Elk Habitat Management in Montana W-179-R Annual interim report, December 2023

Dr. Kelly Proffitt, Research Biologist, Montana Fish, Wildlife & Parks, 1400 S. 19th Ave, Bozeman, MT 59715, kproffitt@mt.gov

Dr. Jay Rotella, Professor, Montana State University, 310 Lewis Hall, Bozeman, MT 59717, rotella@montana.edu

Nicole Bealer, Research Technician, Montana Fish, Wildlife & Parks, 1400 S. 19th Ave, Bozeman, MT 59715, nicole.bealer@mt.gov

Shane Petch, Research Technician, Montana Fish, Wildlife & Parks, 1400 S. 19th Ave, Bozeman, MT 59715, shane.petch@mt.gov

Dr. John Draper, Post Doctoral Researcher, Montana State University, 306 Lewis Hall, Bozeman, MT 59715, john.draper3@montana.edu

State: Montana
Agencies: Fish, Wildlife & Parks and Montana State University
Grant: Elk Habitat Management in Montana
Grant #: F20AF10828-00
Montana Tracking: W-179-R
Time Period: 08/01/2022-09/30/2023

Executive Summary

The Elk Habitat Management in Montana project was initiated to gather information on seasonal habitat use and movements of elk and to evaluate the importance of hunter access management in determining elk distributions during the hunting season. The goals during this reporting period were to 1) collect elk location data in 3 elk populations in central and eastern Montana, including the Devil's Kitchen, Custer Forest, and Missouri Breaks populations; 2) evaluate factors associated with overabundant elk populations across Montana; and 3) conduct a habitat selection analysis in the Devil's Kitchen study area.

We collected location data from collared elk in the Devil's Kitchen area through February 2023, when data collection was scheduled to end. To augment the sample of male and female elk collared in the Custer Forest area, we instrumented 4 male and 5 female elk in the Custer area on 1/29/2023. To augment the sample of male and female elk collared in the Missouri Breaks area, we instrumented 10 male and 6 female elk on 1/30/2023. In both areas, elk were captured using helicopter netgunning or darting and outfitted with Lotek LiteTrack 420 satellite collars programmed to collect hourly location data.

We collected a total of 901,519 locations from 64 individuals in the Devil's Kitchen study area. In the Custer area, we have collected 1,179,068 locations from 78 collared individuals. We are currently monitoring 38 elk (33 females and 5 males). In the Missouri Breaks area, we have collected 552,328 locations from 76 collared individuals. We are currently monitoring 41 elk (33 females and 8 males). Movement information collected in all areas has been compiled into preliminary estimates of seasonal ranges and movement corridors and shared on a monthly basis with state and federal agency partners.

We continued work to evaluate factors associated with overabundant elk populations in Montana FWP Regions 2-7. We are also conducting an elk habitat selection analysis in the Devil's Kitchen area. The objectives of this study are to (1) evaluate the effects of hunting period, harvest regulation, hunter harvest, migratory behavior, and landscape features on female elk selection of hunter access management strategy during the hunting season, and (2) forecast the consequences of potential changes in harvest regulations on elk distributions and harvest risk. To date, we have developed a database of hunter access management strategies by classifying individual land parcels in the study area into discrete categories (open, controlled, and restricted access) based on personal communication with local land and wildlife managers and private landowners. We fit a series of Bayesian multistate models to evaluate the factors influencing the probability that an elk transitioned between hunter access types during the fall hunting season.

Project Background

Recently, there has been a focus in the western United States to identify and conserve big game migration corridors and winter ranges, as highlighted in the 2018 Department of Interior Secretarial Order 3362. Seasonal range and movement information is lacking for many elk populations in Montana, particularly in the central and eastern portion of the State. As part of a Montana Fish, Wildlife and Parks (MFWP) initiative to identify elk migration corridors and winter ranges and work cooperatively with partners to conserve these important habitats, there is a need to collect and assess elk movement data. The purpose of this project is to identify seasonal ranges and movement corridors for the Devil's Kitchen, Custer, and Missouri Breaks elk populations in central and eastern Montana (Figure 1), evaluate the effects of hunter access management and other landscape features on habitat selection in these populations, and provide information to enhance elk management in prairie regions.

Our first goal is to delineate migration corridors and seasonal ranges of 3 elk populations in central and eastern Montana including the Devil's Kitchen, Custer Forest, and Missouri Breaks populations. These areas have been selected based on the local needs identified by MFWP management biologists, and where considerable community, conservation partner, and agency interest in elk habitat conservation exists. A standardized and comprehensive assessment of movement data will ensure seasonal ranges and movement corridors are appropriately quantified, facilitate comparisons among populations, and result in a comprehensive communication tool that FWP can use to inform local stakeholders and agency partners as they consider ways to improve elk habitat in land use and planning decisions.

This component of the project involves collecting elk location data from GPS-collared elk in the 3 study areas for 3 years (Figure 1). We have developed methodologies for delineating seasonal ranges and corridors in collaboration with the USGS corridor mapping team and scientists in other state agencies utilizing Brownian bridge and kernel-based movement models. We will estimate seasonal core use areas during winter (Dec 15 – March 1), calving/fawning (May 25-June 10), summer (July 1 – August 31), and hunting seasons (approx. Sept 1 – Nov 30), and summarize the attributes of seasonal ranges. We will identify important movement corridors by estimating population-level migration routes (e.g., Horne et al. 2007, Kranstauber et al. 2012, Thurfjell et al. 2014, Avgar et al. 2016). Movement-based models are useful for mapping population-level movement corridors and identifying corridors with the highest levels of use. Summaries and maps of location and movement data will be presented in documents designed for landowners and managers that are intended for use in local decision making.

We anticipate that fine-scale location data collected in the Devil's Kitchen study area will help to identify important seasonal habitats and movement corridors and provide information regarding the timing of movements. This information may then be used to refine harvest management strategies that maximize the effectiveness of elk management in the area. Landowners, MFWP, and community members are presently engaged in a longstanding community working group (Devil's Kitchen Working Group) that regularly meets to discuss elk management in the area. The results of this study will aid these conversations on elk management and facilitate stronger conservation-oriented discussions. We anticipate that finescale location data collected in the Custer Forest and Missouri Breaks will also provide new information to inform management aimed at achieving more desirable elk distributions and harvest.

Our second goal is to broadly evaluate factors such as habitat quality, security, and hunter access to investigate and compare attributes of problematic and non-problematic elk distributions. We define problematic elk distributions as elk distributions during the fall and winter hunting seasons that result in failure to achieve female harvest objectives. While it is generally understood that existing problematic elk distributions may be driven by harvest regulations, restrictive hunter access management, landscape factors, or a combination of these factors, a formal assessment is necessary to assess whether elk herds that are or are not characterized by problematic distributions differ among these drivers. This assessment will involve summary analyses of existing data from populations across the state.

To address our second goal, we will combine and analyze existing elk GPS collar data at a statewide scale to broadly evaluate factors associated with problematic elk distributions. Currently, the degree to which elk populations are over objective is hypothesized to relate to the amount of land with restrictive hunter access; however, this hypothesis has not been broadly evaluated, and other landscape attributes may also influence problematic distributions. We plan to utilize a resource selection modeling approach to evaluate how the strength of elk selection for private lands with restricted hunter access varies across populations. We then plan to relate the amount of land with restrictive access and selection coefficients to the degree elk populations exceed objective levels to test the hypotheses that hunter access management and/or elk selection behaviors are associated with the degree to which populations are over objective.

Our third goal is to evaluate the effects of hunter access management and other important factors on elk habitat selection in the Devils Kitchen, Custer Forest, and Missouri Breaks areas, particularly during the fall hunting seasons. We will use location data collected from GPS collared elk in the Devils Kitchen, Custer Forest and Missouri Breaks study areas to evaluate elk habitat selection. Lands with restrictive hunter access may serve as refuges, and elk may aggregate in these areas to escape harvest risk during the hunting seasons (Conner et al. 2001, Vieira et al. 2003, Proffitt et al. 2013). If factors such as security, forage, and hunter access can be identified and related to habitat selection, managers may use this information to design management plans to manipulate these factors and increase the amount of time elk spend on public land. This could facilitate further opportunity for hunters using public lands and reduce game damage incurred on adjacent private lands. By increasing our understanding of these central Montana and prairie elk populations, FWP will be better able to sustainably provide harvest opportunity, minimize game damage and problematic distributions, and work with private and public land stewards to manage habitat that benefits elk.

MFWP and partners have invested considerable resources in evaluating the effects of factors such as hunter access management and elk security on elk distributions in the mountains and forested landscape of western Montana (Ranglack et al. 2017, DeVoe et al. 2019, Lowrey et al. 2020). However, no such studies have been conducted in central Montana and only one study has evaluated factors affecting elk distributions during the hunting season in prairie environments (Proffitt et al. 2016). This lack of information creates a challenge for wildlife managers in central Montana and the prairie regions. To address our third goal, we will build from previous security habitat studies in Montana and provide information and recommendations as to population and habitat management strategies for elk in central Montana and the prairie environments of eastern Montana following a similar approach (Proffitt et al. 2013, 2016, DeVoe et al. 2019, Lowrey et al. 2020).

Information gained from this project will be used for on-the-ground implementation by FWP and partners to manage, protect, and improve important elk habitats and develop strategies to manage elk populations at desired abundances and distributions. Implementation may include working with public and private landowners to improve security and/or habitat quality, remove barriers impeding movement, or may include recommendations for hunter access management.

Our objectives during this reporting period were:

- 1. Capture and collar elk in the Custer and Missouri Breaks study areas to augment sample sizes of collared elk up to 60 elk (20 males, 40 females) in each study area.
- 2. Collect and archive elk location data in the Devil's Kitchen, Custer, and Missouri Breaks study areas.
- 3. Continue state-wide analysis of factors associated with overabundant elk populations.
- 4. Continue work on habitat selection analyses in the Devil's Kitchen study area.

Location

This research is being conducted in portions of Cascade, Lewis and Clark, Garfield, Powder River, Bighorn, and Rosebud River Counties (Figure 1). The Devil's Kitchen elk population occupies Lewis and Clark and Cascade Counties and spans portions of hunting districts (HD) 445, 455, and 446. There are approximately 4,000 elk distributed across several winter ranges.

The Custer elk population occupies Powder River, Bighorn, and Rosebud Counties and spans portions of HD 704 and 705. This elk population has grown to approximately 1,700 elk since surveys began in 2005. The annual range includes a mixture of privately-owned ranchlands, sagebrush and mixed-grass prairies, and xeric ponderosa pine (*Pinus ponderosa*) dominated forest communities.

The eastern Missouri Breaks population (hereafter Missouri Breaks) occupies Garfield County and is within HD 700. In the last 3 surveys conducted during the last six years, the population count ranged from 800 to 1,500 elk. During the most recent survey conducted in winter 2020, a total of 1,300 elk were counted. Survey data suggests the elk population is 500-1200 individuals above the population objective of 200-300 individuals. The annual range includes a mixture of privately-owned ranchlands and sagebrush, mixed-grass prairies, and ponderosa pine forest communities.

Study Area Locations

MONTANA **FWP**



Figure 1. The Devil's Kitchen, Custer Forest, and Missouri Breaks study areas in central and eastern Montana.

Objective 1: Capture and collar elk in the Custer and Missouri Breaks study areas to augment sample sizes of collared elk up to 60 elk (20 males, 40 females) in each study area.

2023 Custer Elk Capture and Collaring

We used aerial darting to capture and collar a total of **9** elk (5 female, 4 male) in the Custer study area on 1/29/23 to augment a sample of previously collared animals in the study area. A total of 78 animals have been collared in the Custer study area to date. We outfitted captured individuals with Lotek LiteTrack Iridium collars programmed to collect hourly locations for 2 years. The collars were programmed to transmit a VHF signal during daylight hours and switch to a mortality signal if stationary for >10 hours. Collars upload locations via Iridium satellites to a web platform where data can be viewed and downloaded in near-real-time.

2023 Missouri Breaks Elk Capture and Collaring

We used a combination of aerial darting and helicopter net-gunning to capture and collar a total of **16** elk (6 female, 10 male) in the Missouri Breaks study area on 1/30/2023 to augment a sample of previously collared animals in the study area. A total of 76 animals have been collared in the Missouri Breaks study area to date. We outfitted captured individuals with Lotek LiteTrack Iridium collars programmed to collect hourly locations for 2 years. The collars were programmed to transmit a VHF signal during daylight hours and switch to a mortality signal if stationary for >10 hours. Collars upload locations via Iridium satellites to a web platform where data can be viewed and downloaded in near-real-time.

Objective 2: Collect and archive elk location data in the Devil's Kitchen, Custer, and Missouri Breaks study areas.

Devil's Kitchen Location and Movement Data Collection

GPS location data collection ended Feb 4, 2023 and drop-off devices released collars from animals. We collected 901,519 locations from 64 individuals in the Devil's Kitchen study area; this data represents the final dataset that has been cleaned of fixes with low precision. We recorded 19 mortalities; 12 were harvested, 2 died of wounding loss, 3 died of natural causes, and 2 were capture-related mortalities.

Estimates of seasonal ranges and movement corridors based on the sample of collared individuals in the final GPS location dataset are shown in Figures 5-7. This information was synthesized from GPS location data using the Migration Mapper application (Merkle et al. 2022) to visually classify migratory behaviors and movement periods using maps of GPS locations and associated net-squared displacement (NSD) curves for each individual. Population-level movement corridors were outlined using two variations of the Brownian bridge movement model

(Horne et al. 2007). We used kernel density estimates (KDE) to delineate seasonal range distributions. Corridors and home ranges were constructed using locations gathered in the Devil's Kitchen area throughout the three-year project.

Movement data from the Devil's Kitchen area (Figure 8) reinforces local reports of a seasonally occurring migratory behavior exhibited by a portion of this population. This movement takes place between the Beartooth Wildlife Management Area (BWMA) and private ranchlands in the valley bottom, with movements onto the BWMA occurring most often in the late fall and early winter months. Seasonal migratory movements occur in other portions of the study area as well. We have also observed movement patterns that appear typical of resident animals dispersed throughout the study area. Individual elk land use in the Devil's Kitchen area shows high proportional use of private lands across all seasons with an increase in proportional use of the BWMA in the fall and winter (Figure 9).



2.1.1 Devil's Kitchen Elk Seasonal Ranges and Movement Corridors

Figure 5. Estimated summer range for elk collared in the Devil's Kitchen area. Seasonal ranges were delineated using 95% kernel density estimates (KDE).



Figure 6. Estimated winter range for elk collared in the Devil's Kitchen area. Seasonal ranges were delineated using 95% kernel density estimates (KDE).



Figure 7. Movement corridors delineated for elk collared in the Devil's Kitchen area. Corridors were constructed using the Migration Mapper application and Brownian bridge movement models. Low use denotes corridors used by one or more, medium use denotes corridors used by 5 or more, and high use denotes corridors used by 15 or more collared elk.





Figure 8. Movements of 64 collared individuals in the Devil's Kitchen study area.



Figure 9. Proportional use of state, federal, and private lands by individual elk and season in the Devil's Kitchen study area. With the exception of some BLM lands that are accessible via helicopter, Montana State Trust and BLM lands in this study area are mostly inaccessible to the public.

2.2 Custer Elk Location and Movement Data Collection

As of September 30, 2023, we have gathered 1,179,068 locations from 78 individuals (49 females, 29 males) in the Custer study area for an average of 15,116 (range = 893 – 24,626) locations per individual. We are currently monitoring 38 individuals (5 males, 33 females). We have recorded 26 collar malfunctions (17 males, 9 females) and 14 mortalities (7 males, 7 females). Nine elk (5 males, 4 females) have been harvested by hunters, 1 female died from mountain lion predation, 1 male and 1 female died from human-related causes, and 1 male and 1 female died from unknown causes. Monthly reports have been generated and distributed to regional MFWP staff as well as other agency partners, private landowners, and other members of the public. Preliminary estimates of seasonal ranges (Figures 10 and 11) and movement corridors (Figure 12) were compiled after one full year of data collection and will be finalized when data collection is complete. An explanation of the process used to delineate seasonal ranges and movement corridors can be found on page 13. The preliminary seasonal range estimations (Figures 10 and 11) demonstrate a lack of strong population-level seasonal shift in the Custer study area.

Throughout the duration of monitoring the Custer elk population, we have observed a variety of individual movement patterns in both male and female collared elk (Figures 13 and 14). In previous reporting periods, multiple males and females have made temporary movements into Wyoming. Additionally, one female traveled to North Dakota before returning to the study area and one male traveled to northwestern South Dakota where he continues to be located. During this reporting period, one male and two females crossed the border into Wyoming and returned back to Montana, but no longer-distance movements occurred. The large movements undertaken by multiple individuals suggest that elk are able to access and connect patches of habitat across a large portion of southeastern Montana. Lands managed by the BLM are an important component of habitat connectivity in this area of the state. We will continue to monitor and evaluate animal movement patterns and will provide this information for use in management decisions.

The location data collected in the Custer area thus far indicates that elk primarily use privately owned lands (48.4% of locations) and the Custer National Forest (40.6% of locations); 6.5% of locations gathered so far have occurred on lands managed by the BLM and 4.5% of locations have occurred on lands managed by the state of Montana. Some collared individuals use BLM lands at much higher rates; a maximum of 41% of an individual's locations have occurred on BLM managed lands thus far. Land managed by the BLM in the southern portion of the study area between the state line and the edge of the Custer National Forest is frequently used by collared elk. Patterns of the distribution of locations across land ownerships are fairly similar across seasons, with mean decreases in use of Custer National Forest and mean increases of use of private lands during fall (Figure 15).



2.2.1 Preliminary Custer Elk Seasonal Ranges and Movement Corridors

Figure 10. Estimated summer range for elk collared in the Custer area based on locations gathered through May 2022. Seasonal ranges were delineated using 95% kernel density estimates (KDE).



Figure 11. Estimated winter range for elk collared in the Custer area based on locations gathered through May 2022. Seasonal ranges were delineated using 95% kernel density estimates (KDE).



Figure 12. Movement corridors delineated for elk collared in the Custer area based on locations gathered through May 2022. Corridors were constructed using the Migration Mapper application and Brownian bridge movement models.

2.2.2 Custer Elk Locations and Movements



Figure 13. Movements of 29 collared males in the Custer study area through September 30, 2023.



Figure 14. Movements of 47 collared females in the Custer study area through September 30, 2023



2.2.3 Custer Elk Land Use

'Private' refers to any lands that are not managed by the state of Montana, MTFWP, USFS, BLM, or USFWS

Figure 15. Proportional use of state, federal, and private lands by individual elk in the Custer National Forest study area by season.

2.3 Missouri Breaks Elk Location and Movement Data Collection

We have gathered 552,328 locations from 76 individuals (30 males, 46 females) in the Missouri Breaks study area for an average of 7,081 (range = 103 - 11,463) locations per individual. We have recorded 17 collar malfunctions (12 males, 5 females) and 15 mortalities (9 males, 6 females); we are currently monitoring 44 individuals (9 males, 35 females). Twelve elk (7 males, 5 females) have been harvested by hunters, one male elk died from natural causes, and 2 elk (1 male, 1 female) died from unknown causes. Monthly reports have been generated and distributed to regional MFWP staff as well as other agency partners, private landowners, and other members of the public. Preliminary estimates of seasonal ranges (Figures 16 and 17) and movement corridors (Figure 18) were compiled after a full year of data collection and will be finalized when data collection is complete. An explanation of the process used to delineate seasonal ranges and movement corridors can be found on page 13. The preliminary seasonal range estimations (Figures 16 and 17) demonstrate a lack of strong population-level seasonal shift in the Missouri Breaks study area.

We have observed a variety of individual movement patterns in both male and female collared elk (Figures 19 and 20). Some individuals have displayed seasonally migratory behavior, while other individuals have displayed behavior more characteristic of resident animals. However, while distinct summer and winter ranges can be distinguished for some individuals, the distance travelled between seasonal ranges has been modest and relatively localized so far. The range of multiple male and female elk has extended across the Musselshell River on the western edge of the study area into elk hunting district 410. One male elk crossed the Missouri River and spent time on the north shore before returning to the study area (Figure 19). Three females made brief movements across Highway 200 east of the Musselshell River in 2022 and two females crossed at the same location in 2023 (including one repeat individual from 2022). This crossing location may offer opportunities for future conservation efforts if it can be identified as a consistent crossing location (Figure 20).

The location data collected in the Missouri Breaks area thus far indicates that elk primarily use privately owned lands (38% of locations), lands managed by the BLM (32% of locations), and lands managed by the US Fish and Wildlife Service (26% of locations). The data collected so far indicate that BLM lands are an important component of elk habitat in the Missouri Breaks area. As in the Custer area, there is variation among individuals in patterns of land use, but a consistently large percentage of total locations across all seasons occur on BLM lands in this study area. Some collared individuals use BLM, USFWS, and private lands at much higher rates; a maximum of 77%, 98%, and 94% of an individual's locations have occurred on BLM, USFWS, and private lands thus far, respectively. Patterns of the distribution of locations across land ownerships are similar across seasons, though on average, use of BLM lands appears to increase during the winter and spring and decrease during summer and fall, whereas use of private land increases during summer and fall and decreases during winter and spring (Figure 21).

2.3.1 Preliminary Missouri Breaks Elk Seasonal Ranges & Movement Corridors



Figure 16. Estimated summer range for elk collared in the Missouri Breaks area based on locations gathered through September 3, 2023. Seasonal ranges were delineated using 95% kernel density estimates (KDE).



Figure 17. Estimated winter range for elk collared in the Missouri Breaks area based on locations gathered through September 30, 2023. Seasonal ranges were delineated using 95% kernel density estimates (KDE).



Figure 18. Movement corridors delineated for elk collared in the Missouri Breaks area based on locations gathered through September 30, 2023. Corridors were constructed using the Migration Mapper application and Brownian bridge movement models.



2.3.2 Missouri Breaks Elk Locations and Movements

Figure 19. Movements of 29 collared males in the Missouri Breaks study area through September 30, 2023.



Figure 20. Movements of 45 collared females in the Missouri Breaks study area through September 30, 2023.



2.3.3 Missouri Breaks Elk Land Use

'Private' refers to any lands that are not managed by the state of Montana, MTFWP, BLM or USFWS

Figure 21. Proportional use of state, federal, and private lands by individual elk in the Missouri Breaks study area by season.

Objective 3: Continue state-wide analysis of factors associated with overabundant elk populations.

3.1 State-wide Overabundance Analysis

The purpose of this project is to evaluate landscape factors associated with overabundant elk populations and provide information to enhance management strategies aimed at achieving more desirable elk distributions and harvest management objectives. Many elk populations in Montana have exceeded the population objectives for their respective management units. Elk populations that are over objective across a management unit may be problematic due to their impact on stakeholders and the environment.

In non-harvested populations of large ungulates, adult female survival is fairly constant with variation in recruitment driving fluctuations in population growth (Gaillard et al. 1998), while in harvested populations, adult female survival is more variable and has the capacity to alter population growth rates (Brodie et al. 2013) making the harvest of female elk the primary method for controlling elk population growth. Harvest of female elk can effectively curtail population growth and even have a residual effect in subsequent years by altering the age structure of a population if harvest targets are achieved (Paterson et al. 2022). However, the level of hunter harvest of elk in some areas has proven insufficient to effectively control elk population growth. This has been seen in Montana where many hunting districts (HD) are over their prescribed population objectives despite having regulations that allow for and encourage female elk harvest. Given that populations exceed their numerical objectives despite liberalized female harvest regulations, it is necessary to explore factors other than harvest regulations that may be limiting hunter efficacy in reducing female survival rates and in turn reducing problematic populations' growth rates.

Hunter harvest rates can be affected by several factors that vary spatially and temporally. The most influential variables include road access, elk abundance, the number of hunters per elk, and weather. Weather's effect on harvest success is highly specific to a given region or herd's response, making generalizations as to the effect of weather on harvest success difficult (Cooper et al. 2002; Hansen et al. 1986). Recent research on elk distributions during the hunting seasons found that in addition to traditional security habitat (far from roads and timbered), elk are finding security on lands that restrict hunter access (DeVoe et al. 2019; Proffitt et al. 2013, 2016). These areas may be public lands that prohibit hunting (Mikle et al. 2019) or private lands not enrolled in access programs (hereon referred to as unknown access) where hunting pressure is lower as compared to public lands that permit hunting or private lands enrolled in access programs (hereon referred to as unknown access) where hunting pressure is two-fold: limiting harvest on large swaths of land and drawing elk away from accessible lands where hunting pressure is greater. Successful reduction of problematic elk populations to within objectives is not possible if elk distributions during the hunting season limit the total harvest of

females. Given the current abundance of problematic elk populations, there is a need to identify the characteristics of HDs with overabundant populations to identify management tools that may be effective in managing these populations toward objective size. The objective of this study is to evaluate factors associated with overabundant elk populations. We will evaluate the effects of factors such as security habitat, hunter access, and landscape variable on two response variables representing attributes of overabundant elk populations: 1) the proportion over or under objective levels and 2) the population growth rate. For each HD, we estimated the proportion over or under objective as the current count/objective number and we estimated the growth rate using an integrated population model.

We assembled all the available elk count, elk harvest, and elk population objective information from Montana hunting districts in administrative regions 2-7 (Table 1). Region 1 lacked sufficient elk count data and was censored from analysis. Each district has been described as the objective number of elk per km² of habitat and hunter effort per km² of habitat, where kilometers of habitat was defined by the FWP elk distribution layer. These quantitative descriptions of hunting districts have been used in a preliminary analysis describing what factors are correlated with a hunting district's objective status. We have initiated the development of spatial data to use in our analysis of factors associated with problematic distributions including the proportion of a district that is security habitat, accessible to the public for hunting, and agriculture or pasture. We developed a state-wide road layer and used this layer to identify security habitat as it varies between archery and rifle seasons.

To estimate population growth rates, we continued the development of an integrated population model (IPM). The IPM incorporates two models, a process model describing the biological processes underlying the population dynamics and an observational model that connects elk survey data to the biological processes. The process model estimates elk adult survival and annual calf recruitment rates across all hunting districts, with individual district variation in harvest as estimated by the annual harvest survey. The observational model uses Poisson and multinomial distributions to estimate each hunting district's total population and bull, calf, and cow classifications respectively given the annual survey observations and the process model. Once complete, the model will be used to estimate the population growth rates for each hunting district.

Population growth rates for each unit were estimated using the integrated population model described in (Paterson et al. 2019). Inputs to the IPM included annual survey counts, classification counts and harvest estimates. Units with fewer than 6 surveys were excluded to ensure that a multi-year geometric growth rate could be estimated after this warmup period. Age and sex class population estimates were made using a Poisson process model and an observational model, including a Poisson estimate of total abundance and a multinomial estimate of age-sex class assignment. The model estimated harvest instantaneously following the previous year's survey prior to estimating adult survival allowing for harvest to be additive to natural

mortality. Per capita, recruitment is estimated as a single variable accounting for the probability of conception, survival to birth, and calf survival to the following spring census. Estimates of survival and recruitment were shared between all units within each region to increase sample size and to improve estimates for units with incomplete survey histories. We assumed that units within a given region experienced similar conditions to justify sharing these demographic rates. Recruitment was allowed to vary annually to account for annual differences in factors such as weather. The process model equations estimating class-based population sizes are as follows:

$$N_{t,hd}^{af} \sim Poisson\left(\phi_{a}\left(0.5 * N_{t-1,hd}^{c} + N_{t-1,hd}^{af} - h_{t,hd}^{af}\right)\right)$$

$$N_{t,hd}^{am} \sim Poisson\left(\phi_{a}\left(0.5 * N_{t-1,hd}^{c} + N_{t-1,hd}^{am} - h_{t,hd}^{am}\right)\right)$$

$$N_{t,hd}^{c} \sim Poisson(\tau_{t}N_{t-1,hd}^{af} - h_{t,hd}^{c})$$

These three equations share a joint likelihood with the equations that make up the observational model. The observational model estimates the relationship between the count data and N using a Poisson process with an observation-level random effect to accommodate potential overdispersion.

$$Count_{t,hd}^{total} \sim Poisson(N_{t,hd}^{total}\gamma_{t,hd})$$

The relationship between the classified count data and model estimates $N_{t,hd}^c$, $N_{t,hd}^{af}$, $N_{t,hd}^{am}$, is estimated using a multinomial distribution that accounts for the proportional difference between the total count and the total classified count.

Progress on this objective is currently paused until a suitable applicant can be found to work on this project. Our goal for the next annual cycle is to hire a research associate and complete analyses. Table 1. The population objective number of elk and hunter effort per km² of elk habitat (average number of hunter days per season 2004-2020) per hunting district. The area of habitat per hunting district was based on the Montana Fish, Wildlife, and Parks (MFWP) elk distribution layer.

Hunting District	Objective Elk	Hunter Days	Area of Habitat
	Per Km ²	Per Km ²	(Km ²)
200	0.49	3.01	712
201	0.44	3.23	649
202	0.19	1.67	941
203	0.90	2.57	611
204	0.56	2.48	974
210	0.81	4.11	686
211	0.70	2.23	2,678
212	0.34	2.77	563
213	1.61	7.64	1,358
214	0.95	2.85	1,560
215	1.16	7.15	1,852
216	0.42	1.72	375
240	0.52	2.24	1,359
250	0.77	0.29	1,096
261	1.14	2.97	2,050
270	2.53	6.21	1,181
281	0.62	3.88	1,106
282, 285	0.73	0.42	1,677
283	0.76	2.93	631
290, 298	0.88	1.12	1,179
291	0.77	2.97	6,104
292	0.78	3.80	663
293	0.68	3.53	810
300	1.21	6.22	859
301, 309	0.56	2.87	1,553
302	0.77	3.44	696
310, 360	2.15	3.28	713
311	2.36	4.59	1,503
312	0.84	4.99	1,929
313	6.16	5.21	1,205
314	2.57	3.80	896

Hunting District	Objective Elk	Hunter Days	Area of Habitat
	Per Km ²	Per Km ²	(Km^{2})
315	0.99	4.36	1,365
317	0.97	3.23	1,169
318	0.70	6.48	1,052
319	0.86	4.33	903
320, 333	0.49	1.33	867
322 - 327, 330	1.31	0.38	3,573
328	0.99	2.90	1,174
329	0.71	4.07	1,029
331	0.83	3.38	1,059
332	0.53	2.26	1,099
335	1.07	7.65	612
339, 343	1.00	1.53	518
340	0.78	5.54	474
341	1.22	5.85	465
350, 370	0.59	3.04	930
360, 361, 362	2.03	2.65	1,021
380	1.35	6.90	1,061
390	1.47	5.02	767
391	1.00	6.49	1,066
392	0.38	3.14	1,007
393	1.36	4.37	968
401	0.26	0.88	174
410	0.80	2.67	429
411, 511, 530	0.28	1.79	514
412	0.29	1.75	1,601
413	0.44	2.04	1,125
415	0.39	0.88	539
416	0.42	4.08	778
417	0.23	1.18	1,501
418	0.40	2.17	2,899
420, 448	1.19	0.90	790
421, 423	0.53	0.86	544
422	0.58	1.69	1,009
424, 425, 442	1.76	0.49	941
426	0.14	2.07	1,018
432	0.37	2.70	1,285
441	0.58	1.55	1,423

Hunting District	Objective Elk	Hunter Days	Area of Habitat
	Per Km ²	Per Km ²	(Km^{2})
455, 445	1.67	1.12	952
446	0.81	2.61	1,482
447	0.74	2.63	2,311
449, 452	0.76	1.58	864
450	0.50	2.77	1,394
454	0.46	4.63	615
500	0.11	2.99	1,111
502, 520, 575	0.48	0.24	1,064
540	1.05	4.69	1,827
560	0.33	1.29	858
570	0.11	1.78	1,132
580	0.58	2.30	1,054
621, 622	0.43	0.58	2,148
631, 632	0.30	0.67	569
680, 690	0.23	0.18	5,860
700, 701	0.04	0.81	2,786

Objective 4: Continue work on habitat selection analysis in the Devil's Kitchen study area.

4.1 Devil's Kitchen Habitat Selection Analysis

The population dynamics of elk and other large ungulate species are largely driven by adult female survival rates (Gaillard et al. 2000, Eacker et al. 2017), and the primary tool available to reduce survival rates and manage overabundant populations is the liberalization of adult female harvest regulations (Sinclair et al. 2006, Loe et al. 2016, Gruntorad and Chizinski 2020). However, when elk distributions overlap private lands, reducing elk abundance through hunter harvest can be challenging (Haggerty and Travis 2006, Proffitt et al. 2016). While the wildlife on private lands is a public resource managed in the public trust by state wildlife managers (Mahoney and Geist 2019), public access to private lands for hunting is provided at the discretion of individual landowners. Where overabundant elk populations and private lands overlap, the success of hunter harvest as a tool for elk population management depends not only on the harvest regulations applied, but also on the availability of hunting access on private lands.

While many have shown that elk preferentially select for areas that restrict hunting access where available (Burcham et al. 1999, Conner et al. 2001, Proffitt et al. 2010, Proffitt et al. 2013, Sergeyev et al. 2020), our understanding of the factors that influence selection for or against strategies of hunter access remains limited. The objectives of this study are to (1) evaluate the effects of hunting period, harvest regulation, hunter harvest, migratory behavior, and landscape features on female elk selection of hunter access management strategy during the hunting season, and (2) forecast the consequences of potential changes in harvest regulations on elk distributions and harvest risk.

We associated elk locations with one of 4 hunting periods: early shoulder (August 15 – September 3), archery (September 4 – October 17), general firearm (October 23 –November 28), and late shoulder (November 29 – February 15). We then classified individual land parcels in the study area into discrete categories for each of the 4 hunting periods according to the hunter access management strategy employed during each period (Figure 22). We defined categories as open, controlled, and restricted. Classifications were based on personal communication with local land and wildlife managers and private landowners. We classified a parcel as open access if publicly owned and accessible or privately-owned and enrolled in Montana's Block Management Access system and not requiring a reservation to hunt. A parcel was categorized as controlled in Montana's Block Management Access system but required a reservation which limited the number of hunters. Parcels were classified as restrictive access if landowners allowed access only for friends and family or outfitted clients, or if no public hunting opportunities were available. Publicly owned but landlocked parcels were classified using the access management strategies of surrounding private lands.

Harvest regulation was a categorical variable describing one of 3 antlerless harvest regulation scenarios elk could encounter in the study area: liberal harvest (if general license and antlerless only license valid), restricted harvest (antlerless harvest by permit only), or no harvest (no antlerless harvest allowed, Figure 23, Table 2). Hunter harvest was a quantitative variable that varied at the hunting district scale. Harvest estimates were gathered during MTFWP's annual hunter harvest survey where a random sample of licensed hunters are called and asked about their effort and success while hunting. We characterized the migratory behavior of each animal in each year based on the overlap of seasonal home ranges (95% kernel utilization distribution; KUD) and core use areas (50% KUD) estimated for summer (Jun-Aug) and winter (Dec-Feb) location data. We defined migrants as individuals with summer/winter seasonal core use areas that did not overlap and residents as individuals with overlapping seasonal core use areas (Barker et al. 2019). Migratory behavior was coded in models as an indicator variable for whether an individual was a migrant or not. We used snow water equivalent (SWE) data from the Snow Data Assimilation System (SNOWDAS; National Hydrological Remote Sensing Center) to calculate the cumulative SWE value for each 30x30 meter pixel in the study area across all hunting periods.

We pooled hunting season locations and ran 6 separate models (1 for each of the five covariates described above and an intercept-only model). Each model tested a different hypothesis about the factors influencing the probability that an elk made a transition from one hunter access class to another. We used WAIC to compare models and rank them based on model fit.

We expected transition probabilities across access types to be highest during the general rifle period due to the dynamic nature of this period relative to others. The hunting regulation model evaluated the hypothesis that the availability of hunting licenses best described transition probabilities. We hypothesized that the probability of an elk transitioning into a restrictive access class would increase under liberal regulations. The hunter harvest model tested the hypothesis that total harvest estimates for each hunting district best described transition probabilities. We expected elk would select the restrictive access class over open access in the hunting districts with the highest estimated hunter harvest. The migratory status model evaluated the hypothesis that the classification of individuals as either migrants or residents would best describe the probability of transitioning across access classes. We hypothesized that migratory individuals would transition more frequently than resident individuals overall, and that migrants would have a higher probability of transitioning into open access than residents. The cumulative SWE model tested the hypothesis that the cumulative presence of snow on the landscape best described the probability of transitioning across access classes. We hypothesized that a threshold might exist where the probability of transitioning into open access would increase along with SWE to a point, but that at the highest SWE values, transition probabilities would stabilize as elk settled

into wintering grounds. The constant model evaluated the null hypothesis that none of the covariates analyzed explained more variation than the regression intercept alone.

To date, we have run preliminary analyses using data from the first two years of the study. The top-performing model in our candidate suite included Hunt Period as an explanatory predictor (Table 3). Estimates from the top performing hunting period model showed that the probability an elk on day t was located in the same access class on day t+1 was much greater than the probability that an elk transitioned into a different access class on day t+1. This general pattern was consistent across all access classes and all hunting periods (Figure 24) but was particularly evident throughout the early shoulder and archery hunting periods. It was rare for elk to transition between access classes during the archery and early shoulder hunt periods, and elk appeared to select for hunter access in similar ways during these hunt periods (Figure 24).

In the general rifle period, elk already present in open access had an 81.51% probability of remaining in open access; the highest probability of remaining in open access found in any hunt period. We found an 18.05% probability that elk transitioned from restrictive access to controlled access and a 9.61% probability that elk transitioned from controlled to restrictive access. During the general rifle period, elk were more likely to transition from restrictive to open access (5.59% probability) and from controlled to open access (9.80% probability) relative to other hunt periods. The general rifle period had the lowest estimated probability of remaining in restrictive access (76.37% probability), though it should be noted that most elk that began the period in restrictive access remained in restrictive access.

During the late shoulder season, the probability that an elk transitioned from open access to restrictive access was 28.97%; the highest estimated probability of transitioning across access classes found in this study (Figure 24). Correspondingly, the probability that elk already present in restrictive access remained in restrictive access was 92.52%; the highest estimated probability of remaining in restrictive access across all hunt periods. Similar to the general rifle period, the probability that elk transitioned from controlled to restrictive access was 11.72%.

Our goal during the next reporting cycle is to finalize transition models as well as the habitat selection model.

Distribution of Hunting Access in Devil's Kitchen Study Area

MONTANA FWP



Figure 22. The distribution of hunter access classes in relation to a 99% kernel utilization distribution (KUD) of fall/winter elk locations. We defined open access as publicly accessible public lands or private lands enrolled in Montana's block management access program (BMA) and not requiring a reservation to hunt. We classified controlled access as areas where landowners granted access to members of the public who enquired or were enrolled in the BMA program but required a reservation. Parcels were classified as restrictive access if landowners allowed access only for friends and family or outfitted clients, or if no public hunting opportunities were available. Publicly owned but landlocked parcels were classified using the access management strategies of surrounding private lands. Devil's Kitchen study area, central Montana, USA, 2021–2022.

Distribution of Hunting Regulation in Devil's Kitchen Study Area

MONTANA FWP



Figure 23. The distribution of hunter regulation classes in relation to a 99% KUD of fall/winter elk locations. Devil's Kitchen study area, central Montana, USA, 2021–2022.



Figure 24. Results from the top performing model investigating the probability of transitioning across hunter access classes during the fall hunting season. The plotted posterior means with 95% credible intervals show the estimated probability of transitioning from an access class on day t (rows) to an access class on day t + 1 (columns) in each of the 4 hunt periods of interest. Licensing years 2020-2021; Devil's Kitchen area of central Montana, USA.

Table 2.Hunting regulations effective in the Devil's Kitchen study area, central Montana, USA, 2021-2022. Generallicenses were valid across the state for the harvest of one elk depending on unit-specific regulations. Individuals could onlypurchase a single general license each year but there was no quota on the total number available for purchase by residenthunters. Elk B-Licenses were only valid for the harvest of antlerless elk. An annual quota of 6,000 B-license 004-00, 25 B-License 392-00, and 250 B-License 455-00 were available during the study period. A hunter in possession of a GeneralLicense could purchase 2 B-Licenses in a given year. Elk permits were only valid with a General License and were allocatedthrough a drawing. A quota of 45 Permit 445-20, 75 Permit 455-20, and 4,000 Permit 900-20 were available annually duringthe study period.

Early Shoulder	District	Hunt Period	License Type	Harvest Regulation	Regulation Class	
Archery General License Brow-tined Bull or Antlerless Liberal 392 General License 392-00 Antlerless Only Restrictive Barly General General License Brow-tined Bull Restrictive B-License 392-00 Antlerless Only Restrictive Late General General License Brow-tined Bull Restrictive Late General General License Brow-tined Bull Restrictive Late Shoulder No Harvest No Harvest Archery General License Either-sex Liberal B-License 004-00 Antlerless Only Liberal Late General General License Either-sex Liberal Late General General License No Harvest No Harvest Archery General License Bilicense 004-00 Antlerless B-License 004-00 Antlerless Liberal <td></td> <td>Early Shoulder</td> <td></td> <td>No Harvest</td> <td>No Harvest</td>		Early Shoulder		No Harvest	No Harvest	
Archery B-License 392-00 Antheriess Only Liberal 392 Early General General License Brow-tined Bull Restrictive Late Shoulder No Harvest No Harvest Archery General License Either-sex Liberal B-License 004-00 Antlerless Only Liberal Late General General License Either-sex Liberal B-License 004-00 Antlerless Only Liberal Liberal Late General General License Either-sex Liberal Late General General License No Harvest No Harvest Archery General License Bilicense Only Liberal Late General General License Either-sex Liberal B-License 004-00 Antlerless Liberal Bilicense 004-00		Archery	General License	Brow-tined Bull or Antlerless		
392 Early General General License Brow-tined Bull B-License 392-00 Antlerless Only Late General General License Brow-tined Bull B-License 392-00 Antlerless Only Late General B-License 392-00 Antlerless Only Restrictive Late Shoulder No Harvest No Harvest Farly Shoulder No Harvest No Harvest Farly Shoulder No Harvest No Harvest Farly General General License Either-sex Liberal B-License 004-00 Antlerless Only Liberal Late General General License Either-sex Liberal B-License 004-00 Antlerless Only Liberal Late Shoulder No Harvest No Harvest Late Shoulder No Harvest No Harvest Archery General License Either-sex Liberal Jate Shoulder No Harvest No Harvest Archery General License Either-sex Liberal Jate General General License Either-sex Liberal Jate General General License Either-sex Liberal Jate General General License Either-sex Liberal<			B-License 392-00	Antlerless Only	Liberai	
312 Lairy General B-License 392-00 Antlerless Only Restrictive Late General General License Brow-tined Bull Restrictive Late Shoulder No Harvest No Harvest No Harvest Early Shoulder No Harvest No Harvest No Harvest Archery General License Either-sex Liberal B-License 004-00 Antlerless Only Liberal Late General General License Either-sex Late Shoulder No Harvest No Harvest Late Shoulder No Harvest No Harvest Late Shoulder No Harvest No Harvest Archery General License Either-sex Liberal Late Shoulder No Harvest No Harvest Archery General License Either-sex Liberal Late Shoulder No Harvest No Harvest Late Shoulder No Harvest Liber	302	Early Conoral	General License	Brow-tined Bull	Destrictive	
Late General General License Brow-tined Bull B-License 392-00 Antlerless Only Restrictive Late Shoulder No Harvest No Harvest No Harvest Early Shoulder No Harvest No Harvest No Harvest Archery General License Either-sex Liberal B-License 004-00 Antlerless Only Liberal Late General General License Either-sex Liberal Late General General License Either-sex Liberal Late General B-License 004-00 Antlerless Only Liberal Late Shoulder No Harvest No Harvest Late Shoulder No Harvest No Harvest Late Shoulder No Harvest No Harvest Archery General License Either-sex Liberal B-License 004-00 Antlerless Liberal Late Shoulder No Harvest No Harvest Late General General License Either-sex Liberal	392	Early General	B-License 392-00	Antlerless Only	- Restrictive	
Late Central B-License 392-00 Antlerless Only Restrictive Late Shoulder No Harvest No Harvest Archery General License Either-sex Liberal Archery B-License 004-00 Antlerless Only Liberal Early General General License Either-sex Liberal Late Shoulder No Harvest No Harvest Late Shoulder No Harvest No Harvest Archery General License Either-sex Liberal Archery General License Either-sex Liberal Archery General License Either-sex Liberal Archery B-License 004-00 Antlerless Liberal B-License 004-00 Antlerless Liberal Late General General License Either-sex Liberal B-License 004-00 Antlerless Liberal Late General General License Antlerless Liberal B-License 004-00 Antlerless		Lata Canaral	General License	Brow-tined Bull	Doctrictivo	
Late ShoulderNo HarvestNo HarvestEarly ShoulderNo HarvestNo HarvestArcheryGeneral LicenseEither-sexLiberalB-License 004-00Antlerless OnlyLiberalEarly GeneralGeneral LicenseEither-sexLiberalB-License 004-00Antlerless OnlyLiberalLate GeneralGeneral LicenseEither-sexLiberalB-License 004-00Antlerless OnlyLiberalLate GeneralGeneral LicenseEither-sexLiberalB-License 004-00Antlerless OnlyLiberalLate ShoulderNo HarvestNo HarvestArcheryGeneral LicenseEither-sexLiberalB-License 004-00AntlerlessLiberalArcheryGeneral LicenseEither-sexLiberalB-License 004-00AntlerlessLiberalLate GeneralGeneral LicenseEither-sexLiberalLate GeneralGeneral LicenseEither-sexLiberalLate ShoulderNo HarvestNo HarvestLate ShoulderNo HarvestNo HarvestB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessLiberalB-License 004-00Antlerless </td <td></td> <td>Late General</td> <td>B-License 392-00</td> <td>Antlerless Only</td> <td>Resultave</td>		Late General	B-License 392-00	Antlerless Only	Resultave	
Early ShoulderNo HarvestNo HarvestArcheryGeneral LicenseEither-sexLiberalB-License 004-00Antlerless OnlyLiberalEarly GeneralGeneral LicenseEither-sexLiberalB-License 004-00Antlerless OnlyLiberalLate GeneralGeneral LicenseEither-sexLiberalLate GeneralGeneral LicenseEither-sexLiberalLate ShoulderNo HarvestNo HarvestLate ShoulderNo HarvestNo HarvestArcheryGeneral LicenseEither-sexLiberalB-License 004-00AntlerlessLiberalArcheryGeneral LicenseEither-sexLiberalB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessLiberalLate GeneralGeneral LicenseEither-sexLiberalB-License 004-00AntlerlessLiberalLate GeneralGeneral LicenseEither-sexLiberalB-License 004-00AntlerlessLiberalLate ShoulderNo HarvestNo HarvestArcheryGeneral LicenseAntlerlessLiberalB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessLiberalPermit 445-20Either-sexLiberalPermit 445-20E		Late Shoulder		No Harvest	No Harvest	
ArcheryGeneral LicenseEither-sexLiberal413Early GeneralGeneral LicenseEither-sexLiberalB-License 004-00Antlerless OnlyLiberalLate GeneralGeneral LicenseEither-sexLiberalLate GeneralB-License 004-00Antlerless OnlyLate GeneralB-License 004-00Antlerless OnlyLate ShoulderNo HarvestNo HarvestArcheryGeneral LicenseEither-sexLiberalArcheryGeneral LicenseEither-sexLiberalB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessB-License 004-00AntlerlessLate GeneralGeneral LicenseEither-sexB-License 004-00AntlerlessLate GeneralGeneral LicenseEither-sexB-License 004-00AntlerlessLate ShoulderNo HarvestKarcheryGeneral LicenseAntlerlessB-License 004-00AntlerlessLiberalArcheryB-License 004-00AntlerlessArcheryB-License 004-00AntlerlessArcheryB-License 004-00AntlerlessArcheryB-License 004-00AntlerlessB-License 004-00AntlerlessLiberalPermit 445-20Either-sexEither-sexLate GeneralB-License 004-00Antlerless <t< td=""><td></td><td>Early Shoulder</td><td></td><td>No Harvest</td><td>No Harvest</td></t<>		Early Shoulder		No Harvest	No Harvest	
Atchely B-License 004-00 Antlerless Only Liberal 413 Early General General License Either-sex Liberal Late Shoulder No Harvest No Harvest Early Shoulder No Harvest No Harvest Archery General License Either-sex Liberal B-License 004-00 Antlerless Liberal Archery General License Either-sex Liberal B-License 004-00 Antlerless Liberal Hate General General License Either-sex Late General General License Either-sex Late General General License Either-sex Late Shoulder No Harvest No Harvest Late General General License Either-sex Liberal B-License 004-00 Antlerless Liberal Archery General License Antlerless Liberal B-License 004-00 Antlerless Liberal Archery B-Lic		Anabami	General License	Either-sex	T '1 1	
413Early GeneralGeneral LicenseEither-sexLiberalB-License 004-00Antlerless OnlyLiberalLate GeneralGeneral LicenseEither-sexLiberalB-License 004-00Antlerless OnlyLiberalLate ShoulderNo HarvestNo HarvestEarly ShoulderNo HarvestNo HarvestArcheryGeneral LicenseEither-sexLiberalB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessLiberalPermit 445-20Either-sexLiberalPermit 445-20Either-sexLiberalPermit 445-20Either-sexLiberalPermit		Archery	B-License 004-00	Antlerless Only	Liberai	
413 Early General B-License 004-00 Antlerless Only Liberal Late General General License Either-sex Liberal B-License 004-00 Antlerless Only Liberal Late General B-License 004-00 Antlerless Only Liberal Itate Shoulder No Harvest No Harvest Archery General License Either-sex Liberal Archery General License Either-sex Liberal B-License 004-00 Antlerless Liberal Harvest General License Either-sex Liberal B-License 004-00 Antlerless Liberal B-License 004-00 Antlerless </td <td>412</td> <td>Early Concert</td> <td>General License</td> <td colspan="2">Either-sex</td>	412	Early Concert	General License	Either-sex		
Late GeneralGeneral LicenseEither-sexLiberalLate GeneralB-License 004-00Antlerless OnlyLiberalLate ShoulderNo HarvestNo HarvestEarly ShoulderNo HarvestNo HarvestArcheryGeneral LicenseEither-sexLiberalB-License 004-00AntlerlessLiberalEarly GeneralGeneral LicenseEither-sexLiberalLate GeneralGeneral LicenseEither-sexLiberalLate GeneralGeneral LicenseEither-sexLiberalLate ShoulderNo HarvestNo HarvestLate ShoulderNo HarvestNo HarvestLate ShoulderNo HarvestNo HarvestLate ShoulderNo HarvestNo HarvestB-License 004-00AntlerlessLiberalLate ShoulderNo HarvestNo HarvestArcheryGeneral LicenseAntlerlessLiberalB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessLiberalPermit 445-20Either-sexLiberalPermit 445-20Either-sexLiberalPermit 445-20Either-sexLiberalLate GeneralB-License 004-00AntlerlessLate GeneralB-License 004-00AntlerlessPermit 445-20Either-sexLiberalPermit 445-20Either-sexLiberalLate ShoulderGeneral LicenseAntlerlessPermit 445-20 <td< td=""><td>413</td><td>Early General</td><td>B-License 004-00</td><td>Antlerless Only</td><td>Liberal</td></td<>	413	Early General	B-License 004-00	Antlerless Only	Liberal	
Late GeneralB-License 004-00Antlerless OnlyLiberalLate ShoulderNo HarvestNo HarvestEarly ShoulderNo HarvestNo HarvestArcheryGeneral LicenseEither-sexLiberalB-License 004-00AntlerlessLiberalEarly GeneralGeneral LicenseEither-sexLiberalLate GeneralGeneral LicenseEither-sexLiberalLate GeneralGeneral LicenseEither-sexLiberalLate ShoulderNo HarvestNo HarvestLate ShoulderNo HarvestNo HarvestLate ShoulderNo HarvestNo HarvestLate ShoulderNo HarvestNo HarvestB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessLiberalHarvestGeneral LicenseEither-sexB-License 004-00AntlerlessLiberalPermit 445-20Either-sexLiberalHarvestGeneral LicenseAntlerlessLate GeneralB-License 004-00AntlerlessPermit 445-20Either-sexLiberalPermit 445-20Either-sexLiberalLate GeneralB-License 004-00AntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralB-License 004-00An		Lata Cananal	General License	Either-sex	Liberal	
Late ShoulderNo HarvestNo HarvestEarly ShoulderNo HarvestNo HarvestArcheryGeneral LicenseEither-sexLiberalB-License 004-00AntlerlessLiberalEarly GeneralGeneral LicenseEither-sexLiberalB-License 004-00AntlerlessLiberalLate GeneralGeneral LicenseEither-sexLiberalLate GeneralGeneral LicenseEither-sexLiberalLate ShoulderNo HarvestNo HarvestLate ShoulderNo HarvestNo HarvestB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessLiberalHarvestGeneral LicenseEither-sexB-License 004-00AntlerlessLiberalPermit 445-20Either-sexEither-sexLate GeneralB-License 004-00AntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralGeneral LicenseAntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralGeneral LicenseAntlerlessLate ShoulderGeneral LicenseAntlerlessLate GeneralGeneral LicenseAntlerlessLate GeneralGeneral LicenseAntlerlessLate GeneralGeneral LicenseAntlerlessLate ShoulderGeneral LicenseAntlerless<		Late General	B-License 004-00	Antlerless Only	Liberal	
Early ShoulderNo HarvestNo HarvestArcheryGeneral LicenseEither-sexLiberalB-License 004-00AntlerlessLiberalEarly GeneralGeneral LicenseEither-sexLiberalB-License 004-00AntlerlessEither-sexLiberalLate GeneralGeneral LicenseEither-sexLiberalLate ShoulderNo HarvestNo HarvestLate ShoulderNo HarvestNo HarvestB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessLiberalPermit 445-20Either-sexEither-sexB-License 004-00AntlerlessLiberalPermit 445-20Either-sexEitheralLate GeneralGeneral LicenseAntlerlessLate GeneralGeneral LicenseAntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralGeneral LicenseAntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralGeneral LicenseAntlerlessLate GeneralGeneral LicenseAntlerlessLate GeneralGeneral LicenseAntlerlessLate GeneralGeneral LicenseAntlerlessLate ShoulderGeneral LicenseAntlerlessLate Shoulder <td></td> <td>Late Shoulder</td> <td></td> <td>No Harvest</td> <td>No Harvest</td>		Late Shoulder		No Harvest	No Harvest	
ArcheryGeneral LicenseEither-sexLiberalB-License 004-00AntlerlessLiberalEarly GeneralGeneral LicenseEither-sexLiberalB-License 004-00AntlerlessLiberalLate GeneralGeneral LicenseEither-sexLiberalLate GeneralB-License 004-00AntlerlessLiberalLate ShoulderNo HarvestNo HarvestLate ShoulderNo HarvestNo HarvestEarly ShoulderGeneral LicenseAntlerlessLiberalB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessLiberalArcheryGeneral LicenseEither-sexPermit 445-20Either-sexLiberalPermit 445-20Either-sexLiberalPermit 445-20Either-sexLiberalLate GeneralB-License 004-00AntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralGeneral LicenseEither-sexLate GeneralB-License 004-00AntlerlessLate GeneralGeneral LicenseAntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralGeneral LicenseAntlerlessLate GeneralGeneral LicenseAntlerlessLate ShoulderGeneral LicenseAntlerlessLate ShoulderGeneral LicenseAntlerlessLate ShoulderGeneral LicenseAntlerlessLate		Early Shoulder		No Harvest	No Harvest	
ArcheryB-License 004-00AntlerlessLiberal416Early GeneralGeneral LicenseEither-sexLiberalB-License 004-00AntlerlessLiberalLate GeneralGeneral LicenseEither-sexLiberalLate ShoulderNo HarvestNo HarvestLate ShoulderNo HarvestNo HarvestEarly ShoulderGeneral LicenseAntlerlessLiberalB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessLiberalArcheryGeneral LicenseEither-sexArcheryB-License 004-00AntlerlessPermit 445-20Either-sexLiberalPermit 445-20Either-sexLiberalPermit 445-20Either-sexLiberalLate GeneralB-License 004-00AntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralGeneral LicenseAntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralGeneral LicenseAntlerlessLate ShoulderGeneral LicenseAntlerlessLate ShoulderGeneral LicenseAntlerlessLate ShoulderGeneral LicenseAntlerlessLate ShoulderGeneral LicenseAntlerlessLate ShoulderGeneral LicenseAntlerlessLate ShoulderGeneral LicenseAntlerlessLate S		Analasma	General License	Either-sex	T '1 1	
416Early GeneralGeneral LicenseEither-sexLiberalB-License 004-00AntlerlessLiberalLate GeneralGeneral LicenseEither-sexLiberalB-License 004-00AntlerlessLiberalLate ShoulderNo HarvestNo HarvestLate ShoulderNo HarvestLiberalEarly ShoulderGeneral LicenseAntlerlessLiberalB-License 004-00AntlerlessLiberalB-License 004-00AntlerlessLiberalArcheryB-License 004-00AntlerlessLiberalPermit 445-20Either-sexLiberalPermit 445-20Either-sexLiberalPermit 445-20Either-sexLiberalLate GeneralB-License 004-00AntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralGeneral LicenseEither-sexLate GeneralGeneral LicenseAntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralGeneral LicenseAntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralB-License 004-00AntlerlessB-License 004-00AntlerlessLiberal		Archery	B-License 004-00	Antlerless		
410 Early General B-License 004-00 Antlerless Liberal Late General General License Either-sex Liberal Late General B-License 004-00 Antlerless Liberal Late Shoulder No Harvest No Harvest Late Shoulder General License Antlerless Liberal B-License 004-00 Antlerless Liberal B-License 004-00 Antlerless Liberal Archery B-License 004-00 Antlerless Liberal Archery B-License 004-00 Antlerless Liberal Permit 445-20 Either-sex Liberal Liberal 445 Early General B-License 004-00 Antlerless Liberal Permit 445-20 Either-sex Eitherat Liberal Late General B-License 004-00 Antlerless Liberal Late General B-License 004-00 Antlerless Liberal Permit 445-20 Either-sex Eitheral Liberal Late General B-License 004-00 Antlerless Liberal Late Shoulder <	417	Early Concert	General License	Either-sex		
Late GeneralGeneral LicenseEither-sexLiberalB-License 004-00AntlerlessNo HarvestNo HarvestLate ShoulderNo HarvestNo HarvestEarly ShoulderGeneral LicenseAntlerlessLiberalB-License 004-00AntlerlessLiberalArcheryB-License 004-00AntlerlessLiberalPermit 445-20Either-sexPermit 445-20LiberalFarly GeneralB-License 004-00AntlerlessLiberalPermit 445-20Either-sexEither-sexLiberalB-License 004-00AntlerlessLiberalPermit 445-20Either-sexEither-sexLate GeneralB-License 004-00AntlerlessLiberalPermit 445-20Either-sexEither-sexLate GeneralB-License 004-00AntlerlessLiberalLate GeneralB-License 004-00AntlerlessLiberalLate ShoulderGeneral LicenseAntlerlessLiberalConceral LicenseAntlerlessLiberalPermit 445-20Either-sexLiberalPermit 445-20Either-sexLiberalLate ShoulderGeneral LicenseAntlerlessLate ShoulderGeneral LicenseAntlerlessLate ShoulderGeneral LicenseAntlerlessLate ShoulderGeneral LicenseAntlerlessContral LicenseAntlerlessLiberalContral LicenseAntlerlessLiberalContral LicenseAntlerlessLiberal<	410	Early General	B-License 004-00	Antlerless		
Late GeneralB-License 004-00AntlerlessLiberalLate ShoulderNo HarvestNo HarvestEarly ShoulderGeneral LicenseAntlerlessLiberalB-License 004-00AntlerlessLiberalArcheryB-License 004-00AntlerlessLiberalPermit 445-20Either-sexLiberalPermit 445-20Either-sexLiberalFarly GeneralB-License 004-00AntlerlessArcheryB-License 004-00AntlerlessLiberalPermit 445-20Either-sexEither-sexB-License 004-00AntlerlessLiberalEarly GeneralB-License 004-00AntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralGeneral LicenseAntlerlessLate GeneralB-License 004-00AntlerlessLate ShoulderGeneral LicenseAntlerlessLate ShoulderGeneral LicenseAntlerless		Late General	General License	Either-sex		
Late ShoulderNo HarvestNo HarvestEarly ShoulderGeneral LicenseAntlerlessLiberalB-License 004-00AntlerlessLiberalArcheryGeneral LicenseEither-sexB-License 004-00AntlerlessLiberal445Early GeneralGeneral LicenseEither-sexB-License 004-00AntlerlessLiberalPermit 445-20Either-sexLiberalB-License 004-00AntlerlessLiberalPermit 445-20Either-sexLiberalPermit 445-20Either-sexLiberalPermit 445-20Either-sexLiberalPermit 445-20Either-sexLiberalLate GeneralB-License 004-00AntlerlessLate GeneralB-License 004-00AntlerlessLate GeneralGeneral LicenseAntlerlessLate ShoulderGeneral LicenseAntlerlessLate ShoulderGeneral LicenseAntlerlessLate ShoulderGeneral LicenseAntlerlessB-License 004-00AntlerlessLiberal			B-License 004-00	Antlerless	Liberai	
Early ShoulderGeneral LicenseAntlerlessLiberalB-License 004-00AntlerlessLiberalArcheryGeneral LicenseEither-sexB-License 004-00AntlerlessLiberalPermit 445-20Either-sexLiberalPermit 445-20Either-sexLiberalB-License 004-00AntlerlessLiberalPermit 445-20Either-sexEither-sexB-License 004-00AntlerlessLiberalPermit 445-20Either-sexLiberalPermit 445-20Either-sexLiberalPermit 445-20Either-sexLiberalLate GeneralB-License 004-00AntlerlessPermit 445-20Either-sexLiberalLate GeneralB-License 004-00AntlerlessPermit 445-20Either-sexLiberal		Late Shoulder		No Harvest	No Harvest	
Early ShoulderB-License 004-00AntlerlessLiberalArcheryGeneral LicenseEither-sexArcheryB-License 004-00AntlerlessPermit 445-20Either-sexPermit 445-20Either-sexEarly GeneralB-License 004-00AntlerlessLiberalPermit 445-20Either-sexPermit 445-20Either-sexLiberalB-License 004-00Permit 445-20Either-sexPermit 445-20Either-sexLate GeneralB-License 004-00B-License 004-00AntlerlessLate GeneralB-License 004-00Permit 445-20Either-sexLiberalDermit 445-20Late GeneralB-License 004-00AntlerlessLiberalPermit 445-20Either-sexLiberalDermit 445-20Permit 445-20Either-sexDermit 445-20Either-sexDermit 445-20Either-sexLiberalDermit 445-20Permit 445-20Either-sexDermit 445-20Dermit 445-20Dermit 445-20Either-sexDermit 445-20Dermit 445-20Dermit 445-20Dermit 445-20 </td <td></td> <td>Early Shouldar</td> <td>General License</td> <td>Antlerless</td> <td>Liberal</td>		Early Shouldar	General License	Antlerless	Liberal	
ArcheryGeneral LicenseEither-sexB-License 004-00AntlerlessLiberalPermit 445-20Either-sexEither-sexFarly GeneralGeneral LicenseEither-sexB-License 004-00AntlerlessLiberalPermit 445-20Either-sexEither-sexB-License 004-00AntlerlessLiberalPermit 445-20Either-sexLiberalLate GeneralGeneral LicenseAntlerlessB-License 004-00AntlerlessLiberalPermit 445-20Either-sexLiberalB-License 004-00AntlerlessLiberal		Earry Shoulder	B-License 004-00	Antlerless	Liberai	
ArcheryB-License 004-00AntlerlessLiberalPermit 445-20Either-sex445Early GeneralGeneral LicenseEither-sexB-License 004-00AntlerlessLiberalPermit 445-20Either-sexEither-sexLate GeneralGeneral LicenseAntlerlessB-License 004-00AntlerlessLiberalPermit 445-20Either-sexEither-sexLate GeneralB-License 004-00AntlerlessPermit 445-20Either-sexLiberalPermit 445-20Either-sexLiberalPermit 445-20Either-sex			General License	Either-sex		
445Permit 445-20Either-sex445General LicenseEither-sexEarly GeneralB-License 004-00AntlerlessPermit 445-20Either-sexLate GeneralGeneral LicenseAntlerlessB-License 004-00AntlerlessLiberalLate GeneralB-License 004-00AntlerlessPermit 445-20Either-sexLiberalLate GeneralGeneral LicenseAntlerlessLate ShoulderGeneral LicenseAntlerlessLate ShoulderDeteral ConseAntlerlessLiberalDeteral ConseAntlerless		Archery	B-License 004-00	Antlerless	Liberal	
445General LicenseEither-sexEarly GeneralB-License 004-00AntlerlessPermit 445-20Either-sexLate GeneralGeneral LicenseAntlerlessB-License 004-00AntlerlessLiberalPermit 445-20Either-sexB-License 004-00AntlerlessLate GeneralGeneral LicenseB-License 004-00AntlerlessLiberalDermit 445-20B-License 004-00Either-sexDermit 445-20Either-sexLiberalLiberal			Permit 445-20	Either-sex		
445 Early General B-License 004-00 Antlerless Liberal Permit 445-20 Either-sex Either-sex Late General General License Antlerless Liberal Permit 445-20 Either-sex Liberal Late General B-License 004-00 Antlerless Liberal Permit 445-20 Either-sex Liberal Late Shoulder General License Antlerless Liberal			General License	Either-sex		
Permit 445-20Either-sexLate GeneralGeneral LicenseAntlerlessB-License 004-00AntlerlessLiberalPermit 445-20Either-sexLiberalLate ShoulderGeneral LicenseAntlerlessLate ShoulderDetermit 400-00Antlerless	445	Early General	B-License 004-00	Antlerless	Liberal	
General License Antlerless Late General B-License 004-00 Antlerless Permit 445-20 Either-sex Late Shoulder General License Antlerless Late Shoulder D.License Antlerless			Permit 445-20	Either-sex		
Late General B-License 004-00 Antlerless Liberal Permit 445-20 Either-sex Late Shoulder General License Antlerless			General License	Antlerless		
Permit 445-20 Either-sex Late Shoulder General License Antlerless Liberal Liberal		Late General	B-License 004-00	004-00 Antlerless		
Late Shoulder General License Antlerless Liberal			Permit 445-20	Either-sex		
Late Shoulder Liberal		Late Shoulder	General License	Antlerless		
B-License (0)4-(0) Antierless			B-License 004-00	Antlerless		

Table 2. Continued

District	Hunt Period	License Type	cense Type Harvest Regulation		
	Early Shoulder	General License B-License 004-00	Antlerless Antlerless	Liberal	
	Archery	General License	Brow-tined Bull or Antlerless		
		B-License 004-00	Antlerless	Liberal	
110	Early General	General License	Brow-tined Bull or Antlerless		
440		B-License 004-00	Antlerless	Liberal	
	Late General	General License	Brow-tined Bull or Antlerless	Liberal	
		B-License 004-00	Antlerless		
	Late Shoulder	General License	Antlerless	Liberal	
_		B-License 004-00	Antlerless		
455	Early Shoulder		No Harvest	No Harvest	
	Archery	Permit 455-20	Either-sex		
		Permit 900-20	Either-sex	Restrictive	
		B-License 455-00	Antlerless		
	Early General	Permit 455-20	Either-sex	Destrictive	
		B-License 455-00	Antlerless	ss Kestrictive	
	Lata Cananal	Permit 455-20	Either-sex Destriction		
	Late General	B-License 455-00	Antlerless	Kesuicuve	
_	Late Shoulder		No Harvest	No Harvest	

Table 3. Results of WAIC comparison of candidate multi-state models. Δ WAIC values indicate the difference between each candidate model's WAIC score and that of the top performing model.

Model	WAIC	ΔWAIC
Hunt Daried	14450 55	0.00
	14450.55	0.00
Hunting Regulation	14300.00	-100.11
Hunter Harvest	14846.05	-395.50
Snow Water Equivalent	14956.30	-505.75
Migratory Status	14994.99	-544.44
Constant/Null	15013.08	-562.53

Literature Cited:

- Avgar, T., J. R. Potts, M. A. Lewis, and M. S. Boyce. 2016. Integrated step selection analysis: bridging the gap between resource selection and animal movement. Methods in Ecology and Evolution 7:619–630.
- Barber-Meyer, S. M., P. J. White, and L. D. Mech. 2007. Survey of selected pathogens and blood parameters of Northern Yellowstone elk: wolf sanitation effect implications. The American Midland Naturalist 158:369–381.
- Burcham, M., W. D. Edge, and C. L. Marcum. 1999. Elk use of private land refuges. Wildlife Society Bulletin 27:833–839.
- Cleveland, S. M., M. Hebblewhite, M. Thompson, and R. Henderson. 2012. Linking Elk movement and resource selection to hunting pressure in a heterogeneous landscape. Wildlife Society Bulletin 36:658–668.
- Conner, M. M., G. C. White, and D. J. Freddy. 2001. Elk movement in response to early-season hunting in northwest Colorado. The Journal of Wildlife Management 926–940.
- Cook, R. C., J. G. Cook, T. R. Stephenson, W. L. Myers, S. M. Mccorquodale, D. J. Vales, L. L. Irwin, P. B. Hall, R. D. Spencer, and S. L. Murphie. 2010. Revisions of rump fat and body scoring indices for deer, elk, and moose. The Journal of Wildlife Management 74:880–896.
- Cook, R. C., J. G. Cook, D. J. Vales, B. K. Johnson, S. M. Mccorquodale, L. A. Shipley, R. A. Riggs, L. L. Irwin, S. L. Murphie, B. L. Murphie, K. A. Schoenecker, F. Geyer, P. B. Hall, R. D. Spencer, D. A. Immell, D. H. Jackson, B. L. Tiller, P. J. Miller, and L. Schmitz. 2013. Regional and seasonal patterns of nutritional condition and reproduction in elk. Wildlife Monographs 184:1–45.
- DeVoe, J. D., K. M. Proffitt, M. S. Mitchell, C. S. Jourdonnais, and K. J. Barker. 2019. Elk forage and risk tradeoffs during the fall archery season. The Journal of Wildlife Management 83:801–816.
- Drew, M. L., V. C. Bleich, S. G. Torres, and R. G. Sasser. 2001. Early pregnancy detection in mountain sheep using a pregnancy-specific protein B assay. Wildlife Society Bulletin (1973-2006) 29:1182–1185.
- Duncan, C., H. Van Campen, S. Soto, I. K. LeVan, L. A. Baeten, and M. W. Miller. 2008. Persistent bovine viral diarrhea virus infection in wild cervids of Colorado. Journal of Veterinary Diagnostic Investigation 20:650–653.
- Eacker, D. R., P. M. Lukacs, K. M. Proffitt, and M. Hebblewhite. 2017. Assessing the importance of demographic parameters for population dynamics using Bayesian integrated population modeling. Ecological Applications 27:1280–1293.
- Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution 13:58–63.

- Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.
- Gruntorad, M. P., and C. J. Chizinski. 2020. Constraints to hunting and harvesting elk in a landscape dominated by private land. Wildlife Biology 2020. Nordic Board for Wildlife Research.
- Haggerty, J. H., and W. R. Travis. 2006. Out of administrative control: Absentee owners, resident elk and the shifting nature of wildlife management in southwestern Montana. Geoforum 37:816–830.
- Hoff, L. 1973. Experimental infection in North American elk with epizootic hemorrhagic disease virus. Journal of Wildlife Diseases. 9:129–132.
- Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis. 2007. Analyzing animal movements using Brownian bridges. Ecology 88:2354–2363.
- Huang, F., D. C. Cockrell, T. R. Stephenson, J. H. Noyes, and R. G. Sasser. 2000. A serum pregnancy test with a specific radioimmunoassay for moose and elk pregnancy-specific protein B. The Journal of Wildlife Management 64:492–499.
- Kranstauber, B., R. Kays, S. D. LaPoint, M. Wikelski, and K. Safi. 2012. A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. Journal of Animal Ecology 81:738–746.
- Kuttler, K. L. 1984. Anaplasma infections in wild and domestic ruminants: a review. Journal of Wildlife Diseases 20:12–20.
- Loe, L. E., I. M. Rivrud, E. L. Meisingset, S. Bøe, M. Hamnes, V. Veiberg, and A. Mysterud. 2016. Timing of the hunting season as a tool to redistribute harvest of migratory deer across the landscape. European Journal of Wildlife Research 62:315–323.
- Lowrey, B., J. Devoe, K. M. Proffitt, and R. A. Garrott. 2020. Hiding without cover? Defining elk security in a beetle-killed forest. The Journal of Wildlife Management 84:138–149.
- Mahoney, S. P., and V. Geist. 2019. The North American Model of Wildlife Conservation. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Mikle, N. L., T. A. Graves, and E. M. Olexa. 2019. To forage or flee: lessons from an elk migration near a protected area. Ecosphere 10:e02693.
- Nol, P., C. Kato, W. K. Reeves, J. Rhyan, T. Spraker, T. Gidlewski, K. VerCauteren, and M. Salman. 2010. Epizootic hemorrhagic disease outbreak in a captive facility housing white-tailed deer (*Odocoileus virginianus*), bison (*Bison bison*), elk (*Cervus elaphus*), cattle (*Bos taurus*), and goats (*Capra hircus*) in Colorado, USA. Journal of Zoo and Wildlife Medicine 41:510–515.

- Noyes, J. H., R. G. Sasser, B. K. Johnson, L. D. Bryant, and B. Alexander. 1997. Accuracy of pregnancy detection by serum protein (PSPB) in elk. Wildlife Society Bulletin (1973-2006) 25:695–698.
- Paterson, J. T., K. M. Proffitt, and J. J. Rotella. 2022. Incorporating vital rates and harvest into stochastic population models to forecast elk population dynamics. The Journal of Wildlife Management 86:1–27.
- Proffitt, K. M., J. L. Grigg, R. A. Garrott, K. L. Hamlin, J. Cunningham, J. A. Gude, and C. Jourdonnais. 2010. Changes in elk resource selection and distributions associated with a late-season elk hunt. The Journal of Wildlife Management 74:210–218.
- Proffitt, K. M., J. A. Gude, K. L. Hamlin, and M. A. Messer. 2013. Effects of hunter access and habitat security on elk habitat selection in landscapes with a public and private land matrix. The Journal of wildlife management 77:514–524.
- Proffitt, K. M., S. Thompson, D. Henry, B. Jimenez, and J. A. Gude. 2016. Hunter access affects elk resource selection in the Missouri Breaks, Montana. The Journal of Wildlife Management 80:1167–1176.
- Ranglack, D. H., K. M. Proffitt, J. E. Canfield, J. A. Gude, J. Rotella, and R. A. Garrott. 2017. Security areas for elk during archery and rifle hunting seasons. The Journal of Wildlife Management 81:778–791.
- Sergeyev, M., B. R. McMillan, K. R. Hersey, and R. T. Larsen. 2020. The influence of habitat use on harvest vulnerability of cow elk (*Cervus canadensis*). PLOS ONE 15:e0242841.
- Sergeyev, M., B. R. McMillan, L. K. Hall, K. R. Hersey, C. D. Jones, and R. T. Larsen. 2022. Reducing the refuge effect: using private-land hunting to mitigate issues with hunter access. The Journal of Wildlife Management 86:e22148.
- Sinclair, A. R. E., J. M. Fryxell, G. Caughley, and G. Caughley. 2006. Wildlife ecology, conservation, and management. 2nd ed. Blackwell Pub, Malden, MA ; Oxford.
- Tessaro, S. V., P. S. Carman, and D. Deregt. 1999. Viremia and virus shedding in elk infected with type 1 and virulent type 2 bovine viral diarrhea virus. Journal of Wildlife Diseases 35:671–677.
- Thorne, E. T., J. K. Morton, F. M. Blunt, and H. A. Dawson. 1978. Brucellosis in elk. II. Clinical effects and means of transmission as determined through artificial infections. Journal of Wildlife Diseases 14:280–291.
- Thurfjell, H., S. Ciuti, and M. S. Boyce. 2014. Applications of step-selection functions in ecology and conservation. Movement Ecology 2:4.
- Vieira, M. E., M. M. Conner, G. C. White, and D. J. Freddy. 2003. Effects of archery hunter numbers and opening dates on elk movement. The Journal of Wildlife Management 717– 728.

- White, P. J., R. A. Garrott, J. F. Kirkpatrick, and E. V. Berkeley. 1995. Diagnosing pregnancy in free-ranging elk using fecal steroid metabolites. Journal of Wildlife Diseases 31:514–522.
- Wood, A. K., R. E. Short, A.-E. Darling, G. L. Dusek, R. G. Sasser, and C. A. Ruder. 1986. Serum assays for detecting pregnancy in mule and white-tailed deer. The Journal of Wildlife Management 50:684–687.
- Zaugg, J. L., W. L. Goff, W. Foreyt, and D. L. Hunter. 1996. Susceptibility of elk (*Cervus elaphus*) to experimental infection with *Anaplasma marginale* and *a. Ovis*. Journal of Wildlife Diseases 32:62–66.