



Federal Aid in Wildlife Restoration Grant W-188-R *Annual report, September 2026*

Integrated Elk Management in Montana

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State: Montana

Agencies: Fish, Wildlife & Parks and University of Montana

Grant: Evaluating Habitat, Carnivore Abundance and Elk Vital Rates in Pilgrim Creek

Grant #: W-188-R

Time Period: *July 1, 2025 – July 1, 2026*

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Executive Summary

Montana Department of Fish, Wildlife, and Parks (FWP) and the Montana Fish & Wildlife Commission are statutorily obligated to manage elk population sizes within ranges specified in the Montana elk management plan; however, the efficacy of FWP management prescriptions and Commission decisions to meet this obligation is hampered by uncertainty about the drivers of elk populations and distributions in different ecological systems. The broad objective of this project is to develop the necessary components for an adaptive management program focused on management of elk populations and distributions in northwest Montana that will help FWP and the Commission manage elk populations and meet statutory obligations.

To initiate this program, we are establishing an adaptive management framework in hunting district (HD) 121, located in northwestern Montana, which includes 1) predicting how hunting, carnivores and habitat may influence elk population and distribution objectives, 2) monitoring habitat conditions, hunter access, elk vital rates, elk distributions and carnivore abundance for 3 years, 3) updating model predictions and reducing uncertainty in predictions for northwest Montana based on monitoring data, and 4) developing a framework for extending the adaptive management program to elk in different regions of Montana. The goal of developing this type of program is to better understand what types of factors influence elk populations and distributions in different ecological systems and develop management programs that integrate habitat management, carnivore harvest, and elk harvest recommendations to achieve elk population objectives.

To identify the current state of elk populations in northwestern Montana, we developed an integrated population model (IPM) that integrates available count and harvest data, and vital rate information from this study to estimate elk population trends, vital rates, and the factors affecting vital rates/population trends in HD 121. Overall, the model suggested that elk populations have been relatively stable or slightly increasing since 2013, with estimated total population sizes averaging approximately 1,790 individuals (339 calves, 1,225 adult females, and 226 adult males) and geometric mean $\lambda = 1.014$ (95% credible interval [CrI] = 1.005 – 1.026). Mean estimated annual natural survival (excluding harvest) of adult elk (≥ 1 year old) from 2013 – 2025 was 0.98 (95% CrI = 0.92 – 1.00), while mean annual natural survival of calves (< 1 year old) was 0.36 (95% CrI = 0.23 – 0.53). Estimated mean harvest rates of adult females, adult males available for harvest (i.e., possessed brow tines), and calves were 0.064 (95% CrI = 0.050 – 0.080), 0.70 (95% CrI = 0.42 – 0.93), and 0.0054 (95% CrI = 0 – 0.016), respectively.

We did not find strong associations of abiotic (winter severity) or biotic factors (nutritional landscape and indices of predator abundance) with calf or adult survival. The lack of evidence for influential factors on survival is likely related to the relatively short time series we evaluated and the somewhat limited annual variability in survival and covariates during that period. Further, the coarseness of this analysis (i.e., associations of population-level survival with HD-level covariates) may limit our ability to identify true relationships if they exist.

In addition to monitoring elk populations, there is shared interest of wildlife managers, public land managers, hunters using public lands, and private landowners in identifying factors affecting elk distributions during autumn hunting seasons. Thus, we used elk location data from

autumn 2023-2025 to identify what resources elk use and how those resources change throughout 4 hunting periods: “prehunt” (August 1 – September 1, 2023; August 1 – September 6, 2024; August 1 – September 5, 2025), “archery” (September 2 – October 15, 2023; September 7 – October 20, 2024; September 6 – October 19, 2025), “rifle” (October 21 – November 26, 2023; October 26 – December 1, 2024; October 25 – November 30, 2025), and “posthunt” (i.e., post-general rifle season; November 27 – December 31, 2023; December 2 – December 31, 2024; December 1 – December 31, 2025). Using three years of data from 133 females (123 adults and 10 yearlings) and 28 males (17 adults and 11 yearlings), we found both males and females became less accessible for harvest (lower proportion of locations on public lands or BMAs) during rifle season; although, there was considerable variability among elk. Average canopy cover, distance to road, and slope used by females also tended to decline in a similar pattern as accessibility, suggesting some elk moved out of forested, steep areas on public lands to low-elevation private lands as hunting seasons progressed. Males followed similar use patterns as females, except differences between hunting periods were more subtle and distance to road increased between archery and rifle seasons.

While there was high variability in selection across individuals, elk generally selected for greater canopy cover, greater distances from roads, and greater forage digestible energy while generally avoiding steeper slopes, terrain ruggedness, and solar radiation during archery and rifle seasons. Elk selection was weaker and more variable for forage biomass and snow water equivalent. Male and female elk selected strongly for accessible lands during the archery season and inaccessible lands during the rifle season. Additionally, male and female elk responses to categories of timber harvest varied significantly, but elk generally avoided areas of more recent timber harvest and selected unharvested forest throughout hunting seasons.

While there were fewer elk locations within accessible areas during the rifle season and elk generally selected for lands with restricted access, a large proportion of elk remained on public lands the majority of the time. Approximately 85% of females and 97% of males were on accessible lands at least half the time during daylight hours in archery season. This percentage dropped to 61% of females during rifle season, while male accessibility dropped to 72%.

To improve our understanding of elk population dynamics, demographic processes, and distributions, we began a monitoring program that included collaring elk and carnivores; estimating elk and carnivore abundance; and measuring the elk nutritional landscape in HD 121. Since December 21, 2022, we have captured and collared 178 elk ≥ 6 months old (124 adult females, 16 female calves, 25 adult males, 13 male calves) with global positioning system (GPS) radio-collars programmed to record a location every 2 hours. As of July 1, 2026, we have collected 1,200,167 locations from these individuals. So far, 42 collared elk > 1 year old have died; 8 due to natural causes (7 adult females, 1 adult male); 11 due to predation by either mountain lions (5 adult females, 2 adult males), wolves (1 adult female, 2 adult males), or unknown predators (1 adult female); 19 due to hunter harvest (9 adult females, 10 adult males), and 4 adult females due to unknown causes. Three additional mortalities (2 adult females, 1 adult male) occurred during capture operations, but these individuals were never included in the sample. Thirty-six collars (6 males and 30 females) have malfunctioned after deployment (stopped collecting and transmitting locations) and 34 collars (28 adult female, 3 adult male, 3 yearling male) dropped as scheduled. Pregnancy rates (adults and yearlings combined) ranged

from 75.8% (95% CI = 60.6% - 90.9%) in 2025 to 87.5% (95% confidence interval [CI] = 77.1% - 95.8%) in 2023. Across years, pregnancy rates were ~84% with yearlings included and 88% with yearlings excluded (i.e., only adults).

We captured and collared 156 elk neonates (95 males and 61 females) with expandable GPS collars in May and June, 2023 - 2025. Since 2023, 69 collared calves (<1 year old) have died (15 mountain lion predation, 15 black bear predation, 2 coyote predation, 1 wolf predation, 4 unknown predation, 7 natural mortality, 3 human harvest, 5 human-related mortality [non-harvest, e.g., vehicle collision], 7 capture-related mortality, and 10 unknown cause). Thirty collars fell off prematurely (active <6 months), 5 collars dropped as scheduled, 20 failed to send GPS locations within a year after deployment, and 24 collars failed to send GPS locations after 1 year of deployment (i.e., past the expected deployment timeframe). We conducted 4 capture efforts (2 helicopter and 2 ground) in winter/spring 2025/26 to recapture elk collared with neonate collars to remove collars that were not dropping in the timeframe expected. We removed 10 collars from elk (6 male and 4 female) as a part of this effort.

In summer 2022, FWP captured and collared a subadult male wolf. This individual emigrated from the study area in December 2022 and was later harvested. During summer 2024 and 2025, FWP collared an adult female wolf and an adult male wolf, respectively. The male collar failed in autumn 2025 and the collared female remains active. During January and February 2023 and 2024, we captured and collared 9 mountain lions (7 females, 2 males). As of July 1, 2026, we collected a total of 22,455 locations from these individuals. One collared adult female mountain lion died due to natural causes in January 2024, 5 mountain lions were harvested in winter 2024-2025 (2 males, 3 females), 1 adult female died due to unknown causes in September 2025, 1 adult female dropped its collar as programmed, and 1 collar failed in May 2025. Since summer 2023, we have captured and collared 1 female and 6 male black bears and collected 9,801 locations from these individuals. One adult male black bear dropped its collar during 2023-24 winter hibernation and was then harvested in May 2024, one adult male died of unknown causes in August 2024, and 4 males dropped their collars. The remaining collared bear likely dropped its collar while in the den last winter, but the collar has not yet been retrieved.

In May and June 2023, we deployed trail cameras at sites randomly located throughout HD 121 to estimate elk and carnivore abundance. At half of these random sites, we placed a “predator camera” on a dirt bottom trail within 250 meters of the random site to increase the likelihood of detecting predators. At each site, we mounted trail cameras to trees or t-posts approximately 1.5 meters off the ground at optimal angles for elk and carnivore species. We set each camera on both “time lapse” and “motion capture” trigger settings to capture images every 10 minutes and when motion triggered the camera. In total, we deployed 80 random cameras paired with 39 predator cameras across HD 121. These cameras were serviced (batteries and SD cards changed) in September/October 2023, May/June 2024, and September/October 2024, and cameras were retrieved in July/August 2025. Preliminary results from summer 2023 and winter 2023-24 suggested estimates of elk, white-tailed deer, mule deer, and black bear abundance varied by time period, camera arrangement (random or non-random), and by the abundance estimator used. We did not estimate abundance for mountain lions or wolves during summer 2023 or winter 2023-24 because we obtained no timelapse photos of these species during those analytical

periods. This reporting period, we classified photos from 50 cameras from winter/spring 2024/2025 and continue to classify the remaining photos.

To understand elk habitat conditions and evaluate the effects of timber harvest history on elk nutritional resources and resource use in HD 121, we generated 375 random sites each year that were spatially-distributed within unique landcover strata combinations of landcover type, timber harvest strategy, and years-since-harvest, with the intent to sample vegetation at each location once from May – August 2023 and 2024. We also collected elk fecal pellet samples each week from May through August to determine important forage species for elk in HD 121. We measured vegetation and collected biomass samples at 222 sites from May – August, 2023 and 224 sites from May – June, 2024 (ranging from 2 – 14 sites per landcover strata). We submitted 14 composite samples representing 14 weeks of elk diet in 2023, and 6 composite samples representing 6 weeks of elk diet in 2024 to determine preferred forage species. We also collected 6 composite fecal pellet samples (3 in lower valley, 3 in higher forest) in winter 2022-23.

The mean preferred summer forage biomass across sampling points was 242.60 kg/ha (1st – 3rd quartiles: 73.89 – 333.02) and varied by landcover type, time-since-harvest, and harvest strategy. Mean preferred forage biomass was slightly higher in even-age cuts than in intermediate cuts with means of 259.6 kg/ha and 220.65 kg/ha, respectively, which was higher than in unharvested forest with a mean of 155.637 kg/ha. Mean preferred forage biomass was highest 1-5 years post-harvest with a mean of 370.10 kg/ha and steadily declined across harvest age classes until arriving at the low levels of unharvested forest. Though digestible energy of preferred forage (DE) in mesic forests was on average 7.1% lower than dry forests, mesic forests harvested within the past 1-5 years saw an increase in DE of approximately 7.2%, effectively bringing DE levels to those of dry forests. Compared to agriculture and grasslands, our models predicted DE to remain much more stable in forests as summer progressed. Thus, by mid-summer, predicted DE levels in dry and recently harvested mesic forests surpassed those of agriculture and grasslands as plants in the open landcovers senesced and forage quality declined. We found that while 1-5 year-old harvest of dry and mesic forests was one of our highest strata in terms of predicted preferred forage biomass, it was far outclassed by grasslands and agriculture for much of the summer. By late summer, however, the predicted preferred forage biomass of these 1-5 year-old cutblocks was more similar to the predicted forage biomass of agriculture.

We also combined elk nutrition data collected from other studies in Montana to develop a model that predicts annual elk and mule deer forage quality and quantity across western Montana from 2012 – 2025 using remotely sensed data. We are using these model predictions as covariates in resource selection analyses and population models to identify how forage quality/quantity affects elk distributions and population dynamics.

We used location data obtained from 92 collared adult female elk to estimate elk resource selection in early (May-June) and late (July-August) summer during crepuscular (dawn/dusk) and daytime periods using resource selection probability functions. We found elk were more likely to use areas in vegetation cover/harvest types associated with higher nutritional metrics (e.g., 1-5 year-old timber harvest and agriculture [in early summer]) during dawn and dusk in early and late summer, time periods when elk are expected to be primarily foraging. Elk were more likely to use areas associated with higher cover (i.e., older harvested forest stands,

unharvested forests) during the day, a time period when their decision-making may be more influenced by considerations of risk avoidance and thermoregulation. Elk use of timber harvest strata was particularly pronounced during late summer, when they switched their patterns of use to avoid agriculture.

The results provided here outline our progress in this project through July 1, 2026.

Project Background and Objectives

Elk (*Cervus canadensis*) management is a high priority to a variety of stakeholders in Montana, due to their popularity as a game species and their wildlife viewing opportunities. Montana Department of Fish, Wildlife, and Parks (FWP) and the Montana Fish & Wildlife Commission are statutorily obligated to manage elk population sizes within ranges specified in the Montana elk management plan; however, the efficacy of FWP management prescriptions and Commission decisions to meet this obligation is hampered by uncertainty about the drivers of elk populations and distributions in different ecological systems. Additionally, the outcomes of FWP management prescriptions and Commission decisions are not always completely predictable because individual decisions by landowners and hunters also affect elk populations and distributions.

Adaptive management programs that emphasize “learning while doing” have been proposed to address uncertainty and improve management outcomes through an iterative learning process that promotes flexible decision making when new data are available (e.g., Williams et al. 2009). An effective adaptive management program for elk would help FWP and the Commission manage elk populations and meet statutory obligations. Thus, the broad objective of this project is to develop the necessary components for an adaptive management program focused on management of elk populations and distributions in northwest Montana. These components include: 1) predicting how hunting, carnivores, and habitat may influence elk population and distribution objectives; 2) monitoring habitat conditions, hunter access, elk vital rates, elk distributions, and carnivore abundance for 3 years; 3) updating model predictions and reducing uncertainty in predictions for northwest Montana based on monitoring data; and 4) developing a framework for extending the adaptive management program to elk in different regions of Montana. This program will help identify what factors influence elk populations and distributions in different ecological systems and develop management programs that integrate habitat management, carnivore harvest, and elk harvest recommendations to achieve elk population objectives.

Ungulate populations are affected by many biotic and abiotic factors, including predation (e.g., Hebblewhite et al. 2002, Creel et al. 2007, Hebblewhite et al. 2018, Tatman et al. 2018, Horne et al. 2019, Proffitt et al. 2020, Berg et al. 2022), habitat/nutrition (Parker et al. 2009, Cook et al. 2016, Proffitt et al. 2016a), and climatic conditions (Wang et al. 2002, Garrot et al. 2003; Hebblewhite 2004; Schooler et al. 2022). However, the contribution of these factors on ungulate population dynamics are often interconnected and can vary across ecosystems with different habitats, carnivore communities, climatic conditions, and hunting regulations (Wang et al. 2009, Proffitt et al. 2014, Proffitt et al. 2020, Trump et al. 2022). To achieve ungulate population abundance goals and address concerns regarding effects of predation, carnivore management programs designed to reduce carnivore populations and increase ungulate recruitment and population growth have been implemented in a variety of ecological systems (e.g., Boertje et al. 1996, Hayes et al. 2003, Schwartz et al. 2003, White et al. 2010, Hurley et al. 2011, Keech et al. 2011, Proffitt et al. 2020). However, the effectiveness of these management programs on ungulate populations has varied across studies and time, highlighting the need for wildlife managers to better understand the uncertainties associated with the effects of predators, and the contribution of other factors on ungulate populations.

The first goal of this project is to develop an adaptive management framework for reducing uncertainty in predicting elk population trajectories and for better understanding the biological effects of integrated habitat-carnivore-ungulate management in northwest Montana (i.e., Region 1; Figure 1). Elk-carnivore studies in Region 3 of Montana revealed the important role of predation from multiple carnivores, particularly gray wolves (*Canis lupus*) and grizzly bears (*Ursus arctos horribilis*), simultaneously limiting elk vital rates and population growth (e.g., White and Garrott 2005, Proffitt et al. 2014). Yet, in Region 2, elk-carnivore studies found mountain lion (*Puma concolor*) predation, and to a lesser extent habitat conditions, limited elk vital rates and population growth (Proffitt et al. 2020). Further, other studies in Montana have demonstrated that habitat/nutrition (e.g., Proffitt et al. 2016a), climatic conditions (Creel and Creel 2009), and the interactions between climate and predation (Wilmers et al. 2020) can affect elk populations and demographic rates. Currently, it is uncertain how different carnivore communities interact with factors such as habitat and weather to influence elk population dynamics in different ecological systems, such as northwest Montana. Thus, additional elk vital rate data from northwest Montana is required to reduce uncertainty in predicting regional elk population trajectories. This effort initially relied on elk vital rate and population dynamics data from other regions in Montana and Idaho to forecast elk population dynamics in northwest Montana. The model now uses elk vital rate data from northwest Montana collected as part of this study to reduce uncertainties in northwest Montana elk population predictions.

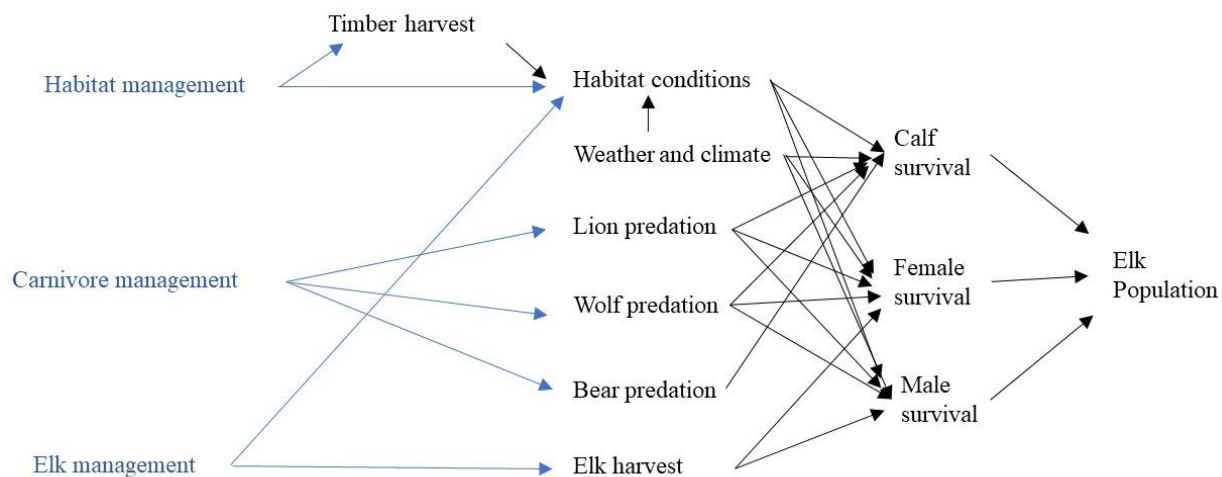


Figure 1. A conceptual model of factors influencing elk population dynamics.

Our second goal of this project is to develop an adaptive management framework for reducing uncertainty in predicting elk distributions and better understand how carnivores, habitat, harvest regulations, and hunter access management influence elk distribution. The distribution of elk across public and private lands provides additional challenges for managing elk populations (Haggerty and Travis 2006) because not all elk may be available for harvest, depending on hunter access management. Even within desired population abundances, problematic distributions of elk across the landscape may increase property damage on private lands and hunter frustrations when elk are not available on public lands (Burcham 1956, Haggerty and

Travis 2006, Krausman et al. 2014, Fontaine et al. 2019, Gruntorad and Chizinski 2020), resulting in harvest that is too low to meet social objectives related to hunter satisfaction. Thus, achieving an acceptable distribution of elk across public and private lands is also required for more effective elk management. FWP has collected elk movement data during the hunting season in > 20 populations across Montana, and these previous studies commonly identify hunter access management as an important driver of elk distributions during the hunting season (e.g., Proffitt et al. 2013, Proffitt et al. 2016b, Ranglack et al. 2017, DeVoe et al. 2019, Lowrey et al. 2020, Snobl et al. 2024). However, there are many diverse factors including landscape features and harvest regulations that also influence elk distributions, creating uncertainty about which set of factors influence elk distributions in different landscapes. In northwest Montana, we predict timber management history (Ruprecht et al. 2023), and the effects on forest successional stage (Irwin and Peek 1983, Proffitt et al. 2019, Monzingo et al. 2023), will be an important driver of habitat conditions and elk distributions. However, little information on the effects of timber management history on elk distributions is available. Therefore, our goal for northwestern Montana is to monitor elk movements, carnivore distributions, habitat conditions, and hunter access and develop elk distribution models that incorporate both the effects of timber harvest management and hunter access (Figure 2). This model will then be used to refine predictions of the effects of changes in habitat management or hunter access on elk distributions in northwest Montana.

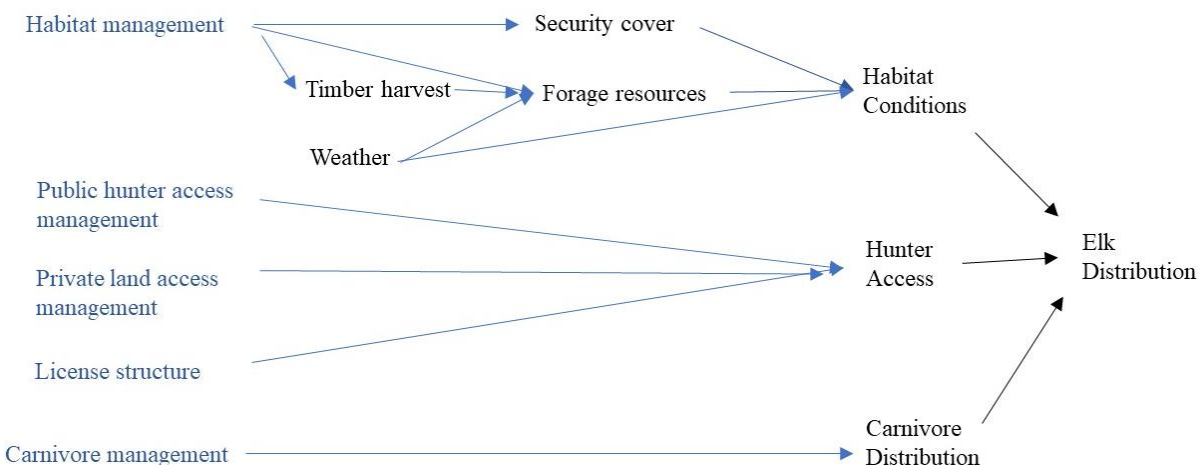


Figure 2. A conceptual model of factors influencing elk distributions during the fall hunting seasons.

We will formally integrate research findings with the northwestern Montana elk and carnivore management programs in a way that will improve FWP and partners' ability to meet elk population and distribution objectives in the future. This study will support development of analytical tools to forecast elk populations and distributions, monitor populations and distributions in northwest Montana, and integrate monitoring results into revised models predicting elk populations and distributions in northwest Montana (Figure 3). This adaptive management framework and the analytical tools developed will be transportable to other areas in

Montana, so that adaptive management and the associated learning can continue and be implemented around the state.

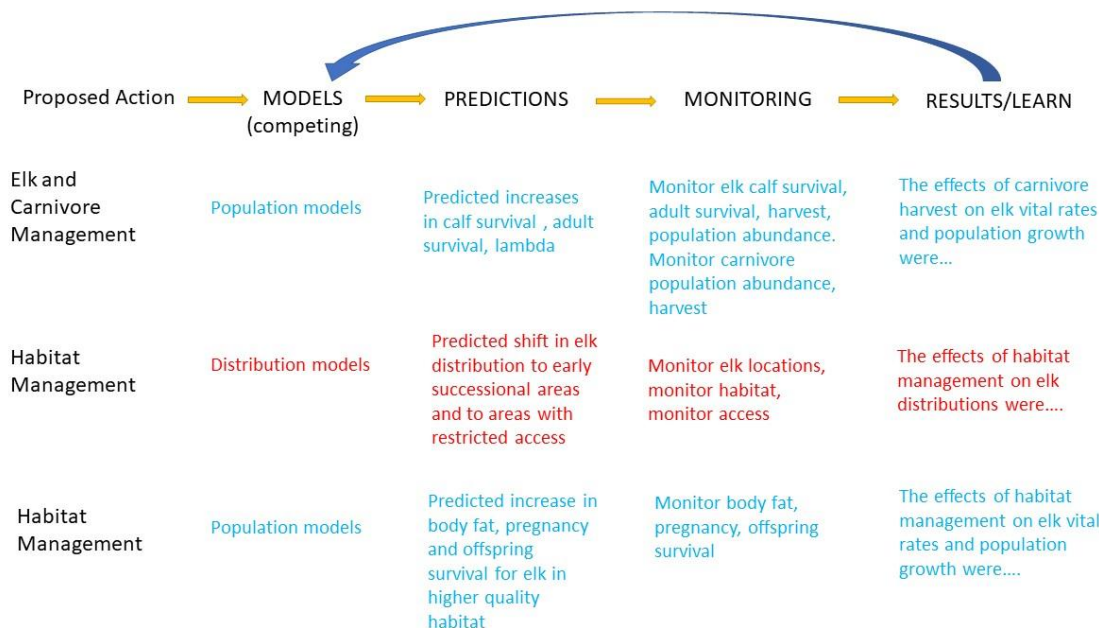


Figure 3. Conceptual diagram of the proposed study design and adaptive learning framework.

The objectives of this project include:

1. Based on past research findings, develop predictive models of elk population dynamics in northwest Montana, including the effects of habitat, elk, and carnivore management decisions.
2. Based on past research findings, develop predictive models of elk hunting season distributions in northwest Montana, including the effects of forest disturbance and hunter access.
3. Design monitoring programs for elk and carnivores that will provide necessary information to evaluate the effects of management actions, as they are implemented on elk population dynamics and hunting season distributions.
4. Integrate findings from the monitoring program into predictive models, such that predictions of elk population dynamics and hunting season distribution become more accurate in the future in northwest Montana and can be exported to other regions of Montana.

Study Location

The study area is defined by the administrative boundary of Hunting District (HD) 121, which is in the Noxon – Thompson Falls area of Sanders County, Montana (Figure 4) and includes the annual range of the Pilgrim Creek elk population. The majority of HD 121 is public land managed primarily by the Kootenai National Forest Cabinet Ranger District, and the lower elevation valley bottom is dominated by private properties. Timber harvest has been common in the study area for decades, although the number of acres harvested per year has declined since the 1980's (Hayes et al. 2021). The forests in the study area are largely dominated by fir (*Abies* spp.), spruce (*Picea* spp.), or Douglas fir (*Pseudotsuga menziesii*). The average minimum elk count over the past 10 years in HD 121 is approximately 1,533 animals and average observed recruitment is approximately 22 calves per 100 adult females. Carnivores include black bear (*Ursus americanus*), mountain lion, and gray wolves.

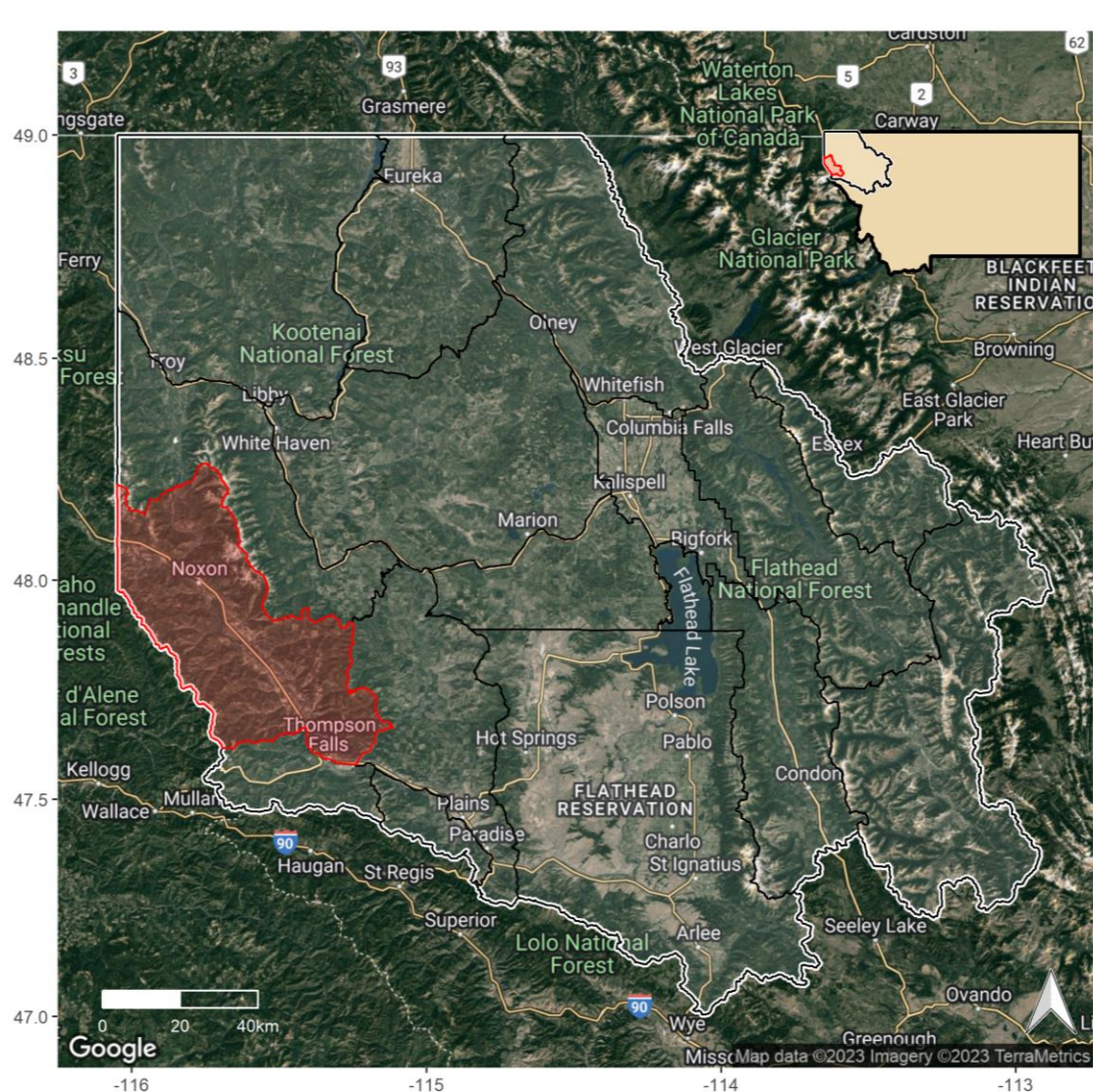


Figure 4. Location of the study area (hunting district 121; red area) within Region 1 (white area) in northwest Montana. Black lines represent borders of elk and deer hunting districts.

Objective #1: Based on past research findings, develop predictive models of elk population dynamics in northwest Montana, including the effects of habitat, elk, and carnivore management decisions.

1.1 Background

Elk population monitoring in Region 1 primarily consists of aerial- or ground-based counts and estimates of hunter harvest via phone surveys. These monitoring methods provide the information necessary for managers to monitor elk populations relative to their objective as defined in the 2023 state Elk Management Plan, but provide less information regarding demographic rates or the factors driving population trends. Due to the difficulty in counting elk in densely forested areas, only portions of the area with good visibility are surveyed and trends in these counts are tracked over time as an index of population performance. Past monitoring methods were not designed to estimate population size or for use in population modeling.

Population models use existing knowledge of life history characteristics and demographic processes of a species to describe and predict population dynamics. Thus, these models can be powerful tools for wildlife biologists and managers to assess the status and trends of wildlife populations, determine the drivers of observed trends (e.g., habitat, predators, disturbance), and predict the outcomes of proposed management actions. Integrated population models (IPMs) have become increasingly more common (Schuab et al. 2004, Johnson et al. 2010, Eacker et al. 2017, Paterson et al. 2022a) because IPMs jointly analyze datatypes which provide insight into the factors influencing population growth and overall population demography (Schuab and Abdai 2011). Further, managers can use IPMs to forecast the consequences of management actions by projecting population trends under different management scenarios. This allows managers to develop management plans based on the observed population vital rates and identify the management actions predicted to be most effective for meeting population objectives. Thus, our first research objective was to develop an IPM with available count and harvest data to estimate elk population trends, vital rates, and the factors affecting vital rates/population trends in HD 121.

While this objective (fitting predictive models with historic data) and Objective #4 (incorporating data from this study to improve models) are separate, we decided to combine them in this report to improve clarity of results. We encourage readers to review Hansen et al. (2025) for a more thorough comparison of model outputs before and after auxiliary data were included.

1.2 Data Collection and Description

1.2.1 Elk Observations

Observation data for the IPM consisted of population counts from aerial surveys and harvest estimates from FWP harvest surveys. During March and April each year, observers in a helicopter count the number of elk in at least three age/sex classes, including calves (young of

the year, approximately 10-11 months old), adult females (any female >1 year old), and adult males (any male >1 year old). In recent years, male elk have also been classified into spikes (nearly 2 years old) and brow-tined bulls (>2 years old). Elk that cannot be identified to age/sex are marked as unknown. In HD 121, as well as most HDs in Region 1, counts are not considered a full population census due to low visibility (e.g., Figure 5). Elk harvest estimates also primarily track three age/sex classes (calves, adult females, adult males) and are assumed to represent harvest across the entire hunting district.

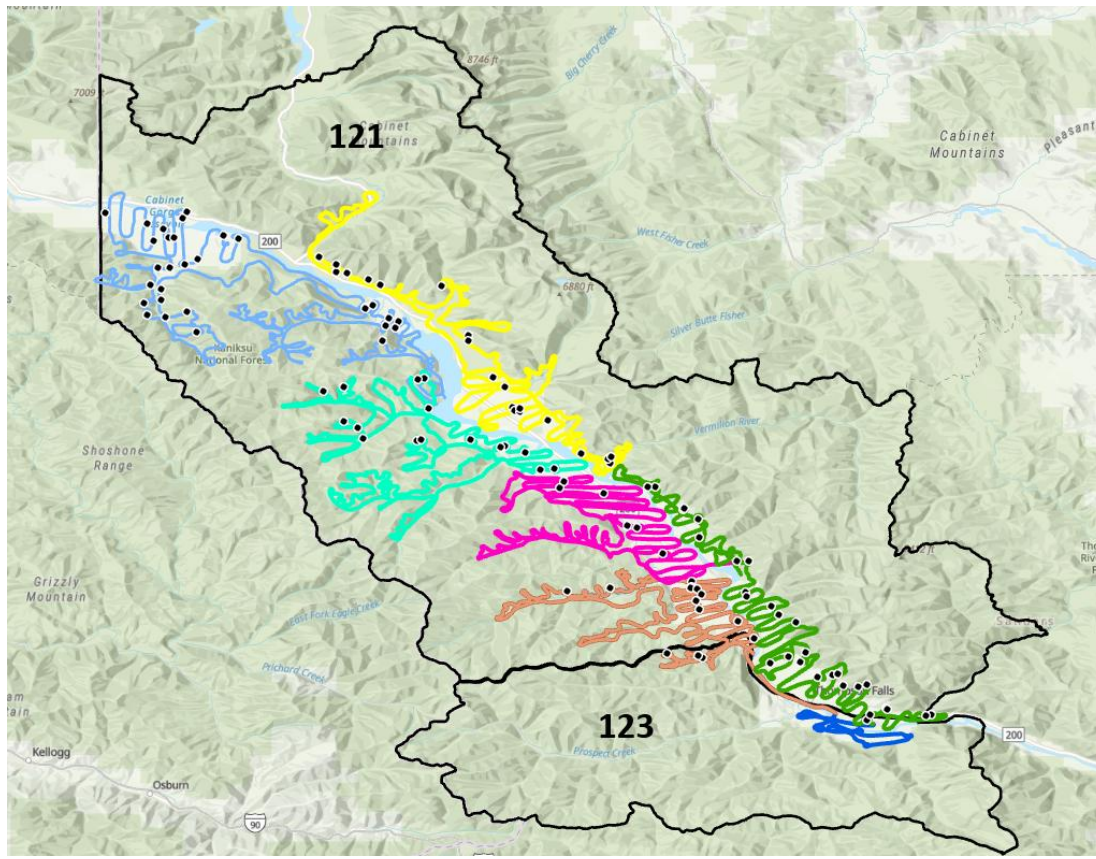


Figure 5. Aerial tracks from elk counts in hunting district 121 and 123 (black borders) in April 2026. Colored lines represent tracks from separate flights completed within approximately one week. Black dots represent locations where elk were observed.

Elk counts since 2005 in HD 121 suggest elk populations have been relatively stable at approximately 1,500 individuals, which is within the population objective range (1,350 – 1,890) outlined in the 2023 Elk Management Plan. However, elk harvest data show that elk harvest, especially adult male harvest, has decreased over time, with a large drop in harvest occurring from 2010 – 2013 (Figure 6). It is largely unknown what factors have caused a drop in harvest, while elk populations appear to be relatively stable. The IPM we developed, in concert with the new data we will collect as part of this study, will help identify the state of elk in HD 121 and Region 1 and identify what factors are most influential on elk population dynamics.

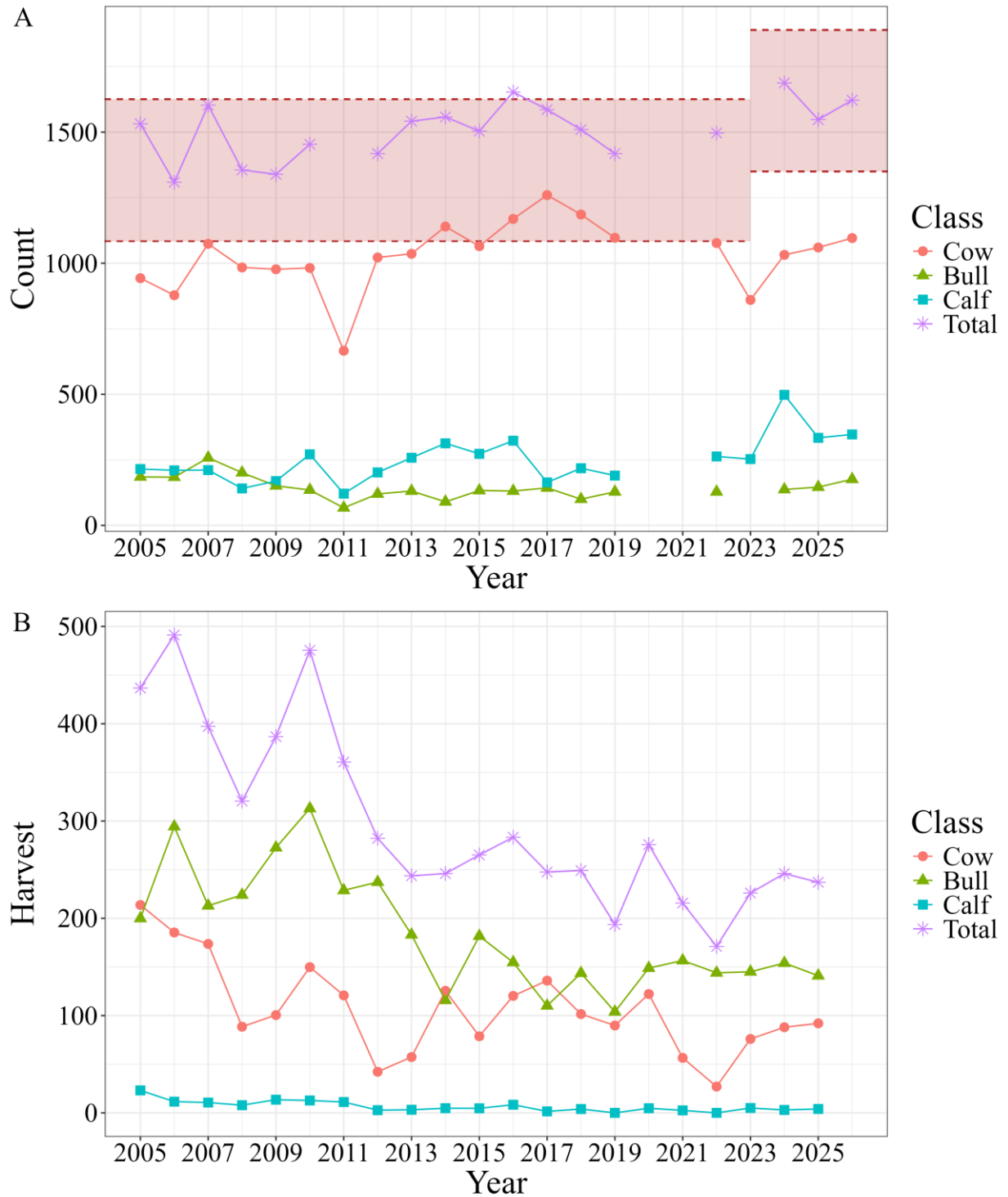


Figure 6. Elk population counts (panel A) and harvest estimates (panel B) for calves (<1 year old) and adult (>1 years old) females and males in hunting district 121 from 2005 – 2026. The red ribbon and dashed horizontal lines in panel A represent the total population objective range. Note, limited aerial surveys were completed in 2011, 2014, 2018, 2020, 2021, and 2023 due either to poor conditions or COVID-19 restrictions.

1.3 Integrated population model development

1.3.1 Population model

Given count data in the region were collected in spring, we defined the population cycle as starting pre-birth, when the age classes observed were calves born the previous spring (approximately 10-11 months old) and “adult” (≥ 22 months old) females and males. Calves observed during aerial counts transitioned to either adult male or adult female classes the following year. A proportion of male calves observed became “available” for harvest (i.e., assumed to possess brow tines, thereby becoming legal to harvest; see below) the following autumn, when they were 1.5 years old; the remaining male calves were assumed to not have brow tines the following autumn, so did not become available for harvest until they were 2.5. Adult females and males stayed within the adult class, and females produced more individuals in the calf class to be observed the following year (Figure 7).

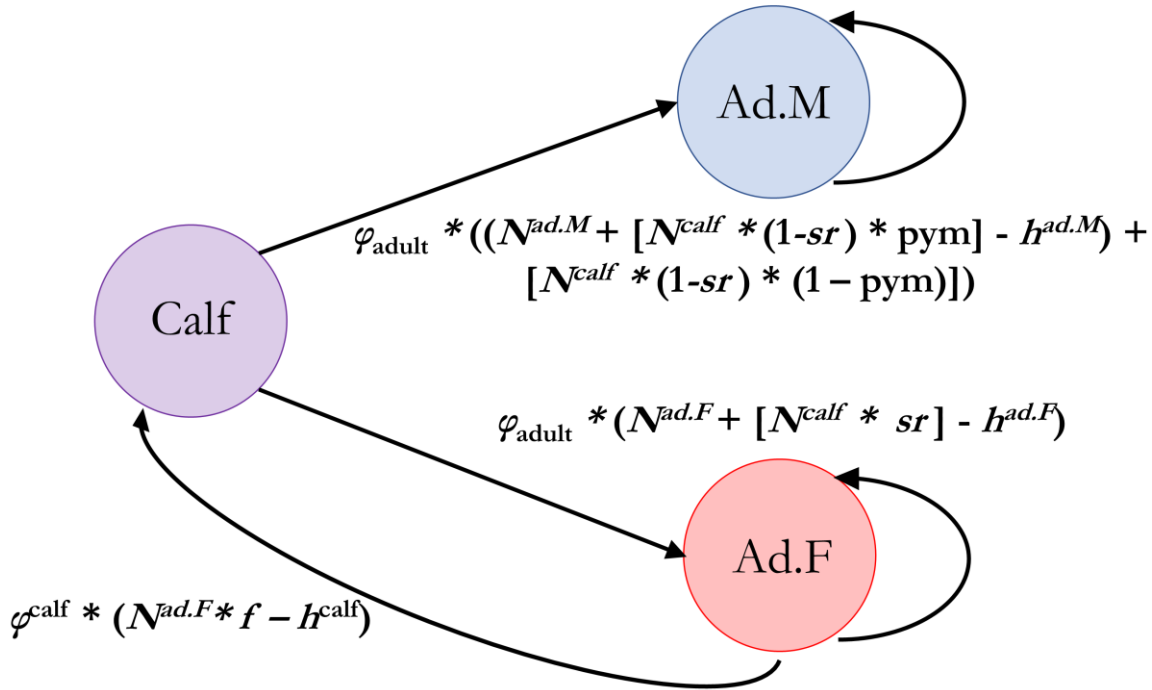


Figure 7. Life cycle diagram demonstrating transition probabilities among sex/age groups included in the integrated population model developed for hunting district 121. sr is the sex ratio at 1 year of age; pym is the proportion of male calves that are legal to harvest as yearlings (i.e., possess brow tines); φ^{adult} and φ^{calf} are annual natural survival of adults (≥ 1 year old) and calves (<1 year old), respectively; h is the harvest number of the designated age/sex class (calf, adult female [ad.F], and adult male [ad.M]); and f is the number of calves produced per adult female, which, assuming 1 calf/pregnant female, reduces down to pregnancy rate.

Thus, the expected number of calves in year t included calves produced in year $t - 1$ that did not get harvested and survived other mortality. Further, the expected number of adult females and males in year t included adult and calf females/males that did not get harvested and survived other mortality in year $t - 1$:

$$\begin{pmatrix} N_t^{calf} \\ N_t^{ad.F} \\ N_t^{ad.M} \end{pmatrix} = \begin{pmatrix} \varphi_{t-1}^{calf} * (N_{t-1}^{ad.F} * f_{t-1} - h_{t-1}^{calf}) \\ \varphi_{t-1}^{ad} * ([N_{t-1}^{ad.F} + N_{t-1}^{calf} * sr] - h_{t-1}^{ad.F}) \\ \varphi_{t-1}^{ad} * \left((N_{t-1}^{ad.M} + [N_{t-1}^{calf} * (1 - sr) * pym] - h_{t-1}^{ad.M}) + [N_{t-1}^{calf} * (1 - sr) * (1 - pym)] \right) \end{pmatrix} \quad \text{Eq. 1}$$

where φ is annual natural survival (excluding harvest), f is the number of calves produced per female, h is the number of individuals harvested, sr is proportion of calves that were female at the time of observation (~10-11 months old), and pym is the proportion of male calves that are available for harvest the following autumn (i.e., possess brow tines). For simplicity, we assumed a 0.5 sex ratio and adult natural survival did not vary by age or sex (e.g., Keller et al. 2015). To determine pym , we consulted check station data and previous literature. If we assume males with 3 points or more on at least one side had brow tines, then check station data in hunting district 121 suggested ~5.4% of 1.5-year-old males (i.e., males that were observed as calves the previous spring in our model) had brow tines. Further, 4.8% of harvested males with 2 points on one or both sides had brow tines (Z. Farley, Montana Fish, Wildlife & Parks, personal communication). Using these criteria, Thelen (1991) and Boyd (1970) suggested ~12% and 8.7% of 1.5-year-old males had brow tines in Washington and Colorado, respectively. Given these data, we assumed 5% of observed male calves possessed brow tines the following autumn, so $pym = 0.05$ each year. If necessary, the pym value could easily be changed, and these changes would only be reflected in male harvest rate estimates (i.e., lower pym values would result in higher harvest rate estimates because fewer males would be available for harvest, but overall male population estimates would not likely change greatly).

We included demographic stochasticity in our population model by assuming the number of individuals in each sex/age class was a realization of a Poisson process with the mean equal to the expected values from Eq. 1 and the variance equivalent to the mean. For example, we estimated the number of calves as:

$$N_t^{calf} \sim \text{Poisson} \left(\varphi_{t-1}^{calf} * (N_{t-1}^{ad.F} * f_{t-1} - h_{t-1}^{calf}) \right) \quad \text{Eq. 2}$$

1.3.2 Observation models

We assumed aerial elk counts were a minimum representation of the true population, so we modeled age/sex counts as a binomial random variable. The binomial model structure is useful when it is assumed that counts represent a minimum population size because it constrains the true population to be equal to (if $p = 1$) or greater than the counts (if $p < 1$), while most other distributions allow the true population size to be less than counts. We set the number of “trials” equal to the latent true population size, the probability of “success” equal to the proportion of

individuals in the population that were counted (p), and the variance equal to $N^{Age/Sex} * p(1 - p)$:

$$\text{Count}_t^{Age/Sex} \sim \text{Binomial}(N_t^{Age/Sex}, p_t^{Age/sex}) \quad \text{Eq. 3}$$

We also assumed adult males would have a different probability of being counted than adult females and calves, so we estimated a separate p for these two age/sex groups.

We modeled harvest observations (h) using a normal distribution with a mean equivalent to the harvest rate (hr) multiplied by the latent true population size immediately after the birth pulse (N), and variance equal to the variance on harvest observations ($h\sigma^2$). For example, we modeled the number of harvested adult females as:

$$h_t^{ad.F} \sim \text{Normal}(hr_t^{ad.F} * [N_t^{ad.F} + N_t^{calf} * sr], h_t^{ad.F} \sigma_t^2) \quad \text{Eq. 4}$$

1.3.3 Incorporating additional data sources

We integrated data collected from this study (see [Section 3.3.1](#)) within the IPM described above. We related elk vital rate and abundance estimates with their associated parameters within the IPM in the year (t) they were collected. For example, we integrated Kaplan-Meier survival estimates from collared individuals (S, σ_S^2) with the IPM survival parameter (ϕ) using a Normal distribution:

$$S_t \sim \text{Normal}(\phi_t, \sigma_{S,t}^2) \quad \text{Eq. 5}$$

We related the number of collared individuals for each age (a) and sex (s) that were harvested ($n.harv$) out of the total number collared ($n.collar$) to the associated harvest rate parameters within the IPM (hr) in the year they were collected using a Binomial distribution:

$$n.harv_t^{a,s} \sim \text{Binomial}(n.collar_t^{a,s}, hr_t^{a,s}) \quad \text{Eq. 6}$$

We related elk STE abundance estimates (see [Section 3.3.7](#)) from randomly-placed trail cameras ($N_c, \sigma_{N_c}^2$) to associated abundance parameters within the IPM (N) using a Normal distribution:

$$N_{c_t} \sim \text{Normal}(N_t, \sigma_{N_{c_t}}^2) \quad \text{Eq. 7}$$

Finally, we related the number of pregnant females ($n.preg$) out of the total females tested ($n.tot$) to associated pregnancy rate parameters within the IPM (f) in the year they were collected using a Binomial distribution:

$$n.preg_t \sim \text{Binomial}(n.tot_t, f) \quad \text{Eq. 8}$$

We fit models using a similar framework as described in Section 1.3.3 and calculated elk abundance, proportion counted, and vital rates from 2013 – 2026.

1.3.4 Covariates

We developed link functions for calf survival, adult survival, and harvest rate parameter, which allowed for the addition of covariates that explained variation in the response. To evaluate how biotic and abiotic factors may have affected elk populations over the past two decades, we collected data related to predators, nutrition, and abiotic processes. We collected similar covariates as those used and described in Paterson et al. (2019), including indices of black bear, mountain lion, and wolf populations; spatiotemporally explicit estimates of elk forage biomass and DE as measures of nutrition (see [Section 3.2.7](#)); and a measure of winter severity that accounted for both snow cover/depth and temperature (Baccante and Woods 2010).

For indices of black bear and mountain lion populations, we used harvest information gathered by FWP, given all hunters are required to report harvest. For the wolf index, we used abundance estimates from an integrated patch occupancy model developed for Montana (Sells et al. 2022). Specifically, we summed abundance estimates across 600 km² pixels located within HD 121, divided this value by the total area of pixels included, then multiplied by the area of HD 121 (2,530.48 km²) each year to arrive at annual wolf abundance values. For nutrition and winter severity metrics, we calculated the mean value of each metric across HD 121 each year. We included each of these covariates in models of adult and calf survival. We also included lagged forms of these covariates in models to identify whether conditions the previous year affected vital rates. We also included a harvest effort covariate, equivalent to the number of elk hunter days in hunting district 121, in linear models predicting harvest rate to account for changes in harvest rates related to effort, rather than population change.

1.3.5 Model fitting

We assigned prior distributions for each demographic parameter within the population model that were informed by past literature (Table 1). Further, we included a temporal random effects structure for annual survival, harvest rate (adult males and females), and proportion of females counted parameters. We structured proportion of males counted and calf harvest rates as independent estimates each year because this structure resulted in better model fit.

We fit models using a Bayesian framework and estimated posterior distributions of parameters by running 3 Markov Chain Monte Carlo (MCMC) chains, each for 500,000 iterations, with a burn-in of 50,000, and thinning of 10. We identified whether models converged by ensuring $\hat{R}$ values were <1.1 and by visually inspecting posterior distributions for adequate mixing. Using the models described above, we estimated true population size for each sex/age class, as well as population growth rates (λ) and demographic rates over time.

Table 1. Prior distributions and references for parameters included in elk integrated population models in hunting district 121 from 2013– 2026. Parameters include calf and adult natural survival (φ), number of calves produced per female (i.e., pregnancy rate; f), harvest rate (hr), and initial population size N_1 .

Parameter	Prior Distribution	Comments and References
φ^{calf}	Unif(0, 0.8)	Singer et al. 1997; Smith and Anderson 1998; Raithel et al. 2007; Eacker et al. 2016; Paterson et al. 2019
φ^{ad}	Unif(0.8, 1)	Unsworth et al. 1993; Raithel et al. 2007; Brodie et al. 2013; Keller et al. 2015; Hegel et al. 2014; Horne et al. 2019; Sergeev et al. 2021; Paterson et al. 2022a
f	Beta(84.15, 14.85)	Sets mean pregnancy rate = 0.85 (derived from FWP statewide database of pregnancy status of adult and yearling females combined) and 95% CI of 0.77 – 0.91
hr^{calf}	Unif(0, 0.1)	Conversations with FWP personnel
$hr^{ad.F}$	Unif(0, 0.2)	Conversations with FWP personnel
$hr^{ad.M}$	Unif(0.2, 1)	Conversations with FWP personnel
$N_1^{calf,ad.F,ad.M}$	$\text{Unif}\left(\frac{\text{Count}_1^{calf,ad.F,ad.M}}{\text{Count}_1^{calf,ad.F,ad.M} * 10}\right)$	NA

1.4 Results

1.4.1 Population Dynamics

Due to uncertainties in elk population dynamics before 2013 (i.e., strong drop in harvest, but consistent aerial counts), we decided to only use data starting in 2013 to estimate elk population dynamics.

Results from the IPM suggested elk populations have been relatively stable or slightly increasing since 2013, with estimated total population sizes averaging approximately 1,790 individuals (339 calves, 1,225 adult females, and 226 adult males) and geometric mean $\lambda = 1.014$ (95% credible interval [CrI] = 1.005 – 1.026; Figure 8). Model results suggested the annual proportion of adult females and calves counted averaged 0.90 (95% CrI = 0.78 – 0.98), while the proportion of adult males counted averaged 0.60 (95% CrI = 0.34 – 0.93).

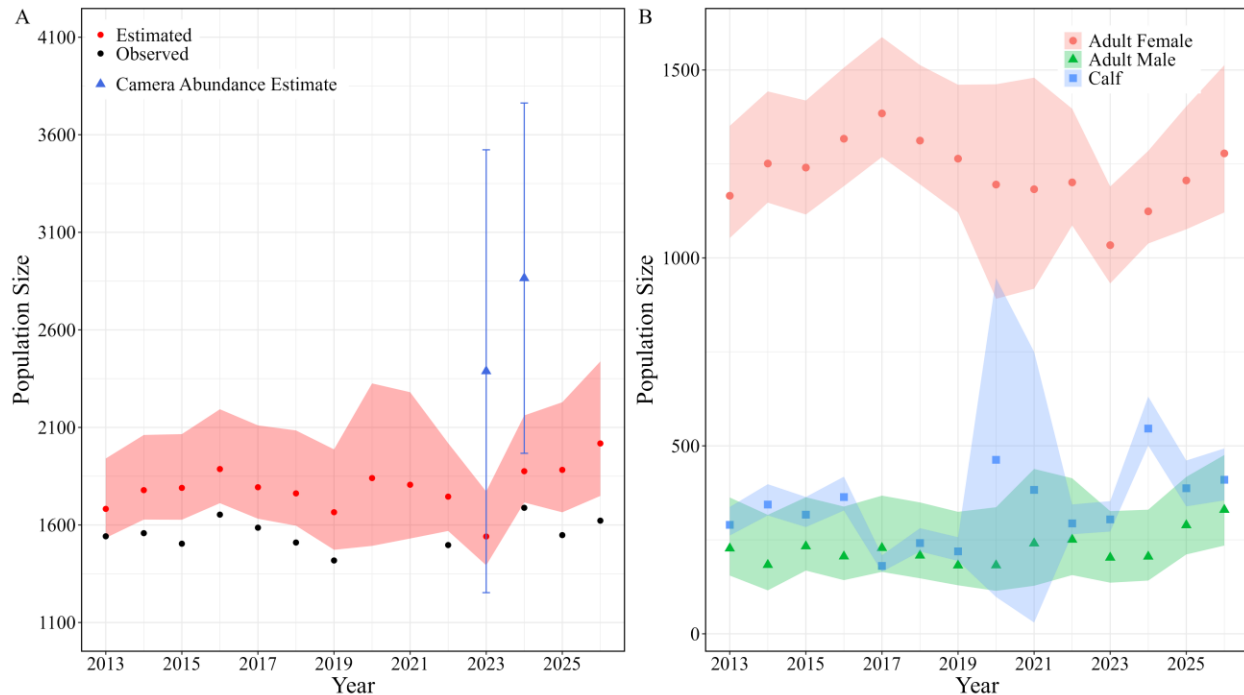


Figure 8. Total elk population estimates (A) and age/sex-specific estimates (B) in hunting district 121 from 2013 – 2026 based on a preliminary elk population model that included abundance estimates, vital rate estimates, and covariate data from our study. Red dots in panel A represent model estimates, while black dots represent observations from aerial counts. Blue triangles represent camera-based elk abundance estimates. All values in panel B are model-estimated and ribbons in both panels represent 95% credible intervals. Note: y-axis scales differ between panels to improve display.

1.4.2 Demographic Rates

Mean estimated annual natural survival (excluding harvest) of adult elk (≥ 1 year old) from 2013 – 2024 was 0.98 (95% CrI = 0.92 – 1.00), while mean annual natural survival of calves (< 1 year old) was 0.36 (95% CrI = 0.23 – 0.53). Estimated mean harvest rates of adult females, adult males available for harvest (i.e., possessed brow tines), and calves were 0.064 (95% CrI = 0.050 – 0.080), 0.70 (95% CrI = 0.42 – 0.93), and 0.0054 (95% CrI = 0 – 0.016), respectively (Figure 9). The model-estimated mean pregnancy rate of females > 1 year old was 0.84 (95% CrI = 0.73 – 0.91).

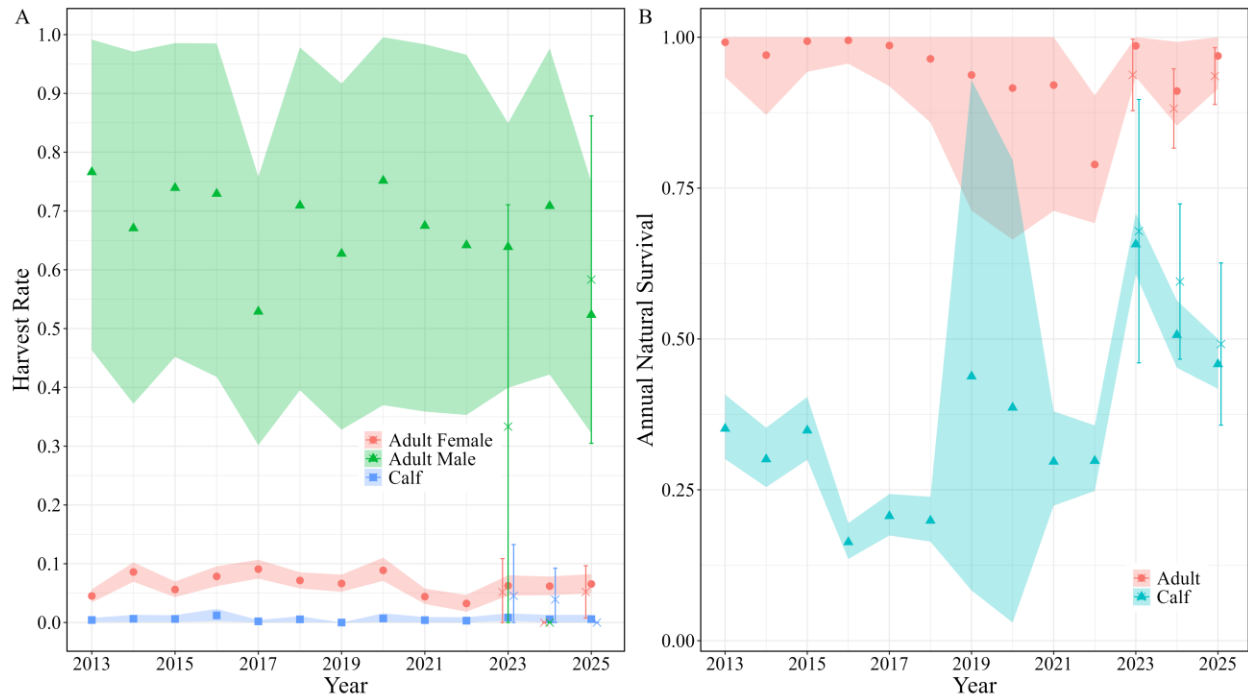


Figure 9. Estimated harvest rates of adult female, adult male, and calf elk (A) and estimated annual natural survival of adult and calf elk (B) from 2013 – 2025 in hunting district 121. Dots represent mean estimates and ribbons represent 95% credible intervals. Exes with error bars represent independent mean estimates and 95% confidence intervals of harvest rate and natural survival from collared individuals.

1.4.3 Covariate Effects on Calf and Adult Survival

No covariates we tested had strong associations with calf or adult survival (Figure 10).

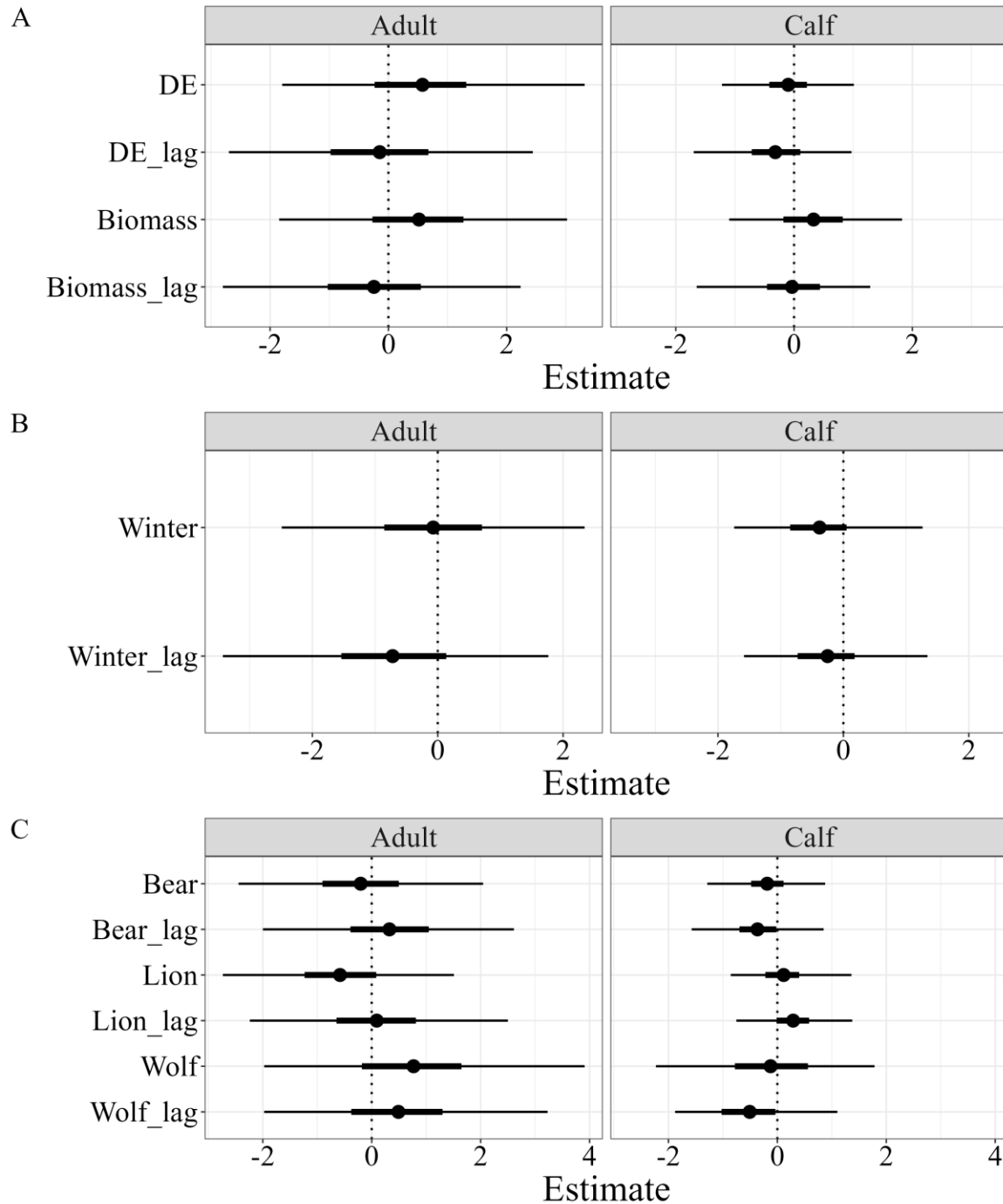


Figure 10. Associations of annual elk nutrition metrics (digestible energy [DE; kcal/g/m²], forage biomass [g/m²]; panel A), winter severity (panel B), and indices of predators (bear harvest, lion harvest, and wolf density estimates; panel C) with adult (>1 year old) and calf (<1 year old) survival from 2013 – 2025 in hunting district 121. Both current year values and lagged values (previous year; “_lag”) were tested for each covariate. Dots represent median estimates, thick horizontal lines represent the 50% credible interval, and thin horizontal lines represent 95% credible intervals. The vertical dotted line represents a beta estimate of 0 (no effect).

1.5 Discussion/Interpretation

Our results suggest that elk populations have been stable or slightly increasing over the past decade and estimated elk demographic rates were consistent with rates documented in other elk literature. Relatively high observed calf:cow ratios and IPM estimates of calf survival in 2024-2026 have resulted in the highest estimated elk abundance since 2013.

While our analyses suggest a stable population in HD 121, we caution interpretation of these results at the current time. The occasional disparity between aerial counts and harvest estimates introduced uncertainty in the model, resulting in model sensitivity to the observation distributions and priors used. Additionally, while we expect elk demographic rates in our study area to be similar to what we estimated, given their consistency with rates in the literature, it is possible that true rates, the annual variability in rates, or the importance of rates in elk population dynamics will differ (e.g., Eacker et al. 2017). We will continue to add demographic information collected as part of this study before finalizing the model and developing management recommendations.

We did not find strong relationships between abiotic and biotic factors and calf or adult survival like other studies (e.g., Eacker et al. 2016, Paterson et al. 2019). The lack of evidence for influential factors on survival is likely related to the relatively short time series we evaluated and the somewhat limited annual variability in survival and covariates during that period. Further, the coarseness of this analysis (i.e., associations of population-level survival with HD-level covariates) may limit our ability to identify true relationships if they exist. Thus, data from collared elk may be more effective at identifying associations between biological/environmental factors and survival.

Another objective of this research was to develop a user-friendly tool to facilitate elk management decisions. Thus, we have continued development of a shiny app that incorporates user data inputs into the IPM described above and provides estimates of elk abundance, vital rates, and population dynamics (Figure 11). Users can forecast management scenarios, such as changing elk harvest or other demographic rates, and view population projections based on those forecasted scenarios. We intend to solicit feedback from biologists and refine this tool in the upcoming year.

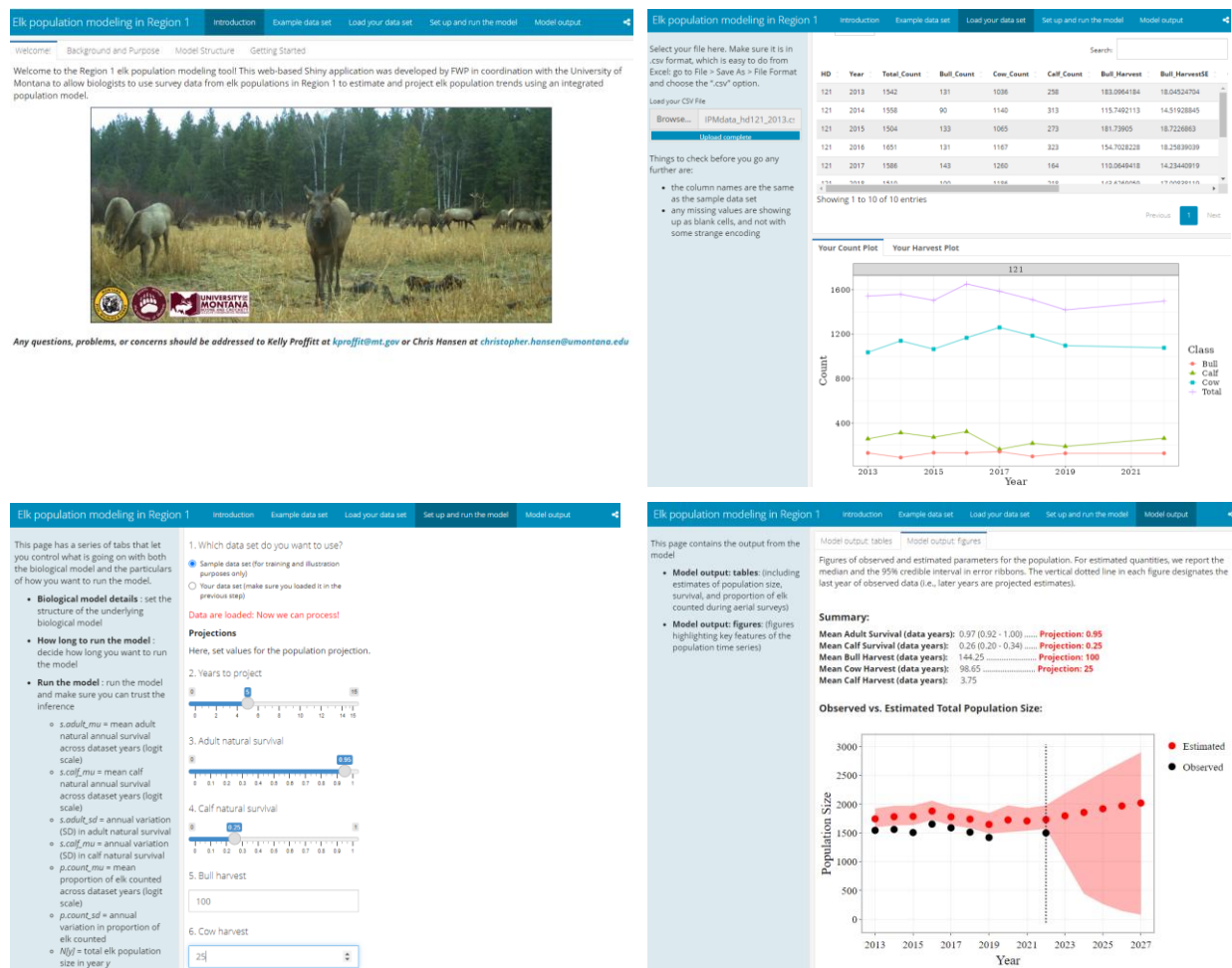


Figure 11. Example workflow of shiny app tool that incorporates user inputs into an integrated population model and provides estimates of elk population dynamics and vital rates.

Objective #2: Based on past research findings, develop predictive models of elk hunting season distributions in northwest Montana, including the effects of forest disturbance and hunter access.

2.1 Background

Elk distribution and migratory behavior are of concern to wildlife managers, land managers, hunters, and private landowners due to concerns with elk availability for harvest and elk-related damage on private lands. In some areas, elk hunters and wildlife managers are observing declines in public-land hunting opportunities and agricultural producers are experiencing increased property damage (Burcham 1956, Haggerty and Travis 2006, Krausman et al. 2014, Fontaine et al. 2019). As such, there is shared interest of wildlife managers, public land managers, hunters using public lands, and private landowners in identifying factors affecting elk distributions during autumn hunting seasons. Our objective was to use elk location data from autumn 2023-2025 to identify what resources elk use and how those resources change throughout hunting seasons. At this time, we present basic summaries of elk landscape use and preliminary results from resource selection models evaluating elk habitat use during the hunting seasons. These models and results will be finalized after data collection is complete.

2.2 Data collection and analytical methods

2.2.1 Elk Habitat Use

We evaluated autumn elk habitat use in hunting district 121 in relation to ten variables that could influence elk resource selection during the hunting season (Ranglack et al. 2017; Table 2, Figure 12). We selected these variables to address hypotheses of elk resource use related to elk avoidance of humans (e.g., publicly accessible vs. inaccessible lands and distance to motorized routes; Proffitt et al. 2016a, Lowrey et al. 2020, Snobl et al. 2024), acquisition of forage/nutrition (predicted forage biomass, predicted forage digestible energy, timber harvest; Weeks 2025), security cover (canopy cover, solar radiation; Proffitt et al. 2016b, DeVoe et al. 2019), topography (slope, terrain ruggedness; Sappington et al. 2007), and snow cover (snow water equivalent [SWE]; Messer et al. 2009, Snobl et al. 2024).

We summarized elk use of these variables (i.e., resources) using location data from collared male and female elk (see [Section 3.2.1](#)) during 4 hunting periods: “prehunt” (August 1 – September 1, 2023; August 1 – September 6, 2024; August 1 – September 5, 2025), “archery” (September 2 – October 15, 2023; September 7 – October 20, 2024; September 6 – October 19, 2025), “rifle” (October 21 – November 26, 2023; October 26 – December 1, 2024; October 25 – November 30, 2025), and “posthunt” (i.e., post-general rifle season; November 27 – December 31, 2023; December 2 – December 31, 2024; December 1 – December 31, 2025). We removed nighttime locations (31 minutes after sunset – 31 minutes before sunrise) so locations represented elk locations during legal shooting light (Figure 13).

Using these data, we calculated each elk’s mean use of every resource during each hunting period, then calculated the mean, median, and variability of these elk-specific values across elk.

We also determined the proportion of elk that had >50% of locations on public or block management area (BMA) lands during each hunting period to identify what proportion of elk were available for harvest.

2.2.2 Elk Habitat Selection

We conducted a preliminary analysis to evaluate elk habitat selection in hunting district 121 during the autumn hunting season in relation to the same ten variables evaluated for elk use. For this analysis, we focused on just the archery and rifle hunting periods. We fit mixed-effects resource selection functions (RSFs) with a used-available design using the ‘lme4’ package in R (Manly et al. 2002, Bates et al. 2015). We randomly generated 10 available locations for each used elk location from that individual’s fall homerange (95% kernel utilization distribution of archery and rifle locations). We standardized all continuous covariates and screened for collinearity, excluding variables with correlation coefficients of $|r| > 0.7$. We fit separate models for each sex in each season with the same global model structure (with the exception of SWE, which was not included in archery models due to no snow accumulation occurring during this period). We included random intercepts and slopes by individual for all covariates except SWE (Muff et al. 2019).

Table 2. Description of variables used to evaluate elk resource use and habitat selection during the hunting season in hunting district 121.

Variable	Description and Source	References
Access	Areas accessible to hunters (public lands and Block Management Areas [BMA; Type 1 and 2]). Developed from Montana Cadastral ownership parcels and FWP BMA shapefiles.	Proffitt et al. 2016b; Ranglack et al. 2017; Lowrey et al. 2020; Snobl et al. 2024
Canopy cover	Percent tree cover. Obtained from Rangeland Analysis Platform (Brown 2026).	Proffitt et al. 2016b; Ranglack et al. 2017; DeVoe et al. 2019
Digestible energy	Predicted forage digestible energy, see Section 3.2.7.	Weeks 2025
Distance to road (archery)	Distance (m) to open motorized routes during the archery season. Developed from a combination of Forest Service (FS) and Montana Department of Transportation (MDT) roads layers.	Ranglack et al. 2017; Lowrey et al. 2020; Snobl et al. 2024
Distance to road (rifle)	Distance (m) to open motorized routes during the rifle season. Developed from a combination of FS and MDT roads layers.	Ranglack et al. 2017; Lowrey et al. 2020; Snobl et al. 2024
Forage biomass	Predicted forage biomass, see Section 3.2.7.	Weeks 2025
Slope	Percent slope. Calculated from DEM.	Ranglack et al. 2017
Snow water equivalent	Daily snow water equivalent (SWE; kg/m ²). Obtained from ORNL DAAC through EarthData.	Messer et al. 2009; Snobl et al. 2024
Solar radiation	Solar radiation (W/m ²). Calculated from DEM using the package solrad (Seyednasrollah 2018).	Proffitt et al. 2016; Ranglack et al. 2017; DeVoe et al. 2019
Terrain ruggedness	Created using package spatialEco (Sappington et al. 2007) from a digital elevation model (DEM) obtained from the National Elevation Dataset (using FedData package in R; Bocinsky 2023).	Bealer et al. 2026
Timber harvest	Timber harvest history classified by time-since-harvest. Developed from Landfire, FS Activity Tracking System, and Montana Department of Natural Resources and Conservation datasets.	Weeks 2025

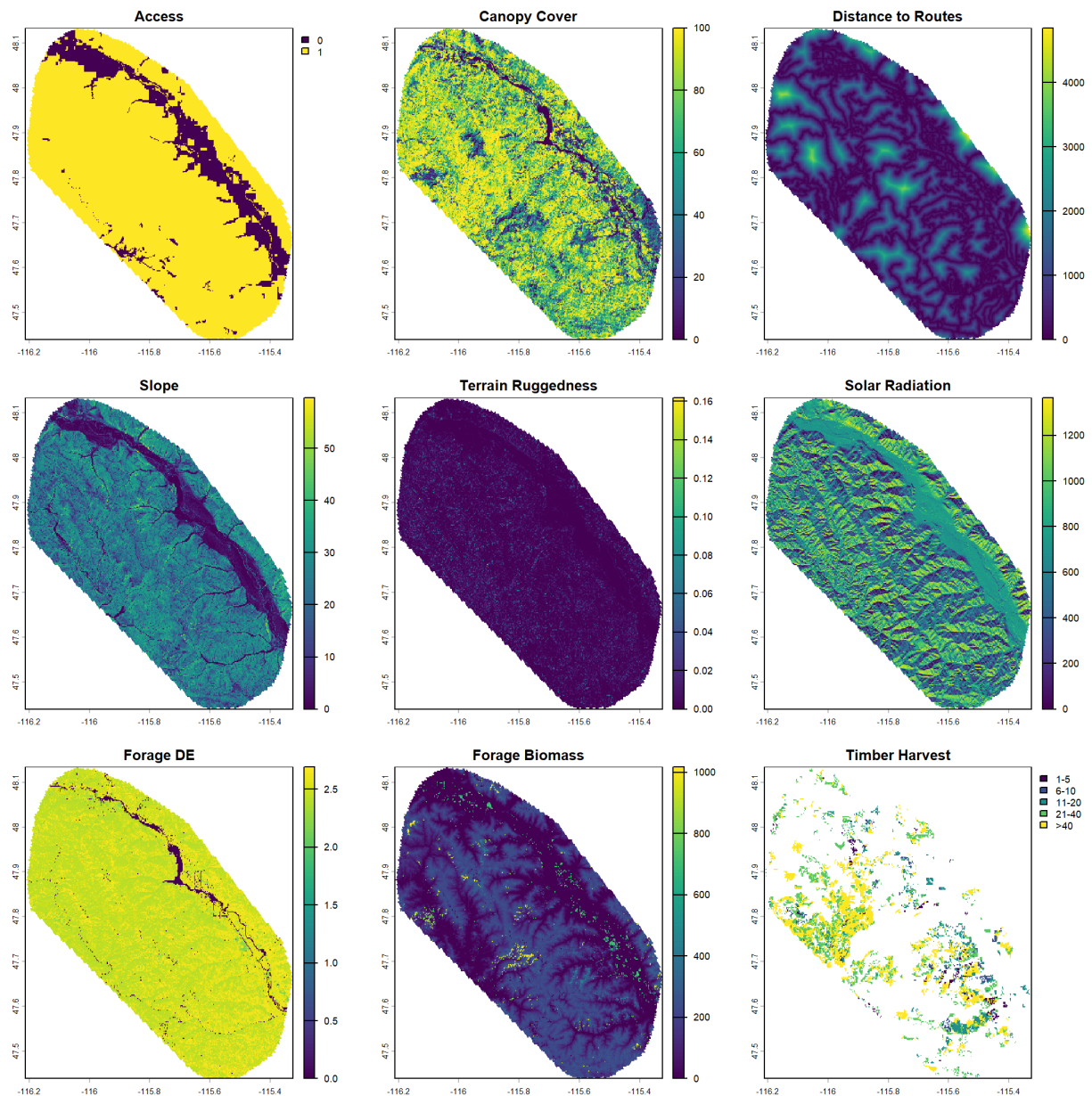


Figure 12. Example rasters of factors potentially influencing elk habitat use and selection during the hunting season in hunting district 121.

2.3 Results and Discussion

2.3.1 Elk Habitat Use

We collected 165,038 daytime locations of 133 females (123 adult and 10 yearling animal-years) and 17,621 locations of 28 males (17 adult and 11 yearling animal-years) during the hunting seasons 2023-2025 (Table 3, Figure 13).

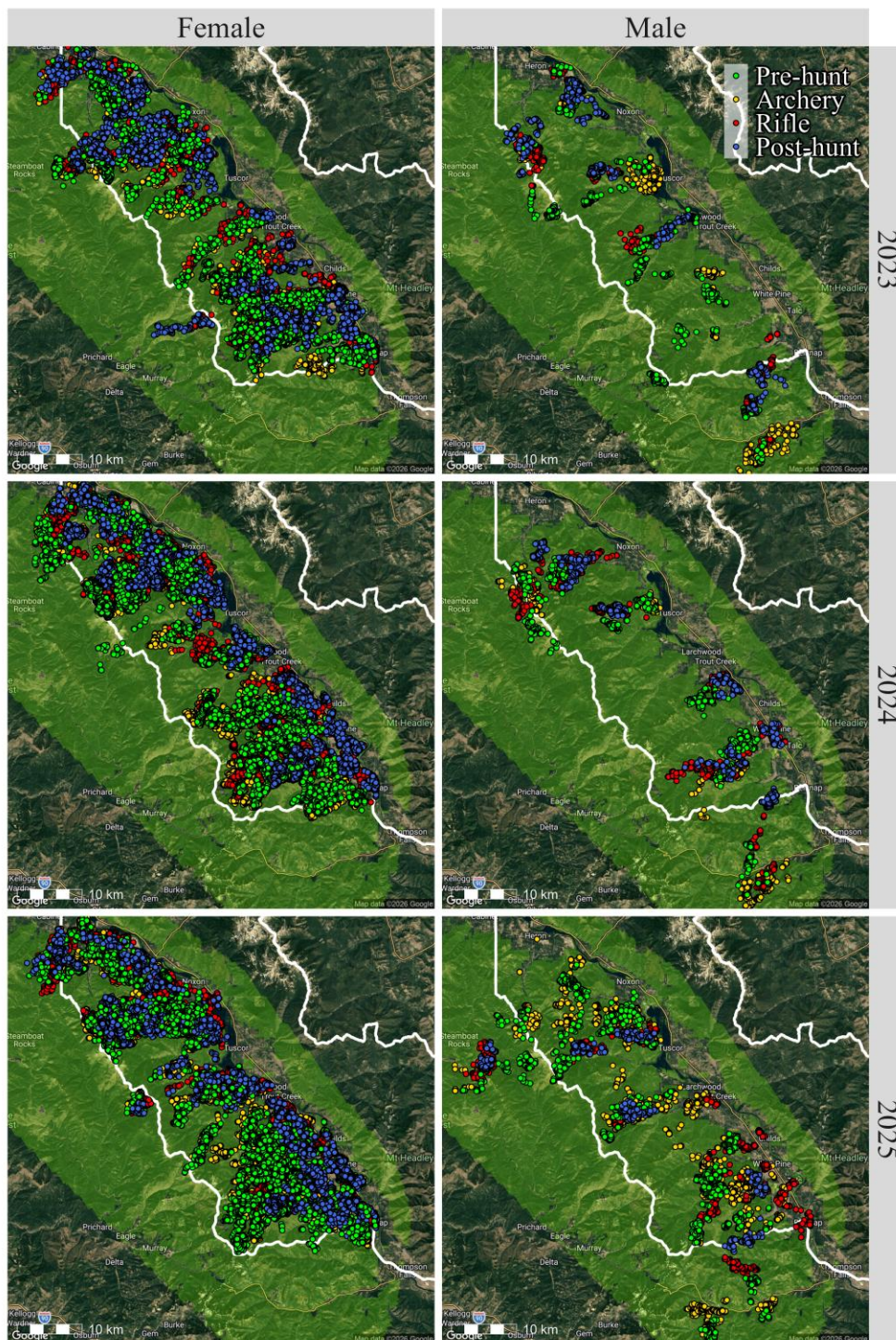


Figure 13. Male and female elk daytime locations during the hunting seasons 2023-2025 within and adjacent to hunting district 121 (white border). Green, yellow, red, and blue dots represent locations during pre-hunt, archery, rifle, and post-hunt periods, respectively. The green overlay represents areas accessible for hunting by the general public (i.e. either public lands or block management areas).

Table 3. Number of daytime elk locations used to summarize elk resource use during hunting periods (prehunt, archery, rifle, posthunt) in hunting district 121 during autumn 2023-2025. “Adult” represents individuals ≥ 2.5 years old and “yearling” represents individuals 1.5 years old.

Sex	Age Class	Hunt Period	Number of Elk	Number of Locations
Female	Adult	Prehunt	123	41,951
		Archery	122	52,821
		Rifle	118	36,274
		Posthunt	113	27,429
	Yearling	Prehunt	10	1,590
		Archery	10	2,153
		Rifle	10	1,618
		Posthunt	9	1,202
Male	Adult	Prehunt	17	3,970
		Archery	17	4,463
		Rifle	13	1,832
		Posthunt	8	1,356
	Yearling	Prehunt	11	1,721
		Archery	10	1,977
		Rifle	9	1336
		Posthunt	9	966

Both female and male elk demonstrated changes in use of some resources from August – December. On average, both males and females became less accessible for harvest (lower proportion of locations on public lands or BMAs) during rifle season; although, there was considerable variability among elk (Table 4, Figure 14, Figure 15). Average canopy cover, distance to road, and slope used by females also tended to decline in a similar pattern as accessibility, suggesting some elk moved out of forested, steep areas on public lands to low-elevation private lands as hunting seasons progressed. Males followed similar use patterns as females, except differences between hunting periods were more subtle and distance to road increased between archery and rifle seasons.

Table 4. Mean female and male elk resource use (see Table 2 for resource descriptions) during pre-hunt, archery, rifle, and post-hunt periods 2023-2025 for individuals collared in hunting district 121. Timber harvest values (TH 1-5 Years, TH 6-10 Years, TH 11-20 Years, TH 21-40 Years, TH 40+ Years, No TH) represent the mean proportion of locations occurring in those timber harvest histories. Accessibility values represent the proportion of elk locations occurring on public lands or block management areas (i.e., available to the public for harvest). Standard deviation of mean values are provided in parentheses.

Sex	Variable	Prehunt	Archery	Rifle	Posthunt
Female	Accessibility	0.87 (0.33)	0.83 (0.38)	0.59 (0.49)	0.63 (0.48)
	Biomass (kg/ha)	136.8 (111.2)	123.8 (117.9)	124.9 (198.8)	130.3 (188.2)
	Canopy Cover (%)	67.8 (24.5)	67.4 (25.2)	57.6 (28.9)	52.3 (29.3)
	DE (kcal/g)	2.47 (0.11)	2.47 (0.12)	2.47 (0.16)	2.49 (0.17)
	Distance to Road (m)	685.2 (605.6)	640.9 (526.1)	568.1 (457.9)	586.1 (470.9)
	Terrain Ruggedness	0.0045 (0.0071)	0.0040 (0.0065)	0.0035 (0.0067)	0.0039 (0.0072)
	Slope (%)	20.9 (8.9)	20.4 (9.7)	16.3 (12.3)	15.8 (11.7)
	Solar (W/m ²)	555.8 (300.82)	537.2 (296.4)	584.7 (290.0)	669.5 (289.7)
	SWE (kg/m ²)	0 (0)	0 (0)	0.024 (0.35)	0.332 (1.52)
	TH 1-5 Years	0.014	0.009	0.012	0.033
	TH 6-10 Years	0.014	0.011	0.009	0.023
	TH 11-20 Years	0.058	0.037	0.029	0.049
	TH 21-40 Years	0.051	0.046	0.037	0.065
	TH 40+ Years	0.13	0.11	0.035	0.042
	No TH	0.73	0.79	0.88	0.79
Male	Accessibility	0.99 (0.11)	0.93 (0.25)	0.79 (0.41)	0.87 (0.34)
	Biomass (kg/ha)	163.4 (108.1)	124.7 (110.4)	151.7 (169.1)	151.4 (144.7)
	Canopy Cover (%)	69.3 (24.5)	68.3 (25.1)	64.0 (28.8)	63.6 (27.9)
	DE (kcal/g)	2.47 (0.12)	2.47 (0.12)	2.47 (0.12)	2.50 (0.14)
	Distance to Road (m)	834.9 (534.0)	719.4 (481.7)	928.7 (634.3)	915.4 (645.3)
	Terrain Ruggedness	0.0059 (0.0091)	0.0049 (0.0076)	0.0047 (0.0082)	0.0058 (0.0092)
	Slope (%)	23.5 (6.8)	21.6 (8.4)	20.1 (11.3)	20.3 (10.8)
	Solar (W/m ²)	536.6 (330.2)	560.9 (304.1)	569.6 (332.0)	671.3 (319.9)
	SWE (kg/m ²)	0 (0)	0 (0)	0.061 (0.58)	0.840 (2.76)
	TH 1-5 Years	0.014	0.012	0.015	0.023
	TH 6-10 Years	0.012	0.011	0.008	0.011
	TH 11-20 Years	0.035	0.028	0.014	0.034
	TH 21-40 Years	0.067	0.075	0.063	0.073
	TH 40+ Years	0.11	0.066	0.039	0.054
	No TH	0.76	0.81	0.86	0.80

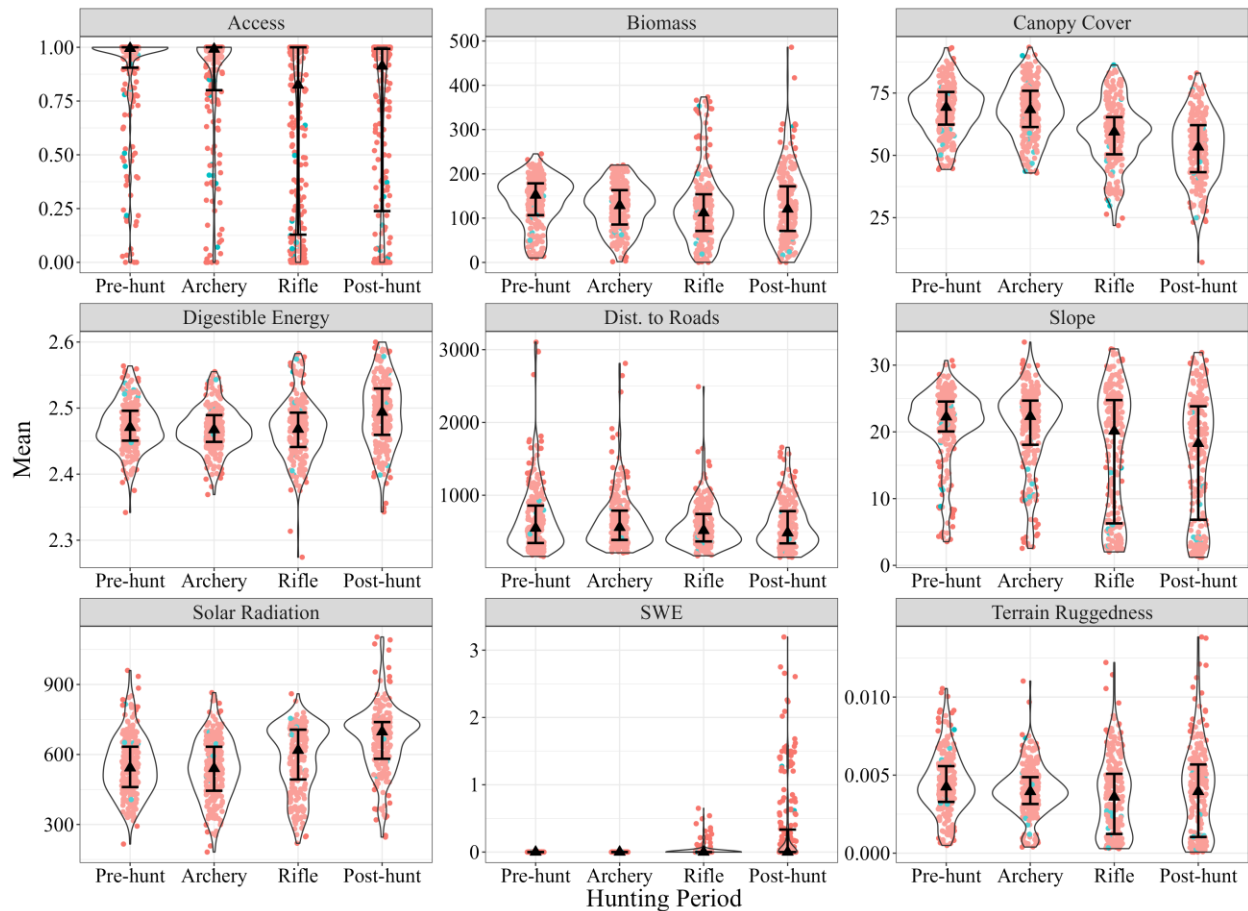


Figure 14. Female elk use of resources (see Table 2 for resource descriptions) during the hunting seasons 2023-2025 for individuals collared in hunting district 121. Red and blue dots represent adult and yearling elk-specific mean use of each resource during hunting periods, respectively. Violin plots show the distribution of use across elk, while the black triangle and bars show the median and 50% quantile of use across elk. Access values represent the proportion of elk locations occurring on public lands or block management areas (i.e., available to the public for harvest).

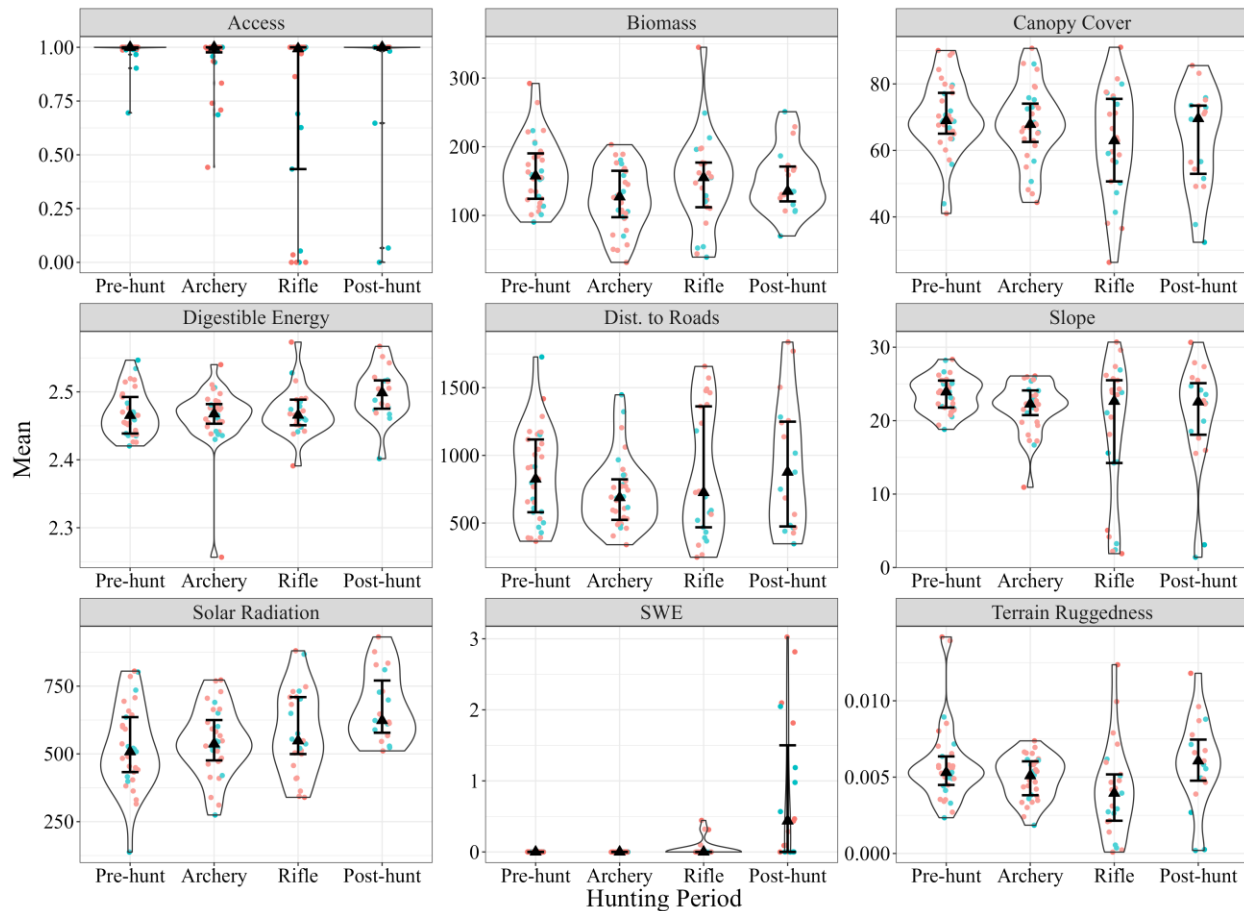


Figure 15. Male elk use of resources (see Table 2 for resource descriptions) during the hunting seasons 2023-2025 for individuals collared in hunting district 121. Red and blue dots represent adult and yearling elk-specific mean use of each resource during hunting periods, respectively. Violin plots show the distribution of use across elk, while the black triangle and bars show the median and 50% quantile of use across elk. Access values represent the proportion of elk locations occurring on public lands or block management areas (i.e., available to the public for harvest).

The pattern of changing resource use throughout autumn was not consistent across all elk, with some individuals increasing, decreasing, or maintaining resource use across hunting periods. For example, many elk maintained accessibility throughout all hunting periods, while others became more accessible. Further, while there were fewer elk locations within accessible areas during the rifle season, a large proportion of elk remained on public lands the majority of the time. Approximately 85% of females and 97% of males were on accessible lands at least half the time during archery season. This percentage dropped to 61% of females during rifle season, while male accessibility dropped to 72% (Figure 16). Approximately 97% of female locations (96%, 97%, 97%, and 97% during pre-hunt, archery, rifle, and post-hunt seasons, respectively) and 80% of male locations (76%, 84%, 78%, and 83% during pre-hunt, archery, rifle, and post-hunt seasons, respectively) occurred in HD121 during the fall. The remaining locations occurred either in other Montana HDs or in Idaho.

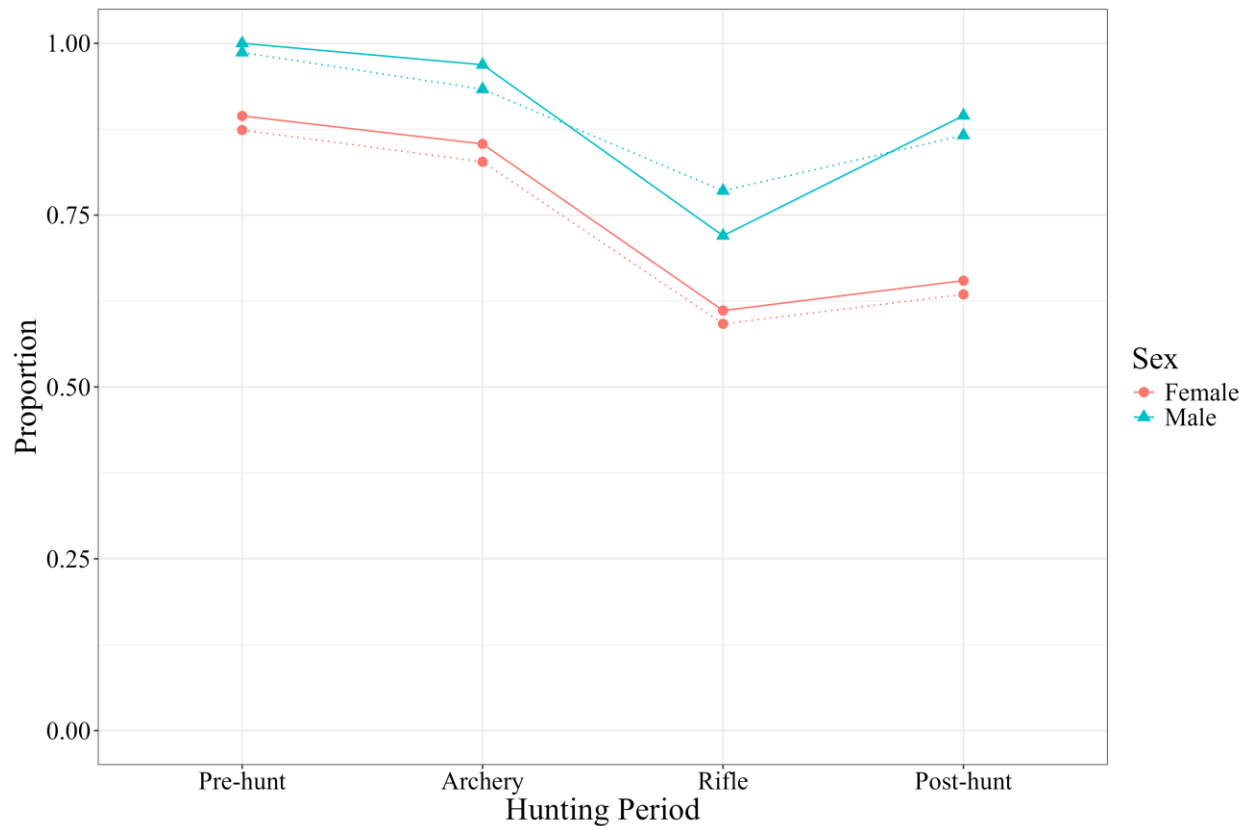


Figure 16. Proportion of collared female and male elk with >50% of daytime locations on publicly accessible land (solid lines) and proportion of total elk locations on publicly accessible land (dotted lines) during each hunting period during 2023-2025 in hunting district 121.

These results suggest that the majority of elk were largely accessible to hunters throughout autumn, regardless of a decrease in proportion of elk locations on publicly accessible lands during the rifle season. However, we caution interpretation of results regarding male distribution, given the low sample size and a significant proportion of yearling males in the sample. Further, the majority of adult males were captured by helicopter at higher elevations and the majority of collared yearling males were caught in the valley in Clover traps. While male elk became more inaccessible during the rifle season, this pattern was in part driven by yearlings that were more likely to move to private land than adult males (e.g., Figure 17). It is possible that males that use the valley in winter (i.e., during capture windows) are also more likely to use private lands in the valley during hunting seasons. Alternatively, our findings could be due to our valley sample of males being primarily composed of yearlings, which may be more likely to follow females onto private lands during rifle season. The final male collaring effort in May 2026 (see [Section 3.2.1](#)) further increased our adult male sample size and will hopefully help disentangle some of these possible relationships for future hunting seasons.

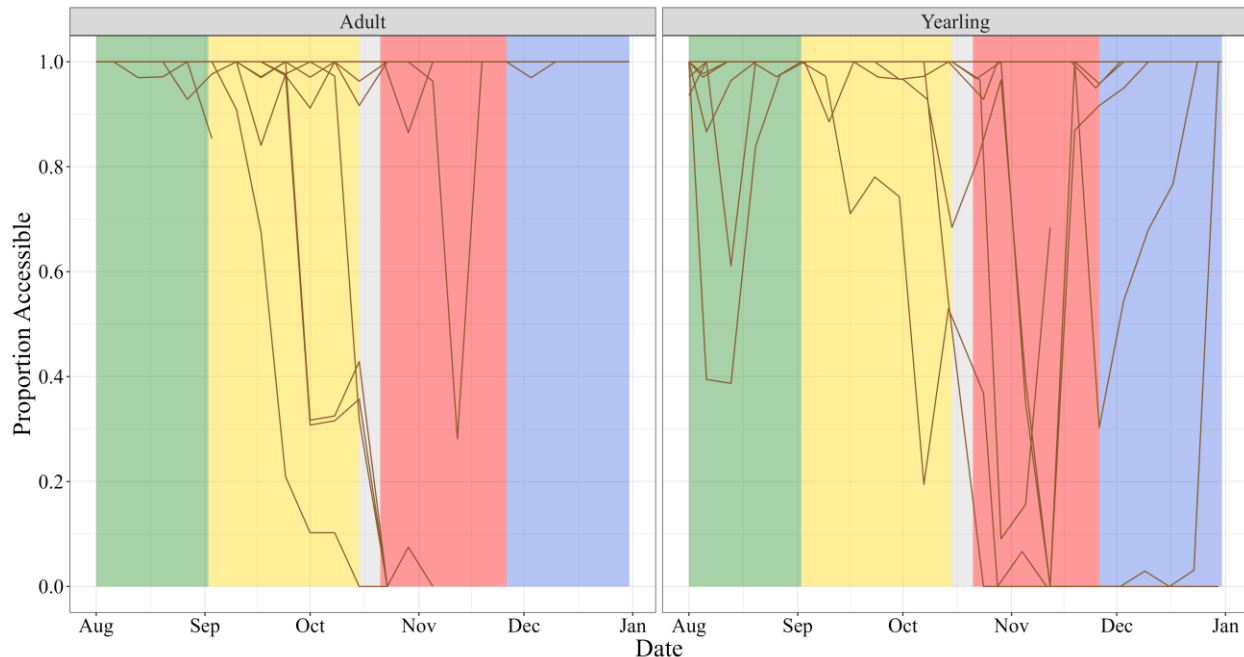


Figure 17. Proportion of accessible locations by week for adult and yearling male elk throughout autumn 2023-2025 in hunting district 121. Brown lines represent elk-specific mean weekly proportion of locations on accessible land. Green, yellow, gray, red, and blue regions represent approximate pre-hunt, archery, rest (no hunting), rifle, and post-hunt periods.

While many elk were on public lands, they may have still been difficult to find and access, given landscape features they used. For example, the 13 adult males (i.e., those likely with brow tines and available for legal harvest) primarily used publicly accessible lands (90.4% of locations) with mean canopy cover 65.7%, mean slope 23.6%, and mean distance from roads 1.2 km during the rifle season. All these values exceeded adult and yearling female and yearling male use values, suggesting adult males used areas more difficult for hunters to access, on average. We will continue to assess this complex “accessibility” landscape in future analyses to help determine the demographic tradeoffs of different resource use strategies by elk during autumn and how this relates to hunter opportunity.

2.3.2 Elk Habitat Selection

Population-level fixed effects results from the preliminary RSFs generally reflect consistent selection or avoidance of certain resources across hunting seasons and sexes (Figure 18). Elk generally selected for greater canopy cover, greater distances from roads, and greater forage digestible energy while generally avoiding steeper slopes, terrain ruggedness, and solar radiation. Elk selection was weaker and more variable for forage biomass and snow water equivalent. Male and female elk selected strongly for accessible lands during the archery season and inaccessible lands during the rifle season. Additionally, male and female elk responses to categories of timber harvest varied significantly, but elk generally avoided areas of more recent timber harvest and selected unharvested forest (Figure 18).

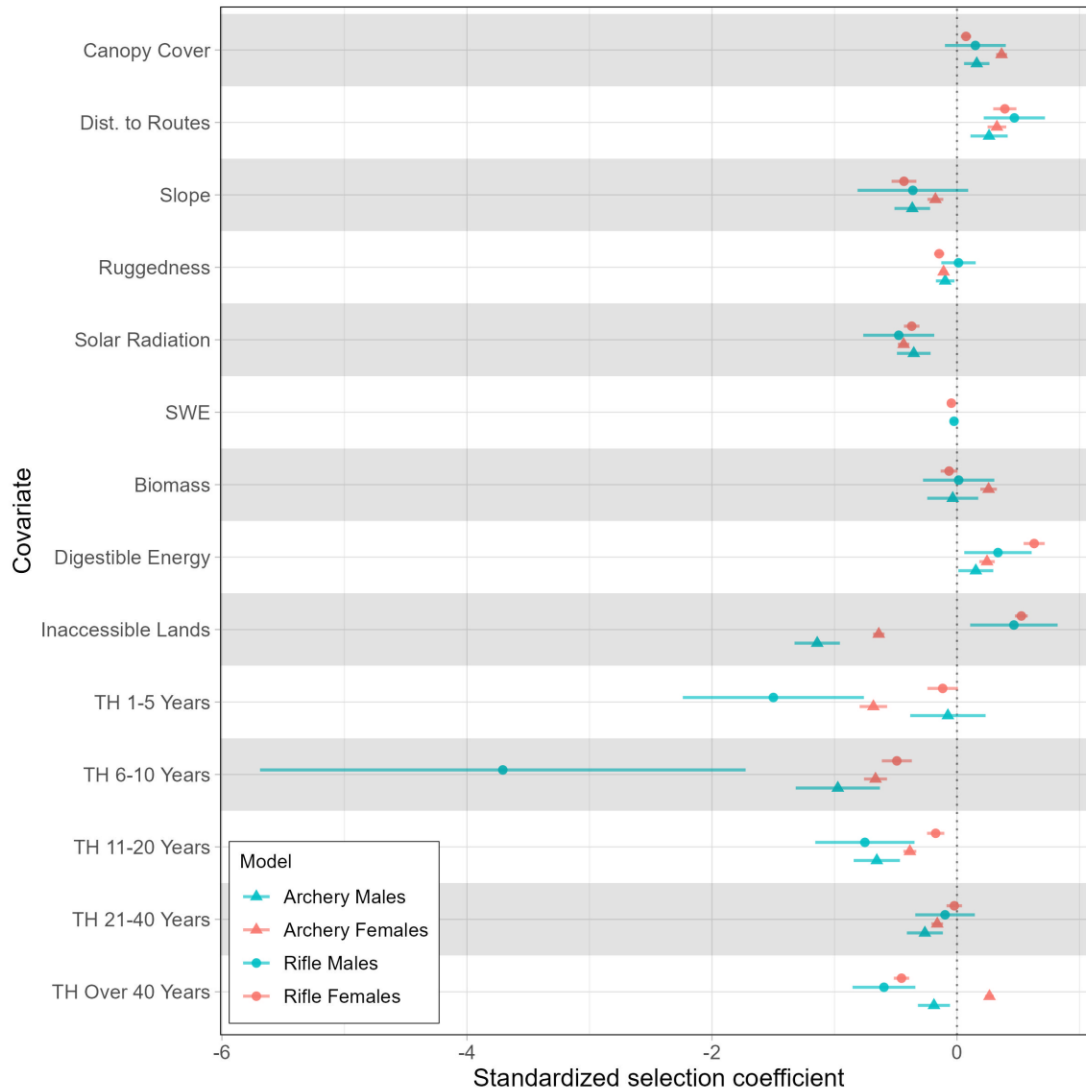


Figure 18. Population-level effects coefficients from preliminary resource selection functions (RSFs) evaluating male and female elk habitat selection during the archery and rifle hunting seasons in hunting district 121, 2023-2025. Coefficients labeled “TH” are categories of timber harvest history where unharvested forest is the reference category.

The individual random slopes for each of the continuous covariates from the preliminary RSF models indicated significant individual variation in habitat selection for several covariates (Figure 19-Figure 25). For example, although elk generally selected for areas farther from motorized routes, the individual slopes demonstrate that some individuals selected extremely strongly for areas farther from routes while others selected weakly for areas closer to routes (Figure 20). Similarly, elk generally avoided steeper slopes and more rugged terrain, but individual random slopes indicate that some individuals selected for these areas (Figure 21, Figure 22). Similar trends of individual variation can be seen in individual elk responses to forage biomass and digestible energy as well (Figure 24, Figure 25). We will continue to explore these relationships in the final reporting year.

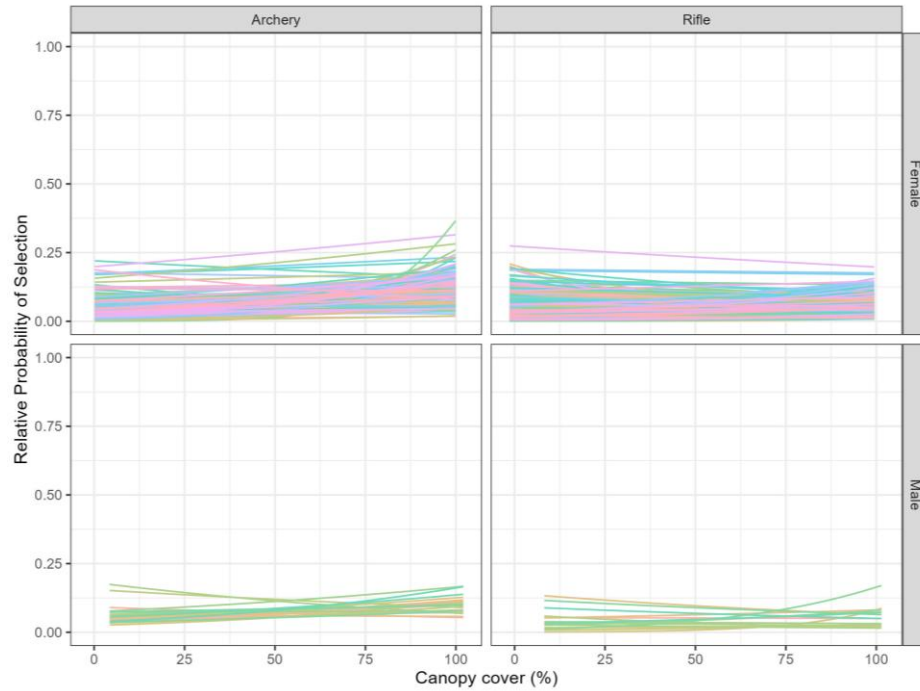


Figure 19. Individual-level random slope coefficients for canopy cover from preliminary resource selection functions (RSFs) evaluating male and female elk habitat selection during the archery and rifle hunting seasons in hunting district 121, 2023-2025.

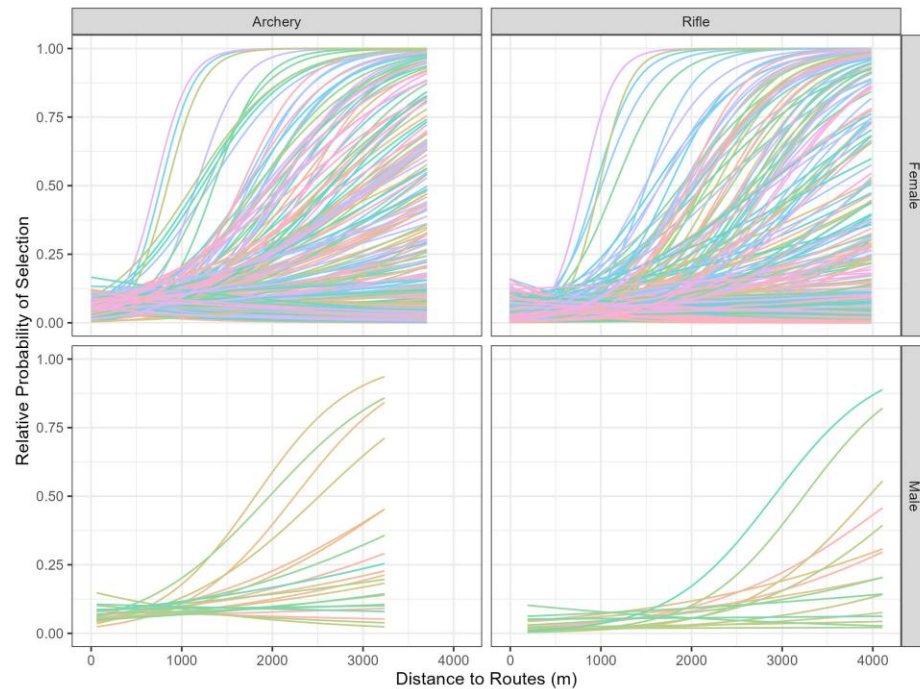


Figure 20. Individual-level random slope coefficients for distance to routes from preliminary resource selection functions (RSFs) evaluating male and female elk habitat selection during the archery and rifle hunting seasons in hunting district 121, 2023-2025.

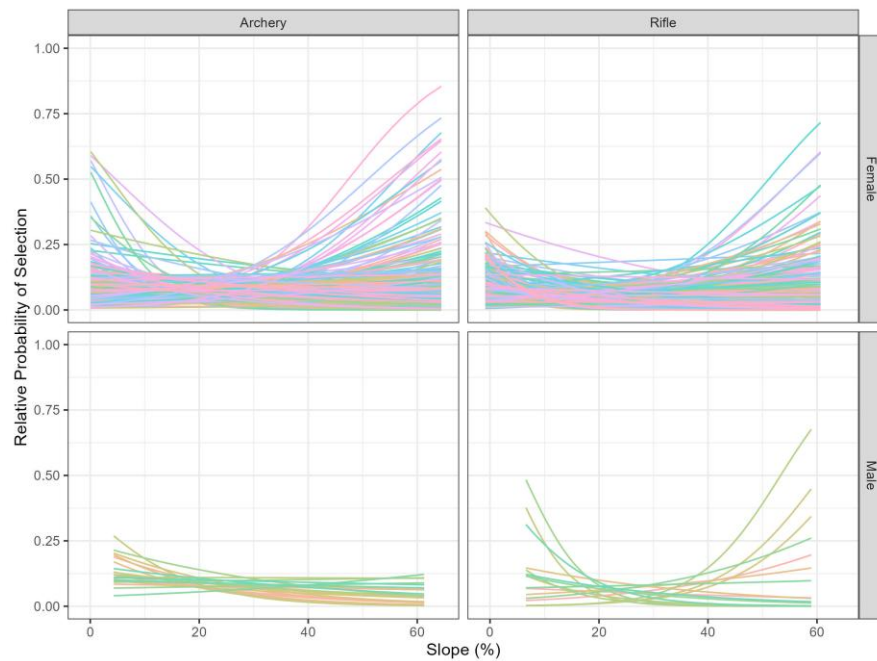


Figure 21. Individual-level random slope coefficients for slope from preliminary resource selection functions (RSFs) evaluating male and female elk habitat selection during the archery and rifle hunting seasons in hunting district 121, 2023-2025.

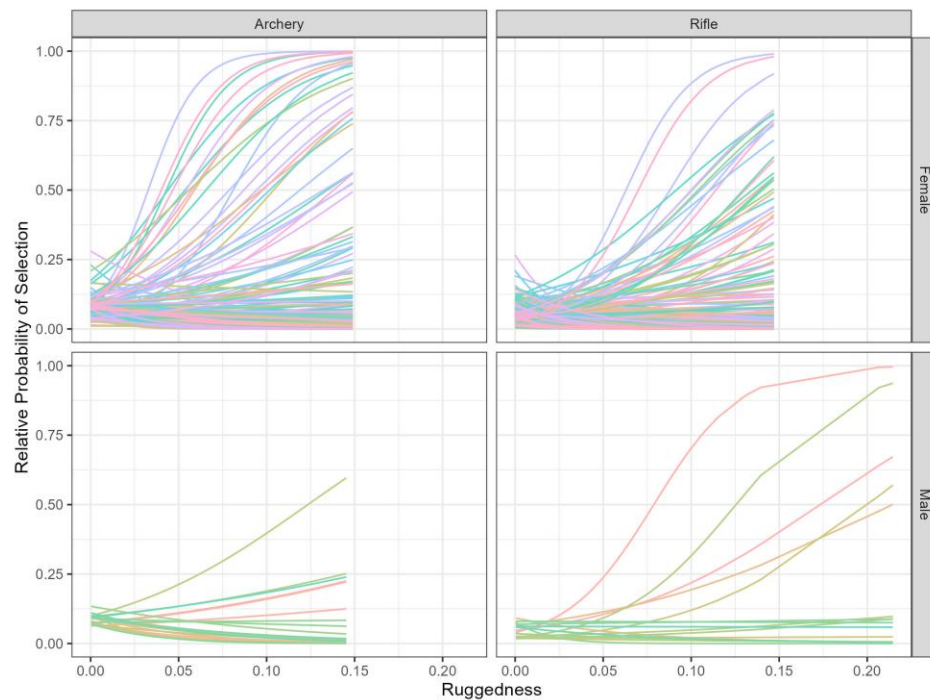


Figure 22. Individual-level random slope coefficients for terrain ruggedness from preliminary resource selection functions (RSFs) evaluating male and female elk habitat selection during the archery and rifle hunting seasons in hunting district 121, 2023-2025.

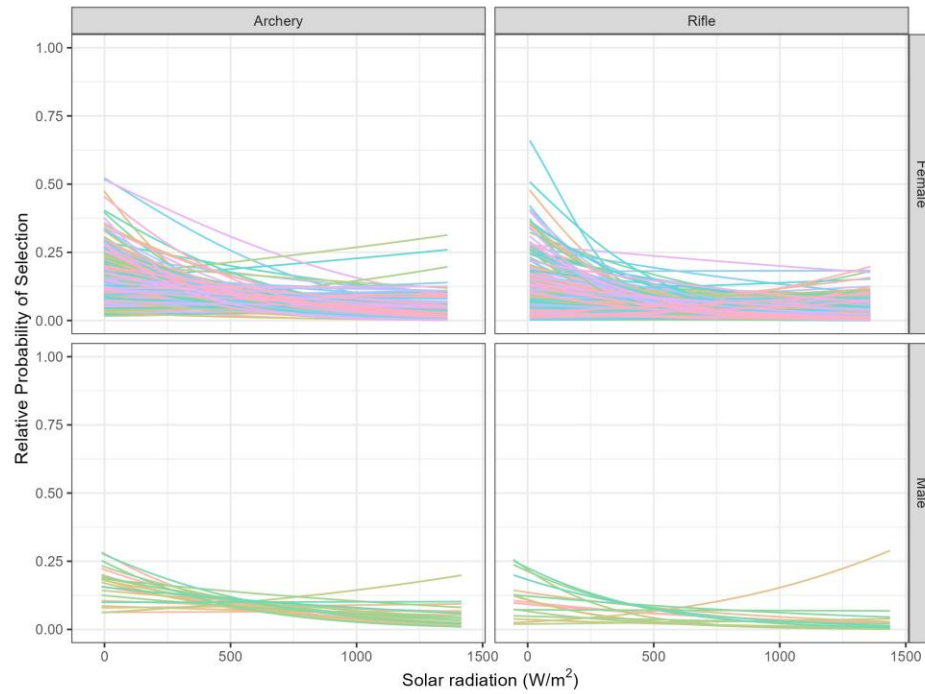


Figure 23. Individual-level random slope coefficients for solar radiation from preliminary resource selection functions (RSFs) evaluating male and female elk habitat selection during the archery and rifle hunting seasons in hunting district 121, 2023-2025.

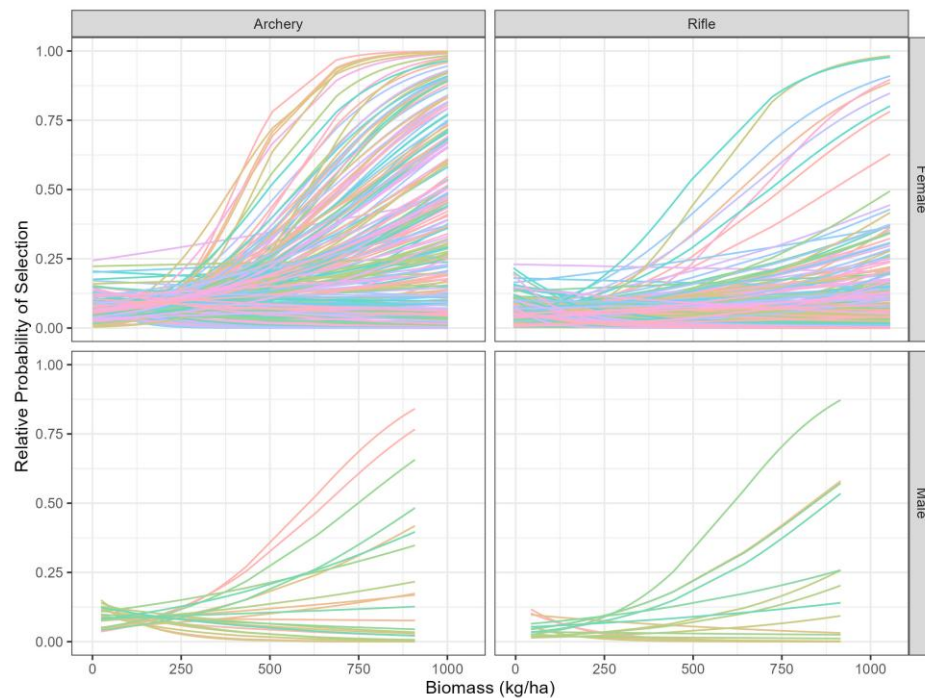


Figure 24. Individual-level random slope coefficients for forage biomass from preliminary resource selection functions (RSFs) evaluating male and female elk habitat selection during the archery and rifle hunting seasons in hunting district 121, 2023-2025.

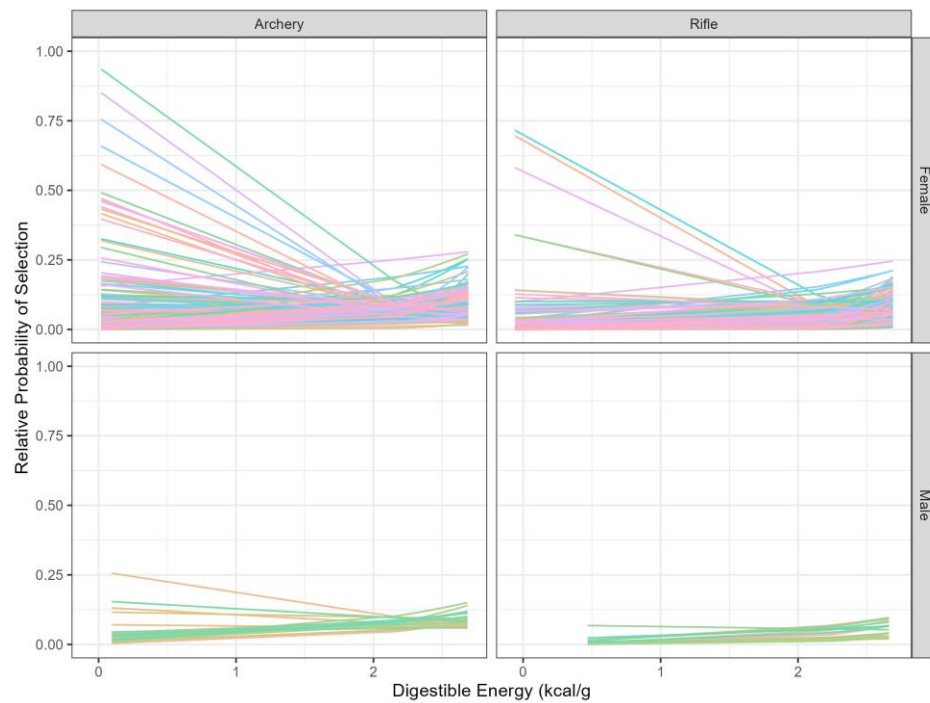


Figure 25. Individual-level random slope coefficients for forage digestible energy from preliminary resource selection functions (RSFs) evaluating male and female elk habitat selection during the archery and rifle hunting seasons in hunting district 121, 2023-2025.

Objective #3: Design monitoring programs for elk and carnivores that will provide necessary information to evaluate the effects of management actions as they are implemented on elk population dynamics and hunting season distributions.

3.1 Background

To improve our understanding of elk and carnivore population dynamics, demographic processes, and distributions in Region 1, information about elk and carnivore survival, movements, and abundances are necessary. Below, we outline our methods and current progress related to collaring of elk and carnivores; estimating elk and carnivore abundance; and measuring the elk nutritional landscape in HD 121.

3.2 Data Collection and Analytical Methods

3.2.1 Adult Elk Capture and Monitoring

Over the winters of 2022–2025 (December–March), we captured male and female elk by a combination of Clover trapping (Thompson et al. 1989; Figure 26) and chemical immobilization from a helicopter following approved University of Montana (003-23JMWB-011823) and FWP (FWP10-2021) animal capture protocols. In May 2025 and 2026, we initiated additional efforts to capture bulls ≥ 2 years old using helicopter chemical immobilization.

Each captured elk was outfitted with Iridium remote upload global positioning system (GPS) radio-collars (Lotek Wireless, model LiteTrack Iridium 420, New Market, Ontario, Canada) programmed to record a location every 2 hours and transmit a mortality notification 8 hours post-mortality.



Figure 26. Female elk captured and chemically immobilized in a Clover trap.

We fit females that were suspected to be pregnant with vaginal implant transmitters (VIT; Lotek Wireless, Newmarket, Ontario, Canada) to assist with neonatal captures in spring (see [Section 3.2.2](#)). We also attempted to collect blood during all captures to confirm pregnancy status based on the presence of pregnancy-specific protein-B in the blood serum (Noyes et al. 1997; Herd Health Diagnostics/BioTracking Testing Lab, Pullman, WA) and extracted a vestigial canine for cementum aging analysis.

In 2023, we assayed blood serum samples for evidence of exposure to pathogens including *Brucella abortus*, Anaplasma bacteria, parainfluenza-3 (P13), bovine respiratory syncytial virus (BRSV), bovine viral diarrhea type 1 (BVD1) and 2 (BVD2), bovine herpesvirus (BHV1), epizootic hemorrhagic disease (EHD), and 5 strains of Leptospira (*L. canicola*, *L. ictero*, *L. grippo*, *L. pomona*, and *L. hardjo*). These pathogens were selected for screening because of their potential to influence individual or herd health in wildlife and/or livestock. All disease assays were conducted by the Montana Veterinary Diagnostic Laboratory (Bozeman, Montana).

We investigated elk mortalities as soon as possible after being alerted of a mortality event. We determined the cause of mortality based on evidence surrounding the mortality site, including teeth marks, carcass condition, and predator signs (e.g., tracks, scat, hair). We calculated annual (June 1 – May 31) natural survival (harvest excluded) for males and females ≥ 1 year old using the Kaplan-Meier estimator in the “survival” package (Therneau 2023).

Ultimately, these data will be used to evaluate elk survival, movements, and space use, which are being used to inform population and distribution models described in Sections 1 and 2.

3.2.2 Neonate Elk Capture and Monitoring

In May and June 2023 – 2025, we located, captured, and collared neonatal elk calves following approved University of Montana (003-23JMWB-011823) and FWP (FWP10-2021) animal capture protocols. We used multiple methods to locate and capture neonatal calf elk, including: 1) monitoring VITs (see [Section 3.2.1](#)) for expulsion from the adult female elk during parturition; 2) monitoring female elk movement metrics to detect parturition behavior (e.g., Figure 27 and narrative below); and 3) opportunistically searching calving areas.

Elk and other ungulates generally display distinct movement patterns around parturition, including a reduction in movement and localization around the birth site and/or neonate. These unique parturition movement patterns may be observed in GPS data from collared female animals. We developed a method to identify potentially parturient female elk by deriving four movement metrics from GPS data and developing parturition-associated thresholds for each metric. The four movement metrics we evaluated were 24-hour rolling MCP home range size, 100m radius residence time with 12-hour rolling average, 24-hour rolling displacement with a 12-hour rolling average, and 12-hour rolling velocity, each of which captured an aspect of reduced or localized movement behavior. To develop threshold values associated with parturition behavior, we used known birth data from the previous neonate capture season and identified the lowest (home range, displacement, velocity) or highest (residence time) value for each metric associated with each individual's known birth event (two days before or after the estimated birth date to account for birth timing uncertainty). We then used the 80th percentile metric value from

this distribution of individual extreme birth values as the threshold for that metric. During calving season, female elk whose movement metric values crossed one or more of these parturition-associated thresholds were flagged as potentially parturient (Figure 27). We examined time series graphs of these individuals' movement metrics as well as raw GPS data for final decision-making before sending a field team to investigate the individual and search for a neonate. We developed a manuscript to describe these methods and make the code/framework available for other researchers capturing neonates. This manuscript is currently in review at *Animal Biotelemetry*.

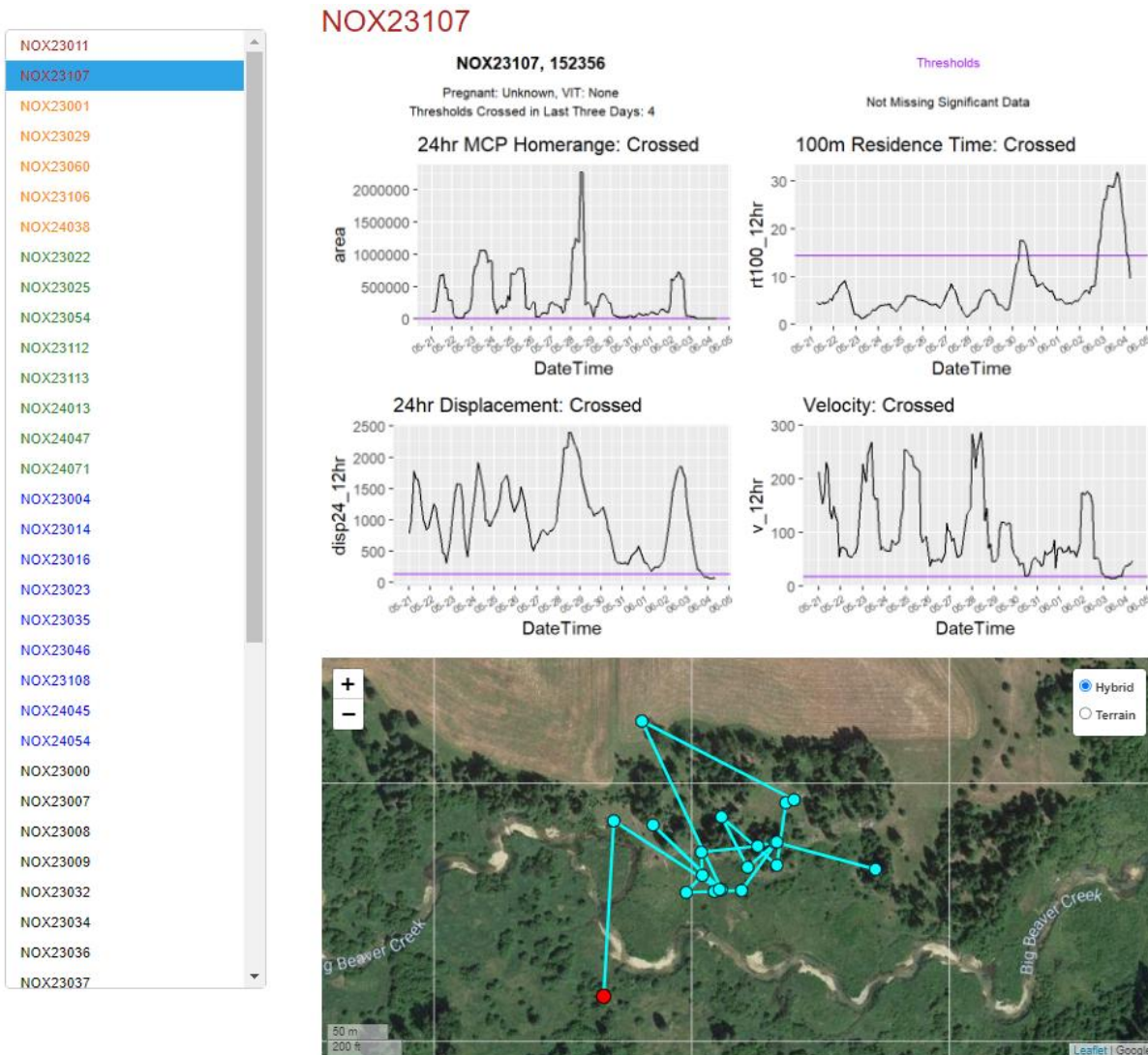


Figure 27. Example output from code developed to identify potential elk parturition events, based on adult female movement metrics in hunting district 121.

Within 12 hours of being alerted of a VIT expulsion (Turnley et al. 2022) or a female elk crossing multiple movement metric thresholds, a team of 2-4 people investigated the area around

the expulsion/GPS cluster, using telemetry to locate both the VIT/parturition site and the collared female. Finally, we used a helicopter during peak calving to help locate “opportunistic” neonates and to assist ground crews in locating well-hidden neonates.

When located, the neonate was caught by hand, blindfolded, and physically restrained with hobbles. We recorded the neonate’s sex, body mass, and estimated age. We outfitted all neonates with expandable GPS collars that collected GPS location data for up to one year or until the collar breaks off (model VERTEX Mini Fawn-1C GLOBALSTAR; VECTRONIC Aerospace Inc.; Figure 28). Due to issues with elastic on collars breaking in 2023, causing the collar to fall off prematurely, collars in 2024 and 2025 were equipped with an abrasion-resistant sheath wrapped around the elastic band. All GPS collars had a mortality sensor that sent a mortality signal if the GPS collar remained motionless for ≥ 6 hours.



Figure 28. Capture and collaring of elk neonates in hunting district 121 in May - June 2023-25.

We searched mortality sites and conducted field necropsies to determine cause of death, including predation, natural mortality (i.e., disease, injury), or hunter harvest. We documented all evidence of predation including claw marks, canine punctures, broken vertebrae, or internal hemorrhaging on the calf carcass (Wade and Bowns 1993, Mattson 1997). We also documented predator sign at and around the kill site including tracks, scat, or hair (Smith et al. 2006, Eacker et al. 2016). We identified black bear predation by evidence of broken vertebrae and puncture

wounds found on or near the dorsal inferior portion of the neck and withers, or a carcass with the hide peeled back and most of the carcass consumed (including the rumen and intestine). We identified mountain lion or felid predation by evidence of puncture wounds or claw marks on or near the head or neck; a cached carcass; plucked hair around areas of consumption; and/or a completely consumed carcass, except the rumen, starting from the hind to front quarters. We identified canid predation by evidence of lacerations and tearing to the ventral superior portions of the neck, or evidence of multiple feeding sites, depending on the number of animals present. For all predation events, we examined subcutaneous hemorrhaging patterns around wounds, including puncture wounds and claw marks, to determine predation (pre-mortem hemorrhaging) versus scavenging (post-mortem seepage). For any unknown predation events, where the carnivore species could not be identified with certainty, we swabbed bite mark locations to collect DNA samples from saliva for carnivore species identification.

In late summer 2025, it became concerning that collars deployed on neonates in 2024 had not fallen off in the timeframe expected (~12 months for the cotton rot-away tab to deteriorate). Due to potential concerns with animal welfare, we underwent 4 separate capture efforts (2 aerial darting from a helicopter and 2 ground darting) to recapture as many of these individuals as possible, assess collar fit, and remove collars. Through these efforts, we recaptured and removed collars from 4 neonates collared in 2024 (2 male, 2 female) and 6 neonates collared in 2025 (4 male, 2 female). Collar fit on individuals collared in 2024 was snug, but with no obvious signs of harm. However, the rot-away tab did not appear to be deteriorating, which continues to be a concern as these individuals grow (particularly males). Fortunately, these collars appeared to be deteriorating at the exposed elastic part of the collar band, and we have observed other collars breaking at this weak point, so it is likely these collars will eventually break off.

3.2.3 Mountain Lion Capture and Monitoring

During winter 2022-23 and 23-24, we used trained hounds to track, tree, and chemically immobilize mountain lions following approved University of Montana (002-23JMWB-010423) and FWP (FWP10-2021) animal capture protocols. We fit adult mountain lions with Iridium remote upload GPS radio-collars (Lotek Wireless, model LiteTrack Iridium 420, Newmarket, Ontario, Canada) programmed to record a location every 4 hours and transmit a mortality notification 6 hours post-mortality (Figure 29).



Figure 29. Mountain lion capture and collaring in hunting district 121 in winters 2022-23 and 2023-24.

3.2.4 Wolf Capture and Monitoring

During summer and fall 2022-2025, FWPs wolf management staff conducted wolf trapping operations. We also conducted aerial helicopter searches for fresh wolf sign or activity during two days in February 2024.

3.2.5 Black Bear Capture and Monitoring

During spring and summer 2023 and 2024, we used culvert traps and chemical immobilization to capture and collar black bears following approved University of Montana (004-23JMWB-012323) and FWP (FWP10-2021) animal capture protocols. We fit captured bears with Iridium remote upload GPS radio-collars (Lotek Wireless, New Market, Ontario, Canada) programmed to record a location every 4 hours and transmit a mortality notification 6 hours post-mortality (Figure 30).



Figure 30. Capture and collaring of black bears with culvert traps in hunting district 121 in summer 2023.

3.2.6 Estimating Elk and Predator Abundance Using Trail Cameras

Trail Camera Deployment and Photo Classification

In May and June 2023, we deployed remote trail cameras (HyperFire 2 Professional Covert IR Camera OD Green) at random locations across HD 121. We selected 100 random locations using generalized random tessellation stratified (GRTS) sampling (Stevens and Olsen 2004), then paired a non-random “predator camera” with 50 of these cameras, selected at random. We placed predator cameras on a dirt bottom trail within 250 meters of the paired random camera to increase the likelihood of detecting predators.

We mounted cameras to trees or t-posts approximately 1.5 meters off the ground at optimal angles for elk and target predator species (Figure 31). We placed predator cameras at a downward angle perpendicular to the trail to capture movement as animals entered or exited the viewshed. We set each camera on both “time lapse” and “motion capture” trigger settings to capture images every 10 minutes and when motion triggered the camera.

In September/October 2023, May/June 2024, and September/October 2024, we returned to the camera sites and switched camera batteries and SD cards. During summer 2025, we recovered all cameras. We ran photos from summer 2023 and fall/winter 2023-2024 through an AI photo classifier that uses Microsoft’s MegaDetector model in Python to identify empty photos and photos with animals present (Beery et al. 2019, Fennell et al. 2022). We classified animal photos to species and counted the number of individuals of each species in each photo. This reporting period, we classified photos from 50 cameras from winter/spring 2024/2025 and continue to classify the remaining photos.



Figure 31. Trail camera deployment in hunting district 121.

Analysis

We used space-to-event (STE) and instantaneous sampler (IS) models from the spaceNtime R package (Moeller and Lukacs 2022) to estimate the abundance of elk, white-tailed deer, mule deer, black bears, mountain lions, and wolves within defined analysis periods in summer/fall 2023 and winter 2023-24. Our analysis periods were based around influential events in an elk's annual cycle, including the ungulate birth pulse (14 March – 30 June, 2023), pre-hunting season/lactation (15 July – 1 September, 2023), and winter (18 December, 2023 – 18 February 18, 2024). We excluded elk calves from abundance estimates during the birth and pre-hunt periods, while the winter period included all ages.

We fit STE and IS models for both random and non-random camera deployment groups. To estimate the bias associated with abundance estimates for each species during each analysis period, we averaged the abundance estimates from both deployment groups, then divided it by the random camera estimate. Then, we used the results of the bias test and the confidence intervals for each target species during each analysis period to determine which deployment method was the most efficient for estimating abundance of multiple species, while considering the difference in sample size for each deployment group.

3.2.7 Quantifying the Nutritional Landscape and Elk Summer Resource Selection

Landcover Layer Development

Before completing vegetation surveys across HD 121, we developed a landcover layer that included vegetation type, timber harvest strategy, and time-since-harvest so that vegetation sampling sites could be appropriately stratified by landcover classification. We obtained landcover type data from LANDFIRE's 30-meter resolution 2020 Existing Vegetation Type raster dataset (USGS 2022a) and reclassified them into 8 generalized landcover types: mesic forest, xeric forest, deciduous forest, shrubland, grassland, agriculture, wetland, and other. Mesic forests included coniferous forests associated with spruce and fir species. Xeric forests included coniferous forests associated with ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*) and limber pine (*Pinus flexilis*). Douglas fir-dominated forests were classified as either mesic or xeric depending on the secondary tree species associated with the vegetation type. Deciduous forests included forests associated with aspen (*Populus tremuloides*), cottonwood (*Populus* sp.), and western larch (*Larix occidentalis*). Shrublands and grasslands included any shrub- or grass-dominated vegetation type, respectively. Agriculture included cultivated crops and irrigated agriculture. Wetlands included wet meadows, marshes, herbaceous riparian areas, or wetlands. "Other" included the remaining cover types such as human development, sparse vegetation, snow or ice, and open water.

We obtained timber harvest strategy and time-since-harvest spatial data from the USFS and the Montana Department of Natural Resources. We defined timber harvest strategy as the various combinations of treatment types, defined by the Forest Activity Tracking System and Powell (1993), and post-treatment activities utilized by managers when harvesting timber designed to result in a certain stand-age class. We categorized timber harvest polygons into one of four timber harvest strategies: even-age, two-age, uneven, and intermediate, as defined in the USFS Forest Service Manual (USFS FSM 2400 Chapter 2470). Even-age cuts are designed to maintain

and regenerate a stand with one age class and <10% leave trees (e.g., clearcutting). Two-age cuts are designed to maintain and regenerate a stand with two age classes (e.g., any method retaining reserve trees). Uneven cuts are designed to maintain and regenerate a stand with 3 or more age classes (e.g., single and group tree selection regeneration). Intermediate cuts are defined as any treatment designed to enhance growth, quality, vigor, and composition of the stand after establishment or regeneration (e.g., commercial thinning, salvage and release cuts). There were very few two-age or uneven cuts in the study area, so we only sampled from even-age and intermediate cuts.

Our final stratified landcover layer included 25 unique strata in combinations of landcover type, harvest strategy, and years-since-harvest (i.e. 1-5, 6-10, 11-20, 21-40, and >40 years). However, we decided to not include deciduous forest, other, or wetland landcover types in sampling strata due to the low occurrence of these landcover types in the study area. We used the GRTS sampling method (Stevens and Olsen 2004) to generate 375 random sites that were spatially-distributed within landcover strata and across the study area (Figure 32), with the intention to visit each location once from May-August 2023 and visit another unique set of 375 random locations from May-August 2024.

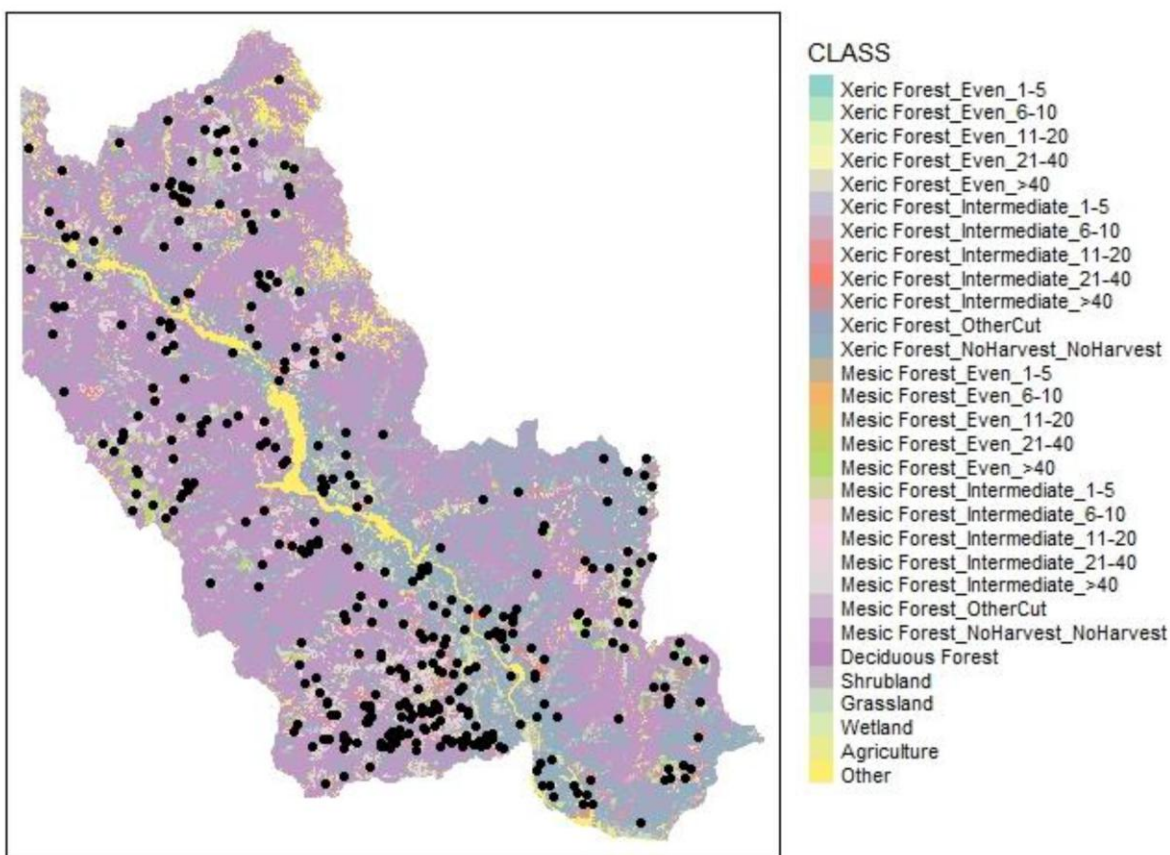


Figure 32. Reclassified landcover strata in hunting district 121 incorporating generalized landcover category, timber harvest strategy, and time-since-harvest. Black dots represent potential vegetation sites randomly selected by strata. The Xeric Forest_OtherCut, Mesic Forest_OtherCut, Deciduous Forest, Wetland, and Other strata were not included in the sampling stratification because of their low prevalence and/or inability to be sampled.

Fecal Pellet Collection

We collected composite elk fecal pellets to evaluate elk diet in the study area and identify the plant species that are important sources of forage for elk in this system. We used GPS locations obtained from collared elk to identify suspected elk bedding sites that were <3 days old. At these sites, we collected 2 pellets <1 week old from each of 2 distinct pellet piles within a 300 m² radius of the site. We collected pellets from 3-5 spatially distributed sites each week of the field season to create weekly composite samples.

We also collected fecal samples during the winter capture season in 2022-23. We combined 1 pellet from 6-8 individuals into a composite sample and assembled 3 composite samples per capture location classified into lower elevation valley and higher mountainous forest environments. Lower valley locations included animals primarily captured by clover traps, and higher forest locations included animals captured by helicopter. No individuals were repeat sampled.

We homogenized and froze composite samples from both seasons in a liquid salt-based RNA stabilizer. Then, we sent all samples to the Species From Feces – Bat Ecology and Genetics Lab at Northern Arizona University, where they used DNA metabarcoding to determine the plant species composition within the pellets. We filtered the lab results through thresholds of 1% relative read abundance and 10% frequency of occurrence (Deagle et al. 2018, Snobl et al. 2022) to determine an elk diet list.

Using these data, we calculated the percentage of composite samples which contained each forage species/item within each sample timing classification and, for winter only, within capture location classifications (i.e., lower valley and higher forest).

Vegetation Surveys

We measured forage quantity and quality at each vegetation sampling site to characterize the summer nutritional landscape for elk across hunting district 121 and to identify how timber harvest affects the nutritional landscape. We established a 40m transect with 1 m² quadrats along the transect at 10m intervals, for a total of five quadrats at each site. At each quadrat, we recorded species composition and visually estimated percent cover of each species. We also recorded phenological stage of each species (emergent, flowering, fruiting, and cured/mature) to be used for forage quality calculations. At the 0m, 20m, and 40m quadrats, we established a 0.25 m² clip plot in the bottom right corner of the quadrat (Figure 33).

We clipped all herbaceous vegetation >2cm above ground within the clip plot and sorted it by growth habit (i.e., shrub, grass, forb). Within 24 hours of sampling, we dried clipped samples for 24-48 hours at 40-60 °C, then weighed the samples. We applied the estimated cover percentages of each species to the clipped sample dry weight to estimate the biomass of each plant species in the clipped plot (g/0.25 m²), which we then used to estimate understory biomass at the greater sampling site (kg/ha; forage quantity).



Figure 33. Vegetation sampling in hunting district 121.

We collected at least 3 samples (at least 20 g dry, total) of each elk forage species in each phenologic stage throughout the study area. Elk forage species were determined via DNA metabarcoding of elk fecal pellets collected in 2023 (see above). We included multiple plants from within a 300 m² radius in each forage sample to reduce individual plant bias. We did not collect any samples from within 15 m of an active road to reduce effects of road dust and chemicals. We placed samples in drying ovens at 40-60 °C within 6 hours of collection and dried them for 48-72 hours. We sent samples to the Forage Laboratory at DairyOne (Ithaca, NY), where they used sequential detergent fiber assays (Goering and VanSoest 1970) to estimate the digestibility of the individual plant cell constituents for each forage item. We then used equations developed by Robbins et al (1987) to relate these values to actual or in vivo (i.e., in the animal) digestibility.

We also collected select samples of forage items for tannin analysis to use in estimation of species and stage specific digestible energy. We collected 2 tannin samples (1 emergent phenostage, 1 cured/mature phenostage) for any forage forbs known to contain tannins and all forage shrub species. We included multiple plants from within a 300 m² radius in each tannin sample to reduce individual plant bias. We did not collect any samples from within 15 m of an active road to reduce effects of road dust and chemicals. We placed samples on ice immediately in the field and moved them to a freezer within 6 hours for storage. We sent samples to the Wildlife Habitat and Nutrition Lab at Washington State University (Pullman, WA), where they used the bovine serum albumin (BSA) method (Hagerman and Butler 1978) to measure tannin concentrations of each forage item.

Calculating Site-specific Forage DE and Biomass

We estimated forage quality as the mean DE value at a sampling point. For each quadrat, we filtered the recorded species to include only forage taxa. We multiplied the phenostage proportions for each taxon by the phenostage-specific DE value for that forage taxon and summed the values for an estimate of DE at the quadrat level. We took the mean of the DE value across the five quadrats at a sampling point to obtain our estimate of a sampling point's DE value (Proffitt et al. 2019, Snobl et al. 2022).

We used a similar approach to estimate forage biomass at each sampling point. For each quadrat, we filtered the recorded species to include only forage taxa. We used the ground cover estimates to calculate the proportion of each forage taxon within its functional group and multiplied that proportion by the dry weight of the functional group to obtain dry weight estimates for each forage taxon in each clipped quadrat. We summed the biomass of forage taxa in each functional group across the 3 clipped plots, multiplied by 4 to convert the data from g/0.25m² to g/m², multiplied again by 10 to convert the data from g/m² to kg/ha, and divided by 3 (i.e., the number of clip plots) to estimate the mean forage biomass of each functional group at a sampling point. We then summed the biomass of each functional group to estimate total mean forage biomass at a sampling point (Proffitt et al. 2019, Snobl et al. 2022).

Modeling the Nutritional Landscape in HD 121

We created separate predictive models for both forage DE and forage biomass. Our primary goals were to understand the influence of timber harvest covariates on forage resources, and to compare the resources of harvested forests to other areas on the nutritional landscape. We compared 22 hypothesis models for both forage DE and biomass which were comprised of different combinations of forest type, harvest strategy, and time-since-harvest. Each hypothesis model also included non-timber-harvest covariates and interactions which were determined via univariate modelling.

The non-harvest covariates that advanced to the forage DE hypothesis models after univariate modeling included grassland, agriculture, and mesic forest landcover types, elevation, Julian day, and E-, S-, SW-, and W-facing aspects. The non-harvest covariates that advanced to the forage biomass hypothesis models included grassland, agriculture, and mesic forest landcover types, elevation, Julian day, and fire history. We used Akaike Information Criterion (AIC) to compare the hypothesis models (Burnham and Anderson 1998) and identify the top models for forage biomass and DE.

Modeling the Nutritional Landscape Across Western Montana

In addition to modeling the nutritional landscape in HD 121, we are combining these data with elk nutrition data collected in Montana to develop a model that predicts annual elk and mule deer forage quality (DE) and quantity (biomass) in western Montana from 2012 forward using remotely sensed data. We are using these model predictions as covariates in resource selection analyses and population models to identify how forage quality and quantity affect elk distributions and population dynamics.

To inform models, we included data on the quality and quantity of available forage from eight unique study areas that have been used in prior study area-specific efforts to quantify elk (Proffitt et al. 2016, 2019, DeVoe et al. 2019, Paterson et al. 2022b) and mule deer forage (Hayes et al. 2022, Snobl et al. 2022). Field methods in each area included the identification of plant species that were consumed as forage by elk and mule deer using either plant fragment analysis or DNA metabarcoding with fecal samples collected in the field. For each ungulate species, we combined the forage plant lists from each prior study and used a combined list that more thoroughly captured the plants available to elk and mule deer. Because the original mule deer forage species were collected across a narrower range of environments than for elk, we added species to the mule deer forage list that were not detected in lab samples but have been identified elsewhere as important components of mule deer diets.

During vegetation sampling, field crews estimated ground cover by species and phenological stage in three to five 1 m² quadrats along 40 m transects. They collected and dried samples of the vegetation cover. Those samples were analyzed for their dry matter digestibility. We then used methods following Proffitt et al. (2016) and Cook et al. (2016) to calculate the mean total forage biomass (g/m²) and digestible energy (DE: kcal/g/m²) of each plot based on species- and phenostage-specific lab estimates for all plants identified as forage species. Where plants were not identified to species, we used genus-level estimates. In our analysis, we combined the field plot data across all studies originally designed for either ungulate species and made estimates of forage quality and biomass based on vegetation data at each field plot, regardless of whether that plot was originally collected as part of an elk or mule deer study.

To build models of ungulate forage that are most likely to be generalizable and repeatable, we derived the model covariates using the Google Earth Engine platform (GEE; Gorelick et al. 2017). GEE is a cloud-based processing service that allows users to access remotely sensed data that might otherwise be difficult to acquire or computationally intensive to process. We selected covariates that are available across large spatial extents—at minimum, the western United States—so the analysis would be easiest to adapt and repeat for researchers in other areas. Broadly, we included covariates in six categories: spectral characteristics, land cover, topography, climate/weather, disturbance history, and soil.

We derived covariates of vegetation properties based on spectral data collected from the Landsat platform. Though Sentinel-2 provides higher spatial and temporal resolution and may be preferable for future work, some of our data were collected before it was launched in 2015. Instead, Landsat has been an active platform for decades and is an invaluable tool for researchers interested in remotely sensed data covering long time periods. From Landsat, we calculated Normalized Difference Vegetation Index (NDVI), Enhanced Vegetation Index (EVI), and the Normalized Difference Moisture Index (NDMI), which measures the water content of vegetation and can be used to approximate its moisture stress (Gao 1996, Sheriff et al. 2025). For each location and in every year, we calculated the minimum, maximum, and range of each of those vegetation indices between October 1 of the previous year and July 15 of the current year. By calculating the range of each index, we hoped to distinguish between evergreen areas of high vegetation activity detectable at the visible surface (e.g., conifer tree canopy cover) from those with a large difference between peak growing season and senesced conditions (e.g., herbaceous cover in mesic areas). We also included in the models annual measures of tree canopy cover from

the US Forest Service (USDA Forest Service 2025) and aboveground herbaceous and total biomass from the Rangeland Analysis Platform (RAP; Jones et al. 2018).

As metrics of topography, we included elevation and two derived indices: multiscale Topographic Position Index (mTPI), a metric used to quantify a pixel's elevation compared to the area around it, and continuous heat-insolation load index (CHILI), a measure of incident solar radiation based on latitude, slope, and aspect (Theobald et al. 2015). To account for the effect of disturbance history on forage, we calculated separately the number of years since timber harvest and fire (Proffitt et al. 2019, Hull et al. 2020, Snobl et al. 2022) based on the US Forest Service Landscape Change Monitoring System (LCMS), which produces annual maps of vegetation loss and its causes. We also included the mean fire return interval (MFRI) from LANDFIRE, a modeled product that estimates the average number of years between fires (U.S. Department of the Interior 2016).

Because soil physical characteristics can affect forest understory cover and biomass (Suchar and Crookston 2010), we included data on soil texture (proportion clay, silt, and sand particles), soil organic carbon content, and soil pH (Poggio et al. 2021). Further, soil moisture balance is a critical component of canopy water use and can both drive and interact with land cover responses to wildfire (Davis et al. 2019, Lyons et al. 2021, Holden et al. 2024). As a measure of total plant and soil water transmission, we therefore calculated the total summer (June 1 – August 31) actual evapotranspiration (AET) with data from the USGS VIIRS platform (Senay et al. 2023). We also used metrics of long-term climatic water balance from TopoTerra (Hoecker et al. 2024), a downscaled (220 m) product that includes historic normal (1961 – 2022) annual AET, climatic water deficit (CWD), mean January low temperature, and mean July high temperature. The TopoTerra historic normal metrics were the only covariates we used that we did not acquire with GEE.

We performed all analyses using random forest (RF) regressions in program R with the *caret* (Kuhn 2008) and *ranger* (Wright and Ziegler 2017) packages for model tuning and training. We modeled forage quality and biomass as separate response variables and did so separately for each ungulate species. In a landscape as forest-covered as western Montana, it is difficult to directly observe the characteristics of vegetation accessible as forage for ungulates. For phenomena where the process is complicated and cryptic, flexible modeling techniques like RF are likely to more accurately capture the nonlinear effects and interactions between variables that drive the outcome, including in models of ungulate nutritional landscapes (generalized additive model: Lopez et al. 2024) and aboveground vegetative biomass (Filippelli et al. 2020, Zhang et al. 2024, Ayushi et al. 2024). Because our goal was to predict nutritional landscapes across a large extent in a wide range of environmental conditions, we divided the study extent into evenly sized spatial blocks of one degree of latitude and longitude. We then used a leave-group-out cross-validation (LGOVCV) in model training wherein the data were grouped by their spatial block and sampling year, then randomly assigned to training (70% of blocks) or testing (30% of blocks) data based on their spatiotemporal block. We repeated the process ten times so different combinations of data were used to build the final ensemble model. In model tuning, we allowed the number of variables randomly selected at each node (*mtry*) to vary between 4, 5, and 7 and used a minimum node size of five points.

After training the models, we evaluated them based on their performance predicting out-of-sample data with R^2 and root mean square error (RMSE). We also calculated variable importance for each model based on the variance of responses and partial dependence for each variable (Greenwell 2017) to evaluate their effects. For both ungulate species, we predicted the nutritional landscape of quality and biomass of suitable forage in each year 2012 – 2024. Because late summer and early autumn are critical periods for elk and mule deer nutrition, we made the predictions based on a September 1 date.

We are in the process of refining model results, so do not present those here. However, we included preliminary predictions from these models (e.g., see Figure 34) in the HD 121 IPM (see [Section 1](#)) to identify the effects of nutrition on elk survival over time.

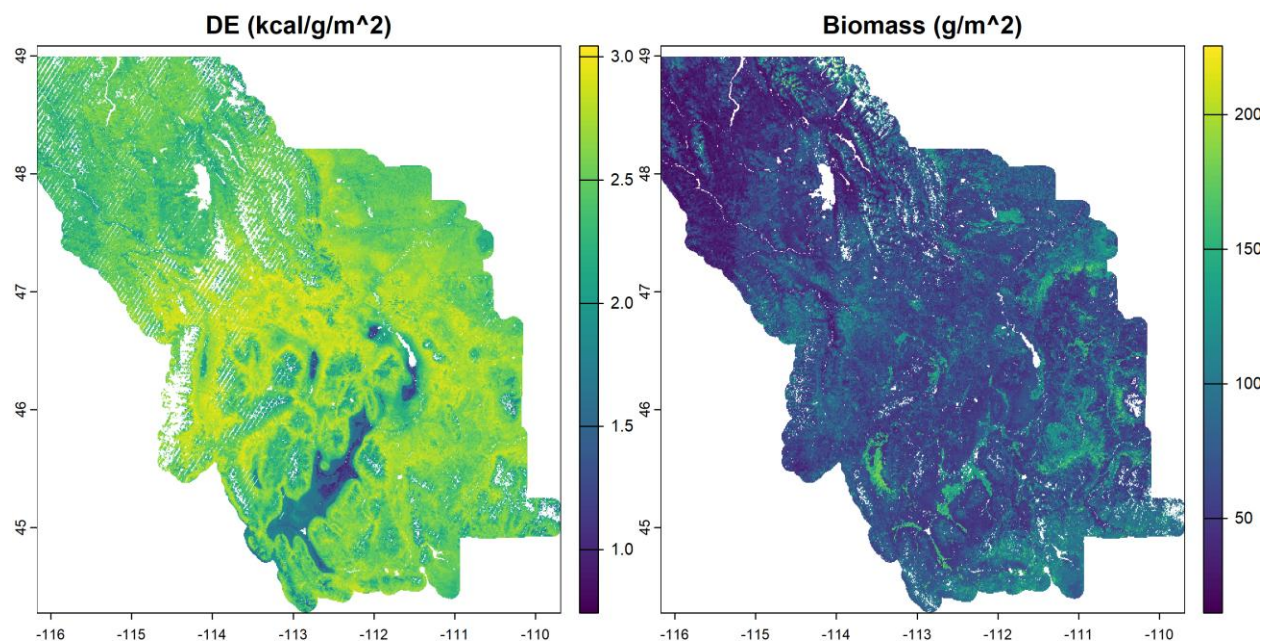


Figure 34. Example predictive maps of elk forage quality (digestible energy; DE; kcal/g/m²) and forage biomass (Biomass; g/m²) across western Montana in 2012.

Elk Resource Selection During Summer

We used location data obtained from 92 adult female elk in our analysis to estimate elk resource selection in early (May-June) and late (July-August) summer during crepuscular (dawn/dusk) and daytime periods. To reduce spatial autocorrelation (Hansteen et al. 1997), we randomly sampled 2 locations per time period per day for each individual, for a total of 6 locations per individual per day. We used the ‘adehabitatHR’ package (Calenge et al. 2006) in R to build 95% kernel density estimate home ranges for each individual and sampled from within each home range (e.g., third order of selection, Johnson 1980) at a 1:10 ratio of used:available points. We extracted covariate values at each location using bilinear interpolation from the four neighboring

grid cells (Klappstein et al. 2022) using the ‘extract’ function in the package ‘terra’ (Hijmans 2025) in R.

We developed separate resource selection probability functions (RSPFs; Rota et al. 2013) for early and late summer during both daytime periods. We evaluated 9 covariates in relation to elk resource selection. Though our primary goal was to determine how elk utilized timber harvest areas, we also included covariates related to other landcover types, fire, roads, carnivores, and topography, recognizing their potential influence on elk resource selection. We included these non-harvest covariates in their simplest hypothesized forms. We derived our landcover-, fire-, and timber harvest-related covariates from a previously developed landcover model (see above). We did not consider canopy cover or distance to cover (DeVoe et al. 2019, Snobl et al. 2024), as these metrics are inherently tied to the timber harvest covariates.

We fit RSPF models with categorical covariates, which included landcover classified into 8 broad categories (i.e. mesic forest, dry forest, agriculture, grassland, shrubland, deciduous forest, wetland, and other); harvest strategy binned into 5 categories (i.e. even-age, intermediate, two-age, uneven, and no harvest); time-since-harvest binned into 5 categories (i.e. 1-5, 6-10, 11-20, 21-40, and >40 years); and wildfire as a binary variable (fire history/no fire history). Any area that had a record of wildfire in the last century was considered burned and otherwise was considered unburned. In practice, almost all fire polygons in the study area had burns occurring within the last 10 years.

We also included continuous covariates in RSPF models, including distance (m) to motorized route, terrain ruggedness index (TRI), and an index of predation risk. We developed species-specific Resource Selection Functions (RSFs) to use as course-scale proxies for variation in predation risk for the three most common large carnivores in our study area: wolves, mountain lions, and black bears. These models were developed using GPS data collected from the radiocollars of carnivores that were captured during the study (n wolves = 2, n mountain lions = 9, n black bears = 5) and utilized covariates identified as important in nearby systems (Peterson et al. 2021, Montana Black Bear Monitoring Progress Report 2024).

We estimated the absolute probability of use (ψ) by elk at a location (i) using the following equation:

$$\psi_i = \frac{\exp(\beta_0 + \ln\left(\frac{n_u}{\pi n_a} + 1\right) + \beta_1 x_{i1} + \dots + \beta_j x_{ij})}{1 + \exp(\beta_0 + \ln\left(\frac{n_u}{\pi n_a} + 1\right) + \beta_1 x_{i1} + \dots + \beta_j x_{ij})} \quad \text{Eq. 9}$$

where β_0 is the intercept, n_u is the number of used locations, n_a is the number of available locations, π is a prevalence term equivalent to the average probability of use by elk, and $\beta_1, \dots, \beta_j$, are the parameter coefficients for the j covariates (Rota et al. 2013). We used the ‘R2jags’ package (Su and Yajima 2024) in R to fit a global RSPF model for each summer–time-of-day period. We included a random effect for each individual elk such that a separate intercept value was calculated for each elk (β_{0e}), drawn from a normal distribution with a population mean ($\beta_{0\mu}$) and standard deviation ($\beta_{0\sigma}$): $\beta_{0e} \sim N(\beta_{0\mu}, \beta_{0\sigma}^2)$ (Snobl et al. 2024). We used slightly informative priors ($\beta_{0\mu} \sim N[0,1]$; $\beta_{0\sigma} \sim \text{Unif}[0,20]$) that allowed adequate sampling of parameter space while

being constrained to reasonable values. We included the centered and scaled covariates described above as fixed effects predictors using vague priors from a normal distribution ($\beta_0 \sim N(0, 1)$). We used a vague prior to estimate prevalence as a fixed term ($\pi \sim \text{Unif}[0.001, 0.999]$), allowing for a broad sampling of parameter space (Rota et al. 2013, Snobl et al. 2024).

We estimated the posterior distribution of parameters by running 3 Markov chain Monte Carlo chains, each for 3,000 – 10,000 iterations, with a burn-in of 50% the number of iterations, and a thinning of 5 (when n iterations = 3,000) or 10 (when n iterations > 3,000). We evaluated the evidence for each parameter's effect based on the 95% credible interval (i.e., the 2.5%–97.5% quantiles of the posterior distribution) and the posterior probability of direction ($P(\beta > 0)$ or $P(\beta < 0)$), defined as the proportion of the posterior distribution that shares the sign of the median estimate (Makowski et al. 2019). We considered there to be strong evidence for an effect if the 95% credible interval did not include zero. If the 95% credible interval overlapped zero, we considered there to be moderate evidence if $P(\beta > 0)$ or $P(\beta < 0) \geq 0.9$. If the 95% credible interval overlapped zero and $P(\beta > 0)$ or $P(\beta < 0) < 0.9$, we interpreted this as no strong evidence for an effect (Rouanet 1996, Makowski et al. 2019). We considered parameters with $\hat{R}$ values ≤ 1.1 adequately converged. We used posterior predictive checks to calculate a Bayesian p-value (pb), assuming adequate model fit if $0.1 < pb < 0.9$ (Gelman et al. 2014).

3.3 Results as of July 1, 2026

3.3.1 Adult Elk Capture and Monitoring

In winter 2022-23, we captured and collared 71 adult elk (54 adult females, 6 female calves, 7 adult males, 4 male calves; Figure 35). We captured 37 of these elk in Clover traps over 314 trap-days (number of Clover traps * number of days active) and captured the remaining 34 elk in 2 days of helicopter captures. We took blood samples from 48 adult female elk, 42 of which were found to be pregnant, resulting in an estimated pregnancy rate of 87.5% (95% confidence interval [CI] = 77.1% - 95.8%), which is similar to the state-wide average for adult females (87%). Age results via tooth eruption/wear patterns and cementum aging suggested female elk >1 year old ranged from 1.5 – 20.5 years old, with a median age of 7.5 years old (Figure 36).

In winter 2023-24, we captured and collared 50 additional elk (40 adult females, 6 female calves, and 4 male calves) and recaptured 5 adult females (Figure 35). We captured 32 of these elk in Clover traps over 346 trap-days and captured the remaining 23 elk in 3 days of helicopter captures. We took blood samples from 41 female elk (37 adult, 4 yearling), 35 of which were found to be pregnant (34 adult, 1 yearling), resulting in an estimated total pregnancy rate of 85.4% (95% CI = 73.2% - 95.1%) and an adult pregnancy rate of 91.2% (95% CI = 81.1% - 100%). Age results via tooth eruption/wear patterns and cementum aging suggested female elk >1 year old ranged from 1.5 – 19.5 years old, with a median age of 6.5 years old (Figure 36).

In winter 2024-25, we captured and collared 36 additional elk (29 adult females, 3 female calves, and 4 male calves) and recaptured 11 adult females (Figure 35). We captured 33 of these elk in Clover traps over 310 trap-days and captured the remaining 14 elk in 2 days of helicopter captures. We took blood samples from 33 female elk (30 adult, 3 yearling), 25 of which were found to be pregnant (25 adult, 0 yearling), resulting in an estimated total pregnancy rate of

75.8% (95% CI = 60.6% - 90.9%) and an adult pregnancy rate of 83.3% (95% CI = 70.0% - 96.7%). Age results via tooth eruption/wear patterns and cementum aging suggested female elk >1 year old ranged from 1.5 – 19.5 years old, with a median age of 6 years old (Figure 36). In May 2025, we captured 11 additional adult males (nine 2-year-olds and two 3-year-olds) in 4 days (15 total hours) of helicopter captures. In May 2026, we captured 7 additional adult males (two 2-year-olds, two 3-year-olds, two 4-year-olds, one 5-year-old) in 2.5 days of helicopter captures.

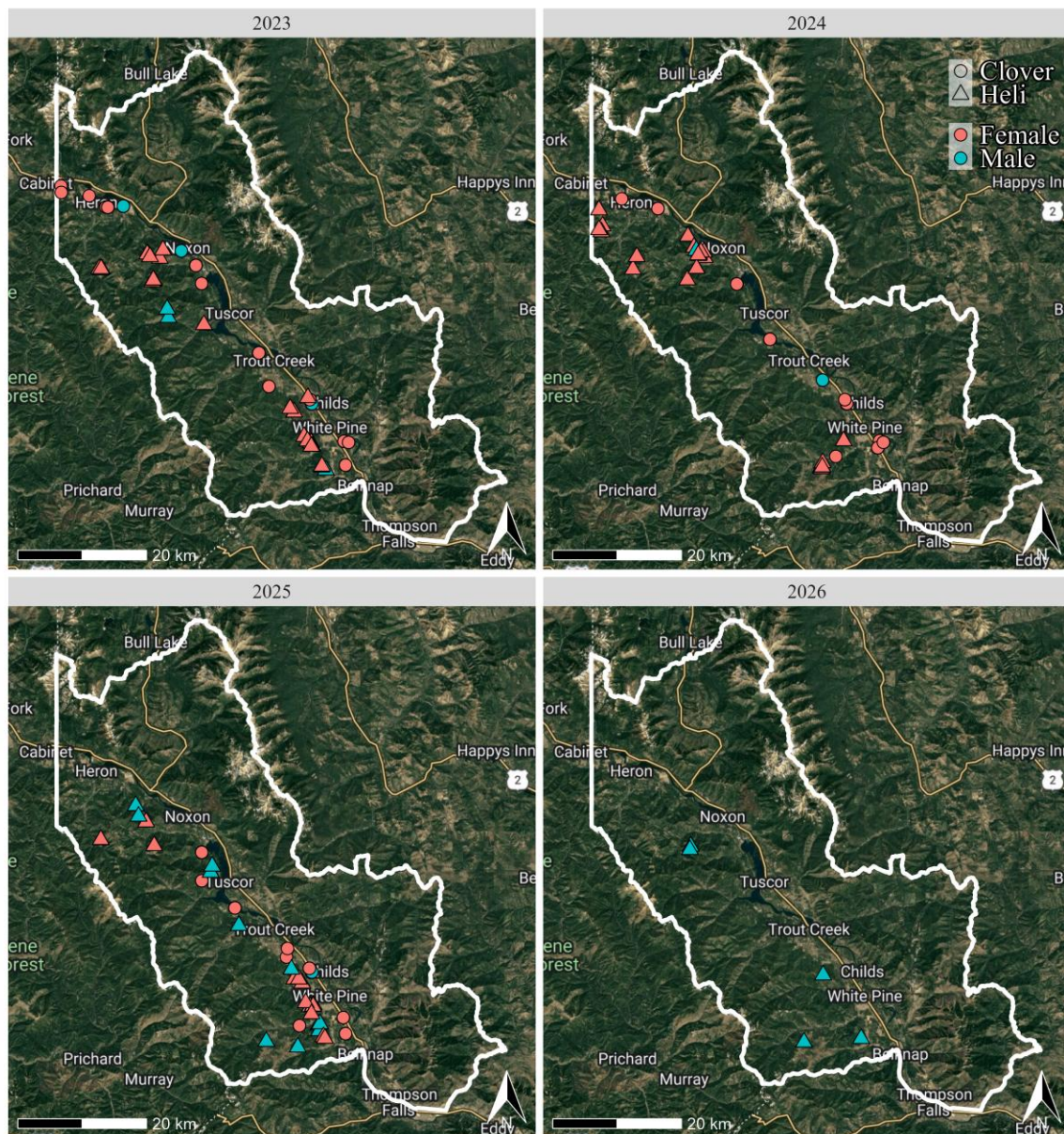


Figure 35. Locations of female (red) and male (blue) elk captures in hunting district 121 (white outline) in winter 2022-23 (“2023”), 2023-24 (“2024”), 2024-25 (“2025”), and May 2026. Elk were captured via Clover trap (circles) and helicopter (triangles) methods. Some captures occurred close together, so locations are difficult to differentiate on the map.

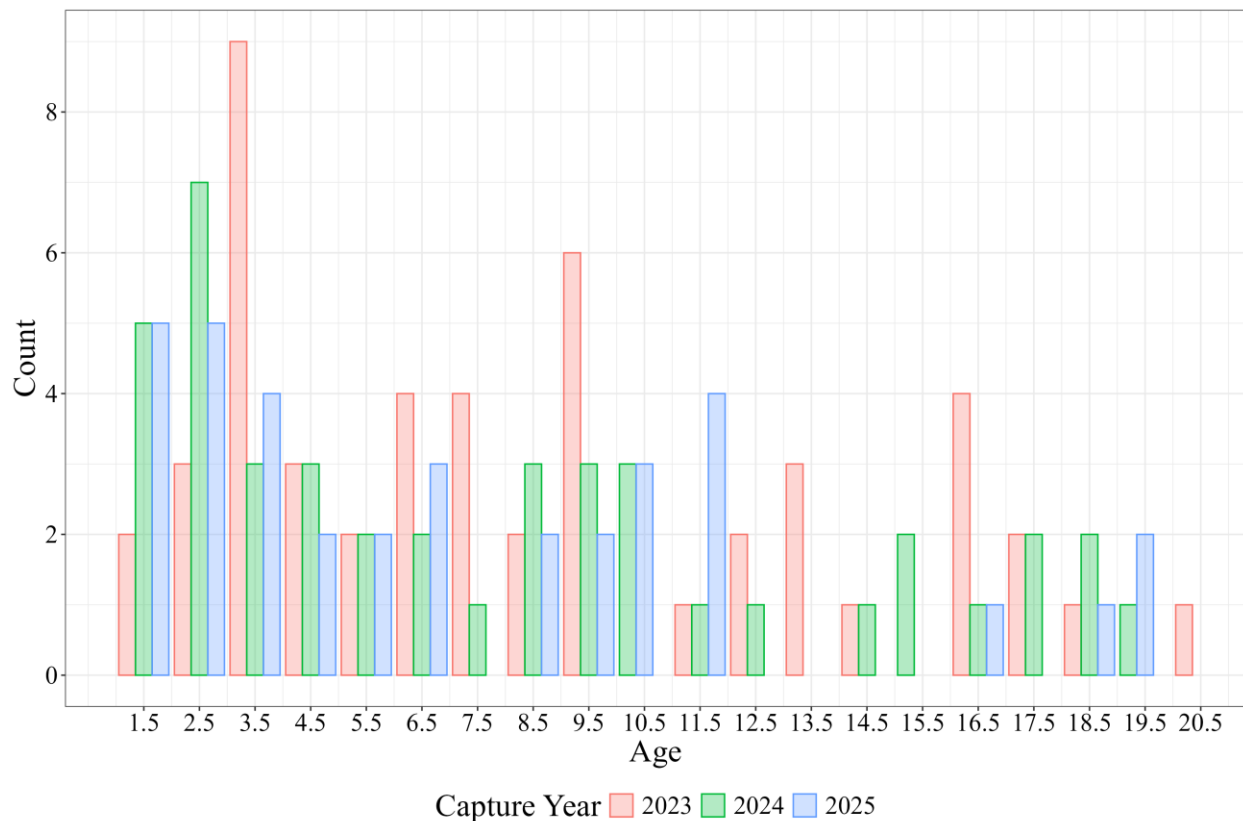


Figure 36. Bar graph of ages of female elk >1 year old captured and collared in hunting district 121 in winter 2022-23 (capture year 2023; red), 2023-24 (capture year 2024; green), and 2024-25 (capture year 2025; blue).

The serology screening in 2023 showed that elk in the area had exposure to multiple diseases known to affect wildlife and/or livestock populations. Evidence for exposure varied by pathogen (Table 5). We found no serological evidence of exposure to brucellosis, BRSV, BVD1, or BVD2. We did find evidence of exposure to Anaplasma (64.6% seroprevalence), PI3 (62.5% seroprevalence), BHV-1 (8.3% seroprevalence), EHD (2.1% seroprevalence), and Leptospira (6.2% seroprevalence). A brief description of each pathogen and its influence (if known) on individual or herd health can be found in Appendix A.

Table 5. Seroprevalence of brucellosis (*Brucella abortus*), anaplasmosis (*Ana*), parainfluenza-3 (PI3), bovine respiratory syncytial virus (BRSV), bovine viral diarrhea type 1 (BVD1), bovine viral diarrhea type 2 (BVD2), bovine herpesvirus-1 (BHV1), epizootic hemorrhagic disease (EHD), and *Leptospira* (*Lepto*) based on serological screening of adult female elk during the winter of 2023.

	Brucella	Ana	PI3	BRSV	BVD1	BVD2	BHV1	EHD	Lepto
#Sampled	48	48	48	48	48	48	48	48	48
#Exposed	0	31	30	0	0	4	1	1	3
%Exposed	0	64.6	62.5	0	0	8.3	2.1	2.1	6.2

As of July 1, 2026, after removing locations with dilution of precision >10, suggesting poor accuracy, we have collected a total of 363,377 locations from 136 female elk and 33,766 locations from 25 male elk in winter (December 1 – March 31); 317,269 locations from 132 female elk and 40,143 locations from 36 male elk in spring (April 1 – June 30); 163,763 locations from 128 female elk and 22,699 locations from 28 male elk in summer (July 1 – August 31); and 233,856 locations from 128 female elk and 25,285 locations from 26 male elk in autumn (September 1 – November 30; Figure 37, Figure 38). All these values exclude locations of individuals with neonate collars.

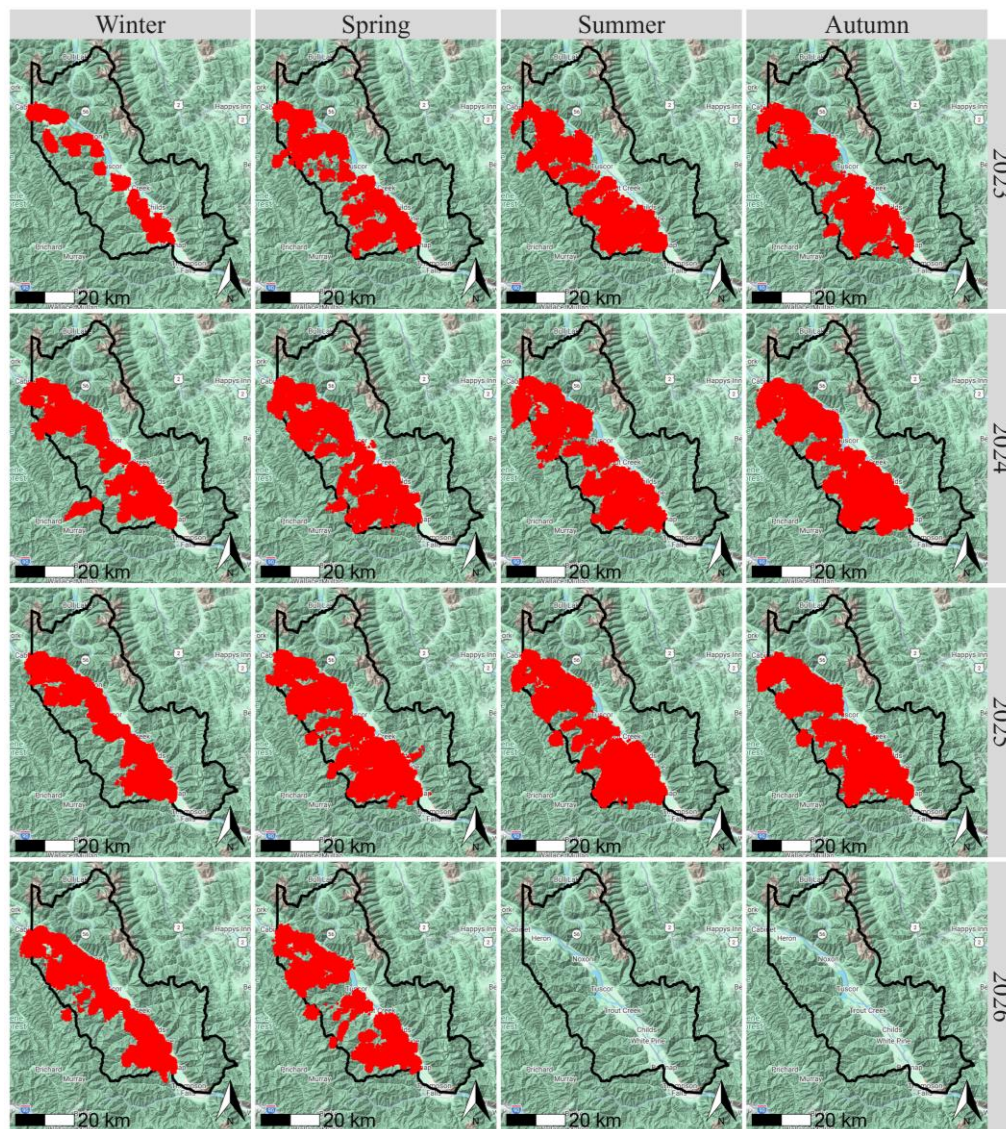


Figure 37. Winter (December 1 – March 31), spring (April 1 – June 30), summer (July 1 – August 31), and autumn (September 1 – November 30) locations of female elk as of July 1, 2026 in and around hunting district 121 (black outline). Locations have been jittered slightly for display.

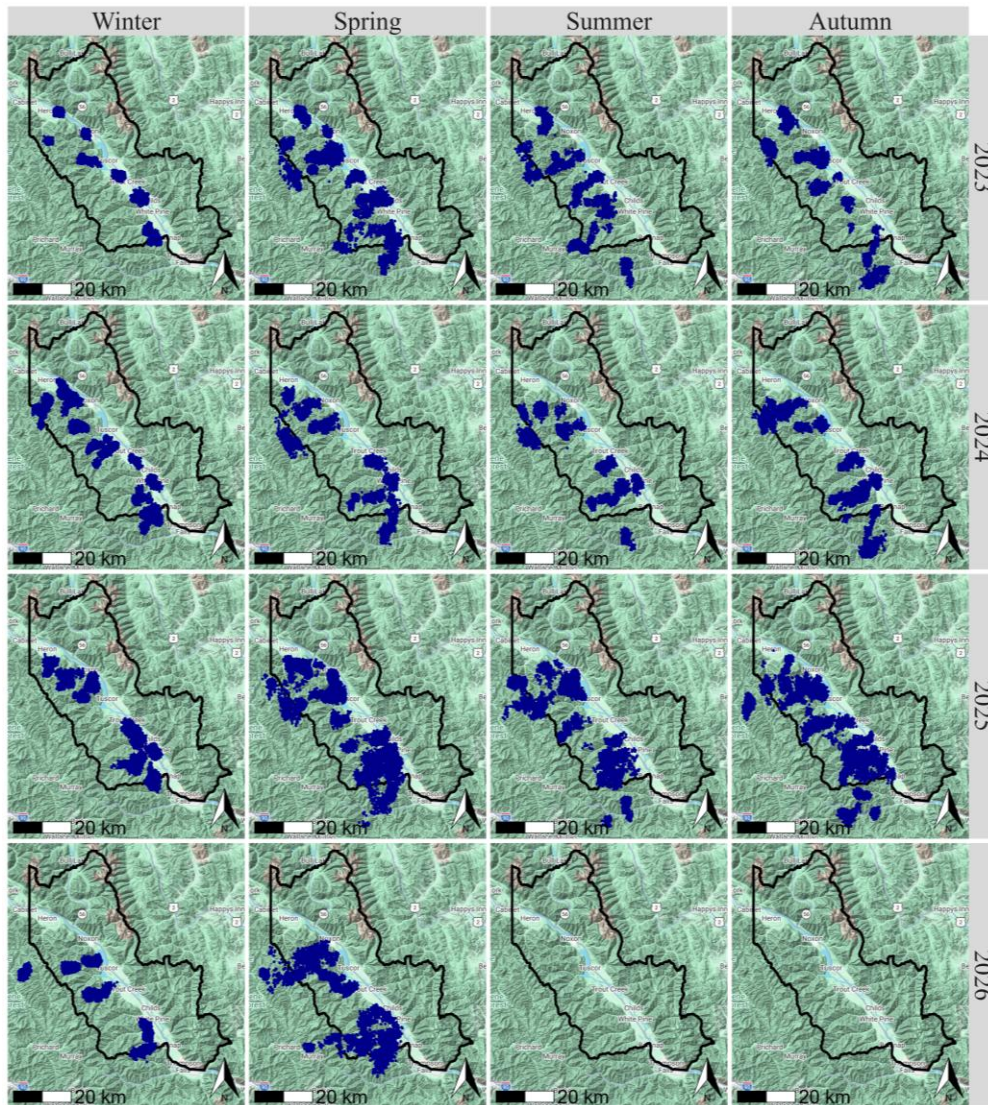


Figure 38. Winter (December 1 – March 31), spring (April 1 – June 30), summer (July 1 – August 31), and autumn (September 1 – November 30) locations of male elk as of July 1, 2026 in and around hunting district 121 (black outline). Locations have been jittered slightly for display.

As of July 1, 2026, we have collected 1,200,167 locations from these individuals. So far, 42 collared elk > 1 year old have died; 8 due to natural causes (7 adult females, 1 adult male); 11 due to predation by either mountain lions (5 adult females, 2 adult males), wolves (1 adult female, 2 adult males), or unknown predators (1 adult female); 19 due to hunter harvest (9 adult females, 10 adult males), and 4 adult females due to unknown causes. Three additional mortalities (2 adult females, 1 adult male) occurred, but these individuals were never included in the sample. Thirty-six collars (6 males and 30 females) have malfunctioned after deployment (stopped collecting and transmitting locations) and 34 collars (28 adult female, 3 adult male, 3 yearling male) dropped as scheduled. Kaplan-Meier estimates of annual natural adult survival (with harvest excluded) were 0.94 (95% CI = 0.88 – 1.00) in 2023 (June 1, 2023 – May 31, 2024), 0.88 (95% CI = 0.82 – 0.95) in 2024 (June 1, 2024 – May 31, 2025), and 0.94 (95% CI = 0.89 – 0.98) in 2025 (June 1, 2025 – May 31, 2026).

3.3.2 Neonate and Calf Elk Capture and Monitoring

We captured and collared 25 elk neonates (9 females, 16 males) in May and June 2023, 66 neonates (27 females, 39 males) in 2024, and 65 neonates (25 females, 40 males) in 2025 (Figure 39). Many neonates collared were associated with collared females ($n = 112$); however, we also collared 44 opportunistic neonates not associated with a collared female. In 2023, neonate weights averaged 17.1 kg (SD = 2.7) for females and 18.3 kg (SD = 4.5) for males, and average age at capture was ~1.7 days (range = 0 – 4 days). In 2024, neonate weights averaged 19.0 kg (SD = 2.9) for females and 20.0 kg (SD = 4.1) for males, and average age at capture was ~2.3 days (range = 0 – 5 days). In 2025, neonate weights averaged 17.1 kg (SD = 3.3) for females and 20.4 kg (SD = 4.3) for males, and average age at capture was ~2.2 days (range = 0 – 5 days).

Since 2023, 69 collared calves (<1 year old) have died (15 mountain lion predation, 15 black bear predation, 2 coyote predation, 1 wolf predation, 4 unknown predation, 7 natural mortality, 3 human harvest, 5 human-related mortality [non-harvest, e.g., vehicle collision], 7 capture-related mortality, and 10 unknown cause). Thirty collars fell off prematurely (active <6 months), 5 collars dropped as scheduled, 20 failed to send GPS locations within a year after deployment, and 24 collars failed to send GPS locations after 1 year of deployment (i.e., past the expected deployment timeframe). Kaplan-Meier estimates of annual calf survival were 0.68 (95% CI = 0.46 – 0.90) in 2023 (June 1, 2023 – May 31, 2024), 0.60 (95% CI = 0.47 – 0.72) in 2024 (June 1, 2024 – May 31, 2025), and 0.49 (95% CI = 0.36 – 0.62) in 2025 (June 1, 2025 – May 31, 2026).

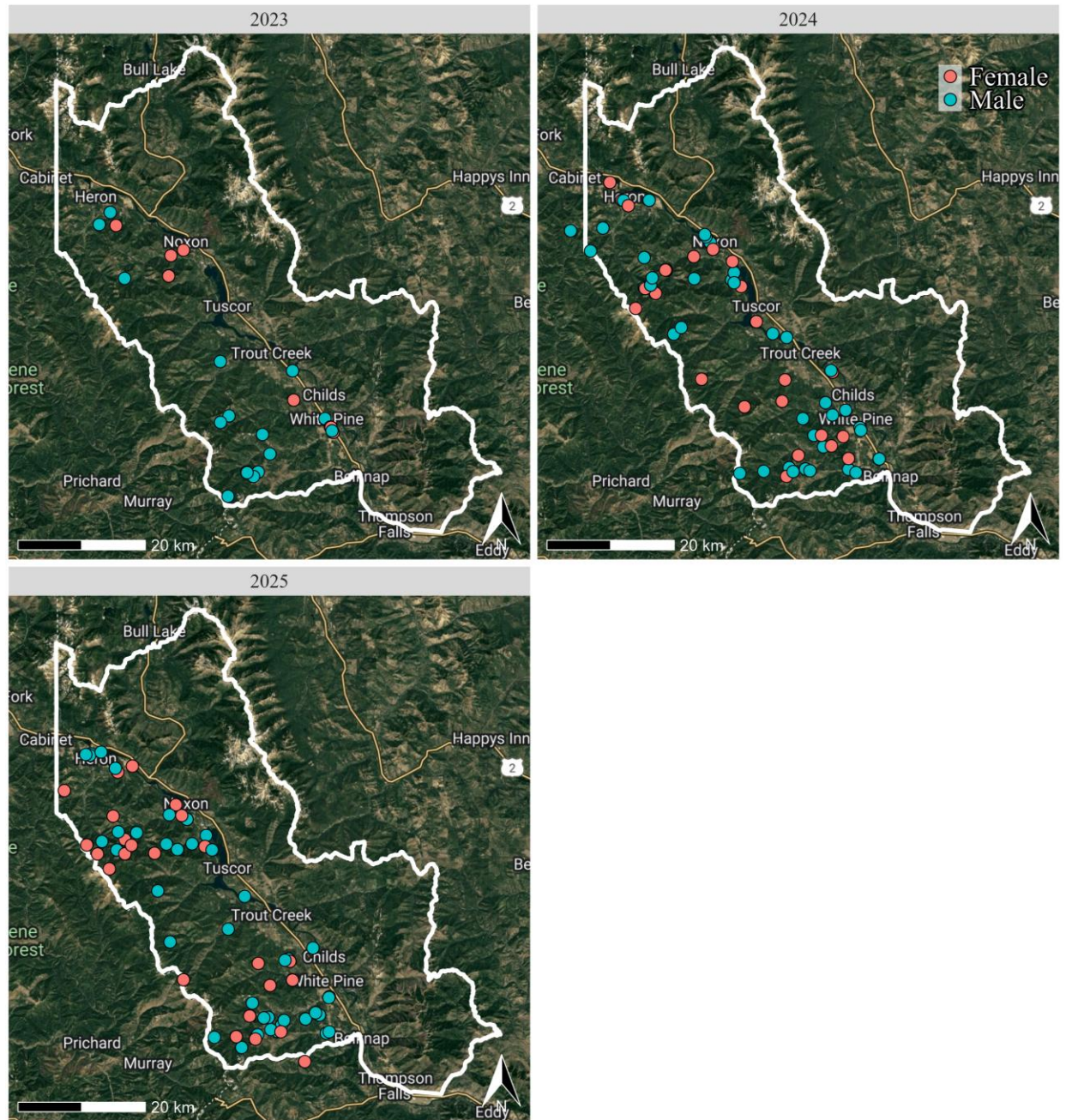


Figure 39. Locations of female (red) and male (blue) elk neonate captures in hunting district 121 (white outline) in May and June 2023 - 2025.

3.3.3 Elk Carcass Monitoring Using Trail Cameras

The occurrence of wolves stealing mountain lion kills has been documented in other areas and may occur in northwestern Montana. If any collared elk were killed by a mountain lion, then stolen by a wolf, it is possible it would have been recorded as a wolf mortality because wolf predation/scavenging events typically result in limited or scattered remains. Given the low number of mortalities recorded as being caused by wolves, it is likely this did not occur often. Further, while it was not a specific objective of the study, researchers placed trail cameras on 10 elk mortalities (6 calf, 4 adult) to identify whether wolves would visit these carcasses and disrupt other predators, such as mountain lions. No wolves were observed visiting elk carcasses. However, black bears visited 5 of 6 calf carcasses and 2 of 4 adult carcasses. Three of these visits were on mountain lion-killed elk (all calves) and the mountain lion did not return to the carcass in 2 of these cases. Coyotes also visited 2 calf carcasses, after black bears had already visited the carcass.

3.3.4 Mountain Lion Capture and Monitoring

We captured and collared 3 adult female mountain lions in January and February 2023, and captured 6 additional mountain lions (4 females, 2 males) in 2024. As of July 1, 2026, we have collected a total of 6,579 locations from these individuals in winter, 6,317 locations in spring, 4,104 locations in summer, and 5,455 locations in autumn (Figure 40). One collared adult female mountain lion died due to natural causes in January 2024, 5 mountain lions were harvested in winter 2024-2025 (2 males, 3 females), 1 adult female died of unknown causes in September 2025, 1 adult female dropped its collar as programmed, and 1 collar failed in May 2025. No collared mountain lions are still active.

3.3.5 Wolf Capture and Monitoring

In summer 2022, one subadult male wolf was captured by FWP management staff. This individual emigrated from the study area in December 2022 and was later harvested. In summer 2024, one adult female wolf was captured by FWP management staff, and an additional adult male wolf was captured in summer 2025. The male wolf collar failed in autumn 2025. The collared female remains alive with an active collar.

3.3.6 Black Bear Capture and Monitoring

In 2023, we captured and collared 1 female and 4 male black bears. We also captured 2 subadult males, but did not fit these individuals with collars. USFWS captured and collared 2 male bears in 2024. As of July 1, 2026, we have collected 407 bear locations in winter, 3,984 locations in spring, 2,507 locations in summer, and 2,903 locations in autumn (Figure 41). One adult male black bear dropped its collar during 2023-24 winter hibernation and was then harvested in May 2024, 1 adult male died of unknown causes in August 2024, and 4 males dropped their collars. The remaining collared bear likely dropped its collar while in the den last winter, but the collar has not yet been retrieved.

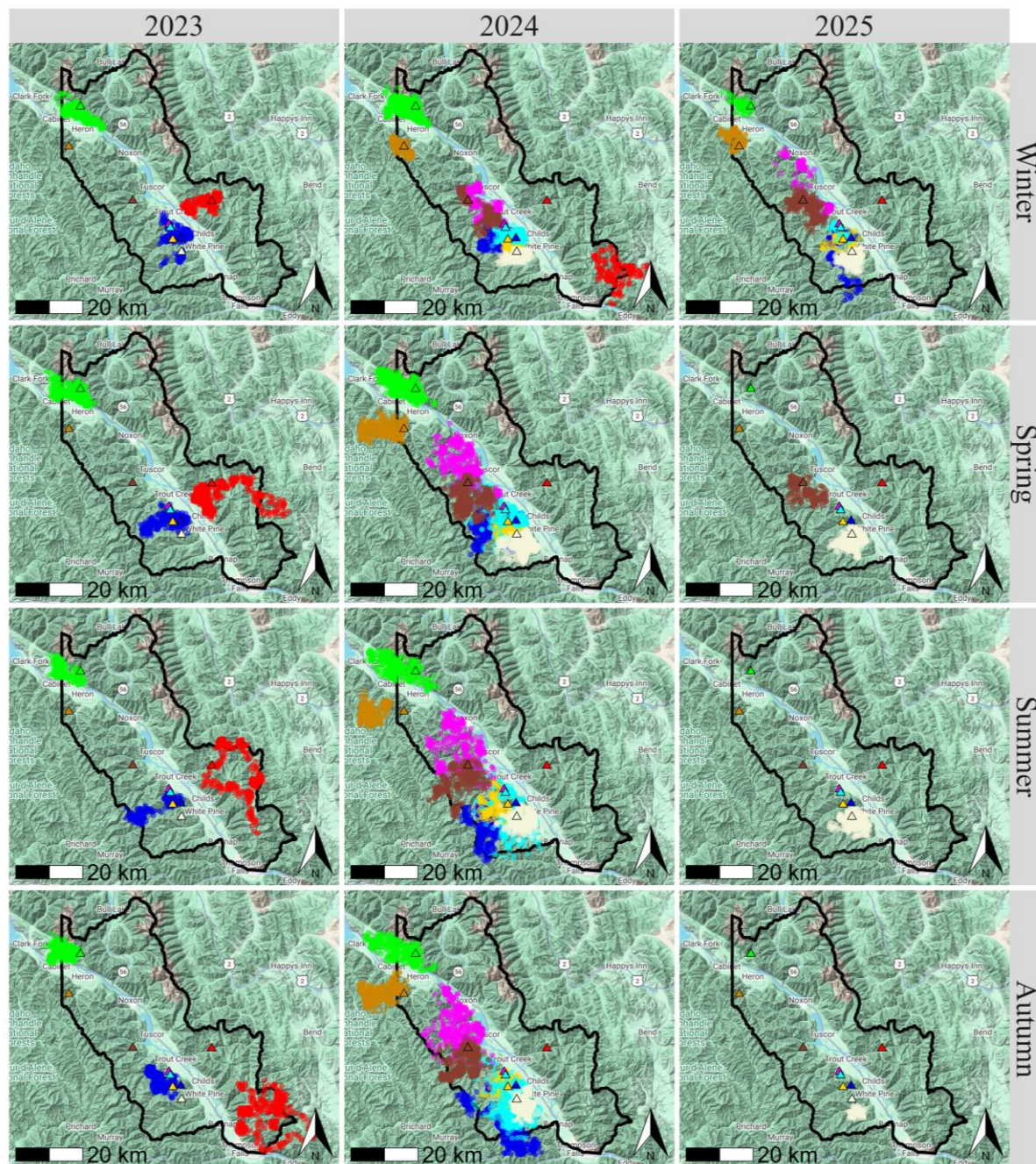


Figure 40. Winter (December 1 – March 31), spring (April 1 – June 30), summer (July 1 – August 31), and autumn (September 1 – November 30) locations of 9 mountain lions captured in hunting district 121 (black outline) as of July 1, 2026. Each color represents a different mountain lion and black outlined triangles represent the capture location for each individual. Locations have been jittered slightly for display.

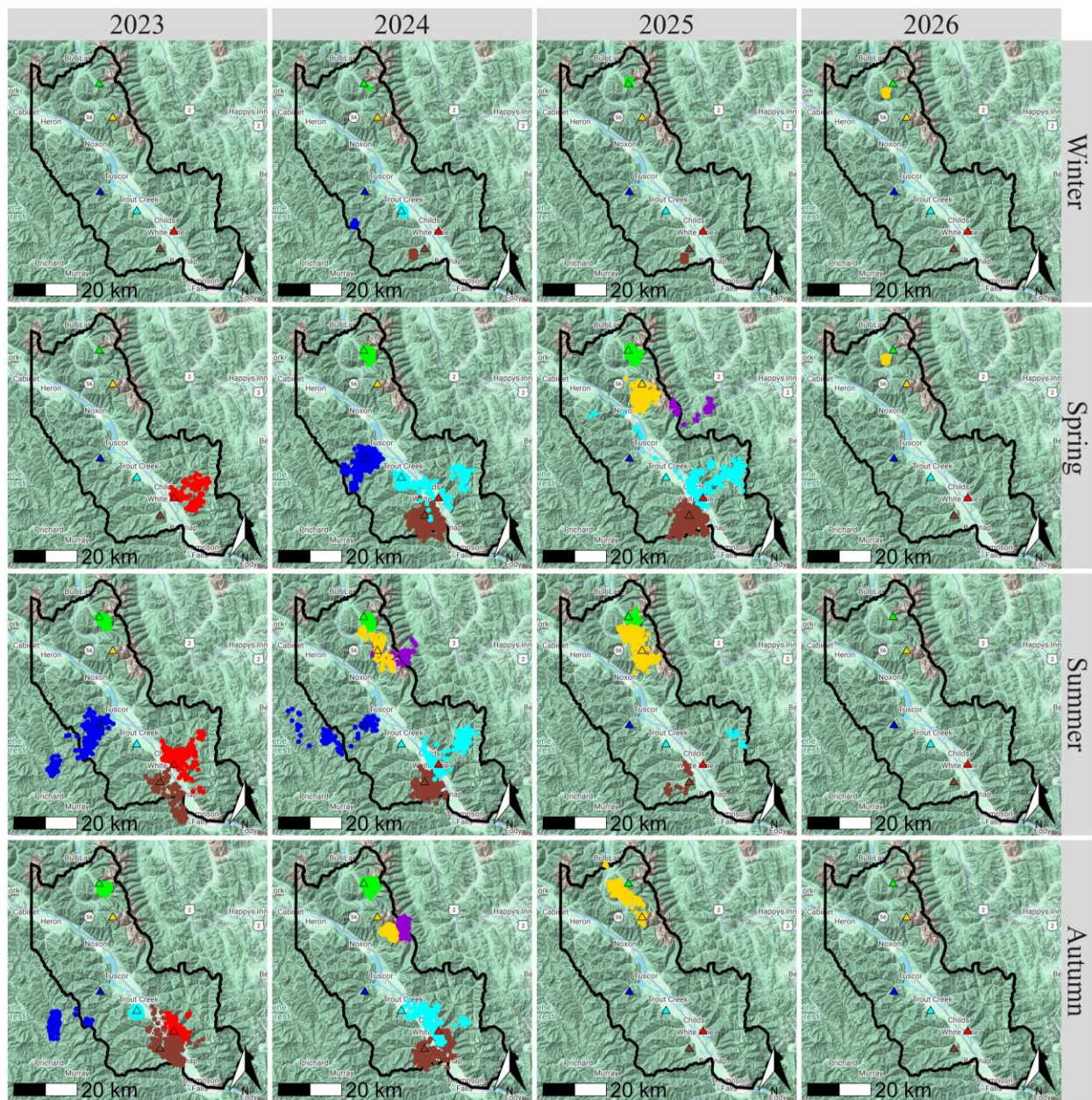


Figure 41. Winter (December 1 – March 31), spring (April 1 – June 30), summer (July 1 – August 31), and autumn (September 1 – November 30) locations of the 5 black bears captured in hunting district 121 (black outline) as of July 1, 2026. Each color represents a different black bear and black outlined triangles represent the capture location for each individual. Locations have been jittered slightly for display.

3.3.7 Estimating Elk and Predator Abundance Using Trail Cameras

In May and June 2023, we deployed 80 random cameras and 39 non-random predator cameras paired with the random cameras across HD 121 (Figure 42). We serviced all 119 cameras in September and October 2023; all cameras except for 2 were functioning as expected (1 camera was missing an SD card and 1 camera only took motion-triggered photos). We serviced all 119 cameras a second time in May/June 2024 and a third time in September/October 2024. We retrieved all cameras in July/August 2025.

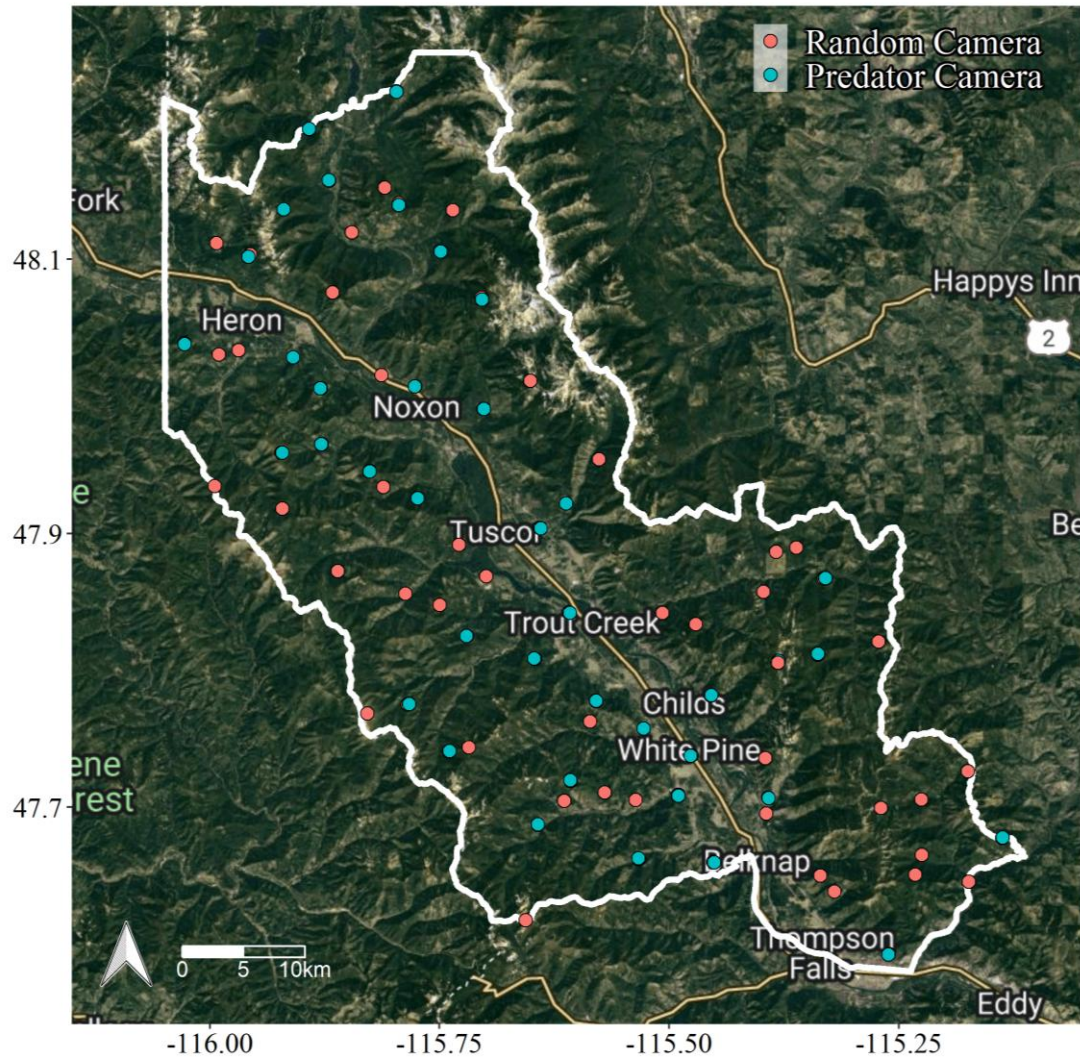


Figure 42. Location of random (red) and predator trail cameras (blue) in hunting district 121. Each predator camera was paired with a random camera within 250 m, so these locations are largely overlapping in the map.

We classified 5,295,299 camera photos from summer 2023 and autumn/winter 2023-2024, identifying multiple species of ungulates and large carnivores (Figure 43). During summer 2023 (May – August), elk were detected on 66 of the total 118 functional cameras (56%), black bears were detected on 68/118 cameras (58%), mountain lions were detected on 4/118 cameras (3%), and wolves were only detected on 1/118 cameras (<1%; Figure 44). During autumn/winter 2023-2024 (September – April), elk were detected on 64/119 cameras (54%), black bears were detected on 16/119 cameras (13%), mountain lions were detected on 10/119 cameras (8%), and wolves were detected on 8/119 (7%) cameras (Figure 45). Other species detected included moose (*Alces alces*), grizzly bear, coyote (*Canis latrans*), red fox (*Vulpes vulpes*), bobcat (*Lynx rufus*), American badger (*Taxidea taxus*), northern raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), short/long-tailed weasels (*Mustela erminea/Neogale frenata*), pine marten (*Martes americana*), lagomorphs (rabbits/hares), sciurids (squirrels/chipmunks), and mice.



Figure 43. Example photos from trail cameras set in hunting district 121 in 2023-24.

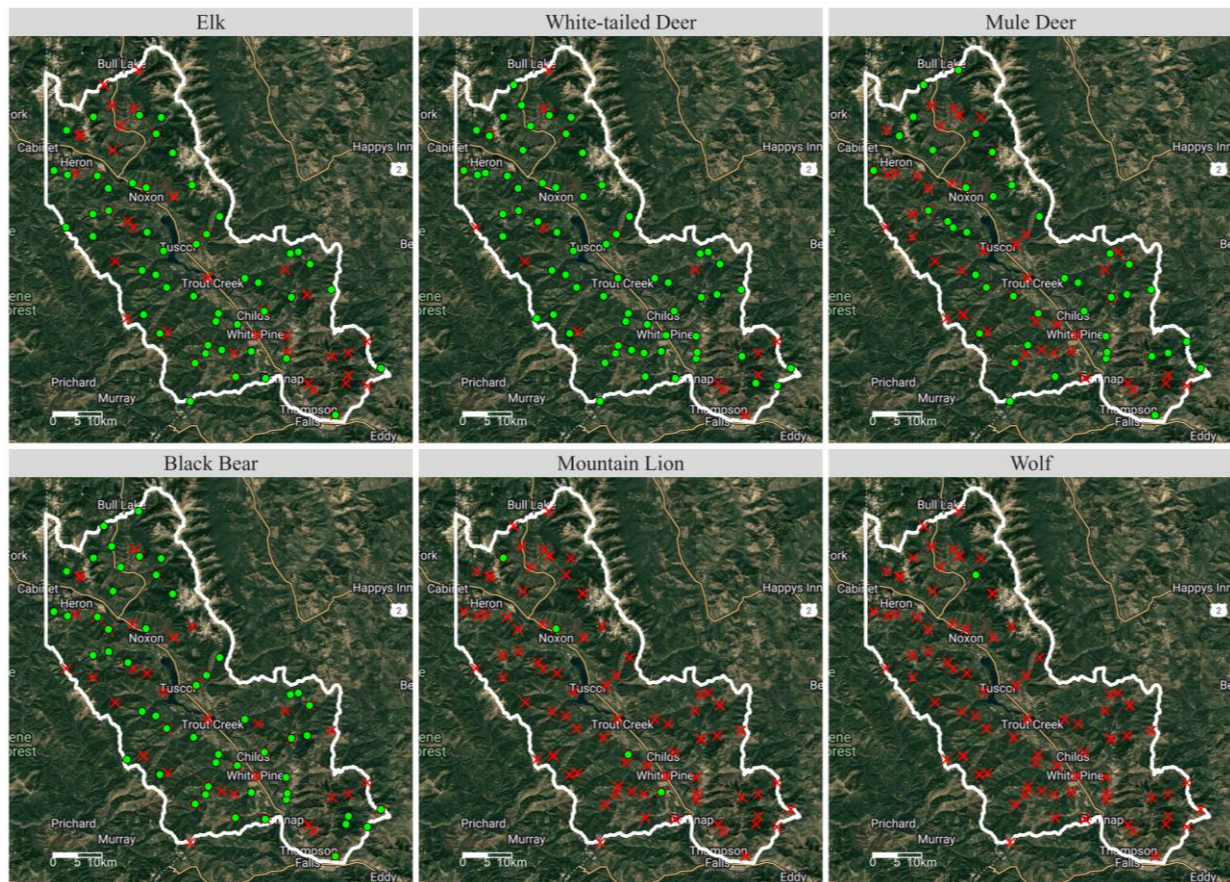


Figure 44. Locations of detections of elk, white-tailed deer, mule deer, black bear, mountain lion, and wolf on trail cameras located across hunting district 121 (white outline) in summer 2023 (May – August). Green dots represent detections of the species, while red exes represent no detection. Note, predator cameras were placed within 250 m of random cameras, so some points appear to overlap.

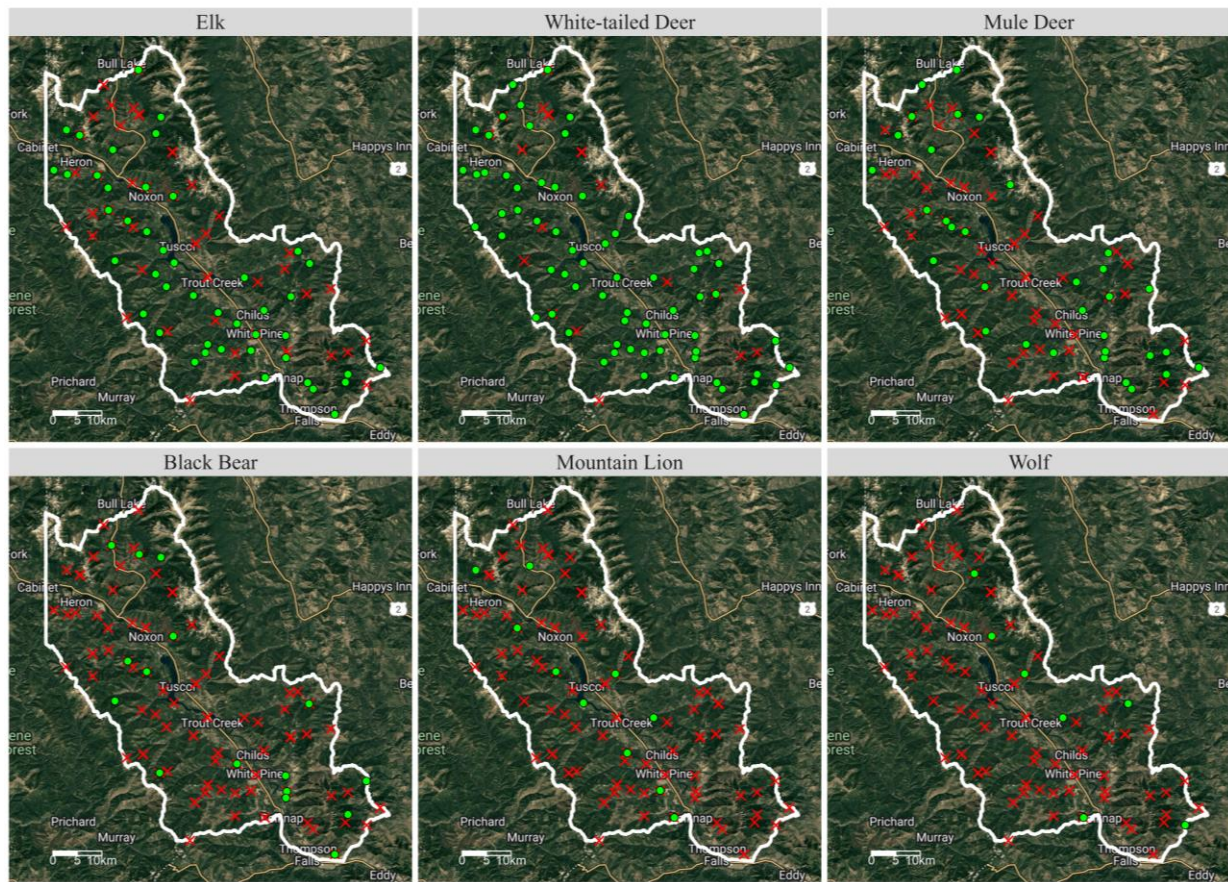


Figure 45. Locations of detections of elk, white-tailed deer, mule deer, black bear, mountain lion, and wolf on trail cameras located across hunting district 121 (white outline) in autumn/winter 2023-2024 (September 2023 – April 2024). Green dots represent detections of the species, while red exes represent no detection. Note, predator cameras were placed within 250 m of random cameras, so some points appear to overlap.

We obtained both motion and timelapse photos of most species during analysis periods in summer/fall 2023 and winter 2023-24 (Table 6). However, we obtained no timelapse photos of mountain lions or wolves during these periods, so we removed them from further analysis. When fitting models, we found that individuals remaining in front of a trail camera for many timelapse intervals resulted in unreasonable abundance estimates. We eliminated these outliers within each analysis period by identifying and censoring the cameras where this occurred (for the appropriate species). This resulted in censoring one camera during each analysis period for white-tailed deer and one camera during the winter period for elk. No cameras were censored from any time periods for mule deer or black bears.

Table 6. Number of photo captures of elk, white-tailed deer (WTD), mule deer (MD), mountain lions (Lion), black bears, and gray wolves (Wolf) from trail cameras located in hunting district 121 in northwestern Montana during 2023 and 2024. “Birth” includes dates: 14 March – 30 June, 2023; “Prehunt” includes dates: 15 July – 1 September, 2023; and “Winter” includes dates: 18 December, 2023 – 18 February 18, 2024. “Motion” trigger type includes only photos that were taken due to animal movement, while “Time Lapse” includes photos automatically taken at 10-minute intervals.

Period	Trigger Type	Elk	WTD	MD	Lion	Black Bear	Wolf
Birth	Motion	2212	9217	1628	12	730	14
Birth	Time Lapse	20	96	29	0	7	0
Prehunt	Motion	3996	9152	1655	9	1147	0
Prehunt	Time Lapse	24	112	30	0	9	0
Winter	Motion	2057	11788	1118	19	0	0
Winter	Time Lapse	72	288	37	0	0	0

Preliminary estimates of abundance using the STE model across the two camera deployment groups during the birth, pre-hunting, and winter period in 2023-24 are summarized in Table 7 and Figure 46. Across all species, average estimated abundance when using non-random cameras was higher, and the confidence intervals were wider than the random camera deployment group. We found no statistically significant differences in abundance when the results were averaged across deployment groups. However, when broken down by deployment group, there were significant differences between abundance estimates from random and non-random groups during the pre-hunting period for elk and white-tailed deer.

The results of our bias test performed for each species and analysis period using the STE model were not always equal to 1, which suggests a difference between the random and non-random deployment group results for some species during some analysis periods (e.g., elk during the pre-hunting period).

Table 7. Abundance estimates for elk, white-tailed deer (WTD), mule deer (MD), and black bears (Bear) in hunting district 121 in northwestern Montana using the space-to-event model across all analysis periods. “Bias” represents the magnitude of bias of the non-random abundance estimates, relative to the random estimate (i.e., $[\text{random} + \text{non-random}] / [2 * \text{random}]$). “Birth” includes dates: 14 March – 30 June, 2023; “Prehunt” includes dates: 15 July – 1 September, 2023; and “Winter” includes dates: 18 December, 2023 – 18 February 18, 2024. “Random” cameras were randomly placed and “Non-random” (i.e., “Predator”) cameras were located on a trail within 250 m of a paired random camera. “N”, “SE”, “LCI”, and “UCI” represent the mean abundance estimate, standard error of the estimate, and lower/upper 95% confidence limits of the estimate, respectively.

Species	Camera	Period	N	SE	LCI	UCI	Density (per km ²)	Bias
Elk	Random	Birth	2388	579	1495	3815	0.94	0.96
	Non-random	Birth	2218	1104	882	5576	0.88	
	Random	Prehunt	1037	329	565	1902	0.41	3.70
	Non-random	Prehunt	6629	1704	4038	10884	2.62	
	Random	Winter	2865	458	2097	3912	1.13	0.77
	Non-random	Winter	1569	781	624	3947	0.62	
WTD	Random	Birth	6463	953	4847	8616	2.56	1.4
	Non-random	Birth	11603	2527	7609	17692	4.59	
	Random	Prehunt	6080	797	4707	7853	2.4	1.76
	Non-random	Prehunt	15371	2596	11065	21354	6.08	
	Random	Winter	13846	1012	12000	15976	5.48	1.07
	Non-random	Winter	15667	2472	11522	21303	6.2	
MD	Random	Birth	3223	673	2150	4832	1.28	1.01
	Non-random	Birth	3304	1348	1531	7127	1.31	
	Random	Prehunt	1976	454	1267	3082	0.78	1.72
	Non-random	Prehunt	4823	1453	2706	8595	1.91	
	Random	Winter	2417	421	1722	3392	0.96	0.91
	Non-random	Winter	1982	878	865	4545	0.78	
Bear	Random	Birth	563	281	223	1418	0.22	1.97
	Non-random	Birth	1657	954	581	4730	0.66	
	Random	Prehunt	727	275	355	1489	0.29	1.11
	Non-random	Prehunt	880	621	253	3058	0.35	

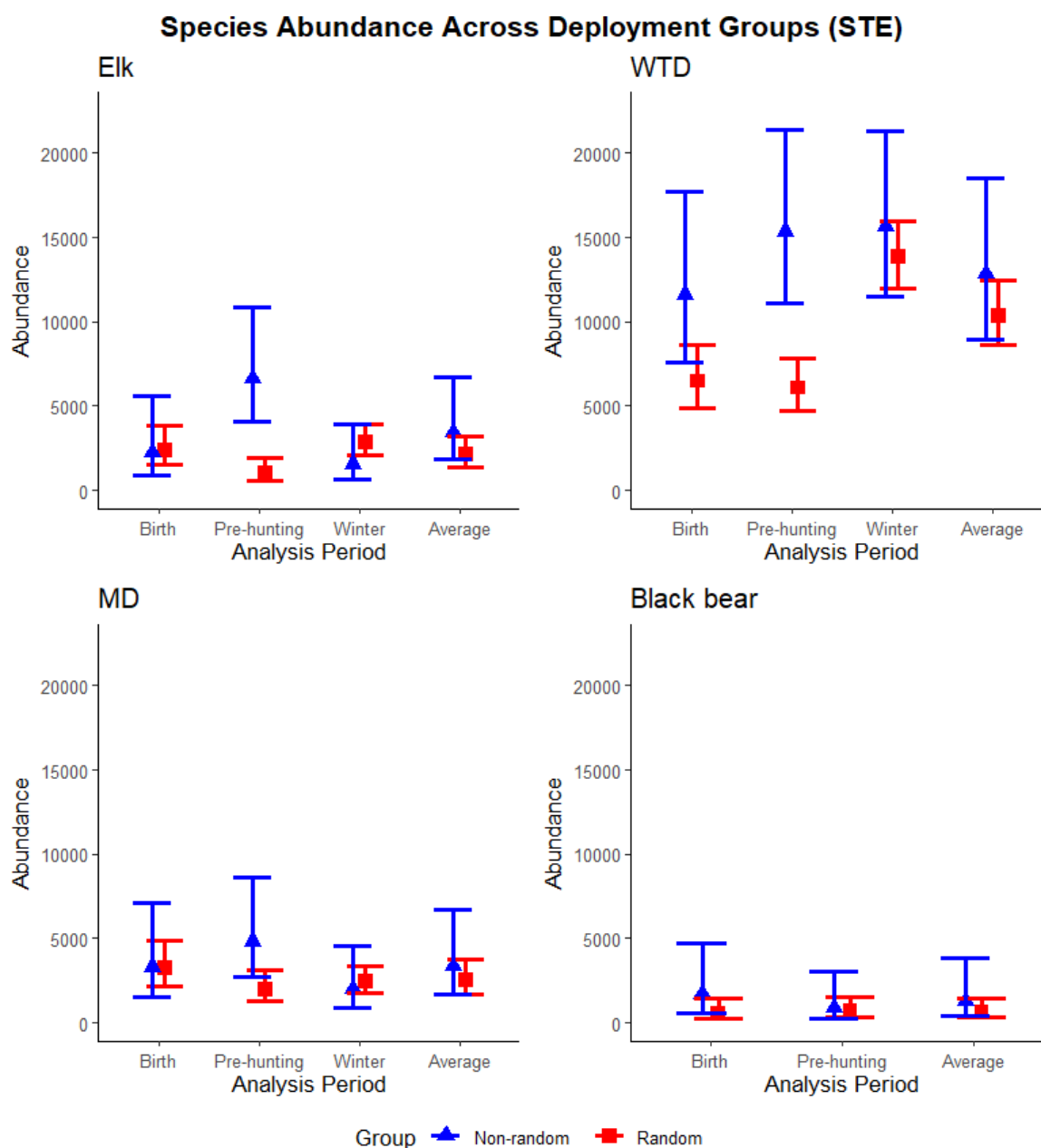


Figure 46. Comparisons of abundance estimates of elk (a), white-tailed deer (WTD) (b), mule deer (MD) (c), and black bears (d) for hunting district 121 in northwest Montana using the space-to-event (STE) model across analysis periods. “Birth” includes dates: 14 March – 30 June, 2023; “Pre-hunting” includes dates: 15 July – 1 September, 2023; “Winter” includes dates: 18 December, 2023 – 18 February 18, 2024; and “Average” includes all periods. Red squares represent “Random” cameras that were randomly placed, and blue triangles represent “Non-random” or “Predator” cameras that were located on a trail within 250 m of a paired random camera. Error bars represent 95% confidence intervals.

Preliminary results suggested the abundance estimates from the IS model were, on average, higher than the STE model across multiple species in 2023-24. Abundance estimates using the IS model across the two camera deployment groups during the birth, pre-hunting, and winter period are summarized in Table 8 and Figure 47. Like the STE estimates, abundance when using non-random cameras had much wider confidence intervals than the random camera deployment group. However, when using the IS model, the abundance point estimate from the random cameras were, on average, higher than the non-random results for half of the species (Figure 47). We again found no statistically significant differences in abundance when the results were averaged across deployment groups. However, when broken down by deployment group, there were three instances of the difference between the abundance results from the random and non-random groups being statistically significant for elk and black bear during the ungulate birth period and white-tailed deer during the pre-hunting period.

The results of our bias test performed for each species and analysis period using the IS model were not always equal to 1, which suggests a difference between the random and non-random deployment group results for some species during some analysis periods (e.g., elk during the pre-hunting period).

Overall, our preliminary results suggest future studies should consider random camera layouts instead of a paired random and non-random camera layout when estimating abundance of multiple common and lower density species because non-random camera placement often resulted in bias from the violation of multiple assumptions. Additional random cameras on the landscape would improve the chances of detecting low-density carnivores and would likely result in more precise abundance estimates for all species. Further, incorporating the abundance estimates obtained from cameras into IPMs along with other existing data sources can increase the precision of estimates without increasing the sample size of cameras.

Table 8. Abundance estimates for elk, white-tailed deer (WTD), mule deer (MD), and black bears (Bear) in hunting district 121 in northwestern Montana using the instantaneous sampler model across all analysis periods. “Birth” includes dates: 14 March – 30 June, 2023; “Prehunt” includes dates: 15 July – 1 September, 2023; and “Winter” includes dates: 18 December, 2023 – 18 February 18, 2024. “Random” cameras were randomly placed and “Predator” cameras were located on a trail within 250 m of a paired random camera. “N”, “SE”, “LCI”, and “UCI” represent the mean abundance estimate, standard error of the estimate, and lower/upper 95% confidence limits of the estimate, respectively.

Species	Camera	Period	N	SE	LCI	UCI	Density (per km ²)	Bias
Elk	Random	Birth	10573	2042	7267	15385	4.18	0.62
	Non-random	Birth	2501	1068	1121	5579	0.99	
	Random	Prehunt	1036	419	483	2222	0.41	3.58
	Non-random	Prehunt	6373	4855	1692	23997	2.52	
	Random	Winter	2067	1475	588	7268	0.82	0.73
	Non-random	Winter	970	907	205	4588	0.38	
WTD	Random	Birth	6222	1727	3648	10612	2.46	1.66
	Non-random	Birth	14465	3068	9589	21822	5.72	
	Random	Prehunt	5642	1231	3697	8611	2.23	2.12
	Non-random	Prehunt	18305	5126	10682	31367	7.24	
	Random	Winter	17028	4103	10689	27125	6.74	0.86
	Non-random	Winter	12370	4967	5798	26393	4.89	
MD	Random	Birth	5681	2493	2496	12932	2.25	0.70
	Non-random	Birth	2299	1929	549	9618	0.91	
	Random	Prehunt	2605	1258	1062	6389	1.03	1.54
	Non-random	Prehunt	5429	4807	1222	24116	2.15	
	Random	Winter	2721	1210	1183	6257	1.08	1.11
	Non-random	Winter	3313	1030	1827	6008	1.31	
Bear	Random	Birth	5344	273	4834	5907	2.11	0.71
	Non-random	Birth	2203	861	1052	4612	0.87	
	Random	Prehunt	1781	387	1169	2713	0.7	0.73
	Non-random	Prehunt	807	589	224	2903	0.32	

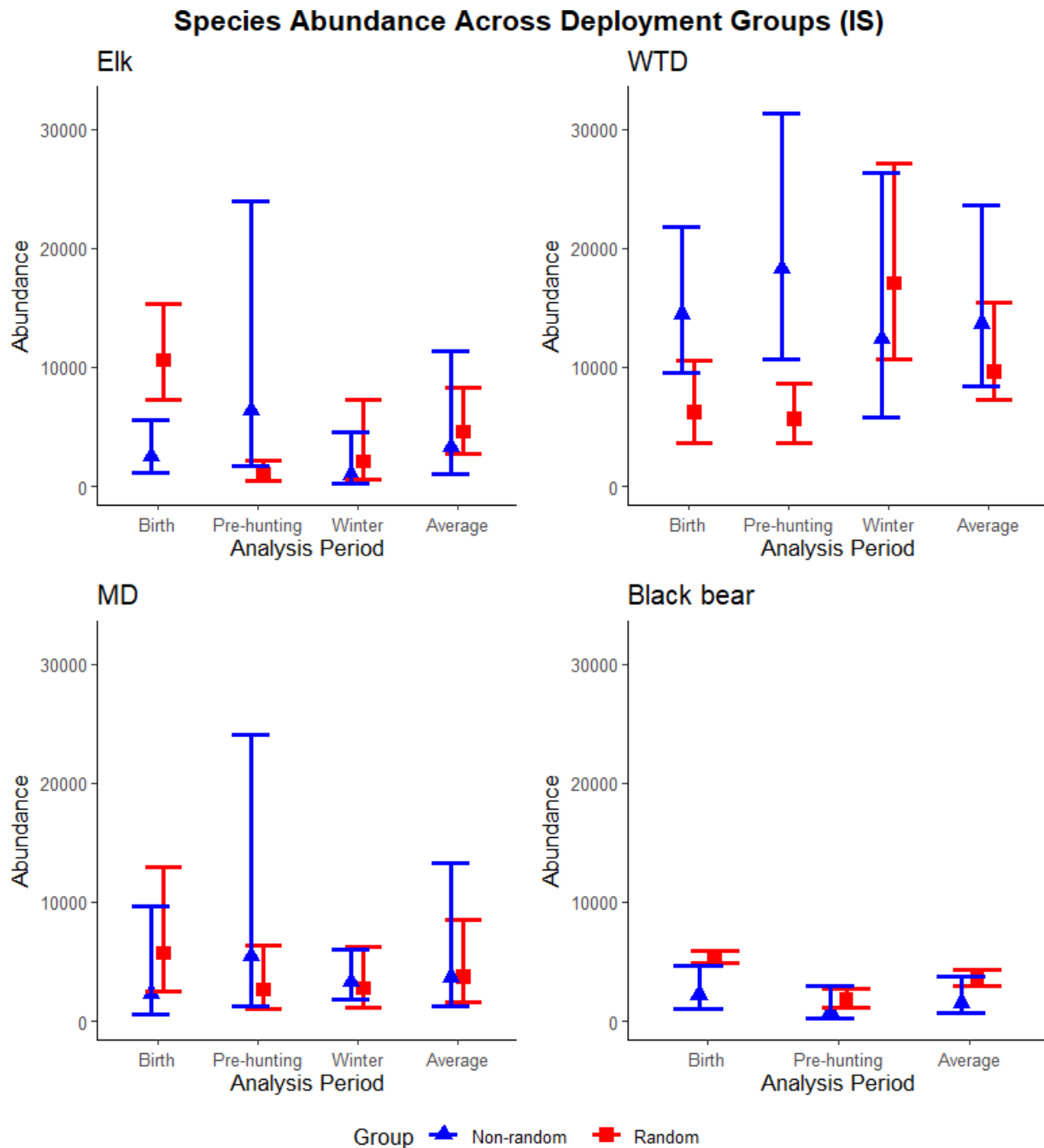


Figure 47. Comparisons of abundance estimates of elk (a), white-tailed deer (WTD) (b), mule deer (MD) (c), and black bears (d) for hunting district 121 in northwest Montana using the instantaneous sampler (IS) model across analysis periods. “Birth” includes dates: 14 March – 30 June, 2023; “Pre-hunting” includes dates: 15 July – 1 September, 2023; “Winter” includes dates: 18 December, 2023 – 18 February 18, 2024; and “Average” includes all periods. Red squares represent “Random” cameras that were randomly placed, and blue triangles represent “Non-random” or “Predator” cameras that were located on a trail within 250 m of a paired random camera. Error bars represent 95% confidence intervals.

3.3.8 Quantifying the Nutritional Landscape and Elk Summer Resource Selection

Vegetation Surveys/Fecal Pellet Collection

We measured vegetation and collected biomass samples at 222 sites from May-August, 2023 and 224 sites from May – June, 2024. We removed 4 datapoints of sites that were erroneously resampled (2 datapoints each year), leaving us with a dataset of 442 vegetation sampling points stratified by landcover type, harvest strategy, and time-since-harvest. We collected fecal pellet samples during May – August both summers, collecting samples from 45 unique sites in 2023 and 20 unique sites in 2024. We submitted 14 composite samples representing 14 weeks of elk diet in 2023, and 6 composite samples representing 6 weeks of elk diet in 2024. We also collected 6 composite fecal pellet samples (3 in low valley, 3 in high forest) in winter 2022-23.

Filtering the 2023 fecal data resulted in a diet list of 45 taxa. We added 2 new taxa to the diet list based on the 2024 fecal results, resulting in a final summer diet list of 47 forage taxa (Table 9). The final diet list included 16 shrub taxa, 28 forb taxa, and 3 grass/grasslike taxa. We recorded 42 of the 47 forage taxa in our vegetation sampling plots during the summers of 2023 and 2024.

*Table 9. Summer diet list of taxa identified via DNA metabarcoding of the ITS2 and rbcL markers that passed the thresholds for relative read abundance (RRA, 1%) and frequency of occurrence (FOO, 10%). ¹ denotes taxa that were identified in the 2023 diet. ² denotes taxa that were identified in the 2024 diet. ³ denotes that the taxon was not found in any of the vegetation plots sampled during the summers of 2023 and 2024. ⁴ denotes that the taxon's status in MT is uncertain (i.e., sources conflict). Taxa are listed alphabetically; the order of listing does **not** denote a hierarchical ranking of diet item importance.*

Taxon	Common Name	Growth Habit
Acer species ^{1,2}	Maples	Shrub
Achillea species ¹	Yarrows	Forb
Adenocaulon bicolor ^{1,2}	American trailplant	Forb
Alnus species ¹	Alders	Shrub
Arnica latifolia ^{1,2}	Mountain arnica	Forb
Berberis repens ²	Oregon grape	Evergreen Shrub
Bromus inermis ¹	Smooth Brome	Grass
Ceanothus species ^{1,2}	Ceanothuses	Shrub
Centaurea stoebe ¹	Spotted knapweed	Forb
Chamerion angustifolium ^{1,2}	Fireweed	Forb
Chenopodium album ¹	Lambsquarters	Forb
Circaea species ¹	Enchanter's nightshades	Forb
Conmitella williamsii ³	William's conimitella	Forb
Coptis occidentalis ¹	Idaho goldthread	Forb

Cornus species ¹	Dogwoods	Shrub
Crataegus species ¹	Hawthorns	Shrub
Eurybia species ¹	Wood asters	Forb
Galium triflorum ¹	Three-flowered bedstraw	Forb
Hordeum species ^{1,3}	Barleys	Grass
Lactuca muralis ¹	Wall lettuce	Forb
Leucanthemum vulgare ^{1,2}	Oxeye daisy	Forb
Lotus species ¹	Trefoils	Forb
Maianthemum species ¹	Solomon's seals	Forb
Moehringia laterifolia ^{1,2}	Bluntleaf sandwort	Forb
Moehringia macrophylla ¹	Largeleaf sandwort	Forb
Osmorhiza species ¹	Sweet-cicelys	Forb
Paxistima myrsinites ¹	Oregon boxleaf	Evergreen Shrub
Phleum pratense ¹	Timothy grass	Grass
Physocarpus species ¹	Ninebarks	Shrub
Plantago lanceolata ¹	English plantain	Forb
Polygonum aviculare ^{1,3}	Prostrate knotweed	Forb
Potentilla species ¹	Cinquefoils	Forb
Rhododendron species ^{1,2}	Rhododendrons	Shrub
Ribes species ^{1,2}	Gooseberries/currants	Shrub
Rosa species ^{1,2}	Roses	Shrub
Rubus species ^{1,2}	Raspberries	Shrub
Rumex acetosella ^{1,2}	Sheep sorrel	Forb
Salix species ¹	Netleaf willow	Shrub
Sorbaria sorbifolia ^{1,3,4}	False spiraea	Shrub
Spergularia rubra ^{1,3}	Red sandspurry	Forb
Symphoricarpos species ¹	Snowberries	Shrub
Taraxacum species ¹	Dandelions	Forb
Trifolium species ^{1,2}	Clovers	Forb
Trillium ovatum ¹	Pacific trillium	Forb
Vaccinium species ^{1,2}	Huckleberries	Shrub
Veronica species ²	Speedwells	Forb
Viola species ^{1,2}	Violets	Forb

Calculating Site-specific Forage DE and Biomass

We submitted 254 forage plant samples to the Forage Laboratory at Dairy One (Ithaca, NY) for sequential fiber analysis during the summer of 2024 (S4. Forage laboratory results). We also submitted 48 samples to the Wildlife Habitat and Nutrition Lab at Washington State University (Pullman, WA) for tannin analysis during the summer of 2024. Our estimated phenostage-specific DE values for forage taxa ranged from 1.946 to 3.375 kcal/g, with a mean value of 2.834 kcal/g. DE values generally declined as phenology progressed, with a mean DE of 2.905 kcal/g for emergent plants, 2.859 kcal/g for flowering, 2.812 kcal/g for fruiting, and 2.722 kcal/g for mature, though some individual forage taxa did not follow this trend.

As expected, the mean proportion of each phenostage at sampling points changed as a function of time, with phenology progressing through the course of the summer. The mean forage DE across sampling points was 2.790 kcal/g (1st – 3rd quartiles: 2.684 – 2.949) and varied by landcover type and time-since-harvest (Figure 48). The mean DE for mesic forests across harvest strategies was highest 1-5 years post-harvest with a mean of 2.825 kcal/g (1st – 3rd quartiles: 2.729 – 2.948) and steadily declined across harvest age classes until arriving at the low DE value of unharvested mesic forest with a mean of 2.649 kcal/g (1st – 3rd quartiles: 2.506 – 2.787). Dry forests appeared to display no trend in digestible energy levels across time-since-harvest, with similar mean DE values in the earliest (2.799 kcal/g) and unharvested (2.834 kcal/g) age classes (Figure 48).

The mean forage biomass across sampling points was 242.60 kg/ha (1st – 3rd quartiles: 73.89 – 333.02) and varied by landcover type, time-since-harvest, and harvest strategy (Figure 49). Mean forage biomass was slightly higher in even-age cuts than in intermediate cuts with means of 259.6 kg/ha (1st – 3rd quartiles: 78.6 – 350.0) and 220.65 kg/ha (1st – 3rd quartiles: 67.45 – 309.55) across harvest age classes, respectively, which was higher than in unharvested forest with a mean of 155.637 kg/ha (1st – 3rd quartiles: 36.533 – 252.000). Mean forage biomass was highest 1-5 years post-harvest with a mean of 370.10 kg/ha (1st – 3rd quartiles: 157.20 – 431.90) across harvest strategies, and steadily declined across harvest age classes until arriving at the low levels of unharvested forest (Figure 49).

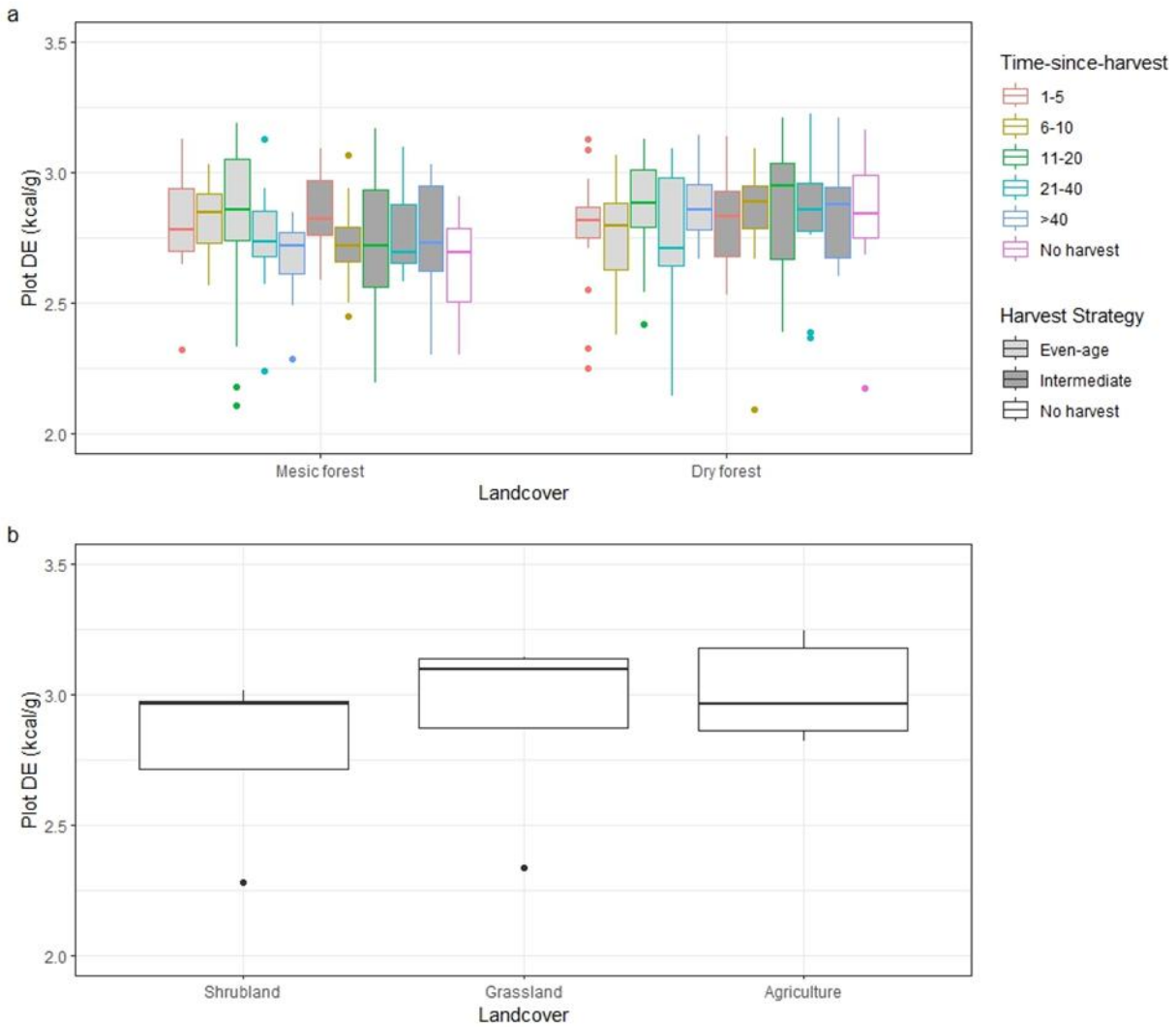


Figure 48. Estimated plot-level forage digestible energy (DE; kcal/g) across 442 vegetation sampling plots surveyed in Montana hunt district 121 during the summers (May-August) of 2023 and 2024. Results are separated into a) forested and b) unforested plots and displayed by landcover type (x-axis), timber harvest strategy (boxplot fill color: light gray = even-age, dark gray = intermediate, white = no harvest), and time-since-harvest (boxplot outline color; orange = 1-5 years, gold = 6-10 years, green = 11-20 years, light blue = 21-40 years, dark blue = >40 years, pink = no harvest).

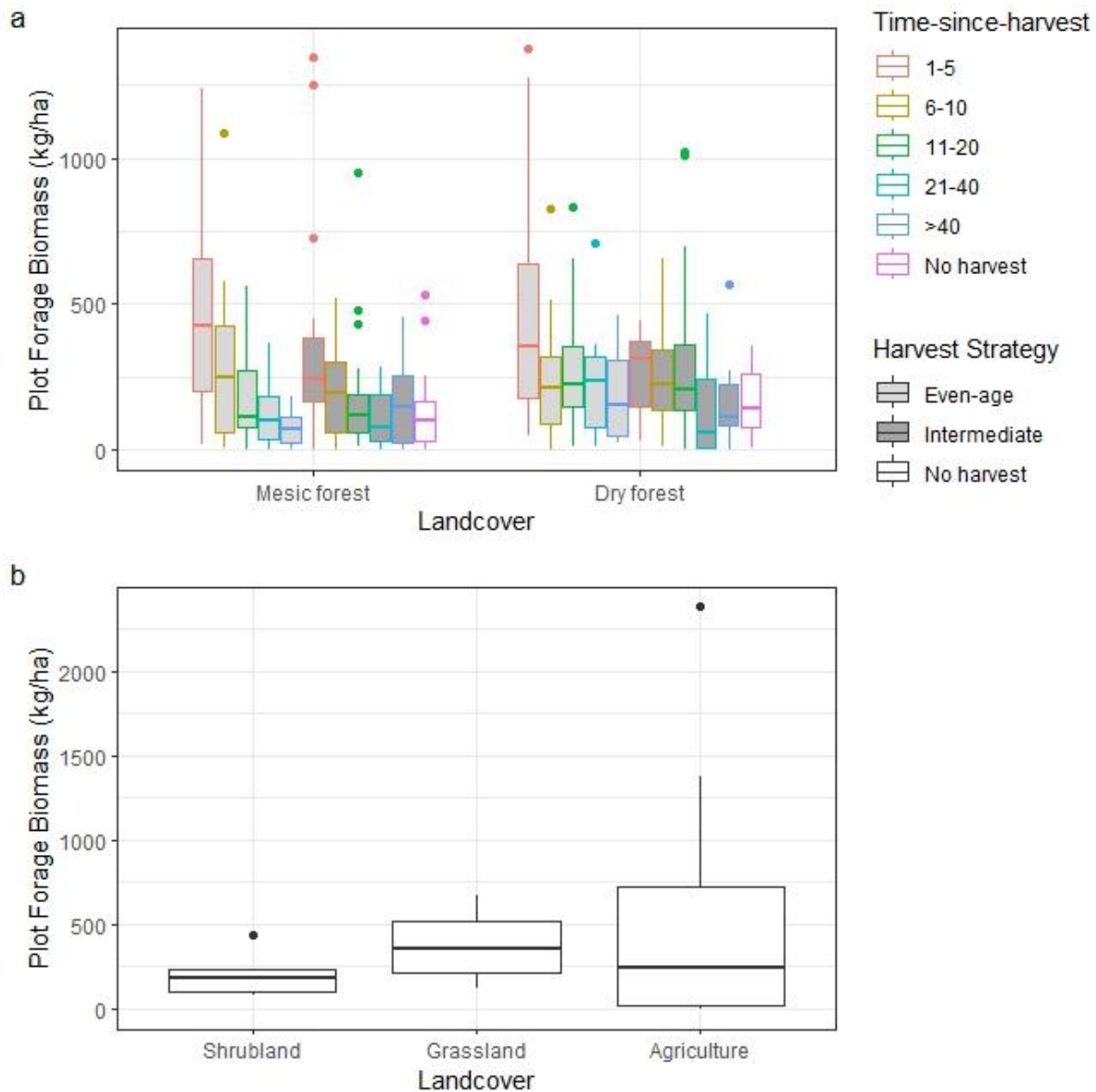


Figure 49. Estimated plot-level forage biomass (kg/ha) across 442 vegetation sampling plots surveyed in Montana hunt district 121 during the summers (May-August) of 2023 and 2024. Results are separated into a) forested and b) unforest plots and displayed by landcover type (x-axis), timber harvest strategy (boxplot fill color: light gray = even-age, dark gray = intermediate, white = no harvest), and time-since-harvest (boxplot outline color; orange = 1-5 years, gold = 6-10 years, green = 11-20 years, light blue = 21-40 years, dark blue = >40 years, pink = no harvest).

Modeling the Nutritional Landscape

The top forage DE model included covariates for time-since-harvest in mesic forests, landcover type, E-, S-, SW-, and W-facing aspects, elevation, a quadratic effect of Julian day, an interaction between elevation and Julian day, an interaction between Julian day and agriculture, and an interaction between Julian day and grassland ($R^2_{adj} = 0.1735$, Table 10). Predicted forage DE in unharvested mesic forests was 7.1% lower than dry forests (95% CI: -13.4, -0.8). However, predicted DE in mesic forests increased by 7.2% 1-5 years post-harvest (95% CI: 0.2, 14.2), increased by 5.4% 6-10 years post-harvest (95% CI: -1.5, 12.4), increased by 4.1% 11-20 years post-harvest (95% CI: -2.9, 11.1), decreased by 0.3% 21-40 years post-harvest (95% CI: -7.3, 6.7), and increased by 3.1% greater than 40 years post-harvest (95% CI: -4.1, 10.2), though many of these confidence intervals overlapped zero.

We found that in mesic forests, timber harvest offset the deficit in DE between mesic and dry forests. Though DE in mesic forests was on average 7.1% lower than dry forests, mesic forests harvested within the past 1-5 years saw an increase in DE of approximately 7.2%, effectively bringing DE levels to those of dry forests (Figure 50, Figure 51). Compared to agriculture and grasslands, our models predicted DE to remain much more stable in forests as summer progressed. Thus, by mid-summer, predicted DE levels in dry and recently harvested mesic forests surpassed those of agriculture and grasslands as plants in the open landcovers senesced and forage quality declined. By late summer, the difference between DE in these forest strata and in agriculture and grasslands was even more pronounced (Figure 50, Figure 51).

The top forage biomass model included covariates for landcover type, time-since-harvest, wildfire history, a cubic effect of elevation, a quadratic effect of Julian day, an interaction between elevation and Julian day, an interaction between Julian day and agriculture, and an interaction between Julian day and grassland ($R^2_{adj} = 0.2001$, Table 11). In harvested forests, predicted forage biomass was 1753% higher 1-5 years post-harvest (95% CI: 744, 2762), 834% higher 6-10 years post-harvest (95% CI: -152, 1821), 829% higher 11-20 years post-harvest (95% CI: -150, 1808), 161% lower 21-40 years post-harvest (95% CI: -1197, 874), and 678% lower greater than 40 years post-harvest (95% CI: -1740, 383) relative to unharvested forest, though many of these confidence intervals overlapped zero.

We found that while 1-5 year-old harvest was one of our highest strata in terms of predicted forage biomass, it was far outclassed by grasslands and agriculture for much of the summer (Figure 52, Figure 53). By late summer, however, the predicted forage biomass of these 1-5 year-old cutblocks was more similar to the predicted forage biomass of agriculture. The stronger interaction between agriculture and Julian day for forage biomass may be largely driven by agricultural practices in the study area, where haying was a common practice in July and August.

Table 10. Coefficient estimates, standard errors, and p-values for the top models predicting forage digestible energy in Hunt District 121 in northwest Montana in May – August of 2023 and 2024. Bolded values indicate coefficients whose 95% confidence interval did not overlap zero. The reference (intercept) is dry forest on a N-facing aspect.

Covariate	Estimate	Standard Error	p-value
Intercept	2.334	0.523	1.047 e-05
Mesic, Harvest Age 1-5	0.168	0.083	0.043
Mesic, Harvest Age 6-10	0.127	0.082	0.122
Mesic, Harvest Age 11-20	0.096	0.083	0.248
Mesic, Harvest Age 21-40	-0.007	0.083	0.934
Mesic, Harvest Age >40	0.071	0.085	0.404
Julian day	0.014	5.565 e-03	0.014
Julian day ²	-5.564 e-05	1.609 e-05	5.967 e-04
Elevation	-7.755 e-04	3.153 e-04	0.014
Mesic Forest	-0.165	0.075	0.028
Agriculture	0.998	0.434	0.022
Grassland	1.076	0.806	0.182
E	0.062	0.037	0.092
S	0.078	0.039	0.050
SW	0.082	0.040	0.042
W	0.045	0.039	0.252
Elevation*Julian day	3.548 e-06	1.690 e-06	0.036
Agriculture*Julian day	-6.003 e-03	2.367 e-03	0.012
Grassland*Julian day	-5.975 e-03	4.535 e-03	0.188

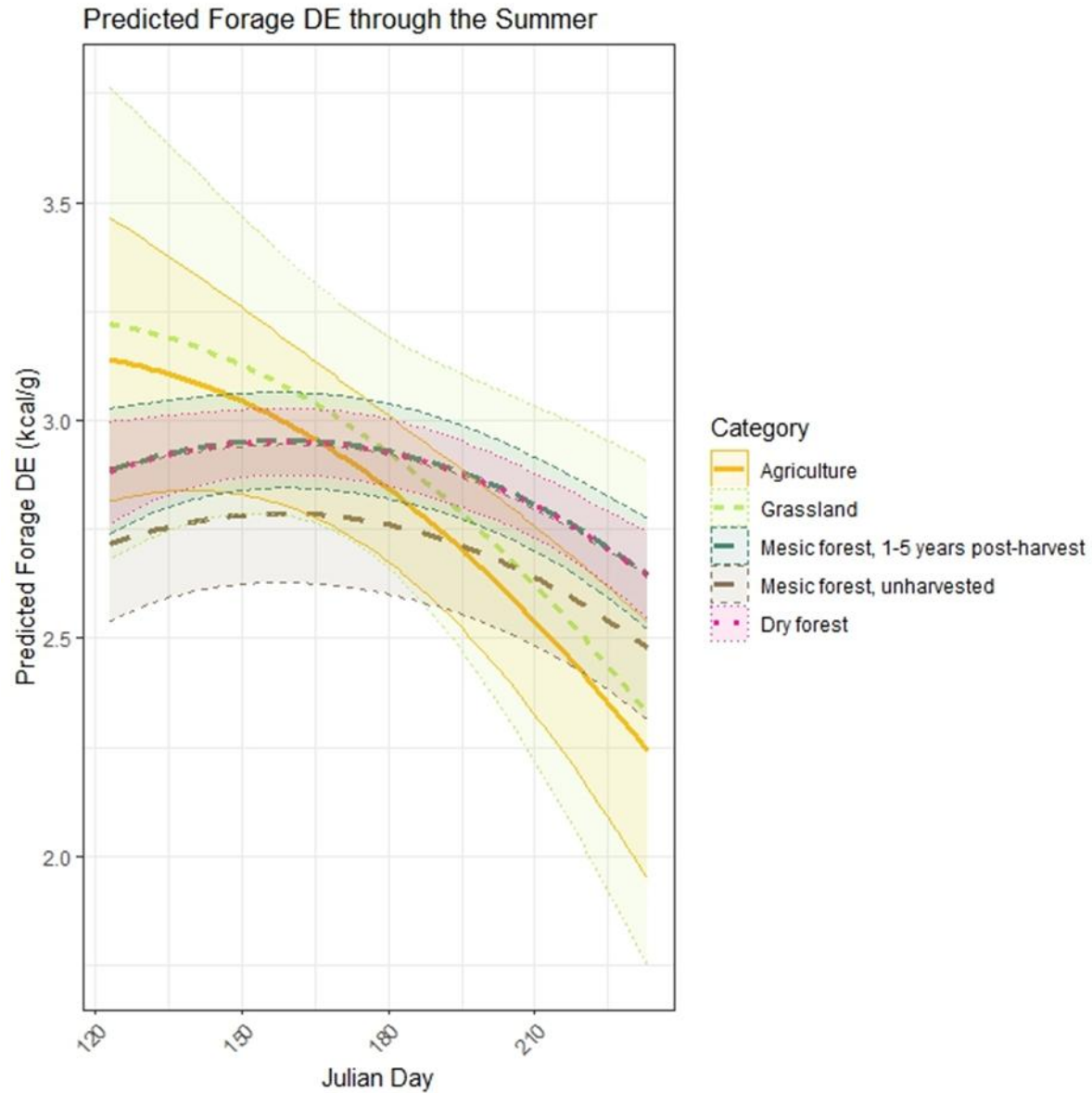


Figure 50. Model-predicted forage digestible energy (DE; kcal/g) as a function of time (Julian day). Julian dates range from the first day of sampling (May 3rd = 123) to the last day sampling (August 20th = 233). Colored lines represent different strata (yellow = grassland, light green = agriculture, dark green = mesic forest 1-5 years post-harvest, brown = unharvested mesic forest). Other time-since-harvest classes of mesic forest fall between the mesic 1-5 and mesic unharvested lines (not displayed for figure clarity). The figure assumes a South-facing aspect with elevation held constant at the mean value.

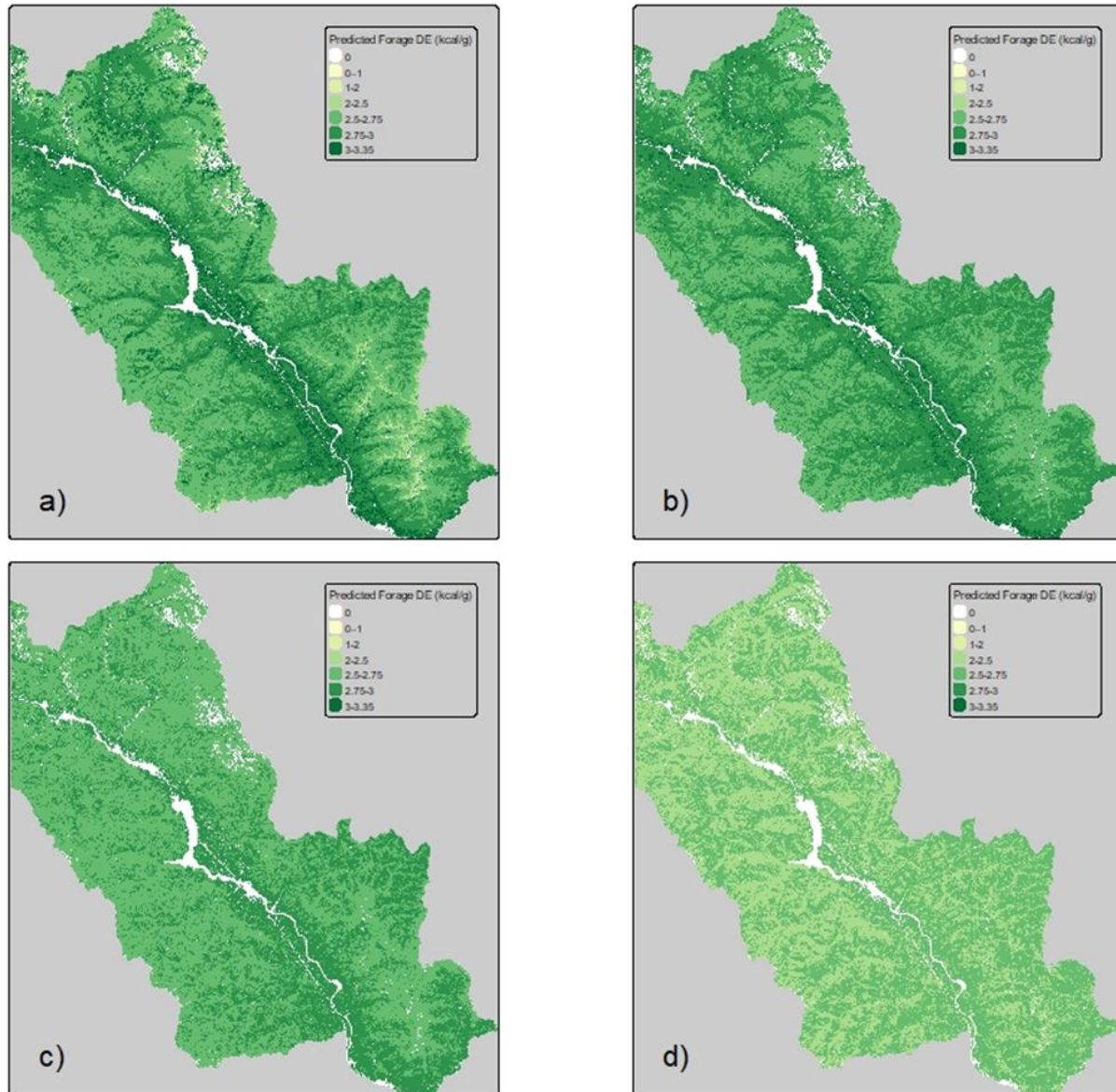


Figure 51. Predicted forage digestible energy (DE; kcal/g) for elk in Montana hunt district 121. Each map illustrates a snapshot of model predictions throughout the summer, including: a) mid-May (May 17th or Julian day 137), b) mid-June (June 17th or Julian day 168), c) mid-July (July 17th or Julian day 198), and d) mid-August (August 17th or Julian day 229). Darker colors indicate higher predicted forage DE values.

Table 11. Coefficient estimates and standard errors for the top models predicting forage biomass in Hunt District 121 in northwest Montana in May – August of 2023 and 2024. Bolded values indicate coefficients whose 95% confidence interval did not overlap zero. The reference (intercept) is unharvested, unburned dry forest.

Covariate	Estimate	Standard Error	p-value
Intercept	-9.719	0.086	0.991
Harvest Age 1-5	170.366	49.894	7.004 e-04
Harvest Age 6-10	81.074	48.787	0.097
Harvest Age 11-20	80.566	48.428	0.097
Harvest Age 21-40	-15.689	51.188	0.759
Harvest Age >40	-65.916	52.480	0.201
Burned	41.241	38.752	0.288
Julian day	18.700	4.945	1.779 e-04
Julian day ²	-0.063	0.014	1.464 e-05
Elevation	-4.007	1.982	0.044
Elevation ²	2.988 e-03	1.673 e-03	0.075
Elevation ³	-8.476 e-07	4.569 e-07	0.064
Mesic Forest	-41.733	22.649	0.066
Agriculture	883.306	388.616	0.024
Grassland	-1245.100	715.070	0.082
Elevation*Julian day	4.189 e-03	1.492 e-03	5.228 e-03
Agriculture*Julian day	-2.712	2.117	0.201
Grassland*Julian day	8.377	4.024	0.038

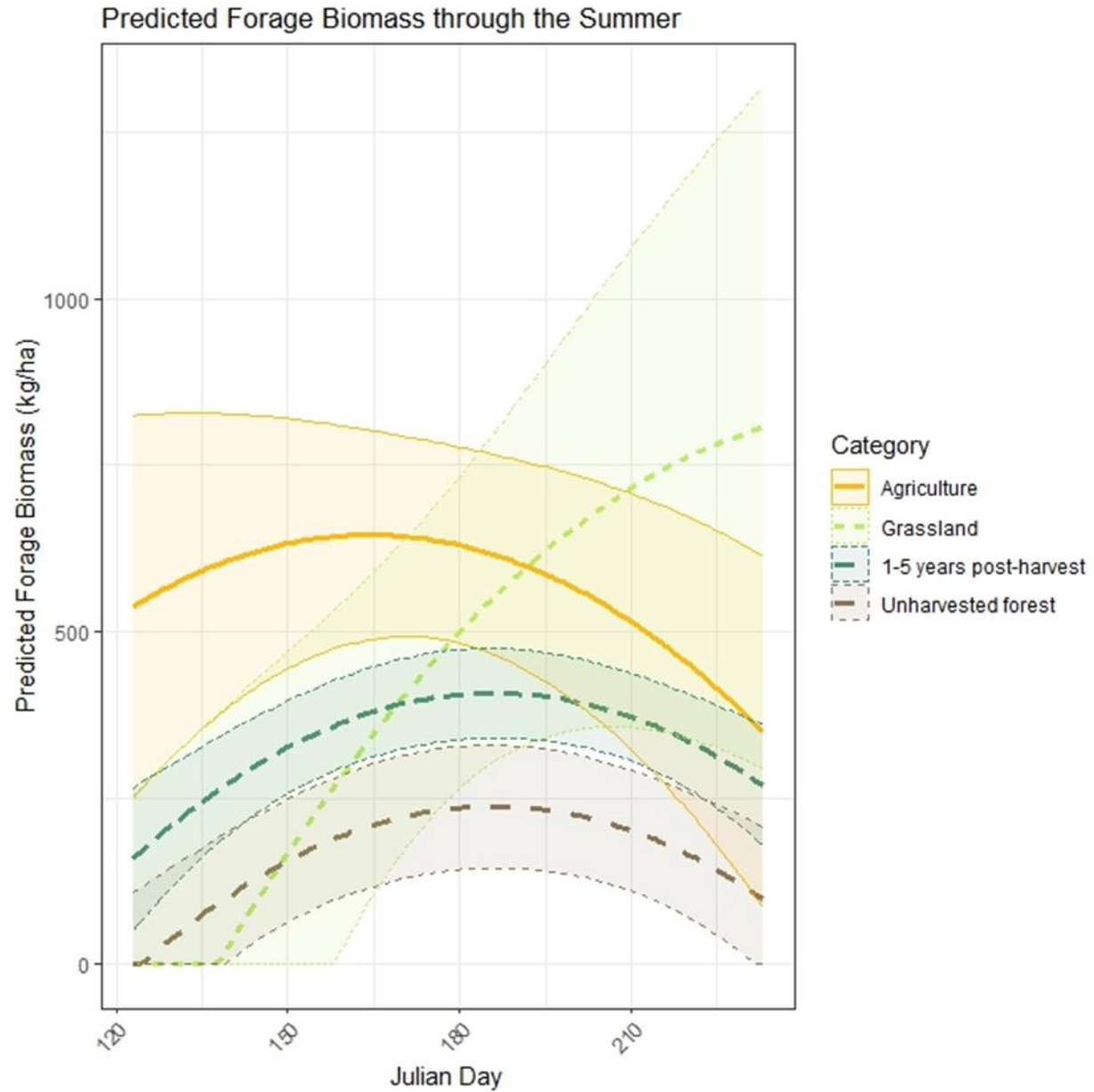


Figure 52. Model-predicted forage biomass (kg/ha) as a function of time (Julian day). Julian dates range from the first day of sampling (May 3rd = 123) to the last day sampling (August 20th = 233). Colored lines represent different strata (yellow = grassland, light green = agriculture, dark green = dry forest 1-5 years post-harvest, brown = unharvested dry forest). Other time-since-harvest classes fall between the 1-5 years post-harvest and unharvested lines, and mesic forests have slightly lower biomass (not displayed for figure clarity). The figure assumes no fire history with elevation held constant at the mean value.

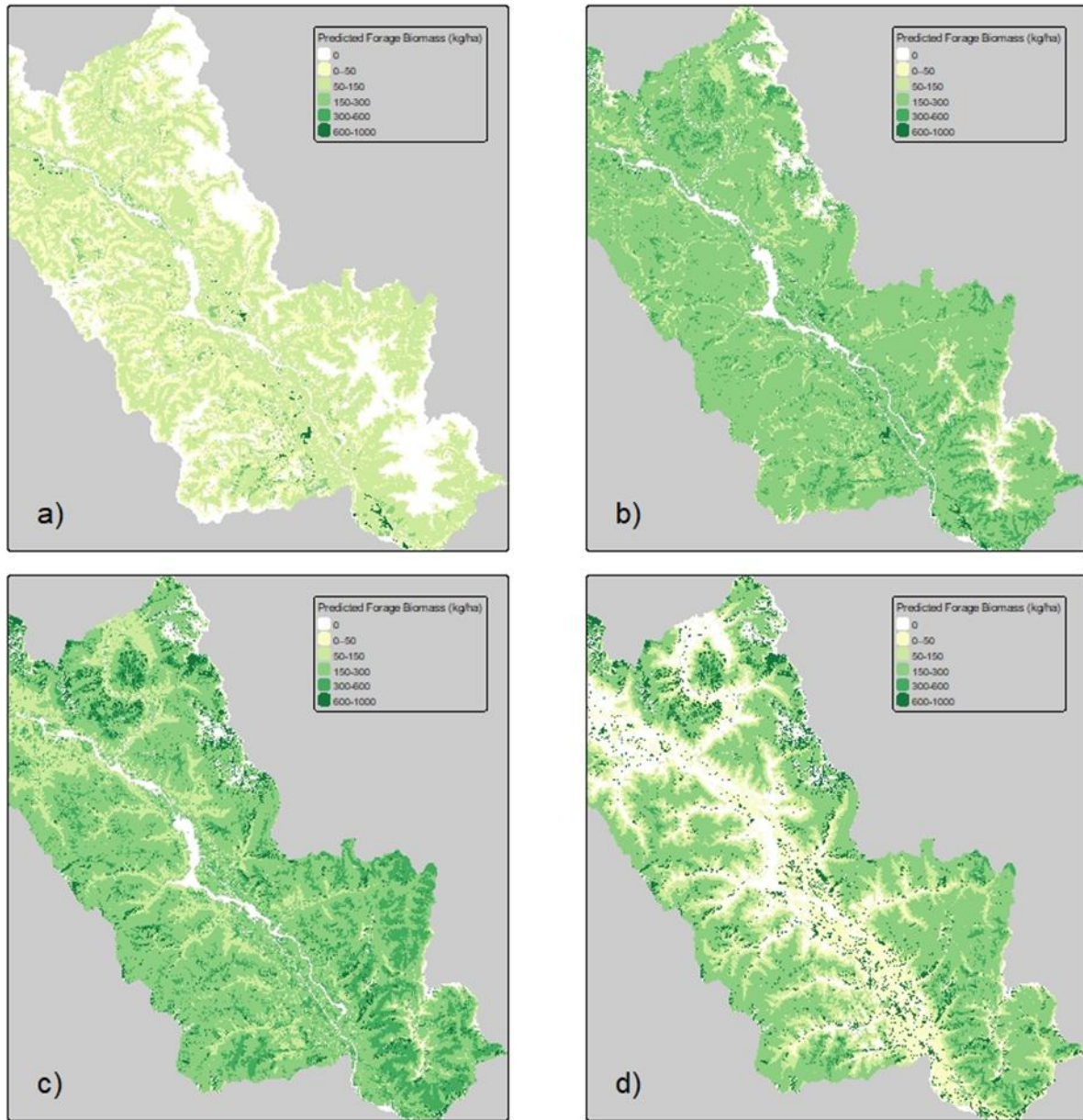


Figure 53. Predicted forage biomass (kg/ha) for elk in Montana hunt district 121. Each map illustrates a snapshot of model predictions throughout the summer, including: a) mid-May (May 17th or Julian day 137), b) mid-June (June 17th or Julian day 168), c) mid-July (July 17th or Julian day 198), and d) mid-August (August 17th or Julian day 229). Darker colors indicate higher predicted forage biomass values.

Elk Resource Selection During Summer

Early Summer Crepuscular

We built our early summer crepuscular model using 16,656 used locations and 166,505 available locations for 92 adult female elk across 2023 and 2024. All hyper-parameters in the model adequately converged, indicated by an $\hat{R}$ value of ≤ 1.1 (Gelman et al. 2014). Model fit based on the Bayesian p-value was adequate ($p_B = 0.101$). Model-estimated prevalence was 0.15 (sd = 0.005).

During crepuscular hours in early summer, adult female elk generally had a low probability of using forests and a high probability of using agriculture ($\beta = 5.981$; 95% CrI = 4.28, 8.765) and grasslands ($\beta = 2.818$; CrI = 2.585, 3.051). Within forests, the odds that female elk used a site were 1.7x higher in dry forests than mesic forests, the reference landcover category ($\beta = 0.541$; 95% CrI = 0.485, 0.6). We found no strong evidence for a difference in the probability of use between even-age harvested areas and the reference category of intermediate harvest ($\beta = 0.021$; 95% CrI = -0.138, 0.176; $P(\beta > 0) = 0.611$). The odds that an elk used a site were 5.5x higher 1-5 years post-harvest ($\beta = 1.7$; 95% CrI = 1.475, 1.924), 4x higher 6-10 years post-harvest ($\beta = 1.387$; 95% CrI = 1.183, 1.606), 2.8x higher 11-20 years post-harvest ($\beta = 1.013$; 95% CrI = 0.861, 1.164), and 1.1x higher 21-40 years post-harvest ($\beta = 0.012$; 95% CrI = -0.027, 0.277; $P(\beta > 0) = 0.942$) relative to sites that were harvested greater than 40 years ago. We found no strong evidence for a difference in the probability of use between unharvested forest and the reference category of forest harvested via an intermediate strategy greater than 40 years ago ($\beta = 0.039$; 95% CrI = -0.064, 0.14; $P(\beta > 0) = 0.758$). During this period, elk also were more likely to use less rugged terrain ($\beta = -0.759$; 95% CrI = -0.797, -0.724), areas closer to motorized roads ($\beta = -0.163$; 95% CrI = -0.196, -0.131), areas more likely to be selected by wolves ($\beta = 0.492$; 95% CrI = 0.457, 0.526), areas less likely to be selected by mountain lions ($\beta = -0.599$; 95% CrI = -0.638, -0.561), and areas less likely to be selected by black bears ($\beta = -0.4$; 95% CrI = -0.439, -0.365; Table 12).

Among landcover types, the estimated probability of use was highest in agriculture ($\psi = 0.965$; 95% CrI = 0.834, .998), and lowest in Other ($\psi = 0.02$; 95% CrI = 0.016, 0.024; Figure 54a).

Among harvest strategies, the estimated probability of use was highest in uneven ($\psi = 0.13$; 95% CrI = 0.079, 0.206), and lowest in intermediate ($\psi = 0.065$; 95% CrI = 0.053, 0.08; Figure 54b).

Across harvest age classes, the estimated probability of use was highest 1-5 years post-harvest ($\psi = 0.276$; 95% CrI = 0.233, 0.323), and lowest greater than 40 years post-harvest ($\psi = 0.065$; 95% CrI = 0.053, 0.08; Figure 54c).

Table 12. Parameter estimates, lower and upper limits of the 95% credible interval (LCL and UCL, respectively), the posterior probability of direction (pd; $P(\beta > 0)$ or $P(\beta < 0)$), and the standard deviation of the random intercepts (σ) for covariates included in the early summer (i.e., May-June) crepuscular resource selection probability function for adult female elk in the Pilgrim Creek elk population in northwestern Montana. The intercept term for categorical covariates is: Landcover, mesic forest; Harvest Strategy, intermediate; Time-since-harvest, > 40 years.

Parameter	Estimate	LCL	UCL	pd	σ
Population Intercept	-2.665	-2.892	-2.445		0.914
TRI	-0.759	-0.797	-0.724	1	
Distance to road	-0.163	-0.196	-0.131	1	
Burned	0.063	-0.084	0.198	0.787	
Wolf RSF	0.492	0.457	0.526	1	
Mountain lion RSF	-0.599	-0.638	-0.561	1	
Black bear RSF	-0.400	-0.439	-0.365	1	
<i>Landcover:</i>					
Dry Forest	0.541	0.485	0.600	1	
Agriculture	5.981	4.280	8.765	1	
Grassland	2.818	2.585	3.051	1	
Deciduous Forest	1.716	1.268	2.196	1	
Wetland	1.562	1.271	1.870	1	
Shrubland	1.394	1.282	1.503	1	
Other	-1.236	-1.434	-1.045	1	
<i>Harvest Strategy:</i>					
Even-age	0.021	-0.138	0.176	0.611	
Two-age	0.282	0.083	0.487	0.998	
Uneven	0.760	0.215	1.313	0.996	
No Harvest	0.039	-0.064	0.140	0.758	
<i>Time-since-harvest:</i>					
ysr1to5	1.699	1.475	1.924	1	
ysr6to10	1.387	1.183	1.606	1	
ysr11to20	1.013	0.861	1.164	1	
ysr21to40	0.124	-0.027	0.277	0.942	

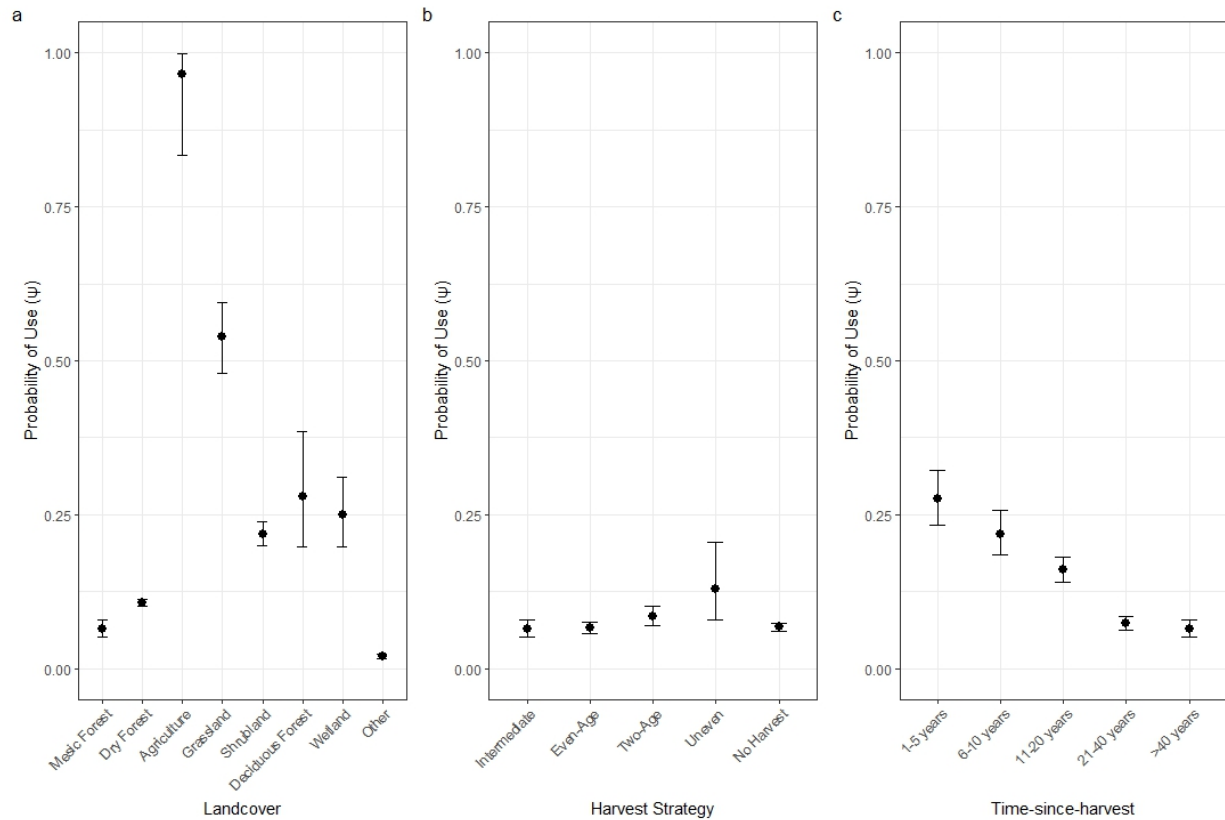


Figure 54. Estimated probability of use (ψ) by adult female elk during crepuscular (dawn/dusk) hours in early summer (May-June 2023-2024) as a function of a) landcover type (mesic forest, dry forest, agriculture, grassland, shrubland, deciduous forest, wetland, other), b) timber harvest strategy in dry and mesic forests (intermediate, even-age, two-age, uneven, no harvest), and c) time-since-harvest in harvested dry and mesic forests (1-5 years-since-harvest, 6-10 years-since-harvest, 11-20 years-since-harvest, 21-40 years-since-harvest, >40 years-since-harvest). Panel a) assumes that mesic and dry forests were harvested >40 years ago using an intermediate harvest strategy. Panel b) assumes that forests were harvested >40 years ago. Panel c) assumes that forests were harvested using an intermediate strategy. All panels assume that continuous covariates are fixed at their mean observed value. Mean estimates are represented by the black dots, and the 95% credible intervals are represented by the error bars.

Early Summer Day

We built our early summer day model using 16,787 used locations and 167,759 available locations for 92 adult female elk across 2023 and 2024. Seventeen out of 21 hyper-parameters in the model converged, indicated by an $\hat{R}$ value of ≤ 1.1 (Gelman et al. 2014). The beta estimate for the TRI, wolf RSF, mountain lion RSF, and Other parameters did not converge ($\hat{R} = 1.359, 1.222, 1.228, \text{ and } 1.237$, respectively). The Bayesian p-value suggested inadequate model fit ($p_b = 1$). Model-estimated prevalence was 0.62 (sd = 0.01).

During daylight hours in early summer, elk generally had a high probability of using forests, agriculture ($\beta = 0.599$; 95% CrI = -0.073, 1.29; $P(\beta > 0) = 0.963$), and grasslands ($\beta = 0.752$; 95% CrI = 0.258, 1.313). Within forests, the odds that female elk used a site were 1.8x higher in dry forests than mesic forests, the reference landcover category ($\beta = 0.593$; 95% CrI = 0.449, 0.724). We found moderate evidence that the odds an elk used a site were 1.3x lower in even-age harvested areas relative to the reference category of intermediate harvest ($\beta = -0.284$; 95% CrI = -0.603, 0.053; $P(\beta < 0) = 0.951$). The odds an elk used a site were 8.6x higher 1-5 years post-harvest ($\beta = 2.147$; 95% CrI = 1.376, 3.122), 2.3x higher 6-10 years post-harvest ($\beta = 0.85$; 95% CrI = 0.376, 1.375), 4.4x higher 11-20 years post-harvest ($\beta = 1.484$; 95% CrI = 1.156, 1.86), and 1.4x higher 21-40 years post-harvest ($\beta = 0.363$; 95% CrI = 0.003, 0.68) relative to sites that were harvested greater than 40 years ago. We found moderate evidence that the odds an elk used a site were 1.1x higher in unharvested forest relative to the reference category of forest harvested via an intermediate strategy greater than 40 years ago ($\beta = 0.136$; 95% CrI = -0.044, 0.321; $P(\beta > 0) = 0.915$). During this period, elk also were more likely to use less rugged terrain ($\beta = -2.393$; 95% CrI = -2.553, -2.23), areas closer to motorized roads ($\beta = -0.308$; 95% CrI = -0.338, -0.224), burned areas ($\beta = 0.82$; 95% CrI = 0.426, 1.259), areas less likely to be selected by wolves ($\beta = -0.656$; 95% CrI = -0.76, -0.53), areas less likely to be selected by mountain lions ($\beta = -1.218$; 95% CrI = -1.335, -1.101), and areas more likely to be selected by black bears ($\beta = 0.866$; 95% CrI = 0.761, 0.982; Table 13).

Among landcover types, the estimated probability of use was highest in deciduous forest ($\psi = 0.891$; 95% CrI = 0.708, 0.974), and lowest in other ($\psi = 0.002$; 95% CrI = 0.001, 0.004; Figure 55a). Among harvest strategies, the estimated probability of use was highest in two-age ($\psi = 0.838$; 95% CrI = 0.752, 0.905), and lowest in even-age ($\psi = 0.655$; 95% CrI = 0.58, 0.727; Figure 55b). Across harvest age classes, the estimated probability of use was highest 1-5 years post-harvest ($\psi = 0.956$; 95% CrI = 0.909, 0.983), and lowest greater than 40 years post-harvest ($\psi = 0.716$; 95% CrI = 0.603, 0.802; Figure 55c).

Table 13. Parameter estimates, lower and upper limits of the 95% credible interval (LCL and UCL, respectively), the posterior probability of direction (pd; $P(\beta > 0)$ or $P(\beta < 0)$), and the standard deviation of the random intercepts (σ) for covariates included in the early summer (i.e., May-June) daytime resource selection probability function for adult female elk in the Pilgrim Creek elk population in northwestern Montana. The intercept term for categorical covariates is: Landcover, mesic forest; Harvest Strategy, intermediate; Time-since-harvest, > 40 years.

Parameter	Estimate	LCL	UCL	pd	σ
Population Intercept	0.925	0.418	1.402		2.004
TRI	-2.393	-2.553	-2.230	1	
Distance to road	-0.308	-0.394	-0.224	1	
Burned	0.820	0.426	1.259	1	
Wolf RSF	-0.656	-0.760	-0.530	1	
Mountain lion RSF	-1.218	-1.335	-1.101	1	
Black bear RSF	0.866	0.761	0.982	1	
<i>Landcover:</i>					
Dry Forest	0.593	0.449	0.724	1	
Agriculture	0.599	-0.073	1.290	0.963	
Grassland	0.752	0.258	1.313	1	
Deciduous Forest	1.179	-0.039	2.712	0.971	
Wetland	-1.560	-2.392	-0.707	0.998	
Shrubland	0.115	-0.222	0.482	0.739	
Other	-7.175	-7.788	-6.510	1	
<i>Harvest Strategy:</i>					
Even-age	-0.284	-0.603	0.053	0.951	
Two-age	0.717	0.184	1.326	0.993	
Uneven	0.337	-0.705	1.568	0.697	
No Harvest	0.136	-0.044	0.321	0.915	
<i>Time-since-harvest:</i>					
yrs1to5	2.147	1.376	3.122	1	
yrs6to10	0.850	0.376	1.375	1	
yrs11to20	1.485	1.156	1.860	1	
yrs21to40	0.363	0.003	0.680	0.975	

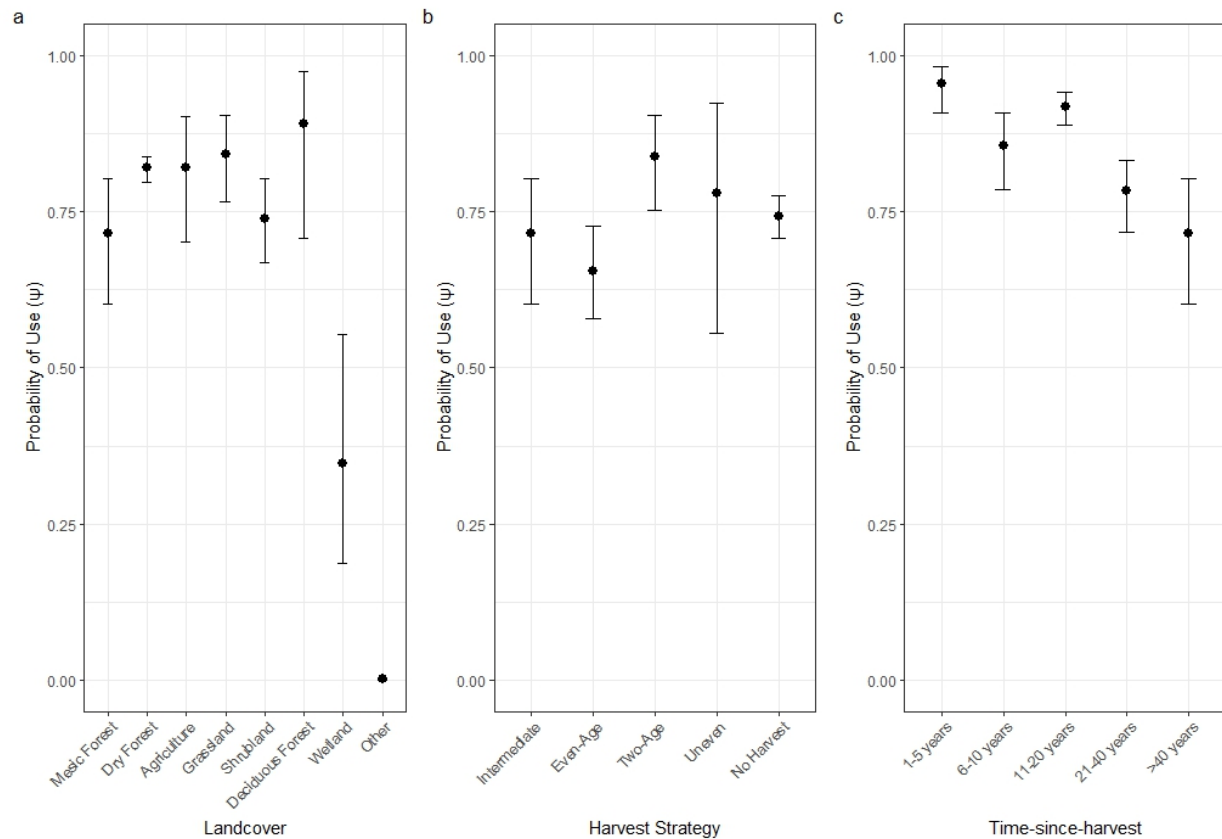


Figure 55. Estimated probability of use (ψ) by adult female elk during daylight hours in early summer (May-June 2023-2024) as a function of a) landcover type (mesic forest, dry forest, agriculture, grassland, shrubland, deciduous forest, wetland, other), b) timber harvest strategy in dry and mesic forests (intermediate, even-age, two-age, uneven, no harvest), and c) time-since-harvest in harvested dry and mesic forests (1-5 years-since-harvest, 6-10 years-since-harvest, 11-20 years-since-harvest, 21-40 years-since-harvest, >40 years-since-harvest). Panel a) assumes that mesic and dry forests were harvested >40 years ago using an intermediate harvest strategy. Panel b) assumes that forests were harvested >40 years ago. Panel c) assumes that forests were harvested using an intermediate strategy. All panels assume that continuous covariates are fixed at their mean observed value. Mean estimates are represented by the black dots, and the 95% credible intervals are represented by the error bars.

Late Summer Crepuscular

We built our late summer crepuscular model using 16,212 used locations and 162,065 available locations for 92 adult female elk across 2023 and 2024. All hyper-parameters in the model converged, indicated by an $\hat{R}$ value of ≤ 1.1 (Gelman et al. 2014). Model fit based on the Bayesian p-value was adequate ($p_B = 0.699$). Model-estimated prevalence was 0.38 ($sd = 0.008$).

During dawn and dusk hours in late summer, elk generally had a low probability of using agriculture ($\beta = -1.203$; 95% CrI = -1.534, -0.878) and forest strata with greater cover, and a high probability of using grasslands ($\beta = 6.363$; 95% CrI = 4.447, 9.98) and more open forest strata. Within forests, the odds that female elk used a site were 1.1x higher in dry forests than mesic forests ($\beta = 0.13$; 95% CrI = 0.053, 0.211). The odds an elk used a site were 13.9x higher in areas of even-age harvest than intermediate harvest ($\beta = 2.632$; 95% CrI = 2.165, 3.176). The odds that an elk used a site were 342.8x higher 1-5 years post-harvest ($\beta = 5.837$; 95% CrI = 3.886, 9.517), 3.5x higher 6-10 years post-harvest ($\beta = 1.258$; 95% CrI = 0.817, 1.712), 2x higher 11-20 years post-harvest ($\beta = 0.669$; 95% CrI = 0.441, 0.884), and 2.7x lower 21-40 years post-harvest ($\beta = -0.989$; 95% CrI = -1.188, -0.781) relative to sites that were harvested greater than 40 years ago. The odds an elk used unharvested forest were 1.4x lower relative to the reference category of forest harvested via an intermediate strategy greater than 40 years ago ($\beta = -0.356$; 95% CrI = -0.462, -0.229). During this period, elk were also more likely to use less rugged terrain ($\beta = -0.46$; 95% CrI = -0.502, -0.413), areas further from motorized roads ($\beta = 0.432$; 95% CrI = 0.387, 0.473), burned areas ($\beta = 1.237$; 95% CrI = 0.988, 1.517), areas more likely to be selected by wolves ($\beta = 0.604$; 95% CrI = 0.561, 0.65), areas less likely to be selected by mountain lions ($\beta = -0.035$; 95% CrI = -0.075, 0.011; $P(\beta < 0) = 0.946$), and areas less likely to be selected by black bears ($\beta = -0.77$; 95% CrI = -0.822, -0.722; Table 14).

Among landcover types, the estimated probability of use was highest in grasslands ($\psi = 0.997$; 95% CrI = 0.981, 0.999), and lowest in other ($\psi = 0.056$; 95% CrI = 0.044, 0.073; Figure 56a). Among harvest strategies, the estimated probability of use was highest in even-age ($\psi = 0.894$; 95% CrI = 0.841, 0.935), and lowest in unharvested forest ($\psi = 0.298$; 95% CrI = 0.276, 0.325; Figure 56b). Across harvest age classes, the estimated probability of use was highest 1-5 years post-harvest ($\psi = 0.995$; 95% CrI = 0.967, 0.999), and lowest 21-40 years post-harvest ($\psi = 0.184$; 95% CrI = 0.156, 0.217; Figure 56c).

Table 14. Parameter estimates, lower and upper limits of the 95% credible interval (LCL and UCL, respectively), the posterior probability of direction (pd; $P(\beta > 0)$ or $P(\beta < 0)$), and the standard deviation of the random intercepts (σ) for covariates included in the late summer (i.e., July-August) crepuscular resource selection probability function for adult female elk in the Pilgrim Creek elk population in northwestern Montana. The intercept term for categorical covariates is: Landcover, mesic forest; Harvest Strategy, intermediate; Time-since-harvest, > 40 years.

Parameter	Estimate	LCL	UCL	pd	σ
Population Intercept	-0.502	-0.675	-0.332		0.502
TRI	-0.460	-0.502	-0.413	1	
Distance to road	0.432	0.387	0.473	1	
Burned	1.237	0.988	1.517	1	
Wolf RSF	0.604	0.561	0.650	1	
Mountain lion RSF	-0.035	-0.075	0.011	0.946	
Black bear RSF	-0.770	-0.822	-0.722	1	
<i>Landcover:</i>					
Dry Forest	0.130	0.053	0.211	1	
Agriculture	-1.203	-1.534	-0.878	1	
Grassland	6.363	4.447	9.980	1	
Deciduous Forest	0.750	0.095	1.549	0.989	
Wetland	2.810	1.486	5.882	1	
Shrubland	0.306	0.150	0.471	1	
Other	-2.320	-2.570	-2.041	1	
<i>Harvest Strategy:</i>					
Even-age	2.632	2.165	3.176	1	
Two-age	2.274	1.814	2.781	1	
Uneven	0.233	-0.474	1.027	0.72	
No Harvest	-0.356	-0.462	-0.229	1	
<i>Time-since-harvest:</i>					
yrs1to5	5.837	3.886	9.517	1	
yrs6to10	1.258	0.817	1.712	1	
yrs11to20	0.669	0.441	0.884	1	
yrs21to40	-0.989	-1.188	-0.781	1	

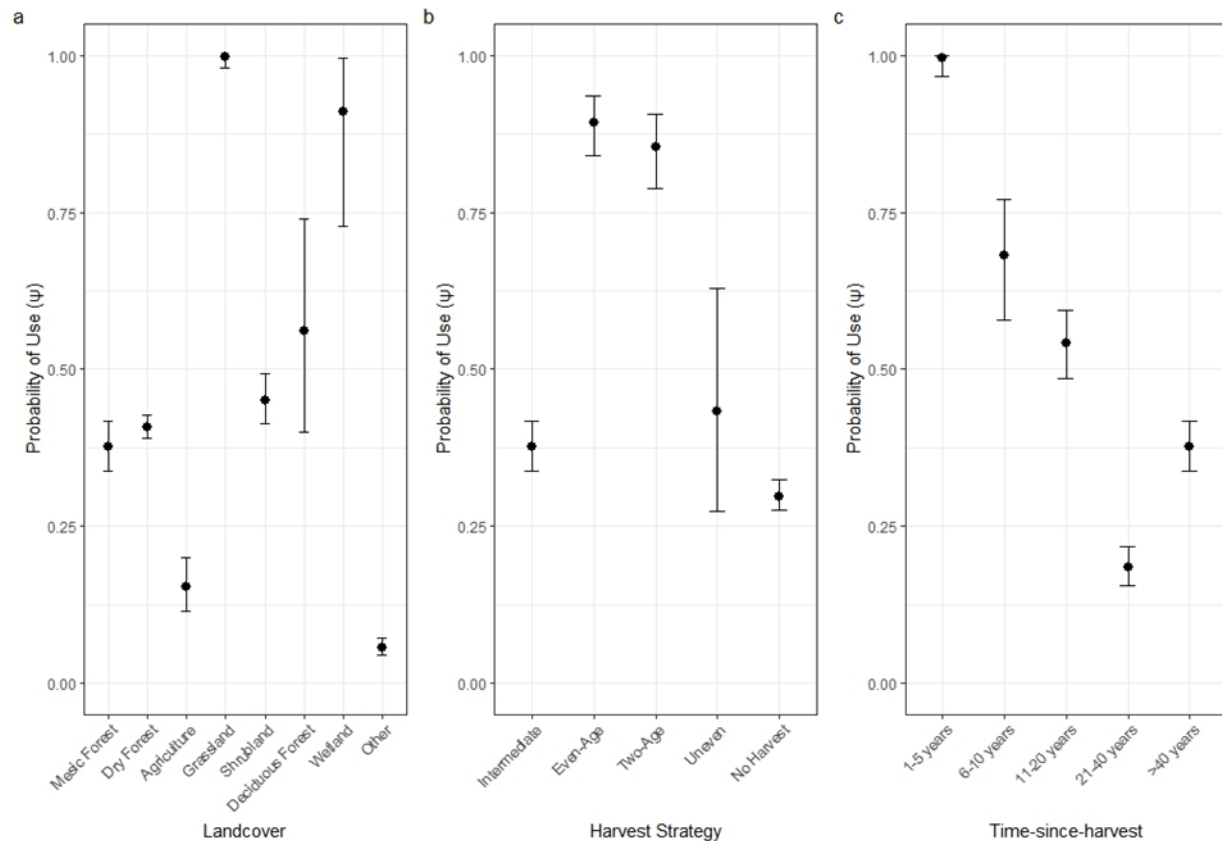


Figure 56. Estimated probability of use (ψ) by adult female elk during dawn and dusk hours in late summer (July-August 2023-2024) as a function of a) landcover type (mesic forest, dry forest, agriculture, grassland, shrubland, deciduous forest, wetland, other), b) timber harvest strategy in dry and mesic forests (intermediate, even-age, two-age, uneven, no harvest), and c) time-since-harvest in harvested dry and mesic forests (1-5 years-since-harvest, 6-10 years-since-harvest, 11-20 years-since-harvest, 21-40 years-since-harvest, >40 years-since-harvest). Panel a) assumes that mesic and dry forests were harvested >40 years ago using an intermediate harvest strategy. Panel b) assumes that forests were harvested >40 years ago. Panel c) assumes that forests were harvested using an intermediate strategy. All panels assume that continuous covariates are fixed at their mean observed value. Mean estimates are represented by the black dots, and the 95% credible intervals are represented by the error bars.

Late Summer Day

We built our late summer daytime model using 16,588 used locations and 165,817 available locations for 92 adult female elk across 2023 and 2024. Eleven out of 21 hyper-parameters in the model converged, indicated by an $\hat{R}$ value of ≤ 1.1 (Gelman et al. 2014). The beta estimate for the distance to road, mountain lion RSF, agriculture, grassland, Other, unharvested forest, 1-5 years-since-harvest, 6-10 years-since-harvest, 11-20 years-since-harvest, and 21-40 years-since-harvest parameters did not converge ($\hat{R} = 1.248, 1.125, 1.231, 2.069, 1.4, 2.665, 1.658, 1.393, 1.789, \text{ and } 1.991$, respectively). The Bayesian p-value indicated inadequate model fit ($p_B = 0.977$). Model-estimated prevalence was 0.64 (sd = 0.009).

During daylight hours in late summer, elk generally had a high probability of using forests and a low probability of using agriculture ($\beta = -6.15$; 95% CrI = -7.018, -5.363) and grasslands ($\beta = -4.304$; 95% CrI = -4.791, -3.891). Within forests, the odds that a female elk used a site were 2.9x lower in dry forests than mesic forests ($\beta = -1.08$; 95% CrI = -1.219, -0.938). The odds that an elk used a site were 1.7x higher in areas of even-age harvest than intermediate harvest ($\beta = 0.505$; 95% CrI = 0.062, 0.951). The odds that an elk used a site were 17.2x lower 1-5 years post-harvest ($\beta = -2.847$; 95% CrI = -3.492, -2.249), 27x lower 6-10 years post-harvest ($\beta = -3.321$; 95% CrI = -3.997, -2.669), 8.8x lower 11-20 years post-harvest ($\beta = -2.17$; 95% CrI = -2.721, -1.707), and 17.2x lower 21-40 years post-harvest ($\beta = -2.842$; 95% CrI = -3.301, -2.411) relative to sites that were harvested greater than 40 years ago. The odds an elk used unharvested forest were 11.5x lower relative to the reference category of forest harvested via an intermediate strategy greater than 40 years ago ($\beta = -2.446$; 95% CrI = -2.825, -2.125). During this period, elk also were more likely to use more rugged terrain ($\beta = 0.247$; 95% CrI = 0.149, 0.351), areas further from motorized roads ($\beta = 2.034$; 95% CrI = 1.834, 2.228), burned areas ($\beta = 1.391$; 95% CrI = 0.869, 1.913), areas less likely to be used by wolves ($\beta = -0.232$; 95% CrI = -0.315, -0.139), areas more likely to be used by mountain lions ($\beta = 1.053$; 95% CrI = 0.943, 1.16), and areas more likely to be used by black bears ($\beta = 0.292$; 95% CrI = 0.199, 0.378); Table 15).

Among landcover types, the estimated probability of use was highest in mesic forest ($\psi = 0.98$; 95% CrI = 0.968, 0.989), and lowest in agriculture ($\psi = 0.096$; 95% CrI = 0.042, 0.188; Figure 57a). Among harvest strategies, the estimated probability of use was highest in uneven ($\psi = 0.999$; 95% CrI = 0.992, 0.999), and lowest in unharvested forest ($\psi = 0.811$; 95% CrI = 0.746, 0.855; Figure 57b). Across harvest age classes, the estimated probability of use was highest greater than 40 years post-harvest ($\psi = 0.98$; 95% CrI = 0.968, 0.989), and lowest 6-10 years post-harvest ($\psi = 0.641$; 95% CrI = 0.477, 0.775; Figure 57c).

Table 15. Parameter estimates, lower and upper limits of the 95% credible interval (LCL and UCL, respectively), the posterior probability of direction (pd; $P(\beta > 0)$ or $P(\beta < 0)$), and the standard deviation of the random intercepts (σ) for covariates included in the late summer (i.e., July-August) daytime resource selection probability function for adult female elk in the Pilgrim Creek elk population in northwestern Montana. The intercept term for categorical covariates is: Landcover, mesic forest; Harvest Strategy, intermediate; Time-since-harvest, > 40 years.

Parameter	Estimate	LCL	UCL	pd	σ
Population Intercept	3.903	3.408	4.460		1.428
TRI	0.247	0.149	0.351	1	
Distance to road	2.034	1.834	2.228	1	
Burned	1.391	0.869	1.913	1	
Wolf RSF	-0.232	-0.315	-0.139	1	
Mountain lion RSF	1.053	0.943	1.160	1	
Black bear RSF	0.292	0.199	0.378	1	
<i>Landcover:</i>					
Dry Forest	-1.080	-1.219	-0.938	1	
Agriculture	-6.150	-7.018	-5.363	1	
Grassland	-4.304	-4.791	-3.891	1	
Deciduous Forest	-0.704	-1.707	0.412	0.899	
Wetland	-1.845	-2.448	-1.243	1	
Shrubland	-1.849	-2.088	-1.605	1	
Other	-5.764	-6.436	-5.122	1	
<i>Harvest Strategy:</i>					
Even-age	0.505	0.062	0.951	0.985	
Two-age	0.822	0.330	1.309	1	
Uneven	2.882	0.958	5.510	1	
No Harvest	-2.446	-2.825	-2.125	1	
<i>Time-since-harvest:</i>					
yrs1to5	-2.847	-3.492	-2.249	1	
yrs6to10	-3.322	-3.997	-2.669	1	
yrs11to20	-2.170	-2.721	-1.707	1	
yrs21to40	-2.842	-3.301	-2.411	1	

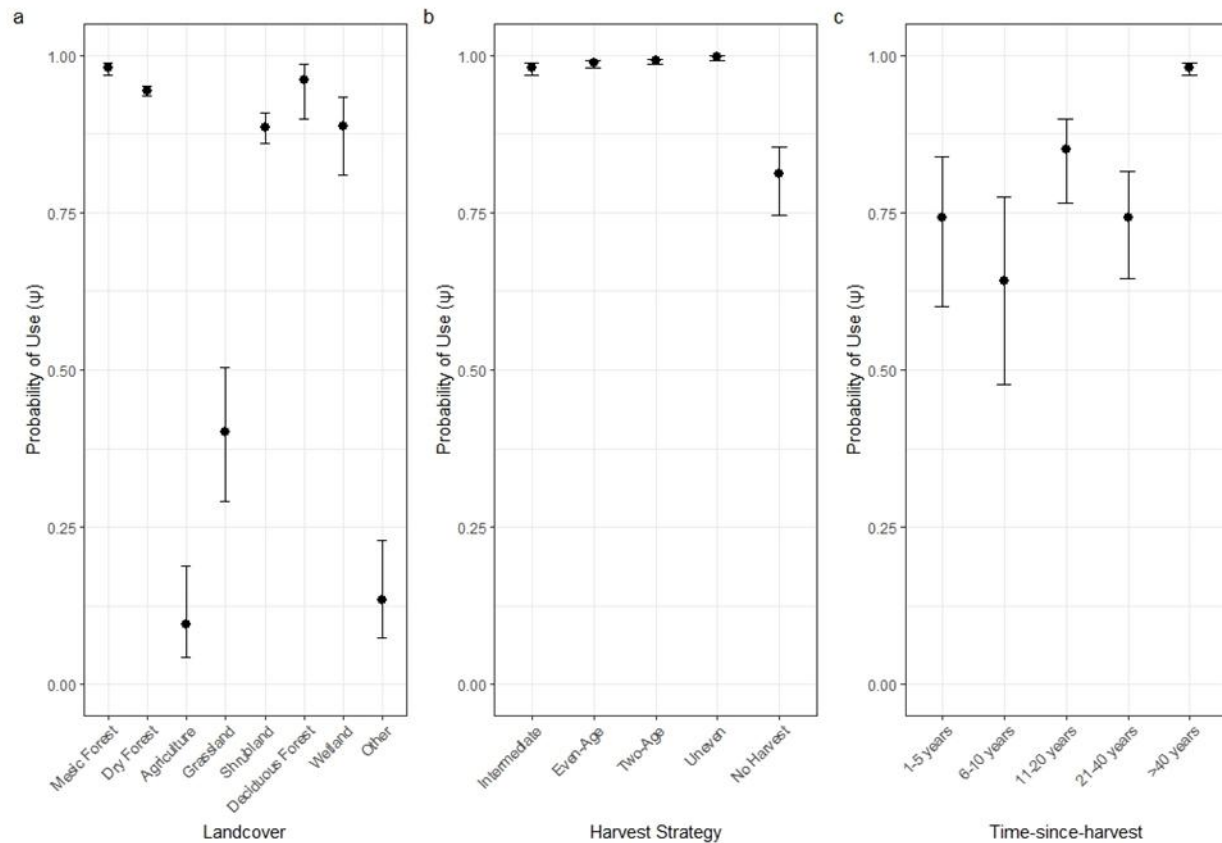


Figure 57. Estimated probability of use (ψ) by adult female elk during daylight hours in late summer (July-August 2023-2024) as a function of a) landcover type (mesic forest, dry forest, agriculture, grassland, shrubland, deciduous forest, wetland, other), b) timber harvest strategy in dry and mesic forests (intermediate, even-age, two-age, uneven, no harvest), and c) time-since-harvest in harvested dry and mesic forests (1-5 years-since-harvest, 6-10 years-since-harvest, 11-20 years-since-harvest, 21-40 years-since-harvest, >40 years-since-harvest). Panel a) assumes that mesic and dry forests were harvested >40 years ago using an intermediate harvest strategy. Panel b) assumes that forests were harvested >40 years ago. Panel c) assumes that forests were harvested using an intermediate strategy. All panels assume that continuous covariates are fixed at their mean observed value. Mean estimates are represented by the black dots, and the 95% credible intervals are represented by the error bars.

Overall, female elk resource selection generally followed predicted patterns that aligned with research performed on elk populations across western North America (e.g., Ager et al. 2003, Rowland et al. 2018, Ruprecht et al. 2023). Elk were more likely to use areas associated with higher nutritional metrics (i.e., even-age forest stands harvested within the past 1-5 years, agriculture, grasslands) during dawn and dusk, time periods when elk are expected to be primarily foraging (Green and Bear 1990, Roberts et al. 2017). Elk were more likely to use areas associated with higher cover (i.e., older harvested forest stands, unharvested forests) during the day, a time period when their decision-making may be more influenced by considerations of risk avoidance and thermoregulation (Merrill 1991, Ruprecht et al. 2023). Elk use of timber harvest strata was particularly pronounced during late summer, when they switched their patterns of use to avoid agriculture (Figure 58).

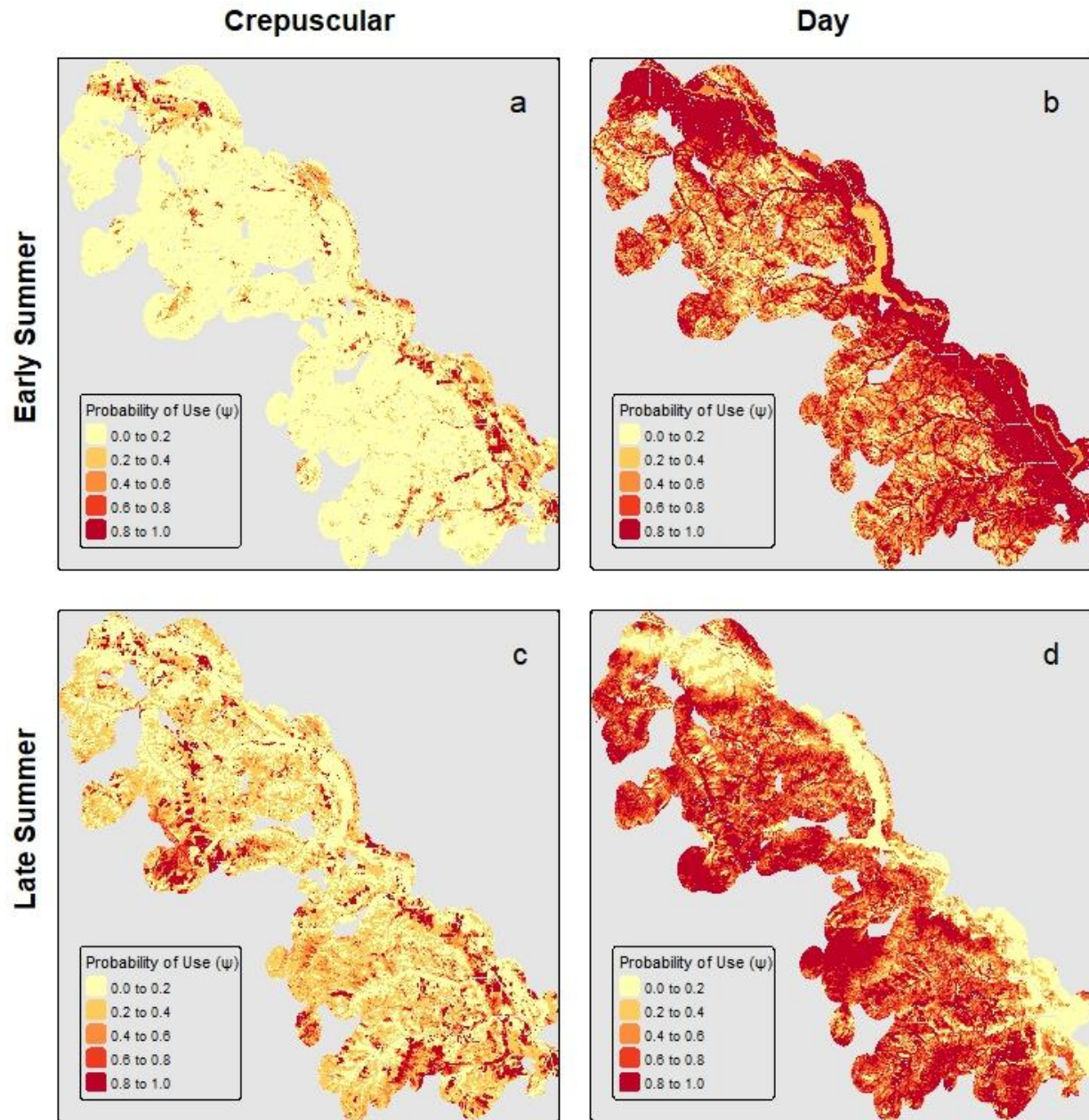


Figure 58. Predicted probability of use (ψ) by adult female elk during early summer (May-June 2023-2024) at dawn and dusk hours (panel a), and daylight hours (panel b), and late summer (July-August 2023-2024) at dawn and dusk hours (panel c) and daylight hours (panel d) in northwestern Montana. Color gradients represent low (yellow) to high (red) probability of use. Note, maps do not depict elk distributions, rather probabilities of use, given site characteristics and model predictions. For example, panels b and d suggest a large proportion of the study area has high predicted probability of use, given site characteristics, but does not necessarily suggest elk occur across these areas of high probability of use.

Objective #4: Integrate findings from the monitoring program into predictive models, such that predictions of elk population dynamics and hunting season distribution become more accurate in the future in northwest Montana and can be exported to other regions of Montana.

4.1 Framework

We are using new information from data collected as part of this study in an adaptive framework that will improve the previous elk IPM for HD 121 described in section 1 and facilitate management actions in Region 1 (Figure 59). See [Section 1](#) for more information regarding results of integrated population models that incorporate study data.

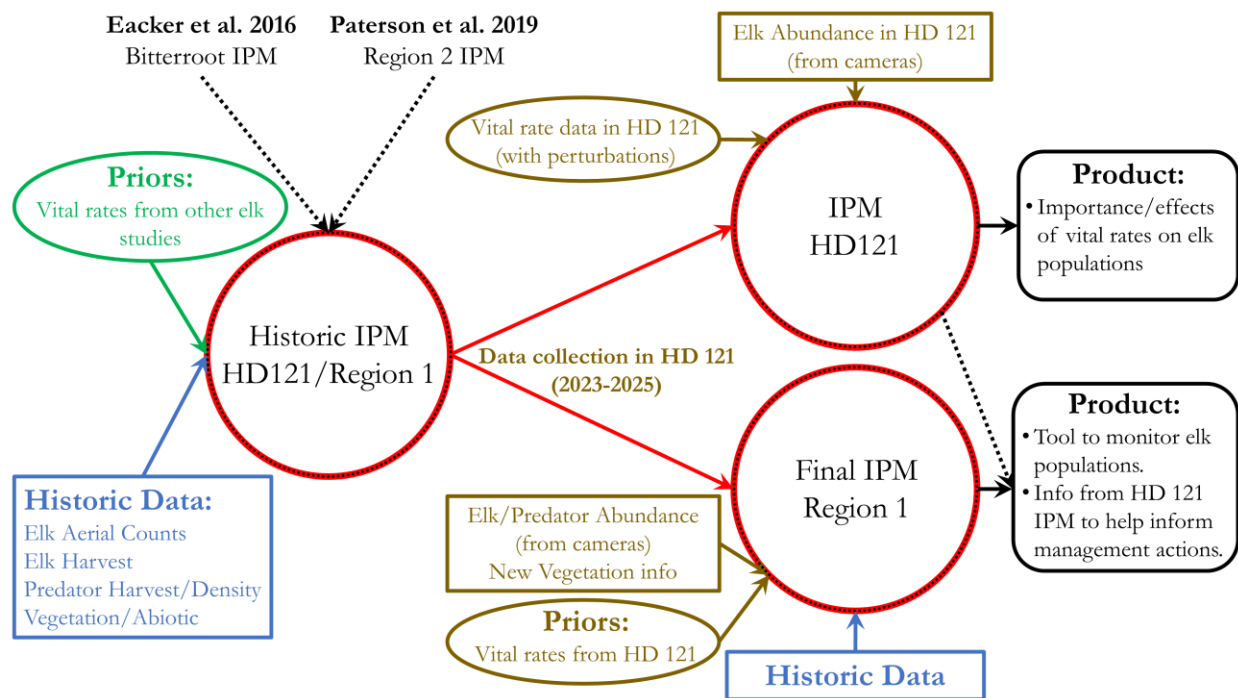


Figure 59. Diagram describing the workflow of our study as it relates to the population model(s) and desired outputs. Red areas represent integrated population models (IPM; all similar structure), green areas represent prior information from previous studies, blue areas represent historic datasets, gold areas represent new data from this study, and black areas represent desired products. In short, we will build upon the previous IPM (see Section 1) to create an IPM for hunting district 121 using only new data, which will be used to evaluate the importance of vital rates on elk populations. In concert with the HD 121 IPM, we will develop an IPM for Region 1 using both historic and new data, as well as information gained from sensitivity analyses with the HD 121, to produce a tool to monitor elk populations which will facilitate elk management throughout Region 1.

Acknowledgments

This research was a collaborative effort and would not have been possible without the cooperation amongst state and federal agency staff, University personnel, non-governmental organizations, and private citizens. We thank the private landowners for providing access and knowledge crucial to the development and implementation of the research. We thank the field technicians and hound handlers for their hard work towards making this project a success. We also thank agency staff across FWP Regions for providing helpful comments and suggestions during research development and for volunteering their time in the field. We thank Rocky Mountain Elk Foundation for providing funding and the U.S. Forest Service for providing housing for our winter crews, and for helping access sites across the Forest.

Appendix A: Description of elk pathogens and their influence (if known) on individual or herd health.

Brucellosis--Brucellosis is an infectious disease caused by the *Brucella abortus* bacterium affecting some elk populations in the Greater Yellowstone Area. The presence of this disease in Montana elk herds is primarily a concern because infected elk can act as a reservoir for transmission to livestock. Naive elk and cattle may experience a high rate of abortion (Thorne et al. 1978); however, brucellosis is not considered a direct threat to the sustainability of elk populations in Montana.

Anaplasmosis--Anaplasmosis, a sickness caused by bacteria of the genus *Anaplasma*, is a vector-borne disease primarily affecting domestic cattle. *Anaplasma marginale*, the species most commonly involved with infections in cattle, affects red blood cells resulting in severe anemia and sometimes death. Elk are susceptible to *Anaplasma* infection; however, serious clinical signs have not been recorded and there is little evidence suggesting elk are important carriers or reservoirs of the disease (Kuttler 1984; Zaugg et al. 1996). The specific *Anaplasma* species that elk are exposed to are unknown because the test detects antibodies for multiple species. This pathogen is not expected to impact individual or herd health in elk.

Leptospirosis--*Leptospira* spp. are a group of several closely related bacteria that can infect nearly all mammals. Infection varies in severity from asymptomatic to fatal depending on the host and the serological variant of *Leptospira*. Naturally occurring *Leptospira* infections in wildlife are usually asymptomatic, but may result in renal failure, destruction of red blood cells, fever, inappetence, hemorrhages on mucous membranes, jaundice, dehydration, infertility, abortion, stillbirths, or weakened neonates. *Leptospira* infection is generally not considered to be of concern in populations of free-ranging elk, but has been widely studied in wildlife due to the possibility of transmission to domestic livestock (Thorne et al. 2002). *Leptospira* spp. infection may cause some mortality; however, clinical disease in wildlife is rare and not likely a major limiting factor in free-ranging elk populations (Thorne et al. 2002).

Parainfluenza-3--Parainfluenza-3 is a common virus that can be involved in respiratory disease in domestic ungulates. The disease associated with PI-3 is usually mild or subclinical, but under severe stress, the virus may predispose animals to coinfection with other respiratory pathogens resulting in development of secondary bacterial pneumonia. It is unknown whether exposure to this virus leads to clinical symptoms in free-ranging elk (Barber-Meyer et al. 2007). Evidence of exposure on serological testing is common in wildlife, but documented clinical cases of disease are not. Exposure to this virus is not expected to impact individual or herd health.

Bovine respiratory syncytial virus--Bovine respiratory syncytial virus can be a primary pathogen causing varying degrees of pneumonia, especially in young calves. Disease is often most severe when secondary bacterial infection occurs. Elk are susceptible to infection by the virus, which is most likely transmitted from cattle; however, serious clinical symptoms may not occur in wild elk (Barber-Meyer et al. 2007).

Bovine viral diarrhea (types 1 & 2)--Bovine viral diarrhea virus (types 1 & 2) can cause bloody diarrhea and can induce immunosuppression resulting in development of secondary bacterial

pneumonia in domestic and wild ungulates. The different types (1 & 2) reflect differences in the antigens found on the viral surface protein and do not relate to the virulence of the virus. Elk are susceptible to infection with BVD, but there is little evidence of serious clinical effects (Tessaro et al. 1999). There is potential for wildlife populations to serve as reservoirs of this virus (Duncan et al. 2008).

Bovine herpes virus-1--Bovine herpes virus-1 is a common virus in cattle and can cause rhinotracheitis, fever, conjunctivitis, a drop in milk production, abortion, encephalitis, and lesions of the mucous membranes of the genital tract. The virus is transmitted most effectively by respiratory infections (Wentink et al. 1993). While most BHV-1 infections in cattle are mild, the virus can predispose animals to secondary bacterial pneumonia. BHV-1 can undergo long periods of latency before being reactivated, when it can again be shed and infect new hosts.

Epizootic hemorrhagic disease--Epizootic hemorrhagic disease (EHD) is caused by a virus that is transmitted by biting midges in the *Culicoides* genus and other arthropods. EHD can cause acute and frequently fatal hemorrhagic disease in domestic and wild ungulates. Recurrent outbreaks of EHD-associated mortality occur in white-tailed deer and mule deer, primarily in southeastern Montana (Montana Fish, Wildlife and Parks Wildlife Health Lab, unpublished data). Elk are susceptible to epizootic hemorrhagic disease, but generally do not suffer high rates of mortality or show clinical symptoms (Hoff and Trainer 1973; Nol et al. 2010). There is some concern that elk could act as reservoirs of EHD and transmit the virus to other wildlife (Thorne et al. 2002), but such relationships are not well studied.

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