elk	4.200 [1.320, 7.07]	--	**-1.690** [-2.960, -0.410]	--	--	--
Moose	-2.66 [-14415, 14410]	-6.58 [-5655, 5641]	383.67 [-10502, 11269]	187.72 [-3440, 3816]	191.41 [-10121, 10503]	-89.98 [-2426, 2245]
Mountain Lion	76.3 [-155.2, 307.8]	--	-102.5 [-385.3, 180.3]	--	-	-0.140 [-2.380, 2.100]
Wolf	-101.9 [-392.2, 188.4]	24.4 [-120.5, 168.8]	--	--		--

Table 4c Occupancy (physical) parameter estimates for single-species models with 95% CI. All estimates are shrunk averages from the top-ranked models (ΔAICc < 2) for each species. Parameters that were not included in the top-ranked models of a species' occupancy process are marked with (--). Significant results are marked in bold.

Species	**Elevation**	**Aspect**	**Slope**	**TRI**	**Human Use**	**Year**
Bear	--	--	--	--	153.5 [-281.9, 588.9]	524.9 [-909.2, 1959]
Coyote	--	--	--	--	--	0.050 [-0.470, 0.580]
Mule Deer	--	0.080 [-0.650, 0.810]	--	-0.670 [-2.940, 1.600]	0.440 [-2.050, 2.940]	7.390 [-97.2, 111.9]
Elk	-0.100 [-0.710, 0.500]	**3.590** [1.380, 5.800]	--	--	--	**8.050** [3.510, 12.58]
Moose	-1.85 [-5193, 5190]	-86.47 [NA]	-128.95 [-6674, 6416]	-8.01 [NA]	237.76 [-14563, 15039]	132.73 [-14791, 15056]
Mountain Lion	-49.7 [-224.1, 124.8]	13.700 [-35.7, 63.1]	-4.690 [-55.9, 46.5]	--	45.2 [-127.2, 217.7]	-122.4 [-557.7, 312.8]
Wolf	--	41.2 [-61.6, 144.0]	-11.26 [-47.0, 24.5]	--	-2.610 [-16.01, 10.79]	162.1 [-288.7, 613.0]

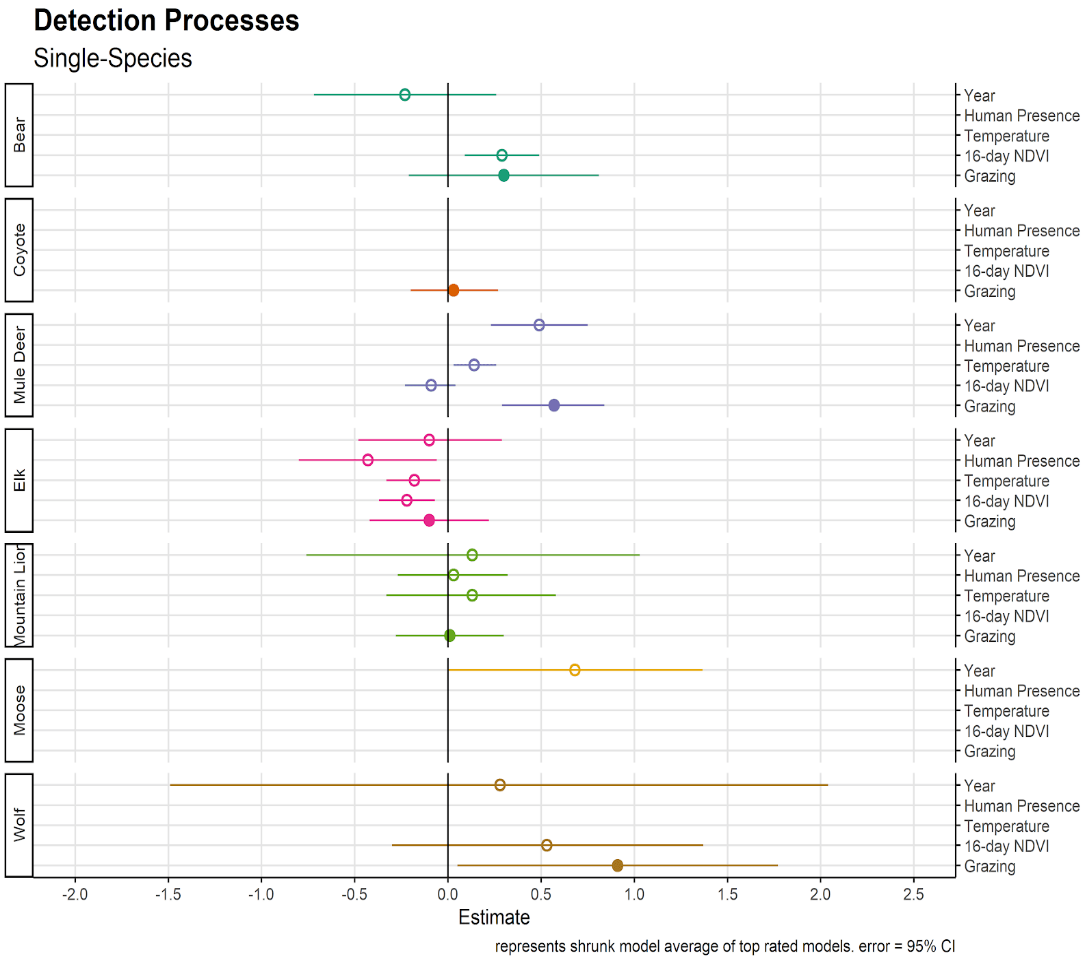


Figure 3 Summary of parameter estimates and 95% CIs from the detection process of single-species models. All estimates are shrunk averages from the top-ranked models (ΔAICc < 2) for each species. The grazing covariate has filled in dots for aid in visualizing this covariate.

Bear

Bears were detected on 47 of 88 camera deployments (2018: 11, 2019: 36) for a total of 124 independent detection events. The averaged model, based on two top-ranked models, featured grazing and 16-day NDVI in the detection process and site NDVI, distance to stream, and human use in the occupancy process. Bear showed a positive, if insignificant, response to grazing and a significant, positive response to 16-day NDVI in the detection process. In the occupancy process, all covariates had large parameter values and their confidence intervals widely overlapped zero. Based on just featured covariates, the top models included for bears suggest they responded to biological covariates (NDVI, distance to stream) and human use. Bears had an insignificant and positive response to grazing, suggesting that detection rates may have increased when sheep were present in the local drainage.

Coyote

Coyote were detected at 52 of 88 camera deployments (2018: 20, 2019: 32) for a total of 132 individual independent detection events. In both the detection and occupancy process, coyotes showed very little response to covariates, with null models ranking highest for both the detection and occupancy process. Coyotes did not respond strongly to any spatial or temporal covariate, suggesting a static probability of detection (13.5% - 19.5%) for any given week and site, and a static probability of occupancy (52.0% - 79.1%) at any given site during the study period. The response of coyotes to grazing was not significant, with the parameter value near zero.

Mule Deer

Mule deer were detected at 86 of 88 camera deployments (2018: 38, 2019: 48) for a total of 718 individual independent detection events. For the detection process, the averaged model included grazing, 16-day NDVI, and temperature. There was a negative, if insignificant, response to NDVI as a temporal covariate and a positive response to temperature, suggesting that as the summer season became hotter and less green, deer detection probability increased. For the occupancy process, the averaged model included site NDVI, aspect, TRI, and human use, but these covariates were not significant. There was a positive response of mule deer to grazing, indicating that detection rates increased significantly when sheep are present in the local drainage.

Elk

Elk were detected at 63 of 88 camera deployments (2018: 23, 2019: 40), for a total of 237 individual independent detection events. In the detection process, covariates of grazing, 16-day NDVI, temperature, and human presence were included in the averaged model. There were two top-ranking models in the detection process: one was the global model, and the other was only lacking the grazing covariate. Elk had a negative, if insignificant, response to temporally varying NDVI and a significant, negative response to temperature, indicating that elk had higher detection rates in the cooler parts of the study period, in areas that tend to be less green. Elk also had a negative response to human presence, which suggests a decrease in detection probability when an area had been used recently by recreationists. The occupancy process included the covariates of aspect, slope, and human use, but these were not significant. Several of the top models included no other covariate besides the year of study, and two were the null model. This suggests that elk had a static occupancy across the landscape regardless of environmental context. Elk had a slight negative, insignificant response to grazing.

Mountain Lion

Mountain lions were detected at 16 of 88 camera deployments (2018: 8, 2019: 8) for a total of 22 individual independent detection events. The detection process included grazing, temperature, and human presence in the averaged model. However, several of the top-ranked models contained no covariates besides year of study or were the null model, and parameter values were near zero and insignificant. This all suggests that mountain lions have a static detection probability across space and time. The occupancy process included the covariates of tree cover, elevation, distance to stream, aspect, slope, and human use. All of the parameter values of these covariates were large and have wide confidence intervals, which supports a lack of significant signal in occupancy for mountain lions or an insufficient number of detections to sufficiently evaluate their responses to environmental conditions. Only one of the top-rated models included grazing as a covariate, and it was highly insignificant.

Moose

Moose were detected at 23 of 88 camera deployments (2018: 9, 2019: 14) for a total of 44 individual independent detection events. Only the top ranked model was included (the next ranked model had ΔAICc > 2), and therefore no model averaging was performed. The detection process included no covariates except for the year of study. The occupancy process selected the global model, which included all covariates, though these were insignificant. The parameter estimates and confidence intervals were very large. Both of these processes suggest that there were insufficient detections of moose to obtain significant responses with this model system. Moose showed no detectable response to the presence of grazing.

Wolf

Wolves were detected at 16 of 88 camera deployments (2018: 1, 2019: 15) for a total of 25 individual independent detection events. The detection process included the covariates of grazing and 16-day NDVI. Wolves had a slightly positive, if insignificant, response to temporal NDVI, suggesting that detection rates increased in greener areas and as areas become greener over the course of a study season, and decreased as areas brown down toward the end of the season. The occupancy process included the covariates of site NDVI, aspect, slope, and human use, although these were not significant. Wolves had a positive response to grazing presence, suggesting that wolf detection rates increase significantly when sheep are present in the local drainage.

Two-Species Models

I evaluated two interspecies interactions: a predator-prey and a competing predator dynamic. I chose to evaluate elk and wolves as a predator-prey dynamic and coyote and wolves as a predator competition dynamic in order to better understand how environmental and grazing factors influence wildlife behavior in this system.

Predation - Wolf and Elk:

Wolves and elk shared detections on 14 of 88 camera deployments (2018: 0, 2019: 14), and were detected at the same site during the same week of observation on 6 separate occasions. The detection process for the top two-species predation models included covariates of grazing, 16-day NDVI, temperature, and human presence (Table 5a, Figure 4). For elk, the inclusion of wolves in the model had little effect, with parameter estimates and confidence intervals remaining largely equivalent to the elk single-species model. For wolves, the inclusion of elk in the model increased the parameter estimate of 16-day NDVI and tightened the confidence interval. Inclusion of elk had the opposite effect on grazing, lowering the estimate and widening the confidence interval. This suggests that when elk, a major prey species for wolves, were included in the model, the effect of sheep presence on wolf detection became less significant, and the importance of the change in greenness over a season (a factor to which elk strongly respond) became more significant. Wolf responses to temperature and human presence remained insignificant.

The occupancy process included the covariates for tree cover, elevation, and aspect (Table 5b). This was different from both species' single-species occupancy results, which for elk contained aspect, slope, and human use, and for wolves contained NDVI, aspect, slope, and human use. Elevation was insignificant for both elk and wolves. Elk have a negative response to tree cover, suggesting that elk were more likely to occupy more open habitats, which correlates with their negative response to temporally informed greenness in the 16-day NDVI covariate in their detection process. Wolves had no significant response to these covariates, as with their single-species model. The elk × wolf interaction intercept was negative, indicating that wolves and elk have a lower probability of occupying the same spaces, when controlling for other environmental and temporal factors. In this predation model, both species showed similar responses to sheep presence as in their single-species models. Elk maintained a negative but insignificant response to grazing, while wolves' positive response to grazing became insignificant in the two-species model.

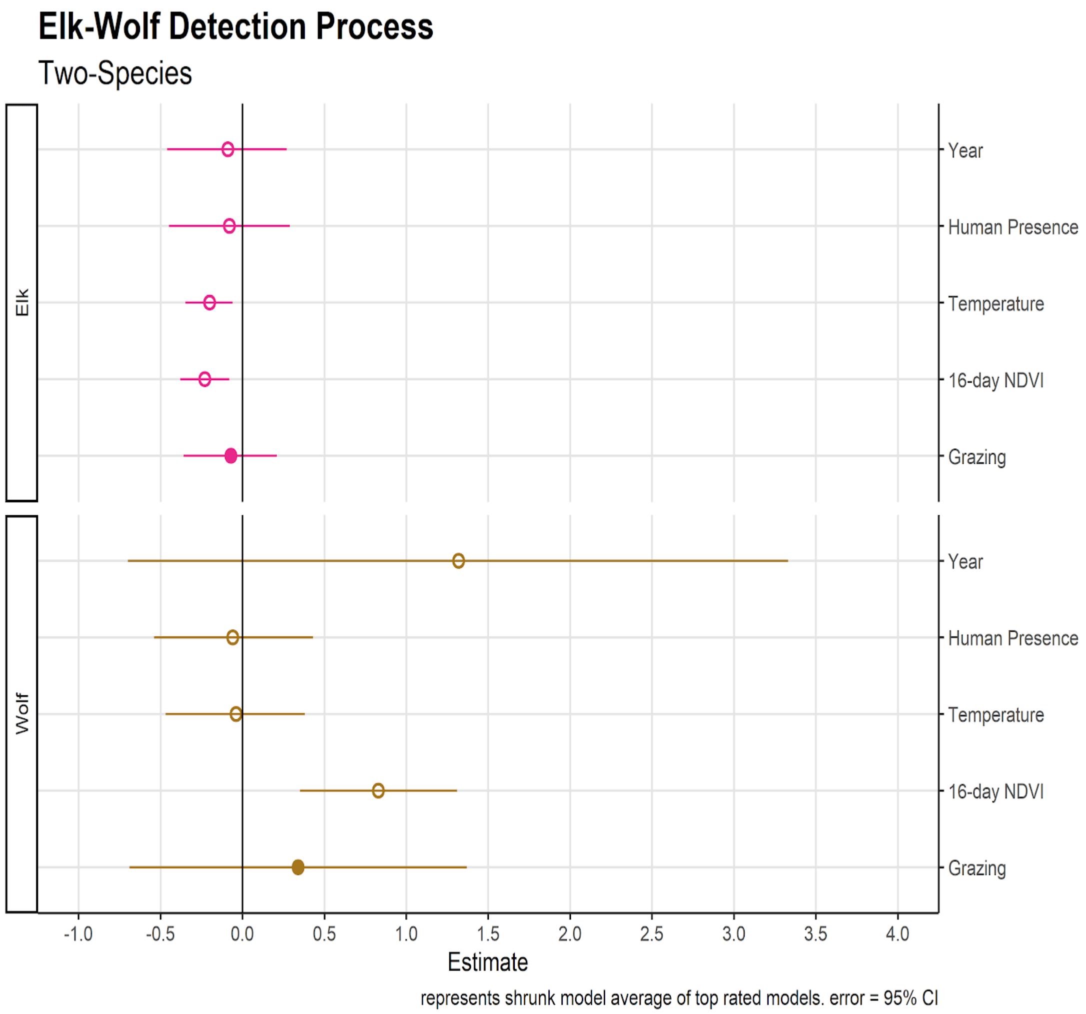


Figure 4 Summary of parameter estimates and 95% CIs from the detection process of the 2-species predation model. All estimates are shrunk averages from the top-ranked models (ΔAICc < 2) for each species. The grazing covariate has filled in dots for aid in visualizing this covariate.

Table 5a **Detection parameter estimates and 95% CI for the 2-species predation model. All estimates are shrunk averages from the top-ranked models (ΔAICc < 2) for each species. Significant results are marked in bold.**

Species	**Intercept**	**Grazing**	**16-day NDVI**	**Temperature**	**Human Presence**	**Year**
Elk	-1.010 [-1.350, -0.670]	-0.070 [-0.360, 0.210]	**-0.230** [-0.380, -0.080]	**-0.200** [-0.350, -0.060]	-0.080 [-0.450, 0.290]	-0.090 [-0.460, 0.270]
Wolf	-5.100 [-7.150, -3.050]	0.340 [-0.690, 1.370]	**0.830** [0.350, 1.310]	-0.040 [-0.470, 0.380]	-0.060 [-0.540, 0.430]	1.320 [-0.700, 3.330]

Table 5b **Occupancy parameter estimates and 95% CI for the 2-species predation model. All estimates are shrunk averages from the top-ranked models (ΔAICc < 2) for each species. Significant results are marked in bold. The Elk:Wolf intercept parameter represents the species interaction intercept between elk and wolf.**

Species	Intercept	Trees	Elevation	Aspect	Year
Elk	4.200 [1.320, 7.07]	**-1.690** [-2.960, -0.410]	-0.100 [-0.710, 0.500]	**3.590** [1.380, 5.800]	**8.050** [3.510, 12.58]
Wolf	-57.2 [-420.5, 306.1]	-52.4 [-252.9, 148.1]	17.86 [-74.6, 110.4]	114.6 [-368.4, 597.5]	204.1 [-592.8, 1001]
Elk:Wolf	**-9.180** [-14.79, -3.580]	--	--	--	--

Competition - Wolf and Coyote:

Coyotes and wolves were both detected at 10 of 88 camera deployments (2018:0, 2019:10), and were detected at the same site during the same week of observation on 5 separate occasions. The detection process for the 2-species competition model included the covariates of grazing and 16-day NDVI (Table 6a, Figure 5). In the detection process, parameter estimates for coyotes remain largely unchanged from the single-species coyote model, with the grazing covariate near zero and insignificant. The added covariate of 16-day NDVI was also near zero and insignificant. For wolves, the detection process in the 2-species competition model was similar to that of the 2-species predation model. When compared to the single-species model, the parameter estimate of 16-day NDVI increased and the confidence interval tightened, while the parameter estimate of grazing decreased and confidence intervals widened. This suggests that the addition of another predator to the wolf model lessened the importance of grazing presence on wolf detection and increased the importance of current greenness, although coyote detection did not have a significant relationship to greenness.

The occupancy process included the covariates NDVI, distance to stream, elevation, aspect, slope, and human use (Tables 6b-6c,). These were all new covariates included for coyotes relative to their single-species model. However, all covariates were insignificant for both wolves and coyotes. The coyote × wolf interaction intercept was negative for 4 of the 7 candidate models, positive for 2 of the 7, and insignificant for 1. The two models that had a positive interaction intercept only contained the slope covariate, while the four that had a negative interaction intercept did not contain the elevation-derived slope covariate. Coyotes did not have a significant response to grazing in these models, and wolves lost the significance of their positive response to grazing, relative to the single-species wolf model.

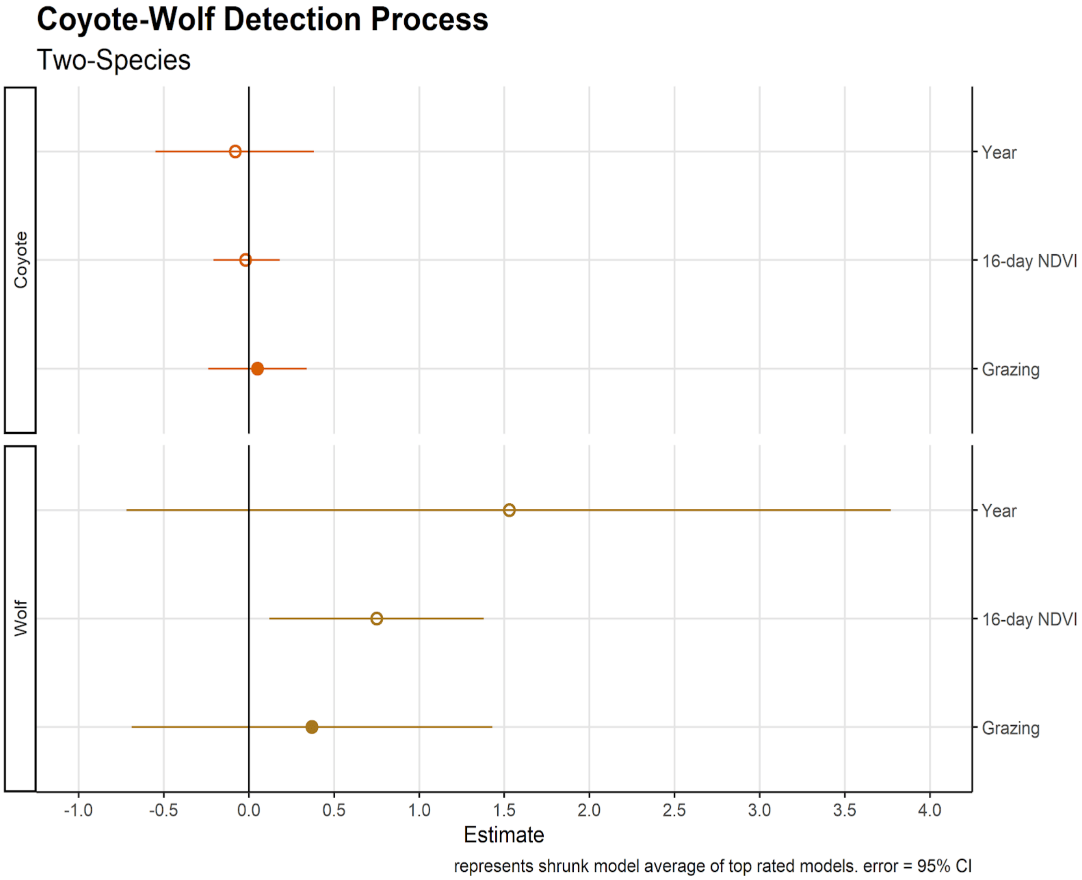


Figure 5 **Summary of parameter estimates and 95% CIs from the detection process of the 2-species competition model. All parameter estimates are shrunk averages from the top-ranked models (ΔAICc < 2) for each species. The grazing covariate has filled in dots for aid in visualizing this covariate.**

Table 6a Detection parameter estimates and 95% CI for the 2-species competition model. All estimates are shrunk averages from the top-ranked models (ΔAICc < 2) for each species. Significant results are marked in bold.

Species	Intercept	Grazing	16-day NDVI	Year
Coyote	-1.580 [-2.000, -1.170]	0.050 [-0.240, 0.340]	-0.020 [-0.210, 0.180]	-0.080 [-0.550, 0.380]
Wolf	-5.310 [-7.720, -2.900]	0.370 [-0.690, 1.430]	**0.750** [0.120, 1.380]	1.530 [-0.720, 3.770]

Table 6b Occupancy (biotic) parameter estimates and 95% CI for the 2-species competition model. All estimates are shrunk averages from the top-ranked models (ΔAICc < 2) for each species. There were no significant results. The Coyote:Wolf intercept parameter represents the species interaction intercept between coyote and wolf.

Species	**Intercept**	**NDVI**	**Stream**
Coyote	0.780 [-2.260, 3.820]	0.020 [-0.230, 0.280]	0.030 [-0.204, 0.300]
Wolf	-34.9 [-328.5, 258.8]	6.060 [-94.9, 107.1]	6.590 [-102.7, 115.9]
Coyote:Wolf	-56.0 [-5568, 5568]	--	--

Table 6c <u>Occupancy</u> (physical) parameter estimates and 95% CI for the 2-species competition model. All estimates are shrunk averages from the top-ranked models (ΔAICc < 2) for each species. There were no significant results. The Coyote:Wolf intercept parameter represents the species interaction intercept between coyote and wolf.

Species	**Elevation**	**Aspect**	**Slope**	**Human Use**	**Year**
Coyote	0.260 [-0.770, 1.280]	0.000 [-0.370, 0.360]	0.430 [-0.830, 1.690]	0.290 [-0.760, 1.340]	56.0 [-5456, 5568]
Wolf	52.2 [-334.1, 438.4]	12.96 [-48.5, 74.4]	-60.2 [-470.6, 350.2]	19.6 [-96.2, 135.3]	278.8 [-5294, 5851]
Coyote:Wolf	--	--	--	--	--

Five-Species Models

I evaluated a five-species model to analyze the study system within a community context. As discussed previously, I excluded mountain lions and moose from the community model due to lack of data for those species and the ways in which their detection processes differed from the other five species in their single-species models.

Only one candidate model emerged as a top-ranked community model, and therefore no model averaging was performed. Only 8 of 88 camera deployments (2018: 0, 2019: 8) detected all five species. There were no sites at which all five species were detected in the same week of observation. The highest rates of co-occurrence were between mule deer and elk, with both species detected at 68 of 88 camera deployments (2018: 28, 2019: 40), and 146 independent detection events (2018: 23, 2019: 123). The lowest rates of co-occurrence were between wolves and coyotes, as described in the competition model, with 10 camera deployments capturing both wolf and coyote detections, and 5 independent detection events.

The detection process for the 5-species model included the grazing and 16-day NDVI covariates (Table 7a, Figure 6). Bears and wolves had a positive response to 16-day NDVI, coyotes had no significant response, mule deer had a slightly negative response, and elk had a negative response. All of these were similar to the NDVI parameter estimates from each single-species model. However, including other species in the model tightened the response to 16-day NDVI for mule deer and wolves, making this parameter more significant for them than in the single-species models.

No environmental factors were included in the best-fitting occupancy process model (Table 7b). The intercept estimate was not significant for any of the species; the confidence intervals had a very large range, and the error was non-computable for mule deer and wolves. None of the occupancy covariates in single- and two-species models were retained in the five-species structure. Every two-species interaction intercept was insignificant, mirroring the noisy occupancy process.

Responses to grazing were similar to single-species and 2-species models for each species in the 5-species model. Bears and mule deer still had a positive response to grazing, but the grazing confidence interval for bears tightened with the inclusion of the other four species. Coyotes maintained an insignificant, near-zero response to grazing. Elk had a more pronounced negative response to grazing when compared to the single-species and predation models, while still having a large confidence interval. Wolves maintained their positive response to grazing while regaining significance in the estimate relative to the predation and competition models, resulting in a response similar to the single-species model. Overall, this describes a system in which the probability of detecting bear, mule deer, and wolf increases when sheep are present in the local drainage, while the probability of detecting elk decreases, and the probability of detecting coyote remains largely the same.

Table 7a Detection parameter estimates and 95% CI for the 5-species community model. Significant results are marked in bold.

Species	**Intercept**	**Grazing**	**16-day NDVI**	**Year**
Bear	-2.367 [-2.904, -1.829]	0.403 [-0.006, 0.813]	0.191 [-0.020, 0.402]	0.456 [-0.091, 1.002]
Coyote	-1.661 [-2.090, -1.232]	0.142 [-0.274, 0.558]	-0.002 [-0.201, 0.198]	-0.012 [-0.481, 0.456]
Mule Deer	-0.082 [-0.306, 0.142]	**0.590** [0.315, 0.865]	**-0.127** [-0.244, -0.011]	**0.452** [0.198, 0.707]
Elk	-1.010 [-1.450, -0.750]	-0.259 [-0.600, 0.081]	**-0.209** [-0.361, -0.057]	0.039 [-0.334, 0.414]
Wolf	-6.272 [-8.260, -4.285]	**0.909** [0.059, 1.759]	**0.831** [0.390, 1.271]	**2.334** [0.314, 4.355]

Table 7b **Occupancy parameter estimates and 95% CI for the 5-species community model. There were no significant results. Pairwise species intercepts represent the interaction intercept for those two species.**

Species	**Intercept**
Bear	-78.3 [-4297, 4141]
Coyote	0.481 [-3.207, 4.169]
Mule Deer	-54.1 [NA]
Elk	-113.1 [-2437, 2211]
Wolf	-12.390 [NA]
Bear:Coyote	0.488 [-1.495, 2.470]
Bear:Mule Deer	79.4 [-4140, 4298]
Bear:Elk	65.3 [-4150, 4281]
Bear:Wolf	-65.2 [-4281, 4151]
Coyote:Mule Deer	54.6 [NA]
Coyote:Elk	3.722 [-10.195, 17.639]
Coyote:Wolf	-58.5 [NA]

Species	**Intercept**
Mule Deer:Elk	41.7 [NA]
Mule Deer:Wolf	68.5 [-3435, 3572]
Elk:Wolf	71.1 [-4144,4287]

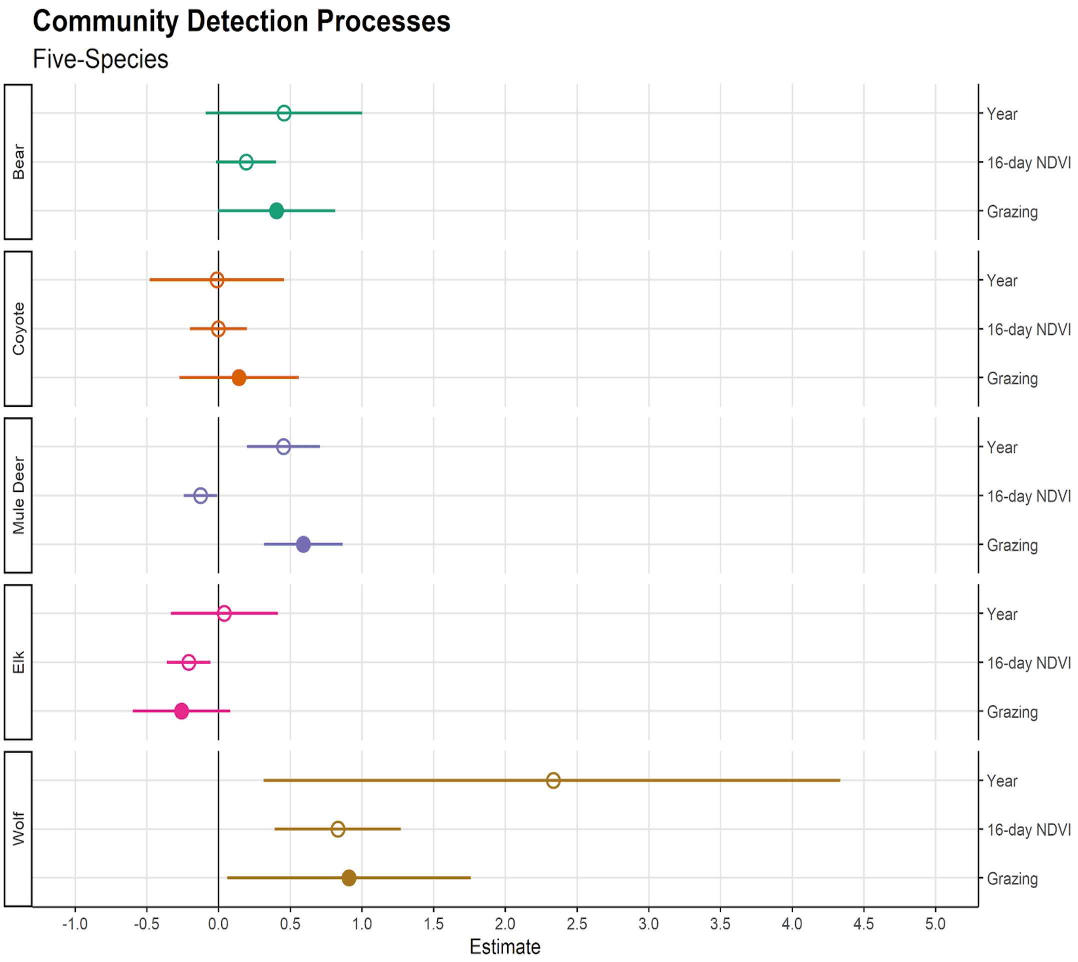


Figure 6 Summary of parameter estimates and 95% CIs from the detection process of the 5-species community model. All parameter estimates are shrunk averages from the top-ranked models (ΔAICc < 2) for each species. The grazing covariate has filled in dots for aid in visualizing this covariate.

DISCUSSION

Spatiotemporal patterns in sheep grazing and NDVI were the best predictors of wildlife activity across all species and models. The temporal detection processes were more important in predicting activity than spatial occupancy processes, which were insignificant for most species and models. This supports my general hypothesis- species have altered occurrence where and when livestock is present. However, exclusively spatial predictions failed to be supported, while temporal predictions were reinforced. Covariates in the community model were more significant for individual species than in single-species models, although single-species models provided insights that were not evident in the general community model. This scaffolded occupancy approach provides a more comprehensive understanding how carnivores and ungulates interact and respond to the presence of grazing.

Grazing Response

Sheep presence was a strong predictor of wildlife detection patterns. It featured in top-ranked models for bear, coyote, mule deer, elk, and wolf. The individual species and community models show that as bands of sheep move into an area, wolf and bear, known predators of sheep, increase in activity and are more readily detected, while ungulate herbivores diverge in response: mule deer activity increases, while elk decrease activity. The responses of these four species all support my general hypothesis by changing occurrence likelihoods where and when livestock are present. However, while carnivores responded as predicted, herbivores split in predicted response. Coyotes, also predators of sheep, had a near-zero, insignificant response to sheep presence. However, grazing was still retained in all models for coyotes, including the single-species model (i.e. without influence from other grazing-directed species). The community model also increased coyote's parameter estimate for grazing, suggesting that coyote may have a weak, positive response to grazing, although this covariate was not significant. This inability to find any significant predictors of coyote activity could be because they are an adaptive, generalist species that thrive under a wide range of conditions (McCue et al. 2014; Bastille-Rousseau et al. 2016).

Sheep not only shifted the likelihood of detecting individual species, but also altered the community structure of large mammals in their spatial and temporal shadow. The movement of sheep into a drainage simultaneously increased predator detectability and caused diverging changes in herbivore detectability, with it becoming less likely to encounter elk and more likely to encounter mule deer. These shifts in community dynamics can have varied downstream effects. Large carnivores exert powerful forces on ungulate populations (Beschta & Ripple 2009). Elk calf mortality, a topic of concern for managing elk populations, is sensitive to differing compositions of predator communities (Griffin et al. 2011). Black bear predation of elk calves, specifically in Idaho, is a prime influence on elk calf mortality and larger population trends (White et al. 2010). The predation of wolves on elk has been an impactful process in western ecosystems affecting not only elk populations but also riparian habitat health and biodiversity; wolf reintroduction in the 1990s has since caused a dramatic reversal in detrimental trophic cascades as wolf predation on elk was restored (Ripple & Beschta 2003; Creel & Christianson 2009; Marshall et al. 2013). Wolves also mediate foraging rates of deer species, dramatically altering vegetative density and structure in areas of high wolf use (Flagel et al. 2016). As sheep draw wolves and bears to an area, they may thus be increasing predation pressure for both of the wild herbivore species, but more so for mule deer than elk.

Environmental Response

NDVI had the largest effect on wildlife detection probability. This measure of spatial and temporal greenness was a significant predictor for the detection processes of bear, mule deer, elk, and wolf. The herbivores, mule deer and elk, had lower detection probabilities with higher 16-day NDVI while the carnivores, bear and wolf, had higher detection probability with higher 16-day NDVI. However, NDVI only gives limited information about vegetation conditions, since it cannot definitively reveal the quality or structure of vegetation, which are important for determining ecologically relevant factors, such as shelter availability and forage palatability (Hopping et al. 2018).Therefore the increase in detection probability for bear and wolf indicate that these species are more likely to be detected in either more densely vegetated or greener spaces and times. These findings are supported by previous studies, which showed that vegetation type based on NDVI was a strong predictor of wolf habitat-selection (Muñoz-Fuentes et al. 2009) and that black bears prefer stands of greener vegetation both in high-undergrowth and dense conifer habitats (Fecske et al. 2002; Brodeur et al. 2008). Additionally, black bear have been shown to come into contact with sheep when following the same high biomass forage (Jorgensen 1983). Bears may be following signals of both livestock prey and greener forage. Conversely, I found that herbivores are more active in either more sparsely vegetated or browner areas and during times that any given area is more sparsely vegetated or browner. Elk had a negative response to tree cover in their occupancy process, suggesting that elk prefer more open habitats with lower NDVI. This pattern might also be a result of predator avoidance, since elk have been shown to move away from areas of recent wolf activity (Middleton et al. 2013). Indeed, wolves had higher detection probability in greener and more densely vegetated areas and elk were negatively associated with wolves in the predation model. Combined, these lines of evidence suggest that elk are responding to predator movements, and that the change in NDVI across space and time mediates wildlife activity and community dynamics.

I found that mule deer were more active during warmer times and elk more active during cooler times, though in areas with browner or sparser vegetation for both species. These responses may be related to the "green wave" of rapidly increasing and short-lived new growth every spring, which some ungulate species have been shown to "surf" as green-up progresses across the growing season and landscape (Merkle et al. 2016). In the study by Merkle and colleagues, elk were shown to not interact with this green wave, while mule deer selected habitat at the crest of it. This helps explain the negative response to 16-day NDVI for mule deer- they reach habitats as temperatures climb but before they reach peak greenness. Then they likely stay in these more open habitats, even after plants begin to senesce. For elk, cooler temperatures and lower NDVI suggests a selection for more open areas, which is a known pattern for elk populations (Sawyer et al. 2007). Aspect and tree cover were two covariates that were significant in the single-species model for elk. Elk may be avoiding the green wave and predation pressure by retreating to cooler, more open areas.

In some models, elk had a decreased detection probability in places and times of human activity. Elk are an important game animal for hunting in the study area. That elk either reduce their activity or retreat to new areas (thereby lowering detection probability at sampled camera sites) when humans are present suggests that they are actively avoiding humans. In particular, recreation in the system is affecting elk activity, given that human presence was greatest during the bow-elk hunting season and that most of the detected humans on cameras were hunters. The spatially explicit covariate of human use was retained in the occupancy process for elk, but was insignificant. This may help to explain elk responses to NDVI and temperature- if elk are avoiding human presence during peaks in summer recreation by retreating to areas of cooler, more open areas, then they would be less detectable in greener, warmer spaces and times.

Multi-species Modeling

Responses to grazing and NDVI changed depending on the species included in the model. Grazing was an especially strong predictor of detection in the community model and the magnitude of the grazing parameter estimate increased and confidence intervals tightened for wolves, bear, and deer when compared to single- or two-species models. Across multi-species modeling, the inclusion of as many species as possible has been linked with clearer, more useful models (Devarajan et al. 2020).

In the 2-species models, the significance of grazing's effect on wolf detections decreased and the magnitude of the 16-day NDVI parameter estimate increased relative to the single- and 5-species models. In these specific multi-species contexts, grazing lost importance and greenness gained importance for patterns of wolf activity. The elk × wolf interaction intercept was significant and negative, showing that elk and wolf have low probabilities of co-occupying space. This aligns with other work that shows elk as highly active in areas and times of recent wolf activity in an attempt to move away (Frair et al. 2005; Middleton et al. 2013). As elk successfully move to spatiotemporal refuges from wolves, they are detected in less-green areas while wolves are detected in greener areas.

The multiple structure approach I used in modeling was useful in revealing both individual species activity and understanding community dynamics. The community model provided the most significant inferences for wildlife activity responses to the environment and grazing, while 2-species models provided insights into trends in wolf and elk activity, and single-species models provided some species-specific responses lost in the sharing of a single model for the community, such as elk response to human presence. This multi-structure, multi-species approach helps fully understand the workings of this carnivore-livestock system.

Insights to Wildlife Management

These findings have several implications for livestock management in this system:

1. Both bears and wolves increase activity when sheep are in the local drainage,
2. The temporal processes of these predator species are more important and predictable than any exclusively spatial process, and
3. These predators are also drawn to greener and more densely-vegetated areas.

Many studies, including those performed in this study system, have focused on wolf-driven mortality of sheep (Treves et al. 2004; Steele et al. 2013; Bradley et al. 2015; DeCesare et al. 2018). However, these data show that black bears are drawn to sheep and kill them as well, as was seen on camera at a bear depredation site and in other studies (Horstman & Gunson 1982; Jorgensen 1983). Focusing on wolves as the main depredation source would not only fail to resolve predation pressure on sheep but could also reduce competitive pressure on bears and increase depredations by them. Wolves and bears have been shown to be interference competitors (Ballard et al. 2003) that depredate similar prey species (Fremmerlid & Latham 2009; Tigner et al. 2014), and bears have been shown to be opportunistic predators of pulse-driven resources (such as a band of sheep would be) (Tigner et al. 2014). Furthermore, it is important to recognize that an exclusively spatial approach to diagnosing risk in this system is not predictive of wildlife activity. As the activity of bears and wolves is tied to the spatiotemporal signals of moving sheep and changing greenness, understanding the temporal variance in depredation risk is key. Finally, both bears and wolves show increased activity and detection probability in areas of greener and more dense vegetation. This can be directly interpreted into insights managers and herders can make as they evaluate depredation risk throughout the grazing season. Adaptive management responses to changing environmental conditions has been successful in promoting coexistence in human-wildlife systems (Stringer et al. 2006; McCarthy & Possingham 2007; Carter & Linnell 2016). Developing tools that can recognize higher-risk spaces and times at fine temporal scales can better inform herder activity during grazing – whether trailing sheep to avoid spatiotemporal risk (Kuiper et al. 2015; Peña-Mondragón et al. 2017) or increased vigilance in spaces and times of higher risk (Stone et al. 2017). These insights form the knowledge needed to make further steps in promoting coexistence.

Study Limitations

The grazing covariate used in these models is representing more than just the physical presence of domestic sheep. Trailing sheep on public lands includes human herders, horses, herding dogs, and guard dogs that operate in the same spaces and times as sheep (Kinka & Young 2018).There is thus a range of activities and non-wildlife species associated with the grazing covariate, which serves as a proxy for an integrated social-ecological process that is difficult to disentangle. More in-depth analyses including dogs, horses, and types of human use (including herding, recreation, and hunting) would have to be included before any independent conclusions could be drawn about how those aspects affect the wildlife activity in this system.

The occupancy process was insignificant or a null (intercept-only) process across species and models. This shows that either the occupancy models did not accurately capture exclusively-spatial processes, or that this system is dominated by temporally-informed processes. The focal species of this study are all large mammals with large home ranges that they can quickly traverse. For example, wolves have been shown to move quickly across long distances (Merrill & Mech 2000) and maintain occupancy over large areas (Mattisson et al. 2013). Elk are considered migratory in many systems, moving long distances yearly (Barker et al. 2019). Black bears have been shown to move continually over home ranges of widely varying sizes (Koehler & Pierce 2003; Karelus et al. 2017). In this system, an exclusively spatial occupancy process is unable to explain trends in wildlife activity. The temporal dynamics of wildlife activity across spaces varying in greenness and sheep presence therefore have more explanatory power in this system.

While it is unsurprising that predator species have increased detection probabilities in the same spatiotemporal places as bands of sheep and increased activity in spaces of denser or greener foliage, it is encouraging that given the relatively coarse spatial and temporal scale of the grazing covariate, the grazing signal was still detectable and significant in some key species. When compared to studies that included a livestock covariate that was exclusively spatial, the importance of having a spatiotemporal grazing covariate becomes readily apparent. Soofi and colleagues used sign survey from trail walks to estimate an exclusively spatial grazing presence covariate, and found that while other species had significant negative responses to grazing, grey wolves had a positive, insignificant response (Soofi et al. 2018). If wolves were responding to temporal pulses of grazing presence in the study area, their occurrence data may not have been enough to receive a significant signal based on the single spatial metric of livestock presence. Karimov and colleagues used distance to nearest herder camp as an exclusively spatial covariate to represent livestock, and found that intensity of wolf use was best explained by either a complex model involving terrain ruggedness, NDVI, and the quadratic of the distance to camp covariate, or simply terrain ruggedness (Karimov et al. 2018). In a rough montane system, the movement of livestock would be temporally dependent on terrain- ruggedness would correlate with slower navigation and so more rugged areas would have a positive response of predators selecting for livestock presence rather than terrain. A finer-scale accounting of the spatiotemporal movements of sheep in these system would have likely strengthened trends and may have made results significant in more species. Work must therefore be done to better quantify livestock movements spatially and temporally during grazing seasons. In addition, it must be noted that these observational studies do not allow for strictly causal interpretations of the effects of sheep on wildlife. Nonetheless, this study shows that an accurate spatiotemporal grazing covariate can provide predictive power and new insight into a livestock-carnivore system.

CONCLUSION

Livestock-carnivore interactions in rangelands are part of a complex human-wildlife system. Understanding how these interactions affect wildlife activity is necessary in promoting coexistence. Analyses that try to quantify grazing effects are a necessary first step. The modeling approach I undertook in this project advanced understanding of how carnivores and herbivores shift activities under the presence of sheep and the environmental and interspecies interactions that accompany and inform those shifts. These shifts revealed changes in community structure that may disrupt predator-prey dynamics when sheep move into an area. Developing and including a spatiotemporal grazing covariate was an important aspect of this study and improved predictive ability of models. Employing a scaffolded, multi-species modeling approach allowed for inferences in both individual species and community contexts.

In order to make these models more informative, we should: 1) develop ways to create a more accurate and fine-scale grazing covariate, 2) perform deeper inquiries into parsing the non-livestock signals of herders, horses, and dogs that lay within the grazing covariate, and 3) focus on analyzing the system using the more informative spatiotemporal detection process rather than the exclusively spatial occupancy process.

Next steps for this analysis include adapting these findings to conservation and management purposes. The creation of decision-support tools is a valuable product in human-wildlife systems (Jackson & Wangchuk 2004; Baruch-Mordo et al. 2011). The confirmed knowledge that predators of sheep increase their detection probability when sheep are in a drainage may not be novel to local stakeholders, but is an important documented step for planning and implementing new adaptive management techniques. Further analyses can also be conducted to determine specific likelihoods of predator detection in areas and times of concern. Modeling approaches can thus provide a more thorough understanding of a human-wildlife system to help promote coexistence in these landscapes.

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APPENDIX

Below are the complete model tables for single-, two-, and five-species models. In total 51 models were included as top-ranking ($\Delta AICc < 2$). The shrunk averaged parameter estimates are also included in these tables. Any significant parameter estimates are in bold.

Single-species Models

Bear

Detection Process

Model	**ΔAICc**	**AICc Wt**	**Intercept**	**Grazing**	**16-day NDVI**	**Year**
Bear Averaged	--	--	-1.870 [-2.340, -1.390]	0.300 [-0.210, 0.810]	**0.290** [0.090, 0.490]	-0.230 [-0.720, 0.260]
Bear 1	0.000	0.378	-1.911 [-2.270, -1.539]	**0.426** [0.016, 0.822]	**0.295** [0.097, 0.499]	-0.217 [-0.682, 0.289]
Bear 2	1.813	0.153	-1.754 [-2.216, -1.344]	--	**0.281** [0.085, 0.481]	-0.250 [-0.671, 0.198]

Occupancy Process

Model	**ΔAICc**	**AICc Wt**	**Intercept**	**Season Mean NDVI**	**Distance to Stream**	**Human Use**	**Year**
Bear Averaged	--	--	-124.2 [-460.6, 212.3]	-131.6 [-484.4, 221.3]	72.9 [-120.1, 265.8]	153.5 [-281.9, 588.9]	524.9 [-909.2, 1959]
Bear 1	0.000	0.378	-136.0 [-170.5, -117.2]	**-144.0** [-159.6, -135.3]	**79.8** [68.4, 87.2]	**168.4** [159.9, 256.6]	**575.2** [498.3, 593.0]
Bear 2	1.813	0.153	-94.9 [-149.8, -89.3]	**-100.8** [-108.6, -79.3]	**55.9** [49.6, 67.2]	**116.6** [108.8, 196.0]	**400.5** [293.3, 435.1]

Coyote

Detection Process

Model	**ΔAICc**	**AICc Wt**	**Intercept**	**Grazing**
Coyote Averaged	--	--	-1.640 [-1.860, -1.420]	0.030 [-0.200, 0.270]
Coyote 1	0.000	0.074	-1.630 [-1.845,-1.428]	--
Coyote 2	1.716	0.031	-1.670 [-1.921, -1.435]	0.140 [-0.284, 0.549]
Coyote 3	1.953	0.028	-1.620 [-1.841, -1.422]	--

Occupancy Process

Model	**ΔAICc**	**AICc Weight**	**Intercept**	**Year**
Coyote Averaged	--	--	0.710 [0.080, 1.330]	0.050 [-0.470, 0.580]
Coyote 1	0.000	0.074	0.738 [0.232, 1.319]	--
Coyote 2	1.716	0.031	0.743 [0.236, 1.327]	--
Coyote 3	1.953	0.028	0.580 [-0.210, 1.606]	0.241 [-0.921, 1.287]

Mule Deer

Detection Process

Model	**ΔAICc**	**AICc Wt**	**Intercept**	**Grazing**	**16-day NDVI**	**Temp.**	**Year**
Deer Averaged	--	--	-0.120 [-0.340, 0.110]	**0.570** [0.290, 0.840]	-0.090 [-0.230, 0.040]	**0.140** [0.030, 0.260]	**0.490** [0.230, 0.750]
Deer 1	0.0000	0.0462	-0.117 [-0.343, 0.110]	**0.564** [0.287, 0.840]	-0.114 [-0.231, 0.002]	**0.139** [0.024, 0.254]	**0.490** [0.232, 0.748]
Deer 2	0.3642	0.0385	-0.119 [-0.347, 0.110]	**0.564** [0.287, 0.840]	-0.115 [-0.231, 0.002]	**0.140** [0.024, 0.254]	**0.492** [0.234, 0.751]
Deer 3	0.9772	0.0283	-0.125 [-0.355, 0.105]	**0.562** [0.286, 0.838]	-0.115 [-0.232, 0.002]	**0.141** [0.026, 0.257]	**0.499** [0.238, 0.760]

Model	**ΔAICc**	**AICc Wt**	**Intercept**	**Grazing**	**16-day NDVI**	**Temp.**	**Year**
Deer 4	1.1079	0.0265	-0.116 [-0.343, 0.111]	**0.565** [0.288, 0.841]	-0.114 [-0.231, 0.002]	**0.139** [0.024, 0.254]	**0.489** [0.232, 0.747]
Deer 5	1.3085	0.0240	-0.106 [-0.332, 0.120]	**0.573** [0.297, 0.849]	--	**0.149** [0.035, 0.264]	**0.482** [0.225, 0.739]
Deer 6	1.5599	0.0212	-0.116 [-0.343, 0.111]	**0.565** [0.289, 0.841]	-0.114 [-0.230, 0.003]	**0.138** [0.023, 0.253]	**0.489** [0.232, 0.747]
Deer 7	1.7348	0.0194	-0.118 [-0.345, 0.110]	**0.564** [0.288, 0.841]	-0.114 [-0.230, 0.003]	**0.139** [0.024, 0.254]	**0.491** [0.233, 0.749]
Deer 8	1.7660	0.0191	-0.108 [-0.335, 0.119]	**0.571** [0.296, 0.847]	--	**0.150** [0.035, 0.265]	**0.484** [0.226, 0.742]

Occupancy Process

Model	ΔAICc	AICc Wt	Intercept	NDVI	Aspect	TRI	Human Use	Year
Deer Averaged	--	--	3.59 [0.960, 6.220]	-0.080 [-0.840, 0.680]	0.080 [-0.650, 0.810]	-0.670 [-2.940, 1.600]	0.440 [-2.050, 2.940]	7.390 [-97.2, 111.9]
Deer 1	0.0000	0.0462	4.060 [0.913, 7.201]	--	--	-1.640 [-4.152, 0.873]	--	9.850 [-164.7, 184.4]
Deer 2	0.3642	0.0385	3.000 [1.504, 4.493]	--	--	--	--	8.820 [-95.2, 112.9]
Deer 3	0.9772	0.0283	3.880 [2.304, 5.448]	--	--	--	--	--
Deer 4	1.1079	0.0265	3.700 [0.445, 6.945]	--	--	-1.300 [-3.979, 1.383]	1.320 [-1.353, 3.994]	7.220 [-22.8, 37.3]

Model	ΔAICc	AICc Wt	Intercept	NDVI	Aspect	TRI	Human Use	Year
Deer 5	1.3085	0.0240	4.050 [0.923, 7.184]	--	--	-1.640 [-4.149, 0.865]	--	8.150 [-66.4, 82.7]
Deer 6	1.5599	0.0212	3.257 [0.771, 5.743]	--	0.813 [-1.006, 2.632]	--	3.028 [-1.571, 7.627]	9.042 [-13.95, 31.05]
Deer 7	1.7348	0.0194	3.441 [1.281, 5.600]	-0.912 [-2.846, 1.022]	--	--	--	9.387 [-10.56, 20.56]
Deer 8	1.7660	0.0191	3.000 [1.511, 4.495]	--	--	--	--	5.000 [-10.56, 20.56]

Elk

Detection Process

Model	**ΔAICc**	**AICc Wt**	**Intercept**	**Grazing**	**16-day NDVI**	**Temperature**	**Human Presence**	**Year**
Elk Averaged	--	--	-0.920 [-1.300, -0.540]	-0.100 [-0.420, 0.220]	**-0.220** [-0.370, -0.070]	**-0.180** [-0.330, -0.040]	**-0.430** [-0.800, -0.060]	-0.100 [-0.480, 0.290]
Elk 1	0.0000	0.0449	-0.933 [-1.284, -0.582]	--	**-0.219** [-0.369, -0.068]	**-0.191** [-0.337, -0.442]	**-0.424** [-0.791, -0.056]	**-0.105** [-0.483, -0.272]
Elk 2	0.4520	0.0358	-0.850 [-1.219, -0.480]	-0.244 [-0.589, 0.100]	**-0.221** [-0.371, -0.071]	**-0.181** [-0.329, -0.034]	**-0433** [-0.801, -0.065]	-0.124 [-0.502, 0.254]
Elk 3	0.5055	0.0349	-0.953 [-1.315, -0.591]	--	**-0.223** [-0.374, -0.073]	**-0.185** [-0.332, -0.038]	**-0.427** [-0.794, -0.060]	-0.086 [-0.473, 0.300]

Model	ΔAICc	AICc Wt	Intercept	Grazing	16-day NDVI	Temperature	Human Presence	Year
Elk 4	0.9341	0.0282	-0.929 [-1.281, -0.578]	--	**-0.218** [-0.368, -0.068]	**-0.189** [-0.336, -0.043]	**-0.426** [-0.794, -0.059]	-0.109 [-0.487, 0.268]
Elk 5	1.0933	0.0260	-0.869 [-1.248, -0.490]	-0.240 [-0.585, 0.105]	**-0.225** [-0.376, -0.074]	**-0.176** [-0.324, -0.029]	**-0.436** [-0.804, -0.068]	-0.436 [-0.494, 0.279]
Elk 6	1.2455	0.0241	-1.016 [-1.378, -0.653]	--	**-0.221** [-0.371, -0.070]	**-0.185** [-0.332, -0.039]	**-0.419** [-0.785, -0.052]	-0.020 [-0.407, 0.367]
Elk 7	1.3404	0.0230	-0.941 [-1.300, -0.583]	--	**-0.223** [-0.373, -0.072]	**-0.185** [-0.331, -0.038]	**-0.431** [-0.798, -0.064]	-0.099 [-0.482, 0.285]
Elk 8	1.4348	0.0219	-0.845 [-1.215, -0.476]	-0.245 [-0.590, 0.099]	**-0.220** [-0.370, -0.070]	**-0.180** [-0.327, -0.033]	**-0.436** [-0.805, -0.067]	-0.128 [-0.507, 0.250]
Elk 9	1.8701	0.0176	-0.936 [-1.319, -0.554]	-0.229 [-0.574, 0.115]	**-0.223** [-0.373, -0.072]	**-0.177** [-0.324, -0.029]	**-0.427** [-0.818, -0.080]	-0.039 [-0.428, 0.351]

Model	**ΔAICc**	**AICc Wt**	**Intercept**	**Grazing**	**16-day NDVI**	**Temperature**	**Human Presence**	**Year**
Elk 10	1.8829	0.0175	-0.963 [-1.331, -0.595]	--	**-0.223** [-0.374, -0.073]	**-0.181** [-0.328, -0.034]	**-0.449** [-0.818, -0.080]	-0.077 [-0.470, 0.316]
Elk 11	1.9651	0.0168	-0.857 [-1.233, -0.481]	-0.242 [-0.587, 0.103]	**-0.224** [-0.375, -0.074]	**-0.176** [-0.323, -0.028]	**-0.440** [-0.809, -0.072]	-0.119 [-0.503, 0.265]

Occupancy Process

Model	**ΔAICc**	**AICc Wt**	**Intercept**	**Aspect**	**Slope**	**Human Use**	**Year**
Elk Averaged	--	--	0.760 [-0.150, 1.680]	0.170 [-0.380, 0.710]	0.130 [-0.400, 0.660]	0.030 [-0.280, 0.330]	0.850 [-0.540, 2.230]
Elk 1	0.0000	0.0449	0.592 [-0.167, 1.352]	--	--	--	1.087 [-0.016, 2.190]
Elk 2	0.4520	0.0358	0.568 [-0.180, 1.316]	--	--	--	**1.108** [0.014, 2.202]
Elk 3	0.5055	0.0349	0.663 [-0.174, 1.499]	0.405 [-0.199, 1.009]	--	--	1.087 [-0.061, 2.235]
Elk 4	0.9341	0.0282	0.836 [-0.070, 1.741]	--	0.408 [-0.271, 1.088]	--	0.689 [-0.614, 1.992]
Elk 5	1.0933	0.0260	0.628 [-0.184, 1.440]	0.390 [-0.200, 0.980]	--	--	1.114 [-0.20, 2.248]
Elk 6	1.2455	0.0241	1.230 [0.646, 1.817]	--	--	--	--

Model	**ΔAICc**	**AICc Wt**	**Intercept**	**Aspect**	**Slope**	**Human Use**	**Year**
Elk 7	1.3404	0.0230	0.887 [-0.038, 1.813]	0.419 [-0.176, 1.013]	0.429 [-0.244, 1.101]	--	0.714 [-0.587, 2.014]
Elk 8	1.4348	0.0219	0.809 [-0.080, 1.699]	--	0.406 [-0.265, 1.077]	--	0.713 [-0.575, 2.002]
Elk 9	1.8701	0.0176	1.210 [0.632, 1.790]	--	--	--	--
Elk 10	1.8829	0.0175	0.503 [-0.398, 1.404]	0.416 [-0.209, 1.042]	--	0.446 [-0.473, 1.365]	**1.554** [0.036, 3.073]
Elk 11	1.9651	0.0168	0.855 [-0.049, 1.760]	0.407 [-0.177, 0.991]	0.427 [-0.237, 1.091]	--	0.739 [-0.547, 2.025]

Mountain Lion

Detection Process

Model	**ΔAICc**	**AICc Wt**	**Intercept**	**Grazing**	**Temperature**	**Human Presence**	**Year**
Mountain Lion Averaged	--	--	-3.450 [-4.160, -2.740]	0.010 [-0.280, 0.300]	0.130 [-0.330, 0.580]	0.030 [-0.270, 0.320]	0.130 [-0.760, 1.030]
Mountain Lion 1	0.0000	0.0531	-3.403 [-4.067, -2.738]	--	--	--	0.322 [-0.546, 1.191]
Mountain Lion 2	0.0047	0.0530	-3.644 [-4.403, -2.884]	--	0.342 [-0.073, 0.757]	--	-171.8 [-0.597, 1.147]
Mountain Lion 3	0.2122	0.0478	-3.771 [-4.493, -3.048]	--	0.348 [-0.053, 0.749]	--	0.367 [-0.516, 1.250]
Mountain Lion 4	0.2592	0.0467	-3.320 [-3.751, -2.898]	--	--	--	--

Model	**ΔAICc**	**AICc Wt**	**Intercept**	**Grazing**	**Temperature**	**Human Presence**	**Year**
Mountain Lion 5	0.5211	0.0409	-3.249 [-3.766, -2.732]	0.083 [-0.833, 0.999]	--	--	--
Mountain Lion 6	0.7486	0.0365	-3.290 [-3.711, -2.859]	--	--	--	--
Mountain Lion 7	0.7947	0.0357	-3.593 [-4.256, -2.931]	--	--	--	0.518 [-0.347, 1.384]
Mountain Lion 8	1.2196	0.0289	-3.300 [-3.724, -2.872]	--	--	--	--
Mountain Lion 9	1.3686	0.0268	-3.565 [-4.341, -2.790]	--	--	0.397 [-0.476, 1.270]	0.361 [-0.510, 1.232]
Mountain Lion 10	1.4239	0.0261	-3.340 [-4.106, -2.573]	--	**0.666** [0.268, 1.064]	--	-0.827 [-1.705, 0.051]
Mountain Lion 11	1.9720	0.0198	-3.310 [-3.737, -2.886]	--	--	--	--

Occupancy Process (a)

Model	ΔAICc	AICc Wt	Intercept	Trees	Distance to Stream	Elevation
Mountain Lion Averaged	--	--	76.3 [-155.2, 307.8]	-102.5 [-385.3, 180.3]	-0.140 [-2.380, 2.100]	-49.7 [-224.1, 124.8]
Mountain Lion 1	0.0000	0.0531	106.9 [-85.5, 299.2]	-152.7 [-435.3, 129.9]	--	-93.2 [-266.8, 80.3]
Mountain Lion 2	0.0047	0.0530	83.2 [-70.7, 237.1]	-118.4 [-347.7, 111.0]	--	-72.3 [-214.3, 69.7]
Mountain Lion 3	0.2122	0.0478	61.6 [-73.9, 197.0]	-73.6 [-235.4, 88.2]	--	--
Mountain Lion 4	0.2592	0.0467	40.1 [-27.3, 107.6]	-48.1 [-130.4, 34.2]	--	--
Mountain Lion 5	0.5211	0.0409	105.3 [-89.3, 300.0]	-150.3 [-436.1, 135.4]	--	-92.0 [-269.0, 84.9]

Model	ΔAICc	AICc Wt	Intercept	Trees	Distance to Stream	Elevation
Mountain Lion 6	0.7486	0.0365	113.7 [-94.2, 321.5]	-146.1 [-420.5, 128.3]	--	-72.7 [-210.8, 65.5]
Mountain Lion 7	0.7947	0.0357	65.8 [-80.5, 212.1]	-79.1 [-256.5, 98.2]	--	--
Mountain Lion 8	1.2196	0.0289	69.4 [-106.6, 245.4]	-58.2 [-208.2, 91.7]	--	-46.8 [-168.0, 74.3]
Mountain Lion 9	1.3686	0.0268	180.8 [-365.5, 727.1]	-247.7 [-877.4, 382.0]	--	-151.9 [-536.9, 233.1]
Mountain Lion 10	1.4239	0.0261	-77.3 [-230.6, 76.1]	--	--	--
Mountain Lion 11	1.9720	0.0198	57.4 [-46.5, 161.3]	-74.3 [-210.0, 61.5]	-2.88 [-11.52, 5.747]	--

Occupancy Process (b)

Model	**ΔAICc**	**AICc Wt**	**Aspect**	**Slope**	**Human Use**	**Year**
Mountain Lion Averaged	--	--	13.700 [-35.7, 63.1]	-4.690 [-55.9, 46.5]	45.2 [-127.2, 217.7]	-122.4 [-557.7, 312.8]
Mountain Lion 1	0.0000	0.0531	25.7 [-22.5, 73.8]	--	--	-221.4 [-623.6, 180.9]
Mountain Lion 2	0.0047	0.0530	19.9 [-18.0, 57.8]	--	--	-171.8 [-499.2, 155.6]
Mountain Lion 3	0.2122	0.0478	--	--	119.2 [-141.4, 379.7]	-42.9 [-159.0, 73.2]
Mountain Lion 4	0.2592	0.0467	--	--	77.8 [-52.8, 208.4]	-27.8 [-82.8, 27.2]
Mountain Lion 5	0.5211	0.0409	25.1 [-22.1, 72.4]	--	--	-218.2 [-627.1, 190.6]

Model	**ΔAICc**	**AICc Wt**	**Aspect**	**Slope**	**Human Use**	**Year**
Mountain Lion 6	0.7486	0.0365	--	--	49.3 [-42.7, 141.2]	-168.7 [-478.9, 141.5]
Mountain Lion 7	0.7947	0.0357	--	--	128.0 [-158.4, 414.4]	-45.9 [-170.1, 78.4]
Mountain Lion 8	1.2196	0.0289	20.7 [-33.8, 75.2]	--	--	-107.8 [-381.9, 166.3]
Mountain Lion 9	1.3686	0.0268	41.2 [-67.2, 149.6]	--	--	-367.6 [-1355, 620.1]
Mountain Lion 10	1.4239	0.0261	20.7 [-20.1, 61.5]	-74.8 [-222.0, 72.4]	31.6 [-32.2, 95.3]	150.7 [-144.7, 446.0]
Mountain Lion 11	1.9720	0.0198	--	--	114.49 [-93.1, 322.0]	-43.3 [-130.5, 43.9]

Moose

Detection Process

Model	**ΔAICc**	**AICc Wt**	**Intercept**	**Year**
Moose 1	0.000	0.237	-2.949 [-3.529, -2.368]	0.681 [-0.004, 1.366]

Occupancy Process (a)

Model	**ΔAICc**	**AICc Wt**	**Intercept**	**NDVI**	**Trees**	**Forbes**	**Shrubs**	**Distance to Stream**
Moose 1	0.000	0.237	-2.660 [-14415, 14410]	-6.580 [-5655, 5641]	383.67 [-10502, 11269]	187.72 [-3440, 3816]	191.41 [-10121, 10503]	-89.98 [-2426, 2245]

Occupancy Process (b)

Model	**ΔAICc**	**AICc Wt**	**Elevation**	**Aspect**	**Slope**	**TRI**	**Human Use**	**Year**
Moose 1	0.000	0.237	-1.85 [-5193, 5190]	-86.47 [NA]	-128.95 [-6674, 6416]	-8.01 [NA]	237.76 [-14563, 15039]	132.73 [-14791, 15056]

Wolf

Detection Process

Model	**ΔAICc**	**AICc Wt**	**Intercept**	**Grazing**	**16-day NDVI**	**Year**
Wolf Averaged	--	--	-3.980 [-5.970, -1.980]	**0.910** [0.050, 1.770]	0.530 [-0.300, 1.370]	0.280 [-1.490, 2.040]
Wolf 1	0.000	0.118	-4.285 [-6.471, -2.099]	**0.981** [0.132, 1.831]	**0.802** [0.329, 1.276]	0.418 [-1.693, 2.528]
Wolf 2	1.369	0.060	-3.365 [-3.882, -2.849]	0.768 [-0.058, 1.593]	--	--

Occupancy Process

Model	**ΔAICc**	**AICc Wt**	**Intercept**	**NDVI**	**Aspect**	**Slope**	**Human Use**	**Year**
Wolf Averaged	--	--	-101.9 [-392.2, 188.4]	24.4 [-120.5, 168.8]	41.2 [-61.6, 144.0]	-11.26 [-47.0, 24.5]	-2.610 [-16.01, 10.79]	162.1 [-288.7, 613.0]
Wolf 1	0.000	0.118	-83.2 [-268.0, 101.7]	--	42.8 [-51.6, 137.2]	-16.9 [-56.4, 22.5]	--	138.0 [-166.6, 442.5]
Wolf 2	1.3694	0.0595	-139.0 [-558.1, 280.1]	72.0 [-149.7, 293.7]	38.0 [-79.5, 155.5]	--	-7.79 [-27.3, 849.7]	210.08 [-429.6, 849.7]

Two-species Models

Predation

Detection Process

Species	**Model**	**ΔAICc**	**AICc Wt**	**Intercept**	**Grazing**	**16-day NDVI**	**Temperature**	**Human Presence**	**Year**
Elk	Predation Averaged	--	--	-1.010 [-1.350, -0.670]	-0.070 [-0.360, 0.210]	**-0.230** [-0.380, -0.080]	**-0.200** [-0.350, -0.060]	-0.080 [-0.450, 0.290]	-0.090 [-0.460, 0.270]
Elk	Predation 1	0.000	0.225	-1.060 [-1.376, -0.744]	--	**-0.211** [-0.377, -0.082]	**-0.211** [-0.355, -0.067]	--	-0.079 [-0.440, 0.281]
Elk	Predation 2	0.805	0.150	-0.991 [-1.324, -0.658]	-0.210 [-0.552, 0.133]	**-0.231** [-0.378, -0.084]	**-0.202** [-0.347, -0.056]	--	-0.096 [-0.457, 0.265]
Elk	Predation 3	1.098	0.130	-0.910 [-1.249, -0.572]	--	**-0.218** [-0.366, -0.070]	**-0.193** [-0.339, -0.048]	**-0.452** [-0.816, -0.088]	-0.132 [-0.497, 0.233]

Species	Model	ΔAICc	AICc Wt	Intercept	Grazing	16-day NDVI	Temperature	Human Presence	Year
Elk	Predation 4	1.234	0.121	-1.062 [-1.380, -0.744]	--	**-0.229** [-0.377, -0.081]	**-0.209** [-0.353, -0.065]	--	-0.076 [-0.438, 0.286]
Elk	Predation 5	1.525	0.105	-0.995 [-1.330, -0.659]	-0.213 [-0.556, 0.130]	**-0.232** [-0.379, -0.084]	**-0.201** [-0.346, -0.056]	--	-0.090 [-0.453, 0.273]
Wolf	Predation Averaged	--	--	-5.100 [-7.150, -3.050]	0.340 [-0.690, 1.370]	**0.830** [0.350, 1.310]	-0.040 [-0.470, 0.380]	-0.060 [-0.540, 0.430]	1.320 [-0.700, 3.330]
Wolf	Predation 1	0.000	0.225	-4.997 [-7.005, -2.988]	--	**0.794** [0.337, 1.250]	-0.046 [-0.470, 0.378]	--	1.325 [-0.696, 3.346]
Wolf	Predation 2	0.805	0.150	-5.305 [-7.323, -3.287]	**0.963** [0.116, 1.811]	**0.892** [0.407, 1.376]	-0.045 [-0.463, 0.373]	--	1.289 [-0.691, 3.269]
Wolf	Predation 3	1.098	0.130	-4.920 [-6.941, -2.898]	--	**0.808** [0.348, 1.268]	-0.035 [-0.462, 0.392]	-0.315 [-1.325, 0.696]	1.308 [-0.715, 3.330]

Species	**Model**	**ΔAICc**	**AICc Wt**	**Intercept**	**Grazing**	**16-day NDVI**	**Temperature**	**Human Presence**	**Year**
Wolf	Predation 4	1.234	0.121	-4.997 [-7.006, -2.988]	--	**0.793** [0.336, 1.250]	-0.049 [-0.473, 0.376]	--	1.323 [-0.699, 3.344]
Wolf	Predation 5	1.525	0.105	-5.363 [-7.432, -3.294]	**0.966** [0.115, 1.817]	**0.894** [0.407, 1.380]	-0.051 [-0.471, 0.370]	--	1.337 [-0.694, 3.368]

Occupancy Process

Species	**Model**	**ΔAICc**	**AICc Wt**	**Intercept**	**Trees**	**Elevation**	**Aspect**	**Year**
Elk	Predation Averaged	--	--	4.200 [1.320, 7.07]	**-1.690** [-2.960, -0.410]	-0.100 [-0.710, 0.500]	**3.590** [1.380, 5.800]	**8.050** [3.510, 12.58]
Elk	Predation 1	0.000	0.225	4.382 [1.427, 7.337]	**-1.756** [-3.047, -0.465]	-0.205 [-1.015, 0.604]	**3.739** [1.477, 6.000]	**8.382** [3.673, 13.090]
Elk	Predation 2	0.805	0.150	4.167 [1.385, 6.950]	**-1.681** [-2.917, -0.446]	-0.192 [-0.981, 0.598]	**3.622** [1.435, 5.810]	**8.113** [3.566, 12.659]
Elk	Predation 3	1.098	0.130	4.150 [1.285, 7.006]	**-1.640** [-2.896, -0.381]	--	**3.520** [1.366, 5.681]	**7.880** [3.538, 12.23]

Species	**Model**	**ΔAICc**	**AICc Wt**	**Intercept**	**Trees**	**Elevation**	**Aspect**	**Year**
Elk	Predation 4	1.234	0.121	4.110 [1.243, 6.973]	**-1.660** [-2.934, -0.381]	--	**3.490** [1.305, 5.669]	**7.800** [3.414, 12.188]
Elk	Predation 5	1.525	0.105	4.000 [1.222, 6.786]	**-1.630** [-2.886, -0.370]	--	**3.440** [1.278, 5.602]	**7.720** [3.371, 12.08]
Wolf	Predation Averaged	--	--	-57.2 [-420.5, 306.1]	-52.4 [-252.9, 148.1]	17.86 [-74.6, 110.4]	114.6 [-368.4, 597.5]	204.1 [-592.8, 1001]
Wolf	Predation 1	0.000	0.225	-92.8 [-700.8, 515.1]	-85.6 [-373.2, 201.9]	33.7 [-96.8, 164.3]	186.4 [-540.5, 913.3]	324.9 [-874.7, 1525]
Wolf	Predation 2	0.805	0.150	-94.4 [-340.4, 151.5]	-84.7 [-306.6, 137.1]	36.4 [-65.8, 138.6]	189.9 [-292.1, 671.9]	322.4 [-469.3, 1114]

Species	Model	ΔAICc	AICc Wt	Intercept	Trees	Elevation	Aspect	Year
Wolf	Predation 3	1.098	0.130	-18.97 [-53.9, 15.95]	-17.69 [-41.8, 6.376]	--	37.4 [-12.53, 87.3]	77.9 [-27.6, 183.4]
Wolf	Predation 4	1.234	0.121	-18.97 [-53.9, 16.01]	-17.68 [-41.8, 6.436]	--	37.3 [-12.71, 87.3]	77.7 [-28.0, 183.4]
Wolf	Predation 5	1.525	0.105	-19.13 [-54.2, 15.94]	-17.69 [-41.9, 6.476]	--	37.3 [-12.79, 87.4]	77.8 [-28.1, 183.8]

Occupancy (Interactions)

Model	Predation-Avg.	Predation 1	Predation 2	Predation 3	Predation 4	Predation 5
Elk:Wolf Intercept	**-9.180** [-14.79, -3.580]	**-9.591** [-15.354, -3.828]	**-9.207** [-14.696, -3.718]	**-9.010** [-14.512, -3.518]	**-8.930** [-14.45, -3.403]	**-8.770** [-14.20, -3.349]

Competition

Detection Process

Species	**Model**	**ΔAICc**	**AICc Wt**	**Intercept**	**Grazing**	**16-day NDVI**	**Year**
Coyote	Competition Averaged	--	--	-1.580 [-2.000, -1.170]	0.050 [-0.240, 0.340]	-0.020 [-0.210, 0.180]	-0.080 [-0.550, 0.380]
Coyote	Competition 1	0.000	0.116	-1.564 [-1.979, -1.148]	--	-0.027 [-0.226,0.172]	-0.079 [-0.559, 0.401]
Coyote	Competition 2	0.038	0.114	-1.573 [-1.991, -1.156]	--	-0.021 [-0.224, 0.183]	-0.087 [-0.572, 0.398]
Coyote	Competition 3	0.237	0.103	-1.622 [-2.062, -1.182]	0.148 [-0.270, 0.565]	-0.016 [-0.221, 0.188]	-0.080 [-0.565, 0.405]
Coyote	Competition 4	0.610	0.086	-1.543 [-1.946, -1.139]	--	-0.005 [-0.210,0.199]	-0.113 [-0.588, 0.363]

Species	**Model**	**ΔAICc**	**AICc Wt**	**Intercept**	**Grazing**	**16-day NDVI**	**Year**
Coyote	Competition 5	1.150	0.065	-1.603 [-2.038, -1.167]	0.126 [-0.290, 0.542]	-0.024 [-0.224, 0.176]	-0.075 [-0.555, 0.404]
Coyote	Competition 6	1.556	0.053	-1.588 [-2.012, -1.164]	0.143 [-0.275, 0.561]	-0.0002 [-0.206, 0.206]	-0.109 [-0.584, 0.366]
Coyote	Competition 7	1.771	0.048	-1.620 [-1.833, -1.415]	--	--	--
Wolf	Competition Averaged	--	--	-5.310 [-7.720, -2.900]	0.370 [-0.690, 1.430]	**0.750** [0.120, 1.380]	1.530 [-0.720, 3.770]
Wolf	Competition 1	0.000	0.116	-4.859 [-6.873,-2.845]	--	**0.749** [0.307, 1.190]	1.109 [-0.918, 3.136]
Wolf	Competition 2	0.038	0.114	-5.556 [-7.537, -3.575]	--	**0.825** [0.373, 1.276]	1.843 [-0.168, 3.853]
Wolf	Competition 3	0.237	0.103	-5.992 [-8.037, -3.947]	**1.012** [0.154, 1.869]	**0.943** [0.463, 1.423]	1.908 [-0.109, 3.925]

Species	**Model**	**ΔAICc**	**AICc Wt**	**Intercept**	**Grazing**	**16-day NDVI**	**Year**
Wolf	Competition 4	0.6095	.0855	-5.553 [-7.544, -3.562]	--	**0.734** [0.304,1.164]	1.991 [-0.210, 0.199]
Wolf	Competition 5	1.1500	.0653	-5.289 [-7.375, -3.204]	**0.915** [0.070, 1.760]	**0.840** [0.374, 1.305]	1.208 [-0.833, 3.248]
Wolf	Competition 6	1.5556	.0533	-5.919 [-7.958, -3.880]	**0.960** [0.118, 1.801]	**0.805** [0.354, 1.256]	**2.028** [0.015, 4.042]
Wolf	Competition 7	1.7713	.0478	-3.230 [-3.637, -2.824]	--	--	--

Occupancy Process (a)

Species	**Model**	**ΔAICc**	**AICc Wt**	**Intercept**	**NDVI**	**Distance to Stream**	**Elevation**
Coyote	Competition Averaged	--	--	0.780 [-2.260, 3.820]	0.020 [-0.230, 0.280]	0.030 [-0.204, 0.300]	0.260 [-0.770, 1.280]
Coyote	Competition 1	0.000	0.116	1.573 [0.029, 3.117]	--	--	--
Coyote	Competition 2	0.038	0.114	-0.887 [-2.179, 0.405]	--	--	--
Coyote	Competition 3	0.237	0.103	-0.889 [-2.186, 0.408]	--	--	--
Coyote	Competition 4	0.610	0.086	2.347 [0.550, 4.145]	--	--	**1.069** [0.075, 2.063]
Coyote	Competition 5	1.150	0.065	1.599 [0.049, 3.149]	--	--	--
Coyote	Competition 6	1.556	0.053	2.397 [0.560, 4.214]	--	--	**1.096** [0.065, 2.127]

Species	**Model**	**ΔAICc**	**AICc Wt**	**Intercept**	**NDVI**	**Distance to Stream**	**Elevation**
Coyote	Competition 7	1.771	0.048	0.707 [-0.211, 1.626]	0.303 [-0.370, 0.977]	0.356 [-0.321, 1.033]	--
Wolf	Competition Averaged	--	--	-34.9 [-328.5, 258.8]	6.060 [-94.9, 107.1]	6.590 [-102.7, 115.9]	52.2 [-334.1, 438.4]
Wolf	Competition 1	0.000	0.116	-48.6 [-146.7, 49.5]	--	--	--
Wolf	Competition 2	0.0383	0.114	-46.8 [-155.6, 62.0]	--	--	--
Wolf	Competition 3	0.237	0.103	-68.9 [-364.8, 227.0]	--	--	--
Wolf	Competition 4	0.610	0.086	55.3 [-84.2, 194.9]	--	--	201.4 [-307.2, 709.9]
Wolf	Competition 5	1.150	0.065	-72.1 [-224.3, 80.1]	--	--	--

Species	**Model**	**ΔAICc**	**AICc Wt**	**Intercept**	**NDVI**	**Distance to Stream**	**Elevation**
Wolf	Competition 6	1.5556	0.0533	68.3 [-199.7, 336.2]	--	--	249.1 [-671.7, 1170]
Wolf	Competition 7	1.7713	0.0478	-125.3 [-842.7, 592.1]	74.0 [-250.5, 398.6]	80.6 [-270.1, 431.3]	--

Occupancy Process (b)

Species	**Model**	**ΔAICc**	**AICc Wt**	**Aspect**	**Slope**	**Human Use**	**Year**
Coyote	Competition Averaged	--	--	0.000 [-0.370, 0.360]	0.430 [-0.830, 1.690]	0.290 [-0.760, 1.340]	56.0 [-5456, 5568]
Coyote	Competition 1	0.000	0.116	-0.015 [-33.9, 105.5]	--	0.774 [-12.47, 44.9]	9.558 [-9.718, 28.8]
Coyote	Competition 2	0.038	0.114	--	**1.162** [0.175, 2.150]	--	-2.065 [-4.160, 0.030]
Coyote	Competition 3	0.237	0.103	--	**1.177** [0.179, 2.174]	--	-2.111 [-4.230, 0.008]
Coyote	Competition 4	0.610	0.086	--	--	0.191 [-0.431, 0.812]	1.323 [-0.161, 2.807]
Coyote	Competition 5	1.150	0.065	-0.011 [-.660, 0.637]	--	0.801 [-0.560, 2.162]	488.2 [-15986, 16962]
Coyote	Competition 6	1.556	0.053	--	--	0.198 [-0.430, 0.825]	1.335 [-0.170, 2.841]

Species	**Model**	**ΔAICc**	**AICc Wt**	**Aspect**	**Slope**	**Human Use**	**Year**
Coyote	Competition 7	1.771	0.048	--	--	--	1.040 [-0.619, 2.699]
Wolf	Competition Averaged	--	--	12.96 [-48.5, 74.4]	-60.2 [-470.6, 350.2]	19.6 [-96.2, 135.3]	278.8 [-5294, 5851]
Wolf	Competition 1	0.000	0.116	35.8 [-33.9,105.5]	--	16.21 [-12.47, 44.9]	138.7 [-137.6, 414.9]
Wolf	Competition 2	0.038	0.114	--	-132.3 [-452.1, 187.5]	--	281.3 [-1446, 2009]
Wolf	Competition 3	0.237	0.103	--	-195.6 [-1033, 641.3]	--	412.6 [NA]
Wolf	Competition 4	0.610	0.086	--	--	53.0 [-93.4, 199.4]	127.6 [-192.7, 447.9]
Wolf	Competition 5	1.150	0.065	52.5 [-55.6, 160.5]	--	23.2 [-21.7, 68.1]	671.2 [-15783, 17126]

Species	**Model**	**ΔAICc**	**AICc Wt**	**Aspect**	**Slope**	**Human Use**	**Year**
Wolf	Competition 6	1.556	0.053	--	--	66.0 [-226.8, 358.9]	157.9 [-423.5, 739.4]
Wolf	Competition 7	1.771	0.048	--	--	--	193.2 [-753.8, 1140]

Occupancy Process (Interactions)

Model	**Competition Averaged**	**Comp. 1**	**Comp. 2**	**Comp. 3**	**Comp. 4**	**Comp. 5**	**Comp. 6**	**Comp. 7**
Coyote:Wolf Intercept	-56.0 [-5568, 5568]	-10.012 [-29.2, 9.164]	**3.549** [1.087, 6.011]	**3.602** [1.112, 6.092]	**-3.048** [-5.226, -0.870]	-488.6 [-16962, 15985]	**-3.090** [-5.307, -0.873]	-1.177 [-3.016, 0.662]

Five-species Model

Detection Process

Species	**Model**	**ΔAICc**	**AICc Wt**	**Intercept**	**Grazing**	**16-day NDVI**	**Year**
Bear	Community 1	0.000	0.674	-2.367 [-2.904, -1.829]	0.403 [-0.006, 0.813]	0.191 [-0.020, 0.402]	0.456 [-0.091, 1.002]
Coyote	Community 1	0.000	0.674	-1.661 [-2.090, -1.232]	0.142 [-0.274, 0.558]	-0.002 [-0.201, 0.198]	-0.012 [-0.481, 0.456]
Mule Deer	Community 1	0.000	0.674	-0.082 [-0.306, 0.142]	**0.590** [0.315, 0.865]	**-0.127** [-0.244, -0.011]	**0.452** [0.198, 0.707]
Elk	Community 1	0.000	0.674	-1.010 [-1.450, -0.750]	-0.259 [-0.600, 0.081]	**-0.209** [-0.361, -0.057]	0.039 [-0.334, 0.414]
Wolf	Community 1	0.000	0.674	-6.272 [-8.260, -4.285]	**0.909** [0.059, 1.759]	**0.831** [0.390, 1.271]	**2.334** [0.314, 4.355]

Occupancy Process

Species	**Intercept**
Bear	-78.3 [-4297, 4141]
Coyote	0.481 [-3.207, 4.169]
Mule Deer	-54.1 [NA]
Elk	-113.1 [-2437, 2211]
Wolf	-12.390 [NA]

Occupancy Process (Interactions)

Species Interaction	**Intercept**
Bear:Coyote	0.488 [-1.495, 2.470]
Bear:Mule Deer	79.4 [-4140, 4298]
Bear:Elk	65.3 [-4150, 4281]

Species Interaction	**Intercept**
Bear:Wolf	-65.2 [-4281, 4151]
Coyote:Mule Deer	54.6 [NA]
Coyote:Elk	3.722 [-10.195, 17.639]
Coyote:Wolf	-58.5 [NA]
Mule Deer:Elk	41.7 [NA]
Mule Deer:Wolf	68.5 [-3435, 3572]
Elk:Wolf	71.1 [-4144, 4287]