

# MONTANA STATEWIDE MULE DEER STUDY: Ecology of mule deer in northern forests and integrated population modeling in the prairie-breaks



## FINAL REPORT

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**MONTANA FISH,  
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## EXECUTIVE SUMMARY

Mule deer (*Odocoileus hemionus*) are an important species in Montana, where Montana Fish, Wildlife and Parks (MFWP) has a long history of science-based deer management. In recent years, mule deer population dynamics and ecology are of particular concern given variable declines in abundance and hunter harvest have been documented in many areas throughout the state. Wildlife managers are tasked with maintaining or recovering deer populations, dampening the magnitude of potential future declines, and stabilizing populations and subsequent hunter opportunity. Therefore, improved quantitative understanding of mule deer ecology and population dynamics is of relevance across Montana. We conducted field research in three study areas of northwestern Montana, where mule deer ecology is lesser studied. Field studies included assessment of seasonal space use and migration, population dynamics and vital rates, summer forage nutrition with particular focus on forest disturbance, summer and winter habitat selection, and fall migration patterns during hunting season. We also conducted a new application of integrated population modelling techniques to mule deer monitoring data collected in eastern Montana which offered several potentially useful advancements for monitoring and management.

*Space use and migration (Section 3):* We captured and collared 134 adult female mule deer across 3 study areas, including 41 in the Cabinet-Salish Mountains, 49 in the Rocky Mountain Front, and 44 in the Whitefish Range. Summer home ranges were generally larger in area than those during winter, though average home range size across all study areas and seasons were  $\leq 10$  km<sup>2</sup>. Deer in all three study areas exhibited partial-migration behavior, where the majority (80–90%) deer migrated to distinct summer ranges. Average migration distances across study areas were 23–33 km, ranging from 3–59 km. The timing of migrations varied widely among individuals, with animals initiating spring migrations on average dates of May 7–20, depending on study area, and the average date of initiation for fall migrations across all study areas was October 19<sup>th</sup>. Deer showed very high fidelity to both winter and summer ranges across years, with 93–100% of deer returning to the same ranges in consecutive years depending on season and study area.

*Nutritional condition and vital rates (Section 4):* We measured nutritional condition in the form of percent body fat, estimated from ultrasonic rump fat measurements and body condition scoring. Nutritional condition varied widely across individual deer, and body fat declined significantly over time as the winter season progressed. After controlling for the effects of capture date, there were no significant differences in body fat among study areas or biological years of capture. In fact, uncorrected median values of % body fat were identical across study areas (Figure 4.2), at 6.9%, which is slightly lower than average values observed in other areas during late-winter (~7.2% in CA and CO studies).

Annual adult female survival averaged 0.77 and was similar across study areas, with mean estimates per study area of 0.79 (0.70–0.90; Cabinet-Salish), 0.77 (0.68–0.87; Rocky Mountain Front), and 0.75 (0.66–0.86; Whitefish Range). All 3 study areas showed highest rates of mortality near the end of the biological year during early spring months of April and May. In all study areas, mountain lion predation was the leading known cause of mortality, imposing 6–11% annual mortality upon adult females across regions. We observed no hunting-based mortality, which was expected in two of the three study areas, where antlerless harvest was prohibited during the study period. Thus, the 21–25% annual mortality observed could mostly be attributed to “natural mortality”, and such rates were high compared to those previously observed in previous eastern Montana studies (5–7%). A pulse of spring mortality observed in the Whitefish Range following the winter of 2018 included consistently poor condition and low marrow fat.

Pregnancy rates were high in all three study areas, averaging 99% in adults across all areas combined, but lower in yearling females (70%). Early winter and/or spring recruitment data were collected in trend areas overlapping two of the study areas. Relatively low spring ratios of 15–25 fawns per 100 adults were observed in the Cabinet-Salish study area, in correspondence with above average winter snowfall during the winters of 2018 and 2019. Similarly low ratios of 17–18 fawns per 100 adults were observed on the Rocky Mountain Front following the winters of 2018 and 2019, along with relatively high winter reduction of fawns (-34 to -46%) when comparing spring to early winter ratios.

*Diet composition (Section 5):* We estimated summer and winter diet composition at the individual level from mule deer fecal samples using fecal DNA-metabarcoding. Summer diets were highly diverse across all three study areas and relatively few species were found consistently across all diet samples. Tallies of species that made up 95% of summer diet samples included 69 species (or groups of species in some cases) in the Cabinet-Salish study area, 63 species in the Rocky Mountain Front, and 71 species in the Whitefish Range. By functional form, forbs and mixed forb/shrub species constituted 42%, 68%, and 48% of summer diets in the Cabinet-Salish, Rocky Mountain Front, and Whitefish Range, respectively, and shrubs made up 39%, 12%, and 19% of summer diets, respectively.

Winter diets contained fewer species, and greater proportional use of conifer (27–66%) and shrub forage species (22–46%). Interestingly, we observed a positive relationship between the amount of conifer species in an individual's diet and the average SWE the individual experiences in their home range, particularly when including deer in deep-snow environments of the Whitefish Range. The relationship was stronger when measuring snow instantaneously when diet samples were collected compared to the average SWE across the entire winter of capture, suggesting this relationship may vary over time for each individual deer.

*Summer habitat relationships (Section 6):* We conducted summer vegetation surveys at 884 field plots across the three study areas and combined these with species-specific forage quality estimates to predict forage digestible energy (kcal/m<sup>2</sup>) over space in each study area. Sampling also included a focus on plant communities in disturbed and undisturbed forest environments. We surveyed plants at paired disturbance and reference conifer plots, specifically sampling 336 points in reference conifer forest, 70 in harvest followed by prescribed fire, 135 in harvest, and 143 in wildfire and prescribed fire patches.

We found management trade-offs when evaluating patterns of plant community response to forest disturbance depending upon the type of disturbance and the metric of plant response. We measured and modeled three metrics of vegetative response: forage nutrition for mule deer, invasive species biomass, and floristic quality, a measure of plant communities' tolerance of disturbances and fidelity to particular environments using native species conservatism scores. We found associations between disturbance and vegetation outcomes that were both desirable and undesirable. Generally, deer forage nutrition and invasive species biomass both increased in disturbed areas, whereas floristic quality increased with disturbance in 2 study areas but decreased in the third. We also used decision analysis to illustrate trade-offs and overall support for different management actions while also accounting for underlying differences among study areas. For example, management actions with the greatest increase in mule deer forage nutrition tended to also increase invasive species biomass. We found low-severity timber harvest to be a productive management approach in 2 study areas due to its association with increased forage nutrition while also limiting invasive species biomass and maintaining floristic quality. However, different weighting schemes according to different management priorities among management outcomes alter the relative ranking of actions.

We also used multi-scale resource selection analysis to study how partially migratory mule deer balance selection for forage and avoidance of predation risk during summer. We compared the availability of forage (kcal/m<sup>2</sup>) and predation risk from wolves (*Canis lupus*) and mountain lions (*Puma concolor*) between summer ranges of study area and according to migratory strategy, then assessed how selection for those factors at the home range (second order) and within-home range (third order) scales varied. As forage availability increased among mule deer summer ranges and individual home ranges, selection for forage decreased at the second-order ( $P = 0.052$ ) and third-order ( $P = 0.081$ ) scales, respectively, but avoidance of predators varied weakly. In 1 study area, summer range of residents contained lower forage and higher risk than summer range of migrants, but residents compensated for this disadvantage through stronger selection of forage and avoidance of risk at finer spatial scales. In the other 2 study areas, summer range of migrants contained lower forage and higher risk than residents, but migrants did not compensate through stronger selection for beneficial resources. The majority of mule deer in our study system were migratory, suggesting partial migration may persist in populations even when measurable benefits in terms of forage and predation risk were not evident.

*Winter habitat relationships (Section 7):* Mule deer in northwest Montana inhabit the northern forests ecoregion, where the winter season can pose relatively challenging climatic conditions. We also studied resource selection during winter, with particular attention to the effects of snow on deer behavior. We found mule deer avoided areas with deeper snow while seeking out patches with greater solar radiation potential. Additionally, interaction between responses to snow and canopy cover showed deer within the deepest snow conditions showed increased selection for high forest canopy, with associated high snow-intercept. This result mirrored our diet results, showing increased use of conifer in deep snow environments. These differences suggest the importance of locally adapted behaviors as mule deer navigate energetic constraints of winter landscapes.

*Fall migration: timing and initiating factors (Section 8):* Deer in all three study areas exhibited summer movements into different hunting districts or management jurisdictions than those occupied during winter. Mule deer captured in the Cabinet-Salish winter range of HD103 were spread across 3 hunting districts during summer, with some not returning to HD103 until the end of general rifle season. Deer captured in the Rocky Mountain Front study area were spread across 8 hunting districts and the Sun River Game Preserve when archery season began in early September. While many deer returned during archery season, some remained in wilderness until after the general rifle season concluded. Lastly, many Whitefish Range deer left winter range in HD109 to summer in HD110, British Columbia, or Glacier National Park, in some cases being fully inaccessible during portions of the hunting season.

Given the management implications of fall migrations, we conducted an additional analysis to explore what drives the initiation of these migrations back to winter range. We hypothesized that factors behind fall migration timing might include precipitation (ie., snow), cold temperatures, senescence of plant forage, human hunting pressure, and the migration distance separating summer and winter ranges. Results supported several of these variables, with the most parsimonious model indicating that the initiation of fall migration is correlated with increased precipitation over the previous week, decreased daily minimum temperatures, and begins earlier with longer migration distances.

*Integrated population modeling in the prairie-breaks (Section 9):* MFWP biologists are charged with managing hunting regulations at hunting district scales yet, aside from harvest estimates, they lack population data sampled at this scale. Here, we used integrated population models (IPMs) to evaluate deer monitoring data within the framework of biological models of deer population growth, and we were able to estimate an important, but previously unavailable metric: harvest rate of antlered buck

mule deer. We used harvest and trend area population data from Region 7 during 1999–2017 and built an IPM founded on data from trend areas. This model returned estimates of population vital rates (e.g., age- and sex-specific survival) that were consistent with prior studies in Montana and elsewhere. It also provided estimates of mule deer antlered buck harvest rates, averaging 46%, that could be used to extrapolate harvest data to HD-scale abundance. We compared these results to those generated from extrapolation of deer densities observed in trend areas to the entire area of surrounding HDs, and we found results to be similar during some periods but quite different during others. Generally, this new IPM-based approach is founded on the assumption that harvest rates, but not necessarily density, are equivalent for those portions of the population within vs. not within trend areas. We feel this assumption may fit many but not all mule deer populations in Montana, and thus warrants further investigation towards robust estimation of HD-scale abundance and sex-age composition of mule deer.

*Management Implications (Section 10):*— Migration imposes a disconnect between population units managed and sampled during the hunting season (via harvest regulations and harvest survey data) and population units monitored during the winter (via post-season and spring trend surveys). This cross-boundary movement of animals may emphasize broad-scale, multi-district, interpretation of both harvest and survey data over finer-scale, single district monitoring data. Season structures that increase harvest opportunity during different portions (early vs. late) of the season may have unequal effects on subgroups of deer, depending upon migration timing and the spatial continuity of regulations. For migratory deer, mirroring regulations in both summer and winter ranges over time may be necessary to avoid undue impacts on those that return early vs. late, though such regulations may ultimately be difficult to implement. Regardless of migration considerations, the high natural mortality rates observed here, driven primarily by predation from mountain lions, leave little to no room for additional hunting opportunity of antlerless deer if mortality from hunting is even partially additive to other natural causes. However, pulses of mortality of animals in poor nutritional condition during early spring do suggest some potential for harvest mortality to be compensatory with winter mortality in these systems, as the effects of winter severity were apparent on both adult and fawn survival.

Responses of summer plant communities to disturbance were highly variable both within and among study areas, and less desirable outcomes such as increased invasive species biomass and decreased floristic quality were also associated with some disturbances. Although different management outcomes led to varying optimal results in each study area, our methods, including SMART analysis, allowed us to predict outcomes in multiple settings and account for uncertainty in vegetative responses to disturbance. Decision analyses suggested that low-severity timber harvest was an appealing forest management action in that it best balanced increased forage nutrition while limiting invasive species and maintaining floristic quality. Regarding the placement of targeted forest management for mule deer habitat, the high fidelity of mule deer to summer ranges and more consistent selection for forage at fine- than broad-scales may suggest limited utility of management-directed forage improvements to individual deer unless placed within existing, often high-elevation, home ranges. Variation in snow conditions across our three study areas was also a primary driver of variation in winter mule deer ecology. In deep-snow environments like the Whitefish Range, management to reduce forest canopy might create additional forage (e.g., shrub) resources but those resources appear to become inaccessible when and where snow is deep enough to inhibit movement or bury plants. In more mild winter environments, habitat management to promote shrubs may be less costly to energy expenditure and increase the biomass of accessible forage, with favorable implications for deer population dynamics.

Lastly, the population modeling approach we pioneered allows novel estimation of a previously unavailable and management-relevant metric: the harvest rate of antlered buck mule deer.

Furthermore, it facilitates absolute deer population estimates at HD- or broader-scales using existing monitoring data collected by MFWP, the use of which has previously been limited to yielding trend index counts for subsets of area and deer populations (i.e., trend survey areas). We recommend further evaluation and validation of this methodology, including parsimonious incorporation of weather covariates to potentially improve or smooth predictions.

## 1. INTRODUCTION

Over the past century, mule deer (*Odocoileus hemionus*) have experienced periods of population growth and decline throughout their range (Mackie et al. 1998, Pierce et al. 2012, Bergman et al. 2015). Studies of mule deer population dynamics have revealed a suite of interacting factors which influence annual variation and trends in population growth (Mackie et al. 1998, Unsworth et al. 1999, Pierce et al. 2012, Monteith et al. 2014, Hurley et al. 2014, Ciuti et al. 2015). The complexity of mule deer population dynamics creates a challenge for biologists seeking to monitor local deer populations and respond with appropriate management decisions in a timely manner (White and Bartmann 1998, Bishop et al. 2005).

Mule deer population trends are of particular concern in Montana, where significant declines in abundance and hunter harvest (correlated) have been documented in many areas throughout the state. Wildlife managers are tasked with the difficult mission of maintaining or recovering deer populations, dampening the magnitude of potential future declines, and stabilizing populations and subsequent hunter opportunity. Therefore, improved quantitative understanding of mule deer ecology and population dynamics is of relevance across Montana.

*Mule deer in the northern forests.*—With this study, Montana Fish, Wildlife and Parks (MFWP), in cooperation with the University of Montana, used detailed studies of mule deer ecology to address several information gaps concerning mule deer within Montana’s portion of the “Northern Forests” ecoregion (Sections 2–8; Hayden et al. 2008). The Northern Forests ecoregion is the northernmost of 7 ecoregions within which the mule deer of North America have been grouped according to similarities in environmental conditions and management challenges. The Northern Forests includes much of western Montana but spans from portions of California across British Columbia and into the Yukon and Alaska. Basic ecological information for mule deer in northwest Montana is limited, and available population monitoring data have indicated declines. Topics of study in this report include vital rate monitoring, detailed assessment of seasonal habitat selection, diet and forage nutrition, and evaluation of seasonal space use, migration routes, and drivers of fall migration timing.

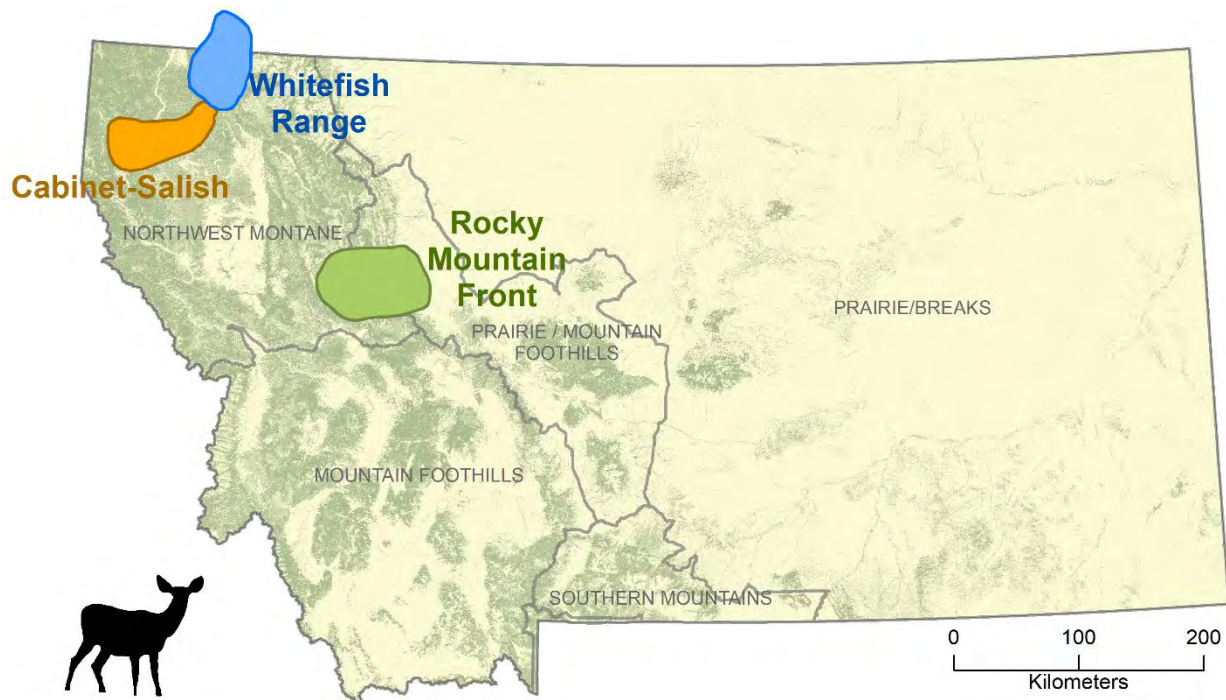
*Integrated population modeling.*—The methods by which MFWP currently monitors and manages mule deer were established in 2001 with the adoption of the Adaptive Harvest Management (AHM) system (MFWP 2001). This system included four primary components: 1) population objectives, 2) monitoring program, 3) hunting regulation alternatives, and 4) population modeling. The population modeling component of AHM was initially designed to predict future deer dynamics given a suite of harvest and weather scenarios. Despite being founded upon very powerful data sets, Pac and Stewart (2007) found the AHM population models achieved mixed results and subsequently recommended they remain in an experimental phase rather than be implemented as a management tool (AHM 2021). With this project, we also seek to leverage existing monitoring and research data together with new integrated population modelling techniques to revisit the modeling component of AHM (Section 9) and explore the application of this technique to MFWP’s current population monitoring data.



# MULE DEER IN THE NORTHERN FORESTS

## 2. STUDY AREAS AND PERIOD

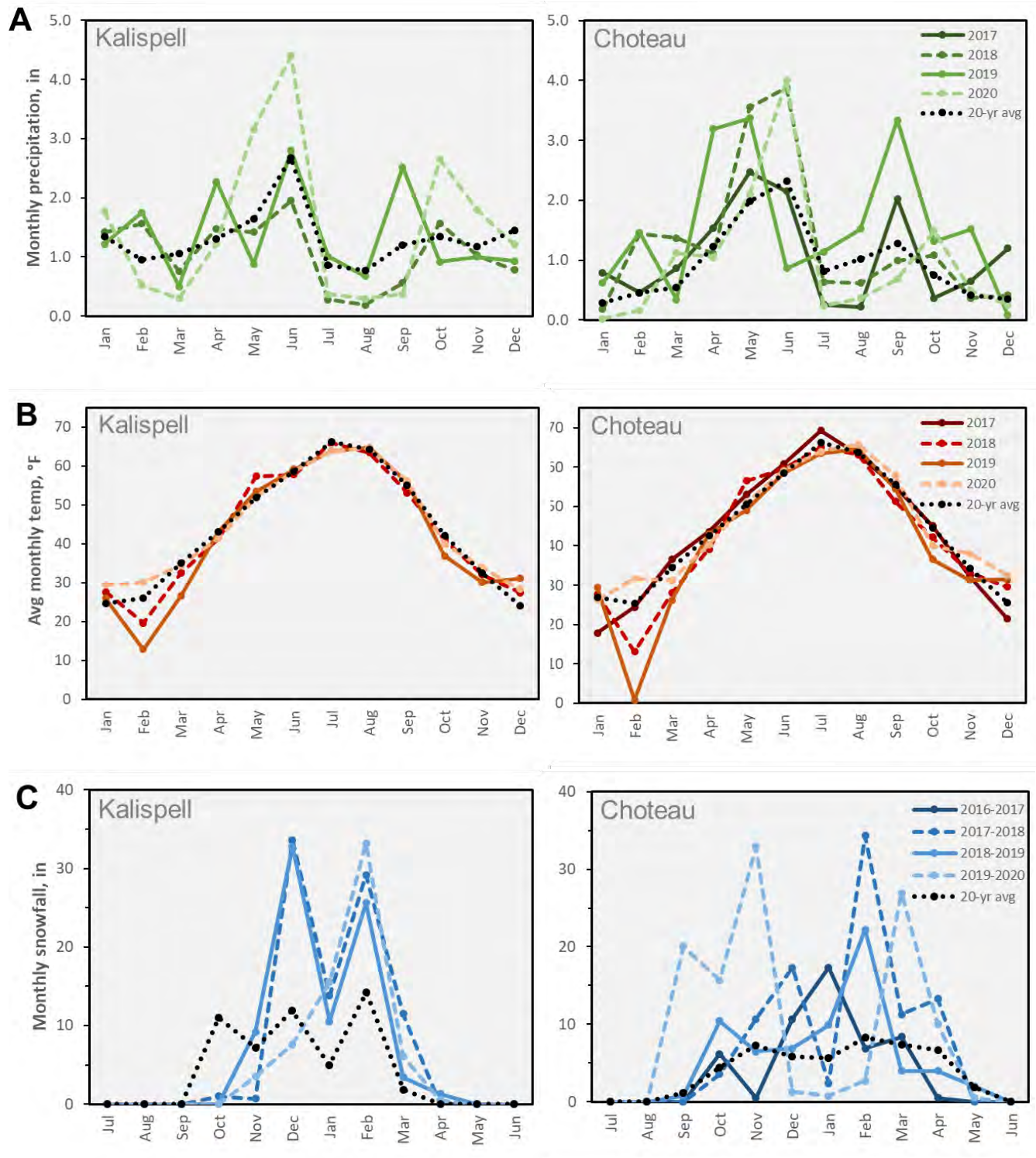
Our research occurred in 3 study areas throughout western Montana (Figure 2.1): The Rocky Mountain Front (47.50° N, -112.99° W), the Cabinet and Salish Mountains (Cabinet-Salish; 48.28° N, -115.31° W), and the Whitefish Range (48.88° N, -114.68° W) during 2017–2020. These areas represented a spectrum of ecological conditions such as dominant vegetation cover types, levels of forest disturbance, and climate, though all fell at least partially within the Northwest Montane mule deer population management unit, as prescribed in AHM (MFWP 2021).



**Figure 2.1.** Study areas for mule deer field research conducted during this study, and MFWP mule deer population management unit boundaries, 2017–2020.

Data collection during this study spanned 2017–2020, with deer captures beginning during the winter of 2016–17 on the Rocky Mountain Front study area and continuing in all three study areas during winters of 2017–18 and 2018–19. Summer forage nutrition and diet sampling primarily occurred during the summers of 2018 and 2019, with a pilot season on the Rocky Mountain Front study area during 2017.

Weather conditions during the study period included some relatively wet spring conditions particularly in the Rocky Mountain Front study area, where precipitation greatly exceeded average conditions during April–June in most years (Figures 2.2, 2.3). In contrast, the summer months of July and August were drier than average in all areas for most years, excluding the summer of 2019 (Figure 2.2). Winter conditions were variable and included relatively low autumn and high winter snowfall in the northwest Montana study areas, as indicated by snowfall at the Kalispell weather station, but somewhat more variable conditions at the Rocky Mountain Front study area (Figures 2.2, 2.3).



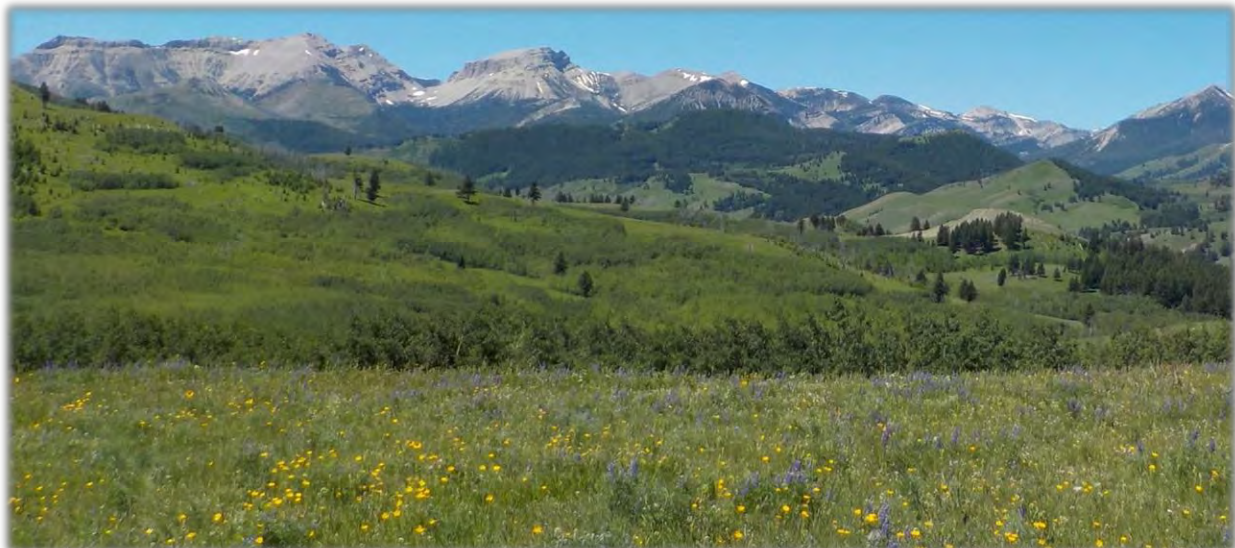
**Figure 2.2.** Monthly weather metrics of A) total precipitation, B) average temperature, and C) total snowfall at 2 regional weather stations in proximity to mule deer study areas during 2017–2020.



**Figure 2.3.** Spring flooding in Augusta, MT (upper photo; USGS, June 2018), was an indicator of generally wet spring conditions on the Rocky Mountain Front during some study years, while periods of heavy, above-average, snow also occurred on mule deer winter ranges in each study area (lower photo; B. Lonner, March 2018).

## 2.1. Rocky Mountain Front

The **Rocky Mountain Front** study area included portions of the Bob Marshall and Scapegoat Wilderness areas (managed by USFS) as well as other public and private lands extending eastward. Elevation ranged from 1,200 to 2,750 m. Mean temperatures averaged  $-10.2^{\circ}\text{C}$  in January and  $22.9^{\circ}\text{C}$  in July, and annual precipitation averaged 81.0 cm (PRISM Climate Group 2020). The study area represents the transition zone between the Great Plains and the Rocky Mountains and contained a pronounced east-to-west gradient in dominant vegetation cover classes, elevation, and topographic complexity. East of the continental divide, lower-elevation areas included riparian areas, agricultural land, and mixed-grass prairie dominated by bunchgrasses (*Pseudoroegneria spicata*) and fescues (*Festuca campestris*, *F. idahoensis*). Moving west, the foothills gave way to shrub- and conifer-dominated ecosystems, then to a diverse mosaic of meadows, alpine steppe, and subalpine conifer areas at higher elevations. Forest stands were generally mixed and composed of lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), spruce (*Picea* spp.), and sub-alpine fir (*Abies lasiocarpa*). Much of this region has experienced a stand-replacement fire regime with fire intervals of 150 to 250 years (Arno et al. 2000).



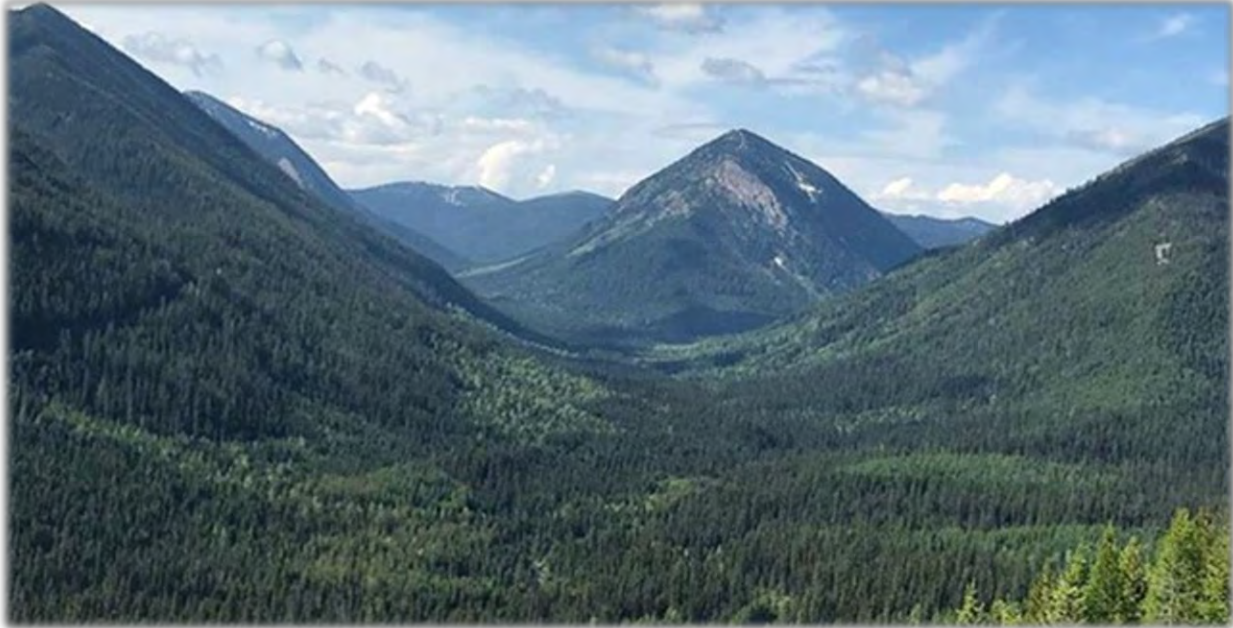
## 2.2. Cabinet-Salish

The **Cabinet-Salish Mountains** study area was centered within the Fisher River drainage and extended westward to the Cabinet Mountains and eastward to the Salish Mountains. Elevation ranged from 600 m to 2,100 m. Mean temperatures averaged  $-8.8^{\circ}\text{C}$  in January and  $25.0^{\circ}\text{C}$  in July, and annual precipitation averaged 76.9 cm (PRISM Climate Group 2020). The study area offered dense- to open-conifer forest with interspersed shrubland and grassland areas. The Salish Mountains in the eastern portion of the study area are characterized by moderate, rolling topography, and were dominated by mesic forests, grasslands, and recently logged forests. Forests were comprised mainly of western larch (*Larix occidentalis*), Douglas fir, lodgepole pine, and Engelmann spruce (*P. engelmannii*). The Cabinet Mountains in the west are steeper and more rugged than the Salish Mountains, and contained wetter forest (e.g., western red cedar [*Thuja plicata*] and western hemlock [*Tsuga heterophylla*]) transitioning upwards to subalpine areas. This region, particularly the Salish Mountains, has received consistent and widespread timber harvest activity for decades from private timber company and U.S. Forest Service harvest actions. Wildfires were dispersed, although larger, more frequent burns tended to occur in the drier Salish Mountains.



### 2.3. Whitefish Range

The **Whitefish Range** was bordered to the east by Glacier National Park and extended north into the East Kootenay region of by British Columbia, Canada. Elevations ranged from 790 m in the Tobacco Valley to 2,440 m in the Whitefish Range. Mean temperatures averaged  $-10.2^{\circ}\text{C}$  in January and  $21.7^{\circ}\text{C}$  in July and annual precipitation averaged 119.0 cm (PRISM Climate Group 2020). Forests generally comprised western larch, Engelmann spruce, Douglas fir, lodgepole pine, and western red cedar. Disturbance includes some areas of small forest thinning projects, and wildfires tended to be relatively small and dispersed.



## 3. SPACE USE, MIGRATION, AND SURVIVAL

### 3.1. Capture and handling

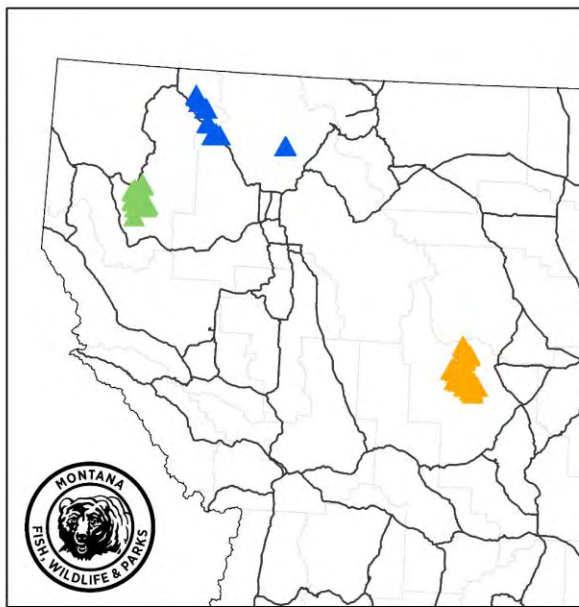
We deployed global positioning system (GPS) collars (Lotek LifeCycle 330 and LifeCycle Pro 330 collars; Lotek, Newmarket, ON, Canada) on 134 female mule deer throughout our 3 study areas during winters 2017–2019 and collected GPS-collar data through winter 2020 (Table 3.1). Collars were programmed to collect and upload locations to satellites every 13 hours. We collared 41 deer in the Cabinet-Salish, 49 in the Rocky Mountain Front, and 44 in the Whitefish Range. We captured mule deer during winter (Dec–Mar) using helicopter net-gunning (Gerlach et al. 1986), clover trapping (Thompson et al. 1989), and ground-darting (Figure 3.1), and attempted to spread the locations of captures throughout winter ranges (Figure 3.2). Institutional Animal Care and Use Committees at the University of Montana and MFWP approved capture protocols (Animal Use Protocols 001-17CBWB-011017 and FWPO3-2016).

**Table 3.1.** Numbers of adult female mule deer captured and radio-collared across 3 study areas, 3 winter seasons, and 3 capture techniques, excluding capture-related mortalities, Montana, 2017–2019.

	Rocky Mtn Front		Cabinet-Salish		Whitefish Range	
	Helicopter net-gun	Ground darting	Helicopter net-gun	Clover trap	Helicopter net-gun	Clover trap
2017	28	1	0	0	2	0
2018	12	0	16	10	0	29
2019	8	0	0	15	0	13
Total	49		41		44	



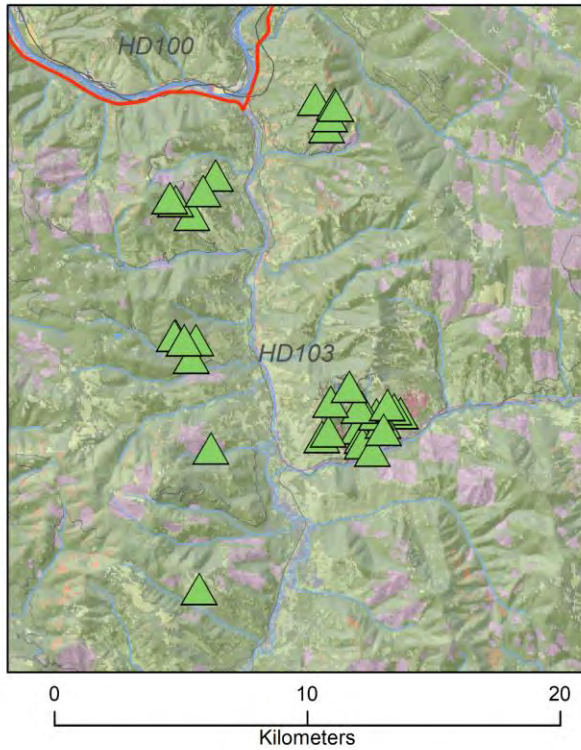
**Figure 3.1.** Mule deer were captured primarily with helicopter net-gun and ground-trapping techniques.



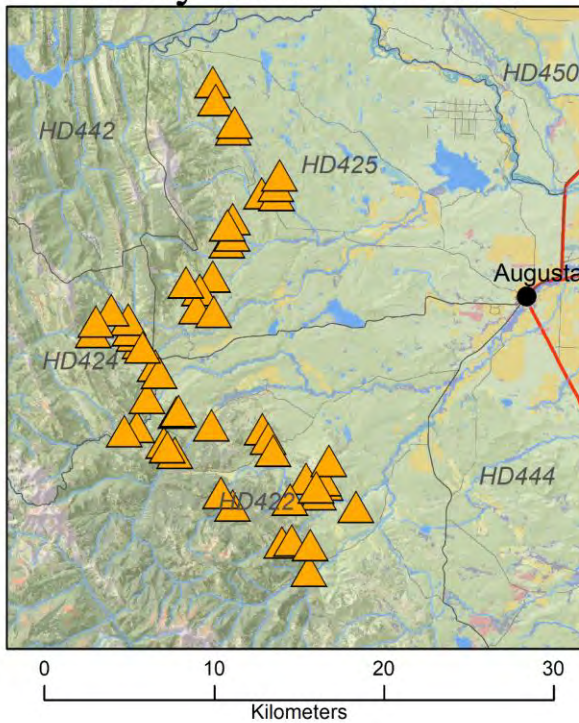
**Study areas**

- ▲ Cabinet-Salish Mountains
- ▲ Rocky Mountain Front
- ▲ Whitefish Range

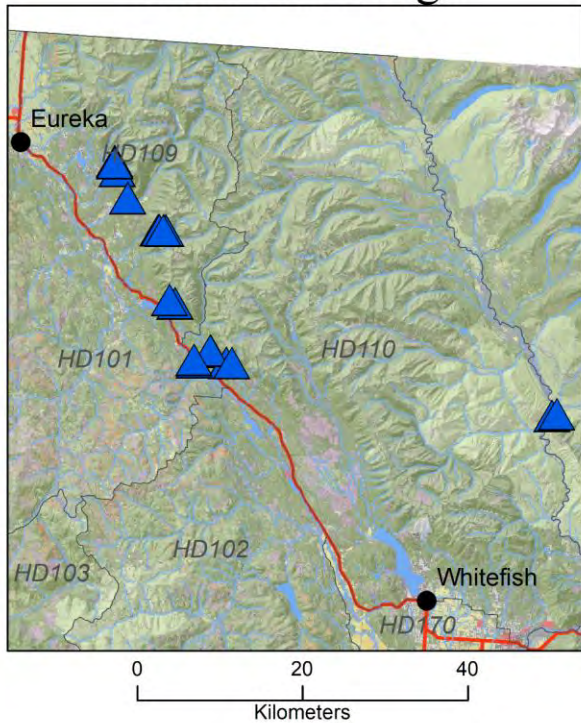
### Cabinet-Salish Mountains



### Rocky Mountain Front



### Whitefish Range

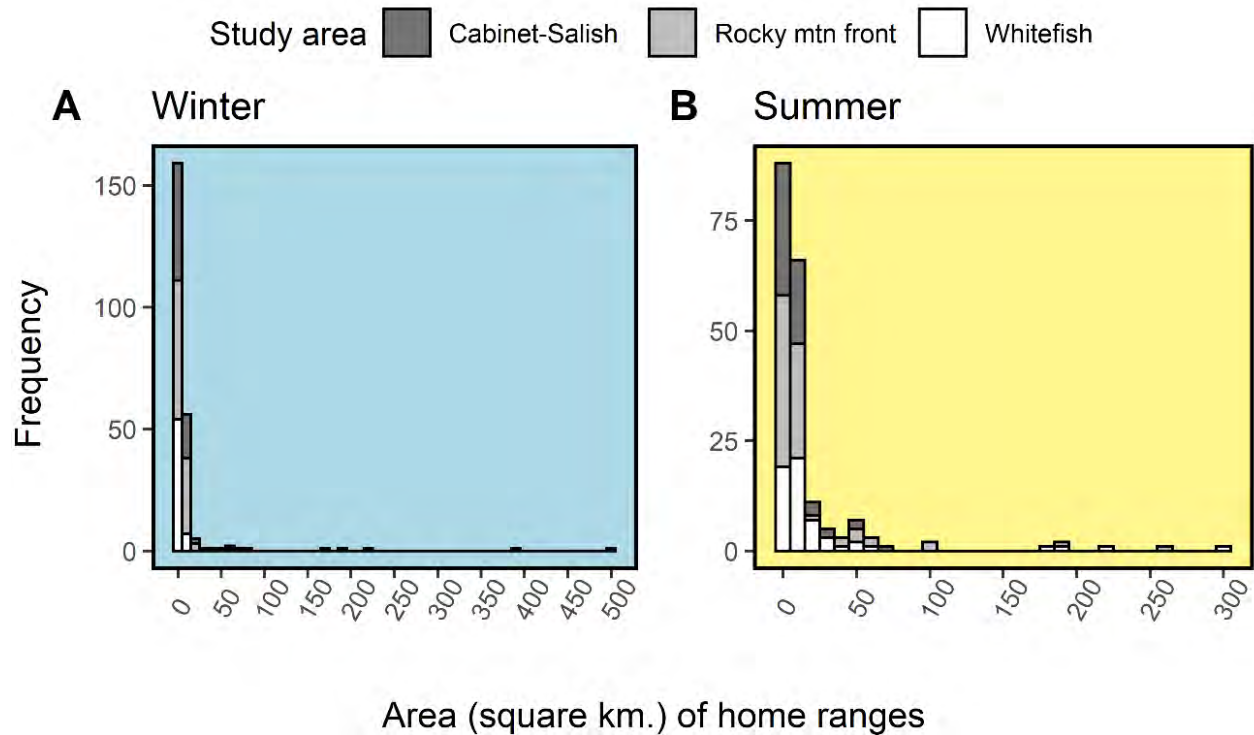


**Figure 3.2.** Capture locations of adult female mule deer in three study areas of western Montana, 2017–2019. Note: Two easternmost Whitefish Range deer shown here were captured near Demers Ridge in 2017, and this area and these deer were later excluded from most analyses.



## 3.2. Space use and migration

**3.2.1. Seasonal home ranges.**— We estimated 90% kernel density estimator home ranges during core seasonal periods for summer (July–August) and winter (January–February) to compile basic descriptions of individual deer space use. Summer home ranges were larger in area than those during winter, though average home range size across all study areas and seasons were  $\leq 10$  km<sup>2</sup> (Figure 3.3, Table 3.2).



**Figure 3.3.** Histogram of the area of 90% kernel density estimate (KDE) home ranges in (A) winter (January-February) and (B) summer (July-August) of individual deer  $\times$  years in 3 study areas in western Montana, 2017–2020.

**Table 3.2.** Home range area and spring migration distance for mule deer collared in 3 study areas of western Montana, 2017–2020.

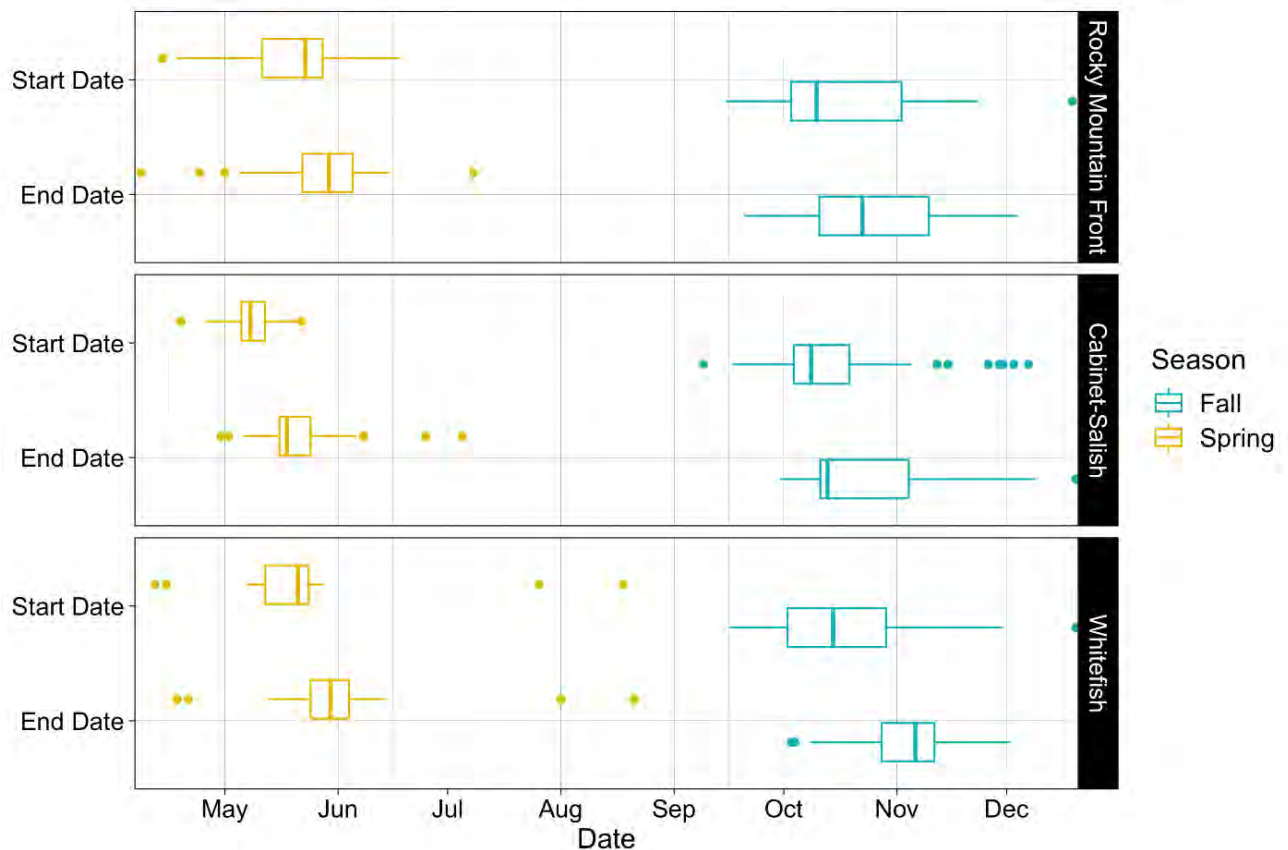
Study area	Home range size, median, km <sup>2</sup>		Spring migration distance, km		
	Winter	Summer	Average	Minimum	Maximum
Cabinet-Salish	3.94	4.45	33.2	20.7	49.6
Rocky Mountain Front	4.07	4.93	23.0	3.1	59.5
Whitefish Range	1.91	10.01	23.1	6.0	43.7

### 3.2.2. Partial migration. —

We assessed migratory behavior using net-squared displacement (NSD) to classify mule deer migration behaviors into either migrant or resident categories (Bunnefeld et al. 2011). NSD measures the straight-line distance between an animal's starting point and subsequent daily locations. We used the R application Migration Mapper (Wyoming Migration Initiative 2020) to view individual mule deer NSD curves to classify their movement behavior as well as the timing and distances of spring and fall migrations. We were able to assess the degree of migratory behavior for 33 deer across 54 deer-years in the Cabinet-Salish, 44 deer across 81 deer-years in the Rocky Mountain Front, and 31 deer across 53 deer-years in the Whitefish Range.

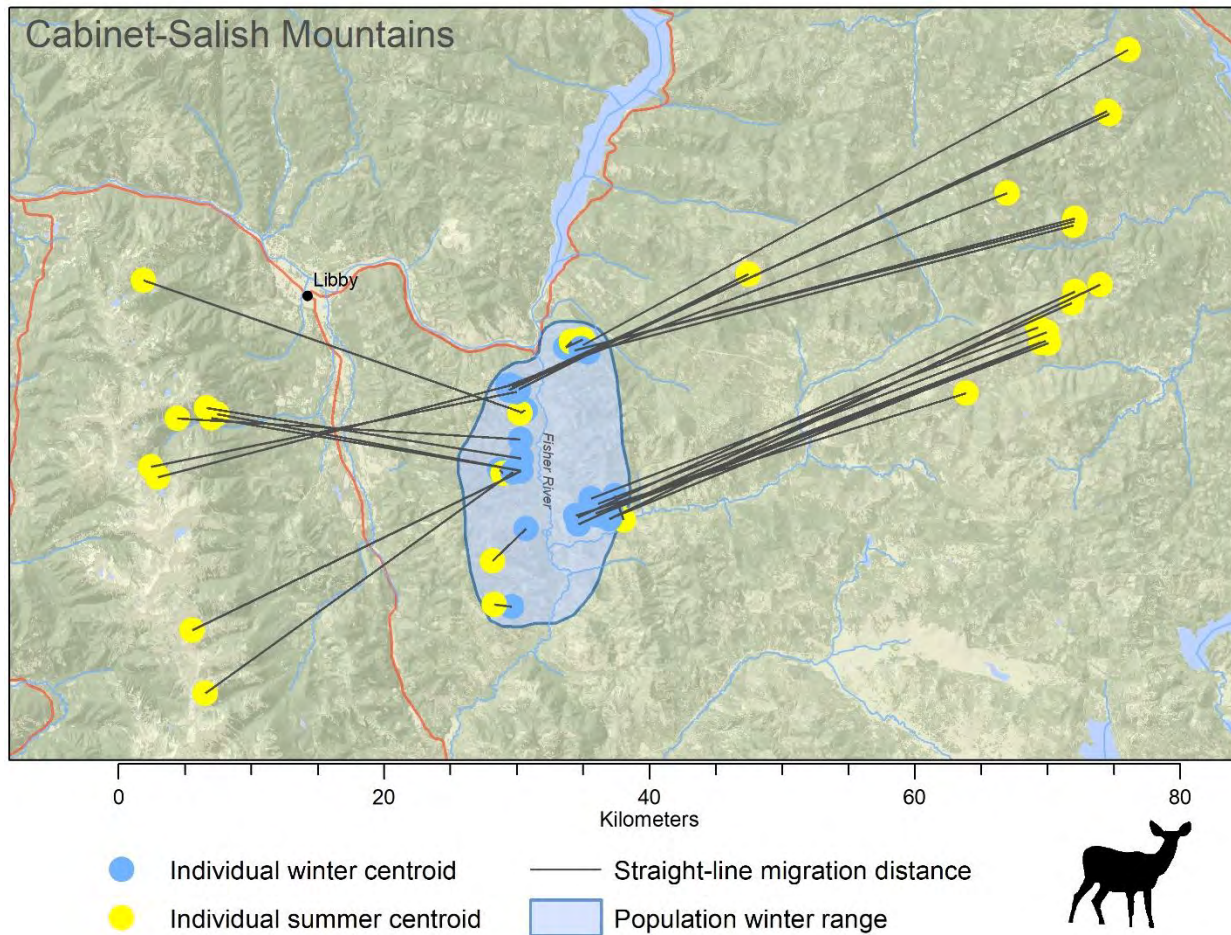
Deer in all 3 study areas exhibited partial-migration behavior whereby some individuals chose to remain resident in a year-round range while others migrate seasonally between spatially distinct ranges (Hebblewhite et al. 2009). However, the majority of animals tended to migrate to distinct summer ranges, with migratory behavior displayed by 82%, 80%, and 90% of deer in the Cabinet-Salish, Rocky Mountain Front, and Whitefish Range study areas, respectively. Average migration distances across study areas were 23–33 km, ranging from 3–59 km (Table 3.2).

The timing of migration was variable across study areas and years (see Section 8 below for detailed assessment of fall migration timing, in particular). Average dates of initiation for spring migrations were May 7 (range Apr 19–May 22), May 16 (range Mar 10–Jun 18), and May 20 (range Apr 12–Aug 18) across the Cabinet-Salish, Rocky Mountain Front, and Whitefish Range study areas, respectively (Figure 3.4).



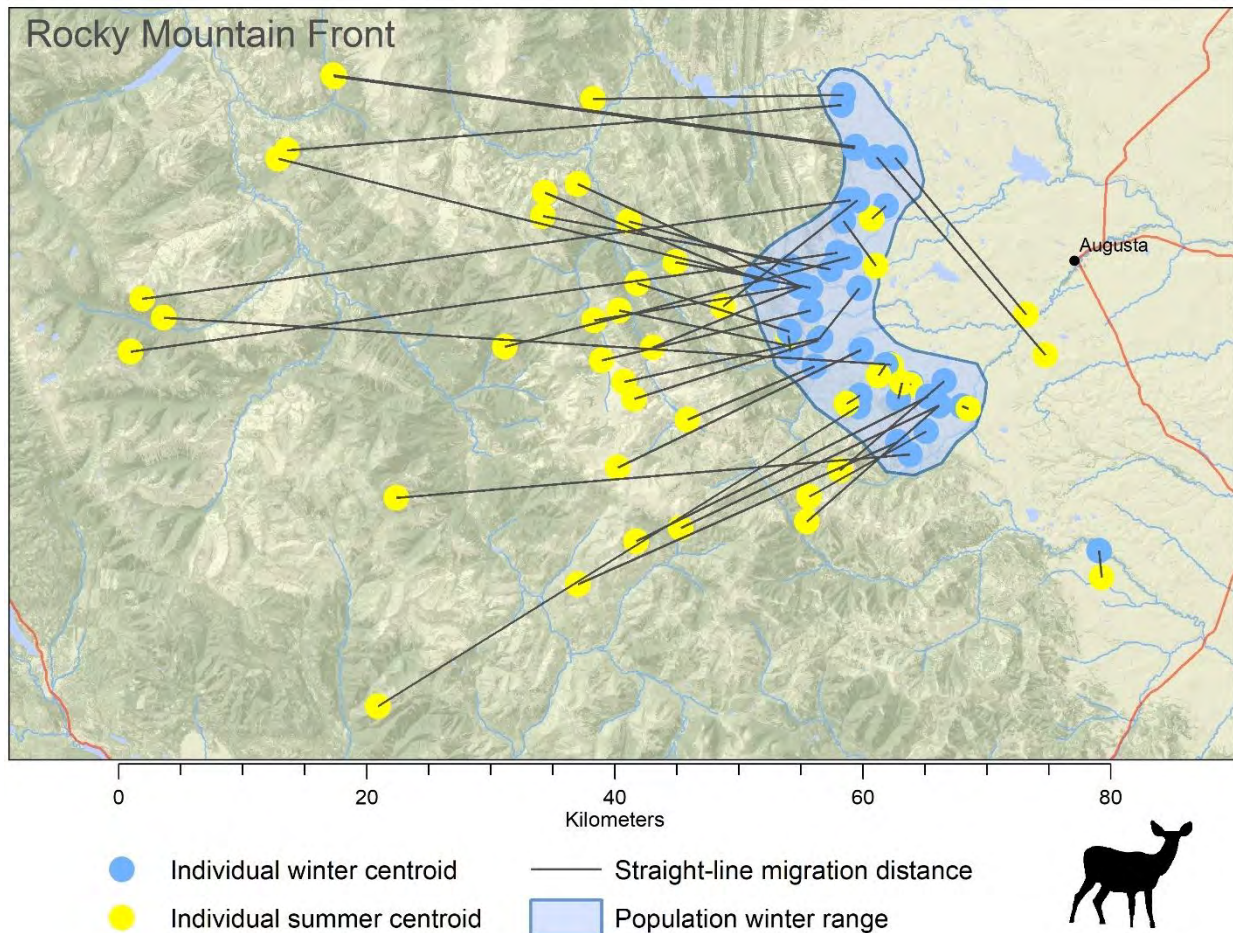
**Figure 3.4.** Start and end dates of the migration period during both spring and fall migrations for each of 3 study areas in Montana, 2017–2020.

In the Cabinet-Salish study area, the direction deer migrated appeared dependent on whether they wintered east or west of the Fisher River (Figure 3.5). Despite relative close proximity between winter ranges on either side of the river, migratory deer that wintered west of the Fisher River primarily migrated westward to the summer ranges in the Cabinet Mountains, and migratory deer that wintered east of the river migrated eastward into the Salish Mountains. There were also deer that remained in summer ranges overlapping winter range on both sides of the river.



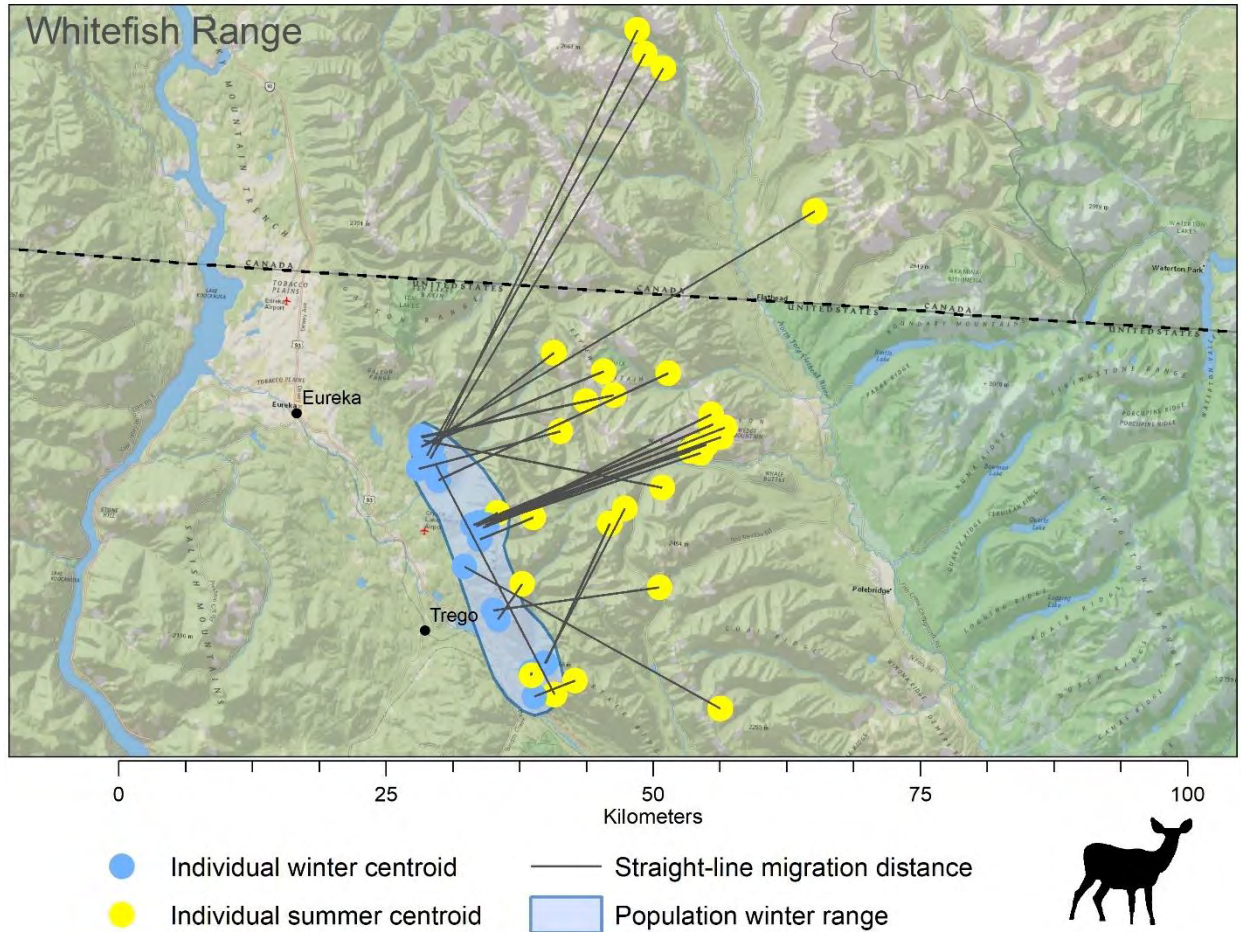
**Figure 3.5.** Partial migration in the seasonal space use of adult female mule deer in the Cabinet-Salish study area, as evidenced by representative winter (February 1<sup>st</sup>) and summer (August 1<sup>st</sup>) locations for individual deer during their first year of monitoring, 2018–2019.

In the Rocky Mountain Front study area, the majority of migratory deer moved westward into USFS National Forest lands and the Bob Marshall Wilderness Complex (Figure 3.6). Exceptions to this pattern included two deer that seasonally migrated southeast along the Rocky Mountain Front from mountain foothill habitat into a more prairie-plains habitat type. Lastly, one deer dispersed out of the study area to prairie-plains habitat to the southeast during the first summer of monitoring, and then remained resident in that area year-round thereafter (Figure 3.6).

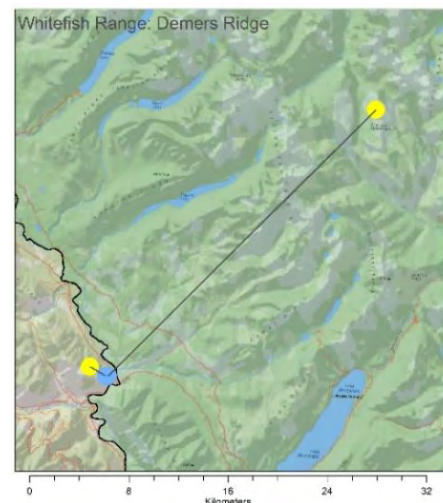


**Figure 3.6.** Partial migration in the seasonal space use of adult female mule deer in the Rocky Mountain Front study area, as evidenced by representative winter (February 1<sup>st</sup>) and summer (August 1<sup>st</sup>) locations for individual deer during their first year of monitoring, 2017–2019. Note one deer dispersed to the southeast of the study area during its first summer, and seasonal locations from its second winter and summer are presented here.

In the Whitefish Range, four deer crossed the Canadian border to summer ranges in British Columbia. The majority of the remaining deer migrated east into the Whitefish Range while a small number remained resident on winter range year-round (Figure 3.7). During the winter of 2016–2017, we also captured two deer within the Whitefish Range but outside of the primary study area, within the North Fork of the Flathead River drainage near Demers Ridge. One of these deer migrated into Glacier National Park during summer while the other remained resident near Demers Ridge year-round.



**Figure 3.7.** Partial migration in the seasonal space use of adult female mule deer in the Whitefish Range study area, as evidenced by representative winter (February 1<sup>st</sup>) and summer (August 1<sup>st</sup>) locations for individual deer during their first year of monitoring, 2017–2019. Note, in the inset (right) are locations for 2 deer captured outside of the study area, in the Demers Ridge area near the border of Glacier National Park.



### 3.3. Seasonal fidelity

Mule deer typically display a strong tendency to return to areas they used during corresponding times of year in the past (Sawyer et al. 2019). Such fidelity to sites can be beneficial because prior knowledge of an area reduces movement costs and search time for forage and refugia from predators (Forrester et al. 2015). However, when resources are unpredictable over time, an inflexible habitat selection strategy may preclude animals from selecting optimal resources available on the landscape (Morrison et al. 2021). Therefore, determining the degree to which mule deer exhibit fidelity to seasonal ranges can help us understand if and how they are optimally using environmental space.

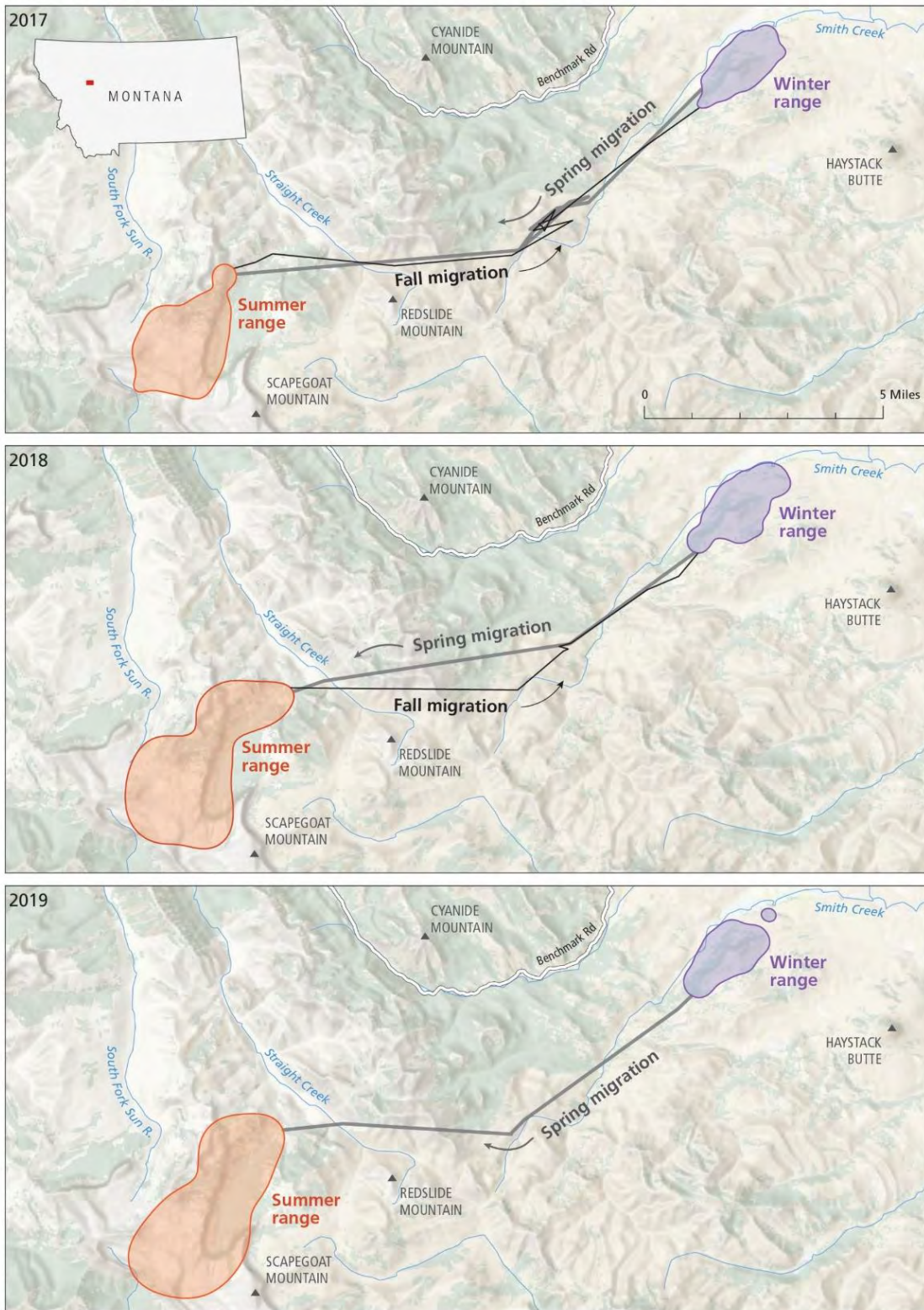
We examined fidelity to winter (January-February) and summer (July-August) ranges of mule deer. First, we determined the geographic centroid of GPS collar locations of individual deer for each season × year that individual’s GPS collar was active. We then calculated the distance between the seasonal centroid of each deer in year  $t$  and year  $t-1$ , a metric we refer to as Inter-Year Distance (IYD). We considered a mule deer to exhibit high fidelity if these centroids were separated by a distance less than the diameter of a typical home range. We determined the diameter of winter and summer home ranges by constructing 90% kernel density estimates (KDEs) for each deer using GPS points that uploaded during Jan-Feb and Jul-Aug, respectively.

Mule deer displayed a strong tendency to return to the same seasonal home range each year. Anecdotally, they also showed high fidelity to the migratory paths between seasonal ranges from year to year (Figure 3.8). During winter, 97% of deer exhibited high fidelity in the Cabinet-Salish, 90% did on the Rocky Mountain Front, and 93% did in the Whitefish Range (Table 3.3, Figure 3.9). All but two out of 93 deer included in this analysis over-wintered within 5 km of their winter range from the previous year. The exceptions included an individual in the Cabinet-Salish and over-wintered in the Fisher River drainage in winter 2018-19 but switched its winter range to an area 52 km away in the eastern Salish Range near Trego, MT in winter 2019-20 (Figure 3.10). The other was an individual captured on the Rocky Mountain Front that moved its winter range 32 km south between winter 2017-18 and 2018-19. During summer, 100% of deer in the Cabinet-Salish and on the Rocky Mountain Front exhibited high fidelity, and 93% did in the Whitefish Range. None of these deer established their summer range more than 3.3 km from where they had the previous year (Table 3.3, Figure 3.9). It is worth noting that complex home ranges of some individuals may have rendered their geographic centroid an irrelevant approximation of home range placement. For example, 1 individual in the Whitefish Range wandered extensively during winter, resulting in an estimated home range  $>400 \text{ km}^2$  in 2019. However, 85% of winter home ranges and 66% of summer home ranges estimated for this purpose were less than  $10 \text{ km}^2$  (Figure 3.3), so geographic centroids were likely a relevant metric for most deer.

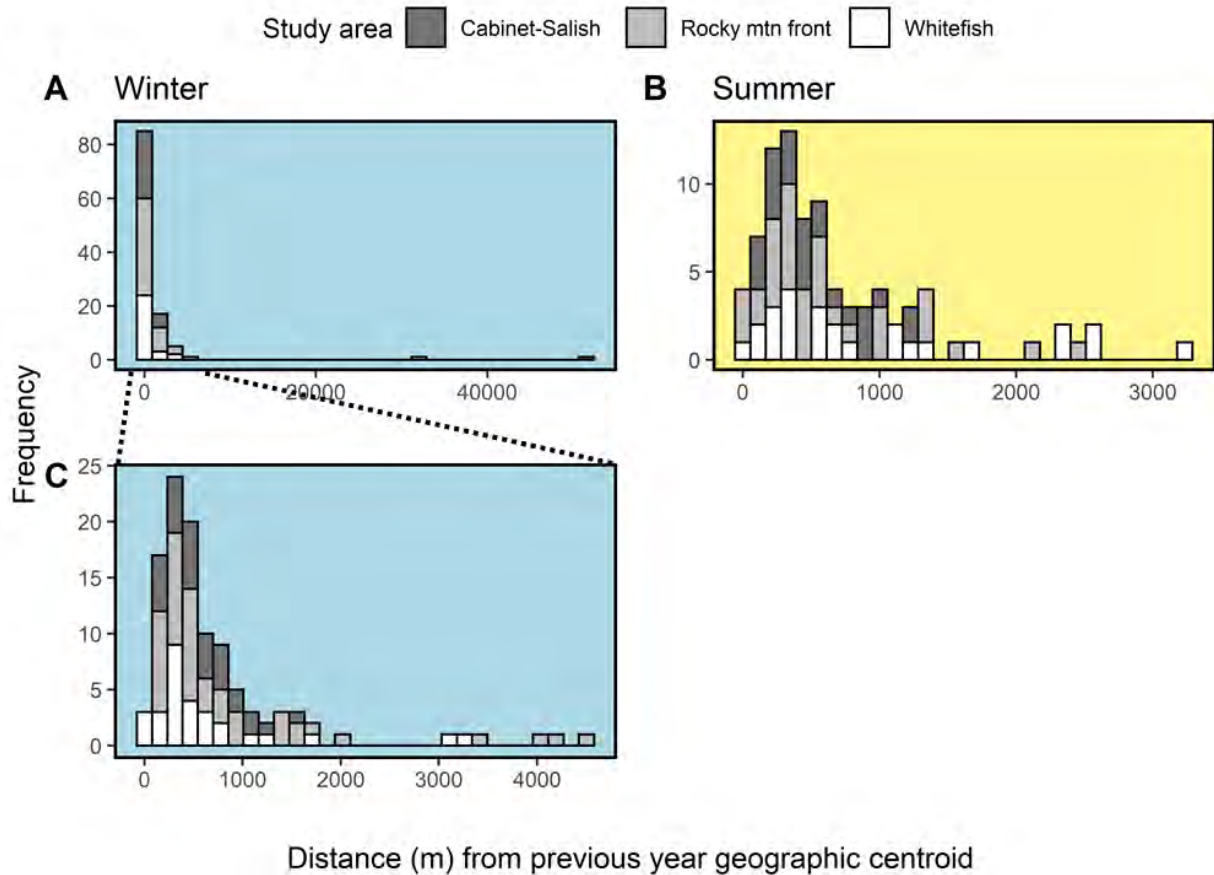
**Table 3.3.** Distances (m) between geographic centroids of individual mule deer winter (January-February) and summer (July-August) home ranges in 3 study areas, western Montana, 2017-2020.

Season	Study area	% High fidelity	Min	Median	Max
Summer	Cabinet-Salish	100	64	443	1,267
	Rocky Mountain Front	100	21	439	2,448
	Whitefish Range	96	52	620	3,256
Winter	Cabinet-Salish	97	141	467	51,591
	Rocky Mountain Front	90	98	511	32,344
	Whitefish Range	93	23	352	3,258

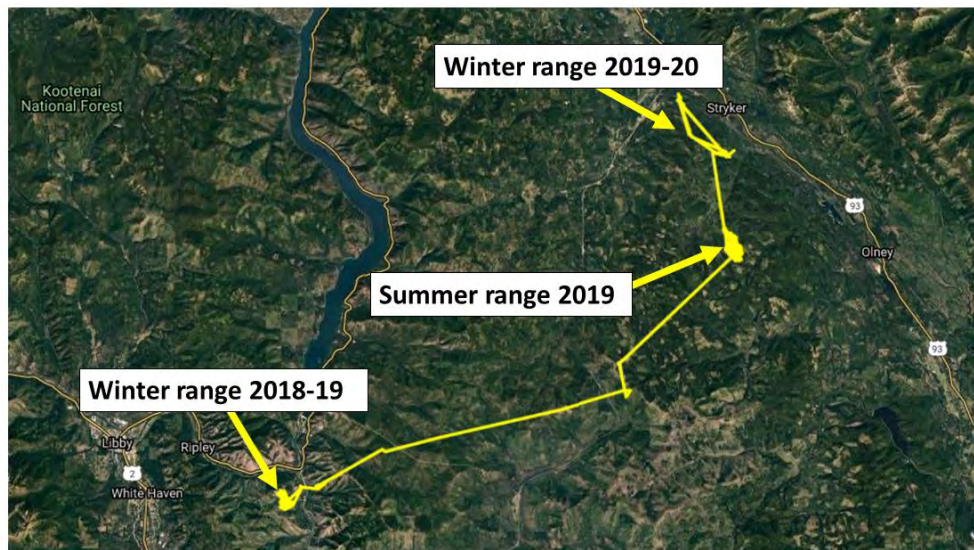
### Migration Fidelity for Mule Deer 19



**Figure 3.8.** A map of summer and winter home ranges and seasonal migratory paths followed by one mule deer collared on the Rocky Mountain Front from 2017-2019. Map produced by the InfoGraphics Lab, Department of Geography, University of Oregon.



**Figure 3.9.** Histogram of inter-year distances (IYD; in meters) between geographic centroids of individual mule deer (A) winter (January-February) and (B) summer (July-August) ranges in 3 study areas in western Montana collared between 2017-2020. We also provide a zoomed in plot of IYD values (C) during winter with outliers removed to better visualize the bulk of the distribution of those data.



**Figure 3.10.** Example of an individual mule deer in the Cabinet-Salish study area exhibiting low site fidelity via dispersal to a new winter range. This individual spent winter of 2018-19 in the Fisher River drainage and transitioned its winter range to an area >50 km east during the subsequent winter.



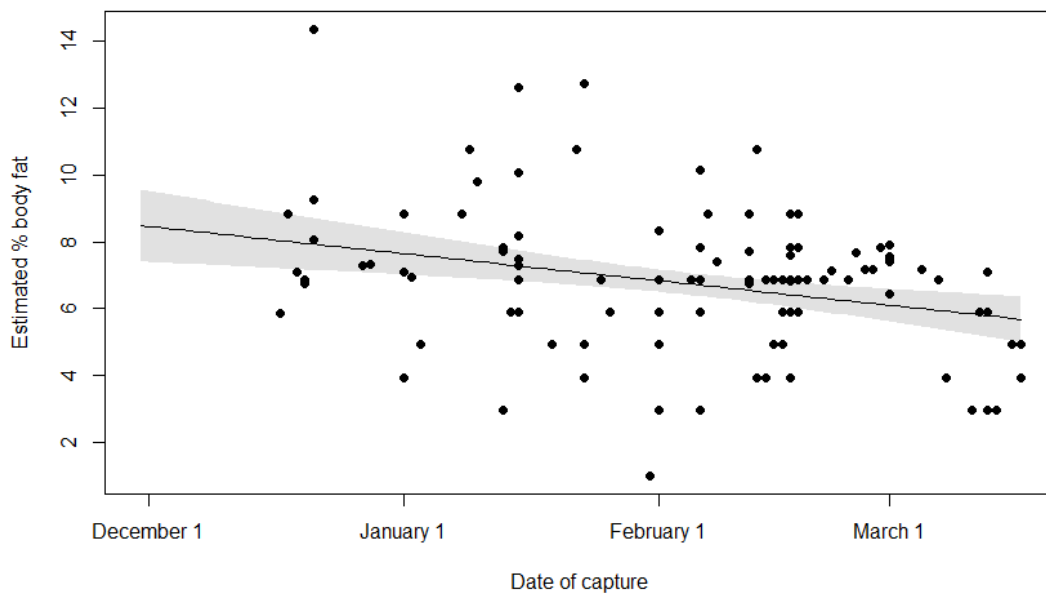
## 4. NUTRITIONAL CONDITION AND VITAL RATES

### 4.1. Nutritional condition

Nutritional condition of ungulates during winter is sensitive to environmental conditions experienced by individuals over space and time, and can be predictive of subsequent patterns of survival, reproduction, and population growth (Bishop et al. 2009, Monteith et al. 2014, Newby and DeCesare 2020).

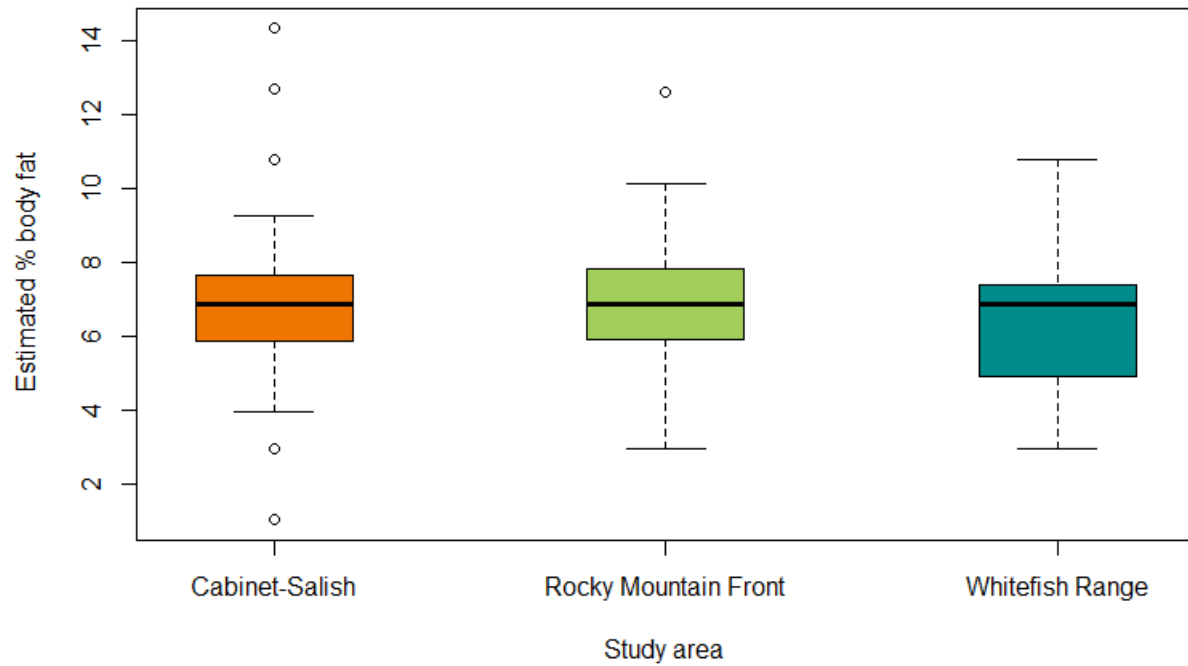
Furthermore, nutritional condition has been proposed as an important metric for monitoring mule deer population status given its role as an integrative link between the environment and fitness (Monteith et al. 2014). We followed the methods of Cook et al. (2010) to estimate percent body fat of captured mule deer, an ideal metric of nutritional condition, using ultrasonic measurements of rump fat and body condition scoring. We then used generalized linear models to assess the effects of capture date, biological year, and study area on variation in body fat from 133 individual adult female mule deer.

Nutritional condition (% body fat) varied widely across individual deer, which was consistent with results from other studies of mule deer (Bergman et al. 2014b, 2018). Body fat declined significantly over time as a function of capture date ( $\beta = -0.026$ ,  $P < 0.001$ ) as the winter season progressed (Figure 4.1).



**Figure 4.1.** Estimated percent body fat of adult female mule deer as a function of capture date during the winter season, western Montana, 2017–2019.

After controlling for the effects of capture date, there were no significant differences in body fat among study areas or biological years of capture. In fact, uncorrected median values of percent body fat were identical across study areas (Figure 4.2), at 6.9%, while mean estimates varied slightly among the Cabinet-Salish (6.8%,  $SD=2.37$ ), Rocky Mountain Front (6.8%,  $SD=1.65$ ), and Whitefish Range (6.4%,  $SD=2.02$ ). These values are slightly lower than average values during late-winter for mule deer populations in Colorado (7.2%; Bergman et al. 2018) and California (7.2%; Monteith et al. 2014). However, substantial variation in late-winter body fat can result from individual metrics that were unmeasured, complicating interpretation of this metric with regards to population management (Bergman et al. 2018).

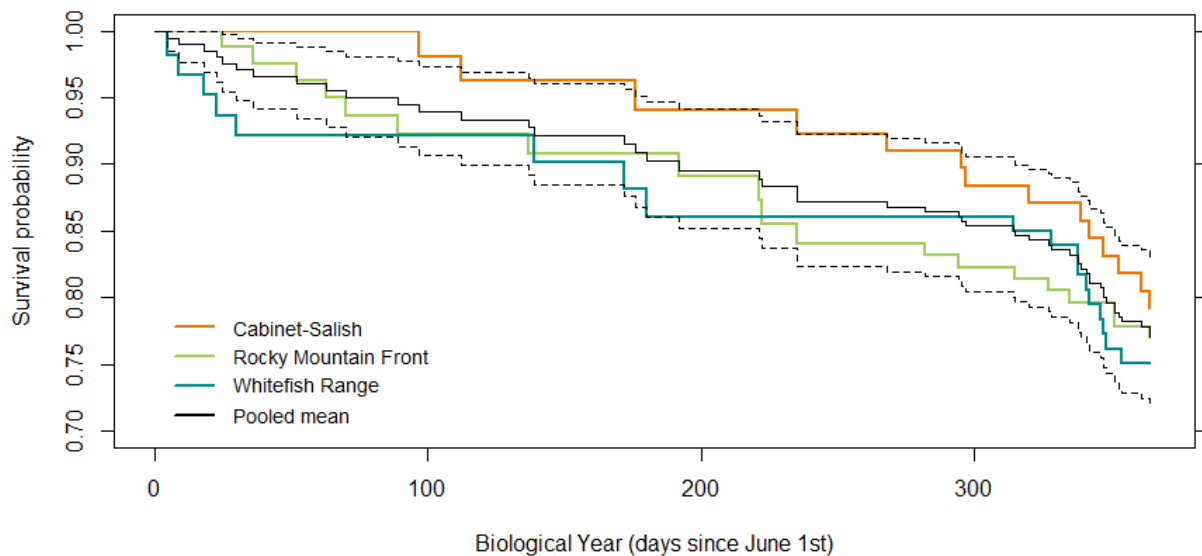


**Figure 4.2.** Box-plots showing median (bold line) and distributions of estimated percent body fat of adult female mule deer in 3 study areas of western Montana, 2017–2019.



## 4.2. Adult female survival, pregnancy, and recruitment

**4.2.1. Adult female survival**—We used the staggered-entry Kaplan-Meier estimator to estimate adult female survival rates over the course of the study, following DeCesare et al. (2016). Annual survival estimates and 95% confidence limits were similar and overlapping across all 3 study areas (Figure 4.3). Mean annual adult female survival across all study areas was 0.77 (0.72–0.83), and estimates for each study area were 0.79 (0.70–0.90; Cabinet-Salish), 0.77 (0.68–0.87; Rocky Mountain Front), and 0.75 (0.66–0.86; Whitefish Range). All 3 study areas showed highest rates of mortality near the end of the biological year during early spring months of April and May (Figure 4.3).



**Figure 4.3.** Kaplan-Meier adult female survival estimates for 3 study areas, 2017-2020.



**Figure 4.4.** Mortality site of deer ‘rmf-21’, showing evidence of mountain lion predation including cache site, trauma to throat, carcass opening at the rib region, and mountain lion tracks at the site, April 2017.

We used a cumulative incidence function estimator developed by Geskus (2011) to estimate cause-specific mortality rates, while accounting for the staggered entry of animals into the data stream throughout the study period. For these estimates we pooled data in the two northwestern Montana study areas to increase sample sizes and produce unified estimates within the Northwest Montane deer population management unit. In all study areas, mountain lion predation was the leading known cause of mortality, imposing 6–11% annual mortality upon adult females across regions (Figure 4.4., Table 4.1). It is noteworthy that there were many cases of unknown causes of mortality; these typically resulted from delays between mortality events and field investigation due to poor satellite transmission from collars and difficulty in promptly accessing backcountry mortality sites.

**Table 4.1.** Annual, cause-specific, mortality rates for adult female mule deer in 2 regions of Montana, 2017–2020.

	Northwestern Montana (Cabinet-Salish & Whitefish Range) <i>n</i> = 84		Rocky Mountain Front <i>n</i> = 49	
	Estimate	SE	Estimate	SE
<i>Predation, mountain lion</i>	0.11	0.027	0.06	0.028
<i>Predation, wolf</i>	0.01	0.007	0.03	0.017
<i>Predation, coyote</i>	0.01	0.006	--	--
<i>Predation, unknown sp.</i>	0.01	0.011	0.02	0.017
<i>Health-related</i>	0.03	0.013	0.03	0.017
<i>Human (fence entrapment)</i>	0.01	0.008	--	--
<i>Unknown</i>	0.06	0.021	0.09	0.033

Considering no hunter harvest of antlerless deer was permitted by regulations in the Cabinet-Salish and Whitefish Range study areas, and we detected no hunter harvest of our collared sample of mule deer in these study areas or the Rocky Mountain Front, these estimates represent “natural” (non-hunting) mortality in absence of harvest. Relative to previous studies elsewhere in Montana, estimates of 21–25% mortality due to natural causes observed in our study were notably high. Mackie et al. (1998) reported natural mortality rates among adult female mule deer averaging 7.3%, 6.2%, and 5.0% in mountain-foothill, timbered breaks, and prairie-badlands study areas of Montana during various studies spanning 1960–1986. Interestingly, Mackie et al. (1998) observed comparatively high hunter harvest mortality rates of 4.8%, 11.0%, and 21.0%, respectively, in these same areas. An important distinction relative to hunter harvest mortality is the variable nature in hunting regulations across years or between areas which dictates opportunity for hunter harvest of antlerless mule deer.

The high natural mortality rates observed here leave little to no room for additional hunting opportunity of antlerless deer, if mortality from hunting is even partially additive to other natural causes. Where combined predation rates approach 10–15% such as observed here, reduced capacity for antlerless hunting may be a consequence of intact predator communities. Reduction of mountain lion populations may have direct implications for mule deer given the paramount importance of adult female survival driving population dynamics in ungulate populations, yet long-term changes in population trend may still be marginal or short-term where such predator management is applied (Hurley et al. 2011). Mountain lion predation can be additive and independent of animal condition in some populations (Bishop et al. 2005) or times of year (Pac and White 2007), but there also is evidence of increased nutrition causing decreased predation rates from mountain lions (Bishop et al. 2009). Roughly half of the observed mortality in our case occurred did occur during the late-winter or early-spring season, and

was associated with animals in poor nutritional condition (<10% marrow fat ) in many cases. Thus, there remains the potential for some compensatory mortality in these systems, wherein a small amount of antlerless harvest might not increase the population-level mortality rates.

It should be noted that annual survival and cause-specific mortality estimates come from relatively modest sample sizes for this vital rate. White and Bartmann (1998) recommended a minimum of 50 marked animals to achieve “reasonable precision” when estimating over-winter fawn survival rates, while at least 20 adults should be monitored for monitoring adult survival. While our sample sizes exceed these minimum recommendations, confidence intervals for annual survival estimates at the study area level were wide.

Furthermore, our estimates are specific to this sample of climatic conditions. Anecdotally, survival and cause-specific mortality estimates in the Whitefish Range may have been unusually influenced by the relatively severe winter conditions in 2017–2018. During approximately one month from April 8, 2018 to May 11, 2018 there were 9 mortalities of collared deer in the Whitefish Range attributed to malnutrition and/or mountain lion predation. Marrow fat estimates were available for 6 of these deer and were all notably low, averaging 3.5% (range 0.2–9.1%). Following the milder winter of 2019 we observed only a single April-May mortality in this study area despite having a comparable number of animals marked. Also possibly contributing to this pulse of mortality in 2018 was a bait attractant (salt block; later addressed by MFWP enforcement staff) that may have drawn deer ( $n=3$ ) into an area of high predation risk where they were killed by one or more mountain lions.

**4.2.2. Pregnancy**—Pregnancy rates were high in all 3 study areas, though a higher proportion of yearlings (with reduced pregnancy rates) was notable in the sample of deer captured in the Cabinet-Salish study area (Table 4.2).

**Table 4.2. Pregnancy rates by age in 3 study areas, Montana, 2017–2019.**

	<u>All females</u> (age ≥ 1.5)		<u>Yearlings</u> (age = 1.5)		<u>Adults</u> (age ≥ 2.5)	
	Pregnancy	<i>n</i>	Pregnancy	<i>N</i>	Pregnancy	<i>n</i>
<i>Cabinet-Salish</i>	81%	31	43%	7	100%	22
<i>Rocky Mtn Front</i>	98%	54	100%	2	98%	48
<i>Whitefish Range</i>	96%	44	82%	11	100%	30
<b>Total</b>	93%	129	70.0%	20	99%	100



**4.2.3. Recruitment**—While this study did not include additional efforts spent monitoring recruitment, existing AHM monitoring protocols for mule deer included early winter and/or spring surveys within trend areas in the Cabinet-Salish and Rocky Mountain Front study areas (MFWP 2021).

In the Cabinet-Salish, spring surveys were conducted via helicopter within an HD103 trend area that overlaps the eastern half of the study area winter range (east of the Fisher River). Spring surveys were conducted in late April or early May each year during 2017–2021, with the exception of 2020, and included classification of mule deer into fawn and adult (male and female) age classes (Table 4.3).

**Table 4.3.** Spring survey data from the HD103 trend area in the Cabinet-Salish study area, 2012–21.

Biological year	Fawns	Adults	Unclassified	Total count	Fawns / 100 adults
2011/12	27	111	3	141	24
2012/13					
2013/14	88	157	5	250	56
2014/15					
2015/16	44	199	0	243	22
2016/17	67	239	15	321	28
2017/18	40	260	17	360 <sup>a</sup>	15
2018/19	66	263	2	360 <sup>a</sup>	25
2019/20					
2020/21	62	153	34	249	41
<i>Average</i>					<b>30</b>

<sup>a</sup>Replicate surveys of total count only were conducted some years, with maximum reported here, while classification by age-class occurred only once; thus classification counts do not sum to total count in some years.

Fawn per adult ratios in the Cabinet-Salish varied from 15–56 fawns/100 does in the previous 10 years. We did not summarize winter weather across this entire 10-year period, nor did we conduct statistical analyses of variation in recruitment in this trend area. However, it is notable that relatively low fawn recruitment values of 28, 15, and 25 fawns/100 adults each occurred during three consecutive winters of this study which all saw notably high snowfall relative to long-term averages (See Section 2, Figure 2.2). That said, over-winter fawn survival in Idaho has been shown to result from both winter conditions (specifically early and late winter snow cover) as well as forage quality during late summer-fall, which we do not discuss here (Hurley et al. 2017).

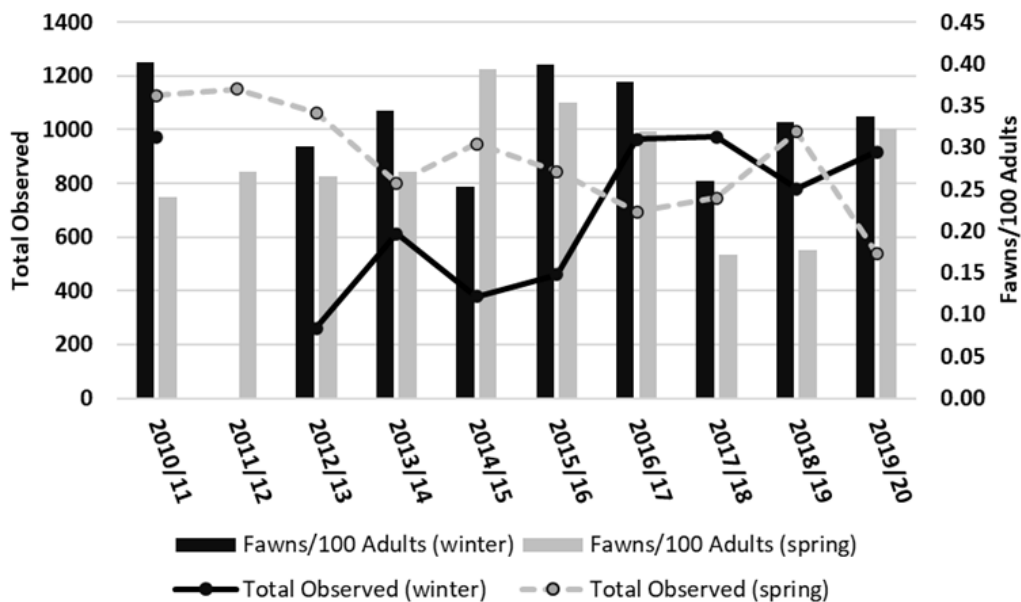


In the Rocky Mountain Front, early winter and spring trend survey data were collected and compiled across multiple trend areas in HDs 422, 424 and 425 that lie within the study area (2010-2020). Early winter surveys are completed around the calendar year changeover and the spring survey data are collected the following spring (approximately 3-4 months later). Age ratio and total count data are tied closely to survey conditions. Generally, fawn/adult ratios decline over the course of the winter due to natural attrition of fawns on winter range, the extent of which we measured as the % reduction in age ratios between early winter and spring surveys (Table 4.4, Figure 4.5). Typically, fewer deer are counted and classified during early winter surveys, with some exceptions.

Similar to patterns observed in the Cabinet-Salish, relatively severe winters of 2018 and 2019 appear anecdotally correlated to observed depression in spring recruitment data (17–18 fawns/100 adults).

**Table 4.4.** Aerial survey data pooled from trend areas overlapping the Rocky Mountain Front study area during early winter (i.e., December) and spring (April), 2010–20.

Biological year	Early winter		Spring		% Reduction in fawns/100 adults (winter to spring)
	Fawns/100 Adults	Total count	Fawns/100 Adults	Total count	
2010/11	40	970	24	1127	-40%
2011/12			27	1150	
2012/13	30	261	27	1063	-12%
2013/14	34	613	27	801	-21%
2014/15	25	379	39	948	NA
2015/16	40	460	35	844	-11%
2016/17	38	965	32	695	-16%
2017/18	26	972	17	745	-34%
2018/19	33	780	18	993	-46%
2019/20	34	918	32	539	-5%
Mean	33	702	28	891	-23%



**Figure 4.5.** Aerial survey data pooled from trend areas overlapping the Rocky Mountain Front study area during early winter (i.e., December) and spring (April), 2010–20.

## 5. DIET COMPOSITION

We estimated diet composition at the individual level from mule deer fecal samples using fecal DNA-metabarcoding (Taberlet et al. 2007; Jonah Ventures, Boulder, Colorado, USA). This method isolates a standardized region (or barcode) from DNA in fecal samples, compares it to a reference database for identification, and returns the relative quantities of plant species in mule deer diets. Most DNA barcodes matched with an existing plant in the database at 98% or greater similarity across the barcode length. However, some species have nearly identical DNA in a given barcode region, making it difficult to distinguish just one species match from the database. In these cases, we used a hierarchical approach to identify the species, genus, or family with the closest match (up to 95% similarity).

### 5.1. Summer diet

During summer, we collected fecal pellets from collared and uncollared mule deer between June 1 and August 31, 2017–2019. We distributed sampling effort across the full spatial extent of each study area and collected 160 samples: 53 from Cabinet-Salish Mountains, 64 from Rocky Mountain Front, and 43 from the Whitefish Range. Each sample consisted of 5-10 pellets collected from a single pellet group. We collected pellet samples only if mule deer were observed defecating, if fresh pellets were found within 100 m of mule deer that were observed in the past 30 minutes, or if moist pellets were located within 500 m of clusters of GPS collar locations and within 1 week of the time of collection.

Summer diets were highly diverse across all three study areas (Tables 5.1, 5.2, 5.3; Figure 5.1). Relatively few species were found consistently across all diet samples, making complete depiction of the breadth of summer diets quite complex. Tallies of species that made up 95% of summer diet samples included 69 species (or groups of species in some cases) in the Cabinet-Salish study area, 63 species in the Rocky Mountain Front, and 71 species in the Whitefish Range.

Amongst this diversity, some species did appear to be most prevalent, within and among study areas. Species that were found to be relatively common across all 3 study areas included *Plantago* species (likely common plantain *P. major* and English plantain *P. lanceolata*), rose family species including strawberry (*Fragaria* spp.) wild rose (*Rosa* spp.) or raspberry/thimbleberry (*Rubus* spp.), primrose (*Oenothera* spp.), serviceberry (*Amelanchier alnifolia*), cheatgrass (*Bromus tectorum*), sulphur-flowered buckwheat (*Eriogonum umbellatum*), *Spiraea* species, and fireweed (*Chamerion angustifolium*). Also locally common were prairie coneflower (*Ratibida columnifera*) in the Rocky Mountain Front study area, and *Ceanothus* spp. in the Cabinet-Salish and Whitefish Range study areas. Also notable was evidence of conifer species (*Pinus* spp. and *Pseudotsuga menziesii*) within summer diets, though these results from fecal samples collected during summer may be somewhat influenced by settling of conifer pollen on fecal piles (J. Craine, Jonah Ventures, pers. comm.).

By functional form, forbs and mixed forb/shrub species constituted 42%, 68%, and 48% of diets in the Cabinet-Salish, Rocky Mountain Front, and Whitefish Range, respectively (Figure 5.1). Shrub species made up 39%, 12%, and 19% of diets, tree species 14%, 10%, and 15% of diets, and graminoids 5%, 10%, and 18% of summer diets in each of the Cabinet-Salish, Rocky Mountain Front and Whitefish Range study areas, respectively (Figure 5.1).



**Table 5.1.** Summer diet species, sorted by % occurrence, and showing cumulative % of diet as each row is added in the Cabinet-Salish (CS) study area, 2018–2019.

Study area	Species name	Form	Mean % diet	Cumulative % diet
CS	<i>Fragaria spp.</i> <sup>a,b</sup> , <i>Rosa spp.</i> <sup>a,b</sup> , <i>Rubus spp.</i> <sup>a,b</sup>	forb/shrub	15.50	15.50
CS	<i>Ceanothus spp.</i> <sup>b</sup>	shrub	11.78	27.28
CS	<i>Chamerion angustifolium</i> <sup>a,b</sup> , <i>Oenothera spp.</i> <sup>a</sup>	forb	9.21	36.48
CS	<i>Pinus spp.</i> <sup>b</sup>	conifer	5.59	42.08
CS	<i>Plantago spp.</i>	forb	4.45	46.53
CS	<i>Alnus spp.</i> <sup>b</sup>	deciduous tree	4.30	50.83
CS	<i>Pseudotsuga menziesii</i>	conifer	4.11	54.94
CS	<i>Amelanchier alnifolia</i> <sup>b</sup>	shrub	3.28	58.22
CS	<i>Rhododendron albiflorum</i>	shrub	2.85	61.06
CS	<i>Bromus tectorum</i> <sup>b</sup>	graminoid	2.63	63.70
CS	<i>Spiraea spp.</i> <sup>b</sup>	shrub	2.46	66.16
CS	<i>Ribes spp.</i> <sup>b</sup>	shrub	2.19	68.35
CS	<i>Eriogonum umbellatum</i> <sup>b</sup>	forb	1.86	70.21
CS	<i>Salix spp.</i> <sup>b</sup>	shrub	1.84	72.05
CS	<i>Mahonia spp.</i> <sup>b</sup>	shrub	1.60	73.64
CS	<i>Medicago spp.</i>	forb	1.38	75.02
CS	<i>Thuja plicata</i>	conifer	1.34	76.36
CS	<i>Poa spp.</i> <sup>b</sup>	graminoid	1.32	77.68
CS	<i>Paxistima myrsinites</i>	shrub	1.32	79.00
CS	<i>Heuchera spp.</i>	forb	1.06	80.06
CS	<i>Abies spp.</i>	conifer	0.91	80.97
CS	<i>Vaccinium spp.</i> <sup>b</sup>	shrub	0.90	81.87
CS	<i>Ratibida columnifera</i>	forb	0.89	82.76
CS	<i>Phleum spp.</i> <sup>b</sup>	graminoid	0.69	83.45
CS	<i>Atriplex spp.</i>	shrub	0.69	84.14
CS	<i>Prunus spp.</i>	shrub	0.68	84.82
CS	<i>Cornus sericea</i>	shrub	0.60	85.41
CS	<i>Comarum spp.</i> <sup>a</sup> , <i>Dasiphora fruticosa</i> <sup>a,b</sup> , <i>Drymocallis spp.</i> <sup>a</sup> , <i>Potentilla spp.</i> <sup>a</sup>	shrub	0.48	85.89
CS	<i>Acer spp.</i> <sup>b</sup>	shrub	0.45	86.34
CS	<i>Potentilla spp.</i>	shrub	0.44	86.78
CS	<i>Rhus trilobata</i>	shrub	0.40	87.18
CS	<i>Oxalis spp.</i>	forb	0.40	87.57
CS	<i>Gilia spp.</i>	forb	0.38	87.96
CS	<i>Apocynum spp.</i>	forb	0.36	88.32
CS	<i>Salsola spp.</i>	forb	0.34	88.65
CS	<i>Populus spp.</i>	shrub	0.34	88.99
CS	<i>Arctostaphylos uva-ursi</i> <sup>b</sup>	sub-shrub	0.32	89.31
CS	<i>Brassicaceae spp.</i>	forb	0.31	89.62
CS	<i>Asteraceae spp.</i> <sup>a</sup>	forb	0.30	89.92

**Table 5.1. (continued).**

Study area	Species name	Form	Mean % diet	Cumulative % diet
CS	<i>Epilobium spp.</i> <sup>b</sup>	forb	0.28	90.20
CS	<i>Penstemon spp.</i>	forb	0.28	90.49
CS	<i>Purshia tridentata</i>	shrub	0.27	90.75
CS	<i>Symphoricarpos spp.</i> <sup>b</sup>	shrub	0.24	90.99
CS	<i>Lilliaceae spp.</i> <sup>a</sup>	forb	0.24	91.23
CS	<i>Hedysarum spp.</i> <sup>a</sup> , <i>Sambucus spp.</i> <sup>a</sup>	forb, shrub	0.23	91.47
CS	<i>Helianthus spp.</i> <sup>a</sup> , <i>Ratibida columnifera</i> <sup>a</sup>	forb	0.23	91.70
CS	<i>Moneses uniflora</i> <sup>a</sup> , <i>Chimaphila umbellata</i> <sup>a</sup>	forb	0.22	91.92
CS	<i>Bromus japonicus</i>	graminoid	0.22	92.14
CS	<i>Chrysosplenium spp.</i>	forb	0.22	92.36
CS	<i>Lonicera spp.</i>	forb	0.21	92.57
CS	<i>Euphorbia spp.</i>	forb	0.20	92.76
CS	<i>Oenothera spp.</i>	forb	0.19	92.96
CS	<i>Galium spp.</i>	forb	0.19	93.14
CS	<i>Caprifoliaceae spp.</i>	forb, vine	0.18	93.33
CS	<i>Avena fatua</i>	graminoid	0.17	93.49
CS	<i>Picea spp.</i>	conifer	0.17	93.66
CS	<i>Solanum spp.</i>	forb	0.16	93.82
CS	<i>Xerophyllum tenax</i>	forb	0.14	93.95
CS	<i>Astragalus spp.</i>	forb	0.14	94.09
CS	<i>Larix occidentalis</i>	deciduous conifer	0.13	94.22
CS	<i>Quercus spp.</i>	deciduous tree	0.12	94.35
CS	<i>Comarum palustre</i>	forb	0.12	94.47
CS	<i>Papaveraceae spp.</i>	forb	0.12	94.58
CS	<i>Pedicularis spp.</i>	forb	0.11	94.69
CS	<i>Lotus corniculatus</i>	forb	0.10	94.79
CS	<i>Dactylis glomerata</i>	graminoid	0.10	94.89
CS	<i>Chimaphila umbellata</i>	forb	0.10	94.99
CS	<i>Triticum aestivum</i>	graminoid	0.09	95.08
CS	<i>Lactuca spp.</i>	forb	0.09	95.17

<sup>a</sup> DNA barcodes from ESV sequencing correspond with multiple forage taxa, resulting in duplicate estimates of % diet.

<sup>b</sup> Digestible energy estimates were collected from samples in these study areas.

**Table 5.2.** Summer diet species, sorted by % occurrence, and showing cumulative % of diet as each row is added in the Rocky Mountain Front (RMF) study area, 2018–2019.

Study area	Species name	Form	Mean % diet	Cumulative % diet
RMF	<i>Plantago spp.</i>	forb	16.09	16.09
RMF	<i>Fragaria spp.</i> <sup>a,b</sup> , <i>Rosa spp.</i> <sup>a,b</sup> , <i>Rubus spp.</i> <sup>a,b</sup>	forb	15.39	31.48
RMF	<i>Pinus spp.</i> <sup>b</sup>	conifer	6.78	38.26
RMF	<i>Oenothera spp.</i>	forb	6.17	44.43
RMF	<i>Ratibida columnifera</i>	forb	3.92	48.35
RMF	<i>Bromus tectorum</i> <sup>b</sup>	graminoid	3.83	52.18
RMF	<i>Eriogonum umbellatum</i> <sup>b</sup>	forb	3.52	55.71
RMF	<i>Rhamnus spp.</i>	shrub	2.43	58.13
RMF	<i>Lactuca spp.</i>	forb	2.28	60.42
RMF	<i>Spiraea spp.</i> <sup>b</sup>	shrub	2.24	62.66
RMF	<i>Hedysarum spp.</i> <sup>a</sup> , <i>Sambucus spp.</i> <sup>a</sup>	forb, shrub	2.23	64.89
RMF	<i>Chamerion angustifolium</i> <sup>a,b</sup> , <i>Oenothera spp.</i> <sup>a</sup>	forb	2.16	67.05
RMF	<i>Poa spp.</i> <sup>b</sup>	graminoid	1.89	68.94
RMF	<i>Sphaeralcea coccinea</i> <sup>a</sup> , <i>Malva parviflora</i> <sup>a</sup>	forb	1.72	70.66
RMF	<i>Amelanchier alnifolia</i> <sup>b</sup>	shrub	1.69	72.35
RMF	<i>Hedysarum spp.</i>	forb	1.50	73.85
RMF	<i>Phleum spp.</i> <sup>b</sup>	graminoid	1.25	75.10
RMF	<i>Asteraceae spp.</i> <sup>a</sup>	forb, shrub	1.24	76.34
RMF	<i>Pseudotsuga menziesii</i>	conifer	1.14	77.48
RMF	<i>Rumex spp.</i>	forb	0.99	78.47
RMF	<i>Salix spp.</i> <sup>b</sup>	shrub	0.94	79.41
RMF	<i>Prunus spp.</i>	shrub	0.81	80.22
RMF	<i>Bromus japonicus</i> <sup>b</sup>	graminoid	0.74	80.96
RMF	<i>Geranium spp.</i>	forb	0.73	81.70
RMF	<i>Rhododendron albiflorum</i>	shrub	0.72	82.42
RMF	<i>Potentilla spp.</i>	forb	0.70	83.12
RMF	<i>Amsinckia spp.</i> <sup>a</sup> , <i>Cynoglossus spp.</i> <sup>a</sup> , <i>Myosotis spp.</i> <sup>a</sup>	forb	0.69	83.81
RMF	<i>Mahonia spp.</i> <sup>b</sup>	shrub	0.67	84.48
RMF	<i>Medicago spp.</i>	forb	0.64	85.12
RMF	<i>Picea spp.</i>	conifer	0.59	85.71
RMF	<i>Ambrosia artemisiifolia</i>	forb	0.58	86.30
RMF	<i>Triticum aestivum</i> <sup>b</sup>	graminoid	0.56	86.86
RMF	<i>Purshia tridentata</i>	shrub	0.55	87.41
RMF	<i>Draba reptans</i>	forb	0.44	87.85
RMF	<i>Avena fatua</i>	graminoid	0.41	88.26
RMF	<i>Ribes spp.</i>	shrub	0.41	88.67
RMF	<i>Vaccinium spp.</i> <sup>b</sup>	shrub	0.40	89.06
RMF	<i>Saxifraga spp.</i> <sup>a</sup> , <i>Mitella spp.</i> <sup>a</sup> , <i>Heuchera spp.</i> <sup>a</sup>	forb	0.39	89.45
RMF	<i>Atriplex patula</i>	shrub	0.33	89.78
RMF	<i>Elymus spp.</i> <sup>a</sup> , <i>Pascopyrum smithii</i> <sup>a</sup> , <i>Triticum aestivum</i> <sup>a,b</sup>	graminoid	0.32	90.10
RMF	<i>Sparganium spp.</i>	forb	0.31	90.41

**Table 5.2. (continued).**

Study area	Species name	Form	Mean % diet	Cumulative % diet
RMF	<i>Koeleria macrantha</i> <sup>a,b</sup> , <i>Sphenopholis spp.</i> <sup>a</sup> , <i>Trisetum spp.</i> <sup>a,b</sup>	graminoid	0.31	90.72
RMF	<i>Geum triflorum</i>	forb	0.29	91.01
RMF	<i>Ericameria nauseosa</i>	forb	0.27	91.28
RMF	<i>Euphorbia spp.</i>	forb	0.27	91.55
RMF	<i>Ceanothus spp.</i> <sup>b</sup>	shrub	0.26	91.81
RMF	<i>Abies spp.</i>	conifer	0.25	92.06
RMF	<i>Astragalus spp.</i>	forb	0.24	92.29
RMF	<i>Moneses uniflora</i> <sup>a</sup> , <i>Chimaphila umbellata</i> <sup>a</sup>		0.23	92.53
RMF	<i>Crataegus spp.</i>	shrub	0.21	92.74
RMF	<i>Linum spp.</i>	forb	0.21	92.95
RMF	<i>Galium spp.</i>	forb	0.20	93.15
RMF	<i>Sanguisorba minor</i>	forb	0.20	93.35
RMF	<i>Plantago lanceolata</i>	forb	0.20	93.55
RMF	<i>Hordeum jubatum</i>	graminoid	0.20	93.75
RMF	<i>Achillea millefolium</i> <sup>a</sup> , <i>Artemisia spp.</i> <sup>a</sup> , <i>Leucanthemum vulgare</i> <sup>a</sup>	forb	0.19	93.94
RMF	<i>Malva parviflora</i>	forb	0.18	94.12
RMF	<i>Antennaria spp.</i>	forb	0.17	94.29
RMF	<i>Thalictrum spp.</i>	forb	0.17	94.46
RMF	<i>Lonicera spp.</i> <sup>a</sup> , <i>Balsamorhiza spp.</i> <sup>a</sup>	forb	0.16	94.62
RMF	<i>Shepherdia canadensis</i>	shrub	0.15	94.78
RMF	<i>Asteraceae spp.</i>	forb	0.15	94.93
RMF	<i>Lotus unifoliolatus</i>	forb	0.15	95.07

<sup>a</sup> DNA barcodes from ESV sequencing correspond with multiple forage taxa, resulting in duplicate estimates of % diet.

<sup>b</sup> Digestible energy estimates were collected from samples in these study areas.

**Table 5.3.** Summer diet species, sorted by % occurrence, and showing cumulative % of diet as each row is added in the Whitefish Range (WF) study area, 2018–2019.

Study area	Species name	Form	Mean % diet	Cumulative % diet
WR	<i>Plantago spp.</i>	forb	15.97	15.97
WR	<i>Fragaria spp.</i> <sup>a,b</sup> , <i>Rosa spp.</i> <sup>a,b</sup> , <i>Rubus spp.</i> <sup>a,b</sup>	forb	8.43	24.40
WR	<i>Pinus spp.</i> <sup>b</sup>	conifer	6.89	31.29
WR	<i>Bromus tectorum</i> <sup>b</sup>	graminoid	6.62	37.92
WR	<i>Hedysarum spp.</i> <sup>a</sup> , <i>Sambucus spp.</i> <sup>a</sup>	forb, shrub	4.17	42.08
WR	<i>Amelanchier alnifolia</i> <sup>b</sup>	shrub	4.14	46.22
WR	<i>Triticum aestivum</i> <sup>b</sup>	graminoid	3.68	49.91
WR	<i>Pseudotsuga menziesii</i>	conifer	3.55	53.46
WR	<i>Chamerion angustifolium</i> <sup>b</sup>	forb	2.92	56.38
WR	<i>Spiraea spp.</i> <sup>b</sup>	shrub	2.40	58.79
WR	<i>Ceanothus spp.</i> <sup>b</sup>	shrub	2.13	60.91
WR	<i>Medicago spp.</i>	forb	2.10	63.01
WR	<i>Poa spp.</i> <sup>b</sup>	graminoid	2.09	65.10
WR	<i>Salix spp.</i> <sup>b</sup>	shrub	1.70	66.80
WR	<i>Eriogonum umbellatum</i> <sup>b</sup>	forb	1.62	68.42
WR	<i>Elymus spp.</i> <sup>a</sup> , <i>Pascopyrum smithii</i> <sup>a</sup> , <i>Triticum aestivum</i> <sup>a,b</sup>	graminoid	1.45	69.87
WR	<i>Lonicera spp.</i>	shrub	1.26	71.13
WR	<i>Vaccinium spp.</i> <sup>b</sup>	shrub	1.24	72.37
WR	<i>Alnus spp.</i> <sup>b</sup>	deciduous tree	1.18	73.56
WR	<i>Linum spp.</i>	forb	1.18	74.73
WR	<i>Phleum spp.</i> <sup>b</sup>	graminoid	1.04	75.77
WR	<i>Rhododendron albiflorum</i>	shrub	0.98	76.75
WR	<i>Atriplex patula</i>	shrub	0.98	77.73
WR	<i>Avena fatua</i>	graminoid	0.92	78.65
WR	<i>Ribes spp.</i> <sup>b</sup>	shrub	0.91	79.56
WR	<i>Asteraceae spp.</i>	forb	0.86	80.42
WR	<i>Oenothera spp.</i>	forb	0.70	81.12
WR	<i>Fragaria vesca</i> <sup>b</sup>	forb	0.70	81.82
WR	<i>Sphaeralcea coccinea</i> <sup>a</sup> , <i>Malva parviflora</i> <sup>a</sup>	forb	0.68	82.50
WR	<i>Bromus japonicus</i> <sup>b</sup>	graminoid	0.67	83.16
WR	<i>Fraxinus spp.</i>	deciduous tree	0.60	83.76
WR	<i>Sanguisorba minor</i>	forb	0.57	84.33
WR	<i>Mahonia spp.</i> <sup>b</sup>	shrub	0.52	84.85
WR	<i>Purshia tridentata</i>	shrub	0.50	85.35
WR	<i>Picea spp.</i>	conifer	0.49	85.85
WR	<i>Crepis spp.</i>	forb	0.48	86.33
WR	<i>Gilia spp.</i>	forb	0.39	86.72
WR	<i>Crataegus spp.</i>	shrub	0.39	87.10
WR	<i>Epilobium spp.</i> <sup>b</sup>	forb	0.38	87.48
WR	<i>Trifolium spp.</i>	forb	0.38	87.86
WR	<i>Quercus spp.</i>	deciduous tree	0.37	88.23
WR	<i>Festuca spp.</i> <sup>a,b</sup> , <i>Vahlodea spp.</i> <sup>a</sup>	graminoid	0.37	88.60

**Table 5.3. (continued).**

Study area	Species name	Form	Mean % diet	Cumulative % diet
WR	<i>Hordeum jubatum</i>	graminoid	0.37	88.96
WR	<i>Acer spp.</i> <sup>b</sup>	shrub	0.36	89.32
WR	<i>Heuchera spp.</i>	forb	0.34	89.66
WR	<i>Erigeron spp.</i> <sup>a</sup> , <i>Ericameria nauseosa</i> <sup>a</sup>	forb	0.33	90.00
WR	<i>Thuja plicata</i>	conifer	0.33	90.32
WR	<i>Abies spp.</i>	conifer	0.31	90.63
WR	<i>Apiaceae spp.</i>	forb	0.28	90.91
WR	<i>Apocynum androsaemifolium</i>	forb	0.27	91.18
WR	<i>Potentilla spp.</i>	forb	0.27	91.45
WR	<i>Viola spp.</i>	forb	0.24	91.70
WR	<i>Ambrosia artemisiifolia</i>	forb	0.24	91.94
WR	<i>Juniperus spp.</i> <sup>b</sup>	shrub	0.22	92.16
WR	<i>Galium spp.</i>	shrub	0.22	92.38
WR	<i>Lactuca spp.</i>	forb	0.21	92.59
WR	<i>Rumex spp.</i>	forb	0.20	92.79
WR	<i>Saxifraga spp.</i> <sup>a</sup> , <i>Mitella spp.</i> <sup>a</sup> , <i>Heuchera spp.</i> <sup>a</sup>	forb	0.20	92.99
WR	<i>Stipa spp.</i>	forb	0.19	93.18
WR	<i>Ericameria nauseosa</i>	shrub	0.17	93.35
WR	<i>Brassicaceae spp.</i>	forb	0.14	93.49
WR	<i>Dactylis glomerata</i>	graminoid	0.14	93.63
WR	<i>Stachys spp.</i>	forb	0.13	93.76
WR	<i>Antennaria alpina</i>	forb	0.12	93.88
WR	<i>Ratibida columnifera</i>	forb	0.12	94.00
WR	<i>Populus spp.</i>	deciduous tree	0.20	94.20
WR	<i>Penstemon spp.</i>	forb	0.23	94.43
WR	<i>Liliaceae spp.</i>	forb	0.10	94.53
WR	<i>Rhus trilobata</i>	shrub	0.09	94.62
WR	<i>Betula spp.</i>	deciduous tree	0.09	94.71
WR	<i>Bromus hordeaceus</i>	graminoid	0.08	94.79

<sup>a</sup> DNA barcodes from ESV sequencing correspond with multiple forage taxa, resulting in duplicate estimates of % diet.

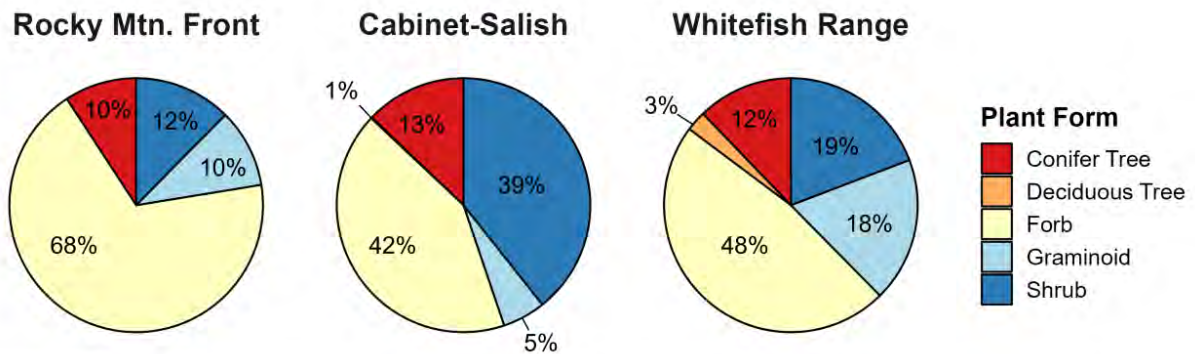
<sup>b</sup> Digestible energy estimates were collected from samples in these study areas.

## 5.2. Winter diet

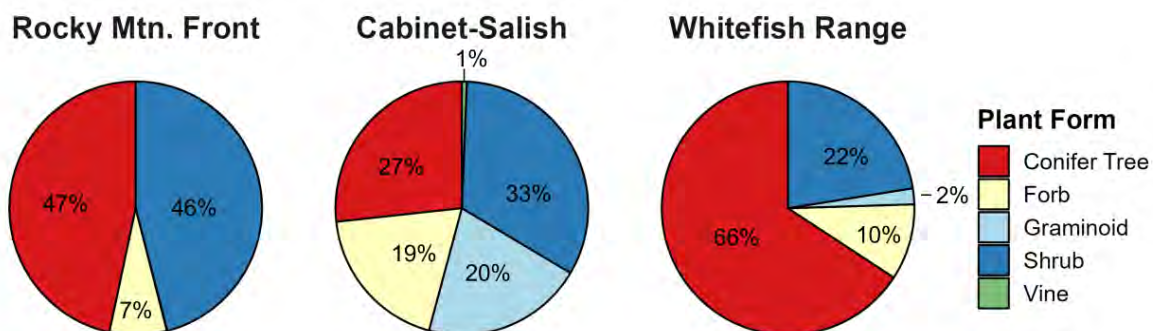
During winter, we collected fecal samples from captured deer plus a small number of additional samples from other individuals collected incidentally during capture efforts, totaling 136 samples: 45 in Cabinet-Salish, 49 on the Rocky Mountain Front, and 42 in the Whitefish Range.

In Cabinet-Salish, mule deer consumed Douglas fir (*Pseudotsuga menziesii*) more than any other plant taxa (26.7% of diet), followed by *Ceanothus* spp. (19.5%) and *Poa* spp. (15.5%; Table 5.4). On the Rocky Mountain Front, mule deer consumed Douglas fir more than other taxa (46.7%) followed by *Juniperus* spp. (13.4%) and *Ceanothus* spp. (11.6%; Table 5.5), and in the Whitefish Range, mule deer consumed Douglas fir (65.8%) the most, followed by Oregon grape (*Mahonia repens*, 5.3%) and Western red cedar (*Thuja plicata*, 4.6%; Table 5.6). After grouping species by functional type, conifer and shrub forage species were most used in all study areas, with their relative ranking differing among areas (Figure 5.1).

### A SUMMER



### B WINTER



**Figure 5.1.** Mule deer diet estimates summarized by plant functional group in each of three study areas for the A) summer and B) winter season, 2017–2019.

**Table 5.4.** Winter diet species, sorted by % occurrence within plant functional groups in the Cabinet-Salish (CS) study area, 2018–2019.

Study area	Species name	Growth form	Percent of diet	Percent by form
CS	<i>Pseudotsuga menziesii</i>	Conifer	23.64	26.72
CS	<i>Pinus spp</i>	Conifer	3.08	
CS	<i>Plantago spp</i>	Forb	11.35	19.1
CS	<i>Eriogonum umbellatum</i>	Forb	3.66	
CS	<i>Medicago lupulina</i>	Forb	2.10	
CS	<i>Heuchera cylindrica</i>	Forb	0.56	
CS	<i>Taraxacum spp.</i>	Forb	0.54	
CS	<i>Lactuca serriola</i>	Forb	0.28	
CS	<i>Verbascum thapsus</i>	Forb	0.20	
CS	<i>Potentilla recta</i>	Forb	0.15	
CS	<i>Solidago missouriensis</i>	Forb	0.12	
CS	<i>Geranium viscosissimum</i>	Forb	0.06	
CS	<i>Leucanthemum vulgare</i>	Forb	0.05	
CS	<i>Urtica dioica</i>	Forb	0.03	
CS	<i>Poa spp.</i>	Graminoid	15.54	20.64
CS	<i>Dactylus glomerata</i>	Graminoid	1.31	
CS	<i>Phleum pratense</i>	Graminoid	1.15	
CS	<i>Elymus spp. or Elymus spp.</i>	Graminoid	1.03	
CS	<i>Trisetum spicatum</i>	Graminoid	0.86	
CS	<i>Bromus inermis</i>	Graminoid	0.70	
CS	<i>Calamagrostis montanensis</i>	Graminoid	0.04	
CS	<i>Thinopyrum intermedium</i>	Graminoid	0.02	
CS	<i>Ceanothus spp.</i>	Shrub	19.52	32.92
CS	<i>Mahonia repens</i>	Shrub	7.79	
CS	<i>Amelanchier alnifolia</i>	Shrub	4.49	
CS	<i>Lonicera spp.</i>	Shrub	0.63	
CS	<i>Crataegus chrysocarpus</i>	Shrub	0.17	
CS	<i>Populus spp.</i>	Shrub	0.17	
CS	<i>Dasiphora spp. or Potentillas spp.</i>	Shrub	0.15	
CS	<i>Lonicera ciliata</i>	Vine	0.63	0.63



**Table 5.5.** Winter diet species, sorted by % occurrence within plant functional groups in the Rocky Mountain Front (RMF) study area, 2017–2019.

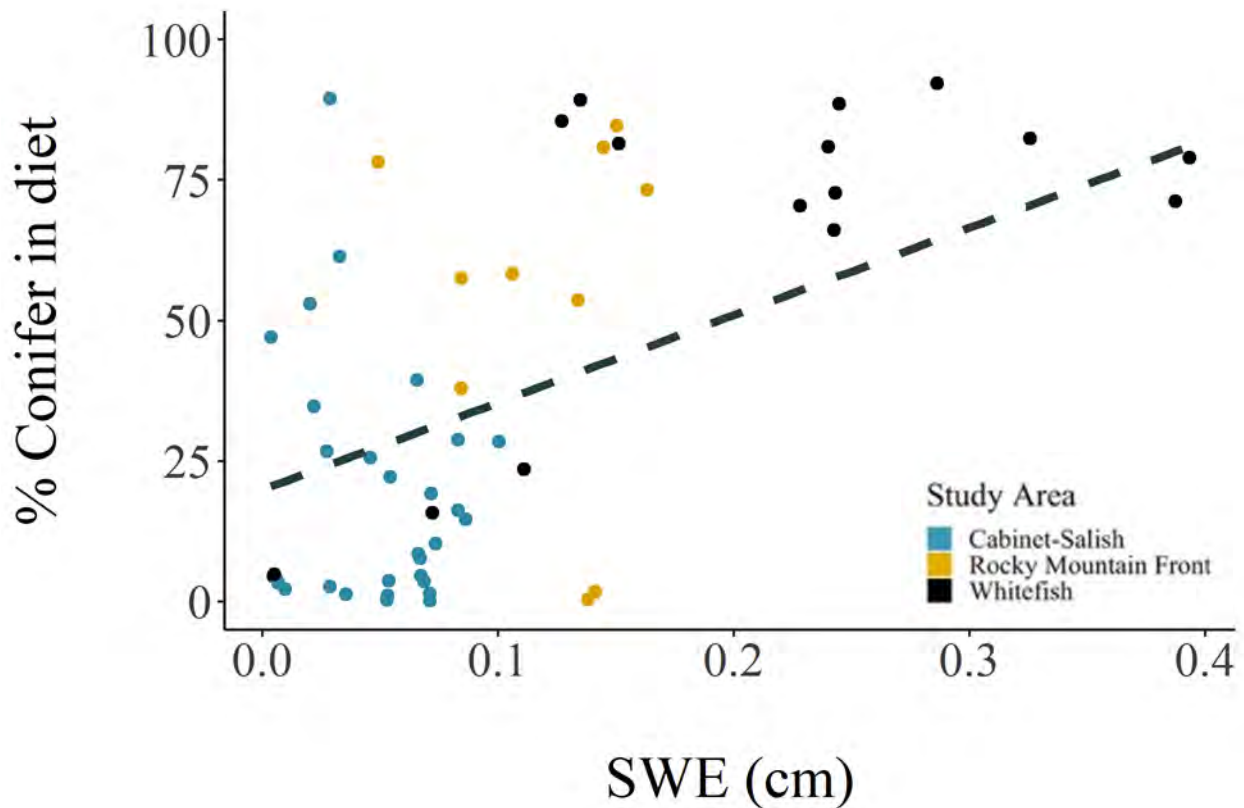
Study area	Species name	Growth form	Percent of diet	Percent by form
RMF	<i>Pseudotsuga menziesii</i>	Conifer	33.99	46.67
RMF	<i>Pinus contorta</i>	Conifer	10.33	
RMF	<i>Pinus ponderosa</i>	Conifer	2.35	7.32
RMF	<i>Heuchera spp.</i>	Forb	3.31	
RMF	<i>Hedysarum alpinum</i>	Forb	3.26	
RMF	<i>Cornus canadensis</i>	Forb	0.64	
RMF	<i>Leucanthemum vulgare</i>	Forb	0.06	
RMF	<i>Ratibida columnifera</i>	Forb	0.04	
RMF	<i>Polemonium sp</i>	Forb	0.02	
RMF	<i>Trisetum spicatum</i>	Graminoid	0.04	0.05
RMF	<i>Hordeum jubatum</i>	Graminoid	0.01	
RMF	<i>Juniperus spp.</i>	Shrub	13.37	45.96
RMF	<i>Ceanothus velutinus</i>	Shrub	11.60	
RMF	<i>Mahonia repens</i>	Shrub	5.23	
RMF	<i>Rhus trilobata</i>	Shrub	5.04	
RMF	<i>Amelanchier alnifolia</i>	Shrub	4.14	
RMF	<i>Prunus virginiana</i>	Shrub	3.09	
RMF	<i>Ribes spp.</i>	Shrub	1.08	
RMF	<i>Populus spp.</i>	Shrub	0.87	
RMF	<i>Acer glabrum</i>	Shrub	0.75	
RMF	<i>Cornus sericea</i>	Shrub	0.64	
RMF	<i>Sorbus scopulina</i>	Shrub	0.16	

**Table 5.6.** Winter diet species, sorted by % occurrence within plant functional groups in the Whitefish Range (WR) study area, 2017–2019.

Study area	Species name	Growth form	Percent of diet	Percent by form
WR	<i>Pseudotsuga menziesii</i>	Conifer	61.17	65.77
WR	<i>Thuja plicata</i>	Conifer	4.60	
WR	<i>Medicago lupulina</i>	Forb	4.07	9.72
WR	<i>Plantago lanceolata</i>	Forb	2.18	
WR	<i>Fragaria vesca</i>	Forb	0.78	
WR	<i>Erigeron spp.</i>	Forb	0.62	
WR	<i>Taraxicum officinale</i>	Forb	0.54	
WR	<i>Eriogonum umbellatum</i>	Forb	0.47	
WR	<i>Heuchera spp.</i>	Forb	0.39	
WR	<i>Lactuca serriola</i>	Forb	0.32	
WR	<i>Leucanthemum vulgare</i>	Forb	0.20	
WR	<i>Potentilla gracilis</i>	Forb	0.13	
WR	<i>Astragalus americanus</i>	Forb	0.01	
WR	<i>Elymus spp. or Pseudoregnaria spp.</i>	Graminoid	0.69	2.02
WR	<i>Phleum pratense</i>	Graminoid	0.60	
WR	<i>Dactylus glomerata</i>	Graminoid	0.45	
WR	<i>Bromus japonicus</i>	Graminoid	0.28	
WR	<i>Mahonia repens</i>	Shrub	5.33	22.49
WR	<i>Paxistima myrsinites</i>	Shrub	4.23	
WR	<i>Rhamnus alnifolia</i>	Shrub	3.24	
WR	<i>Acer glabrum</i>	Shrub	2.70	
WR	<i>Ceanothus velutinus</i>	Shrub	2.48	
WR	<i>Salix sp</i>	Shrub	2.16	
WR	<i>Prunus virginiana</i>	Shrub	0.77	
WR	<i>Sorbus spp.</i>	Shrub	0.53	
WR	<i>Alnus viridis</i>	Shrub	0.52	
WR	<i>Rhododendron columbianum</i>	Shrub	0.40	
WR	<i>Potentilla spp.</i>	Shrub	0.13	

**5.2.1. Snow-affected use of conifer in the winter diet.**— Our diet data revealed notable variation (30–66%) in the percentage of winter diets composed of conifer species. We hypothesized that conifers may become more important when snow restricts access to herbaceous and shrub forage. To further explore this hypothesis, we conducted a simple post-hoc analysis exploring proportionate use of conifer as a function of the snow conditions faced by each deer. We used daily snow water equivalent (SWE; Barrett 2003) rasters at 1-km<sup>2</sup> resolution to quantify snow conditions over time and space in each study area. We then summarized the average SWE for each deer using individual deer home ranges and according to 2 treatments of time: 1) first, using SWE conditions on the date the deer was captured, and 2) second, using mean SWE across the entire winter when the animal was captured. We used beta regression to statistically assess this relationship, considering both linear and log-transformed treatments of SWE during modeling.

We found a significant relationship ( $\chi^2_{(1, 71)} = 28.66, p < 0.001$ ), and a  $R^2$  of 0.27 (Figure 5.2) between the amount of conifer species in an individual’s diet and the average SWE the individual experiences in their home range. The relationship was stronger when measuring snow at the time of capture (when fecal samples were collected) compared to the average SWE across the entire winter of capture, suggesting this relationship may vary over time for each individual deer.



**Figure 5.2.** Positive correlation ( $R^2=0.27$ ;  $P<0.001$ ) between an individual mule deer’s proportionate use of conifer in its diet and the average snow accumulation (snow water equivalent [SWE]) at the time of sample collection, western Montana, 2017–2019.

## 6. SUMMER HABITAT RELATIONSHIPS

### 6.1. Vegetation sampling and forage modeling

As a currency for indexing nutritional resources available to mule deer on the landscape during summer, we integrated the biomass and digestible energy (DE, in kcal/g) per unit biomass of forage on the landscape into a metric reflecting the spatial distribution of kilocalories (kcal) of forage/m<sup>2</sup> across each of our study areas. Our methods for indexing nutritional resources fell into 5 stages: 1) estimating species-specific biomass (in g/m<sup>2</sup>) of forage on the landscape through ground-based vegetation sampling; 2) estimating the composition of mule deer diets via fecal DNA-metabarcoding; 3) estimating DE of forage species in mule deer diets; 4) combining estimates of species-specific forage biomass and DE to estimate kcal of forage/m<sup>2</sup> at each of our vegetation sampling sites; and 5) developing generalized linear models (GLMs) for predicting the spatial distribution of nutritional resources across each of our study areas.

Within each study area, we conducted summer vegetation surveys at a stratified sample of random points (Figures 6.1, 6.2), with stratification factors of 3 undisturbed cover types (conifer forest, grassland, shrubland) and 4 disturbance types (wildfire, prescribed fire, harvest, and harvest followed by prescribed fire; Figure 6.3). We defined disturbance patches using LANDFIRE polygons global forest change (GFC) data. Concurrent with field sampling of disturbance patches, we also sampled points in undisturbed forest to capture vegetative differences between disturbed and undisturbed forest. We selected reference locations in undisturbed forests with similar slope, aspect, and elevation to that at sampled points within disturbance patches. To improve field efficiency, reference points were placed ≤1.5 km from sampled disturbance patches. To avoid edge effects on plant responses (Ries et al. 2004), both disturbance and reference points were ≥100 m from disturbance patch boundaries.

At each sampling site (Figure 6.1), we established a 40-m transect along the contour of the hillslope. At the 0, 20-m, and 40-m mark on the transect, we recorded plant species composition and visually estimated percent cover of each vascular plant species within a 1-m<sup>2</sup> quadrat (Proffitt et al. 2016). In the corner of each 1-m<sup>2</sup> quadrat, we established a 0.5-m<sup>2</sup> clip plot in which we visually estimated percent cover of graminoids, forbs, and shrubs, then clipped and collected all the aboveground biomass of these forage classes within the clip plot into separate paper bags.

To evaluate quality of forage taxa, we estimated their mean DE (in kcal/g) across phenological stages present during summer using sequential detergent fiber analysis (Van Soest 1982) for a subset of forage taxa collected in the field, and used DE or dry-matter digestibility (DMD) values from previous studies for remaining taxa. For forage taxa collected during this study, we calculated the mean phenological stage-specific DMD adjusted for tannin content using an equation from (Robbins et al. 1987a, b):

$$DMD = [(0.9231 e^{-0.0451 \times ADL} - 0.03 \times AIA) (NDF)] + [(-16.03 + 1.02 NDS) - 2.8 \times P], \text{ (eq. 5.1)}$$

where ADL is acid detergent lignin (%), AIA is acid insoluble ash (%) of monocots, NDF is neutral detergent fiber (%), NDS is neutral detergent soluble (%), and P is the reduction in protein digestion (%). We estimated P as  $11.82 \times BSA$ , where BSA is the level of bovine serum albumin (Robbins et al. 1987b); BSA is an index of the inhibiting effect of increasing tannins measured in milligrams of BSA precipitated per milligram of dry matter forage. We obtained ADL, AIA, NDF, and NDS values from DairyOne laboratories (Ithaca, NY, USA). We obtained BSA values for shrubs containing tannins from the Wildlife

Habitat Nutrition Laboratory (Pullman, WA, USA) and assumed BSA values to be zero for forbs and graminoids that typically do not contain tannins. We then estimated phenological stage-specific DE of each forage plant collected using an equation from Cook et al. (2016):

$$DE = (DMD/100) \times GE, \quad (\text{eq. 5.2})$$

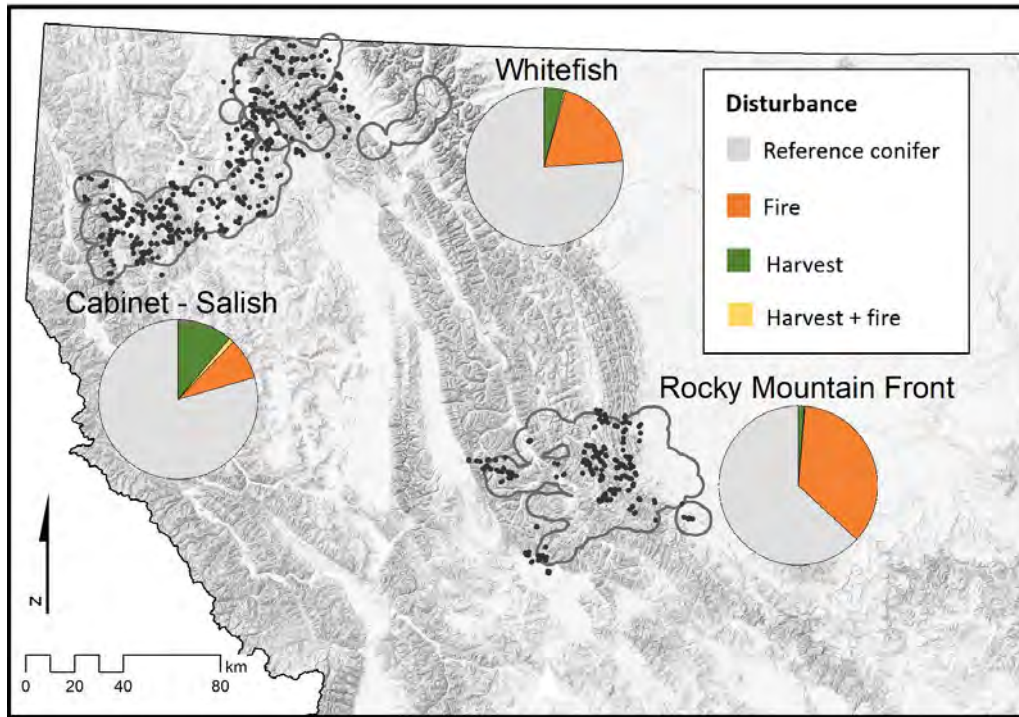
where GE is gross energy content estimated as 4.53 kcal/g for forbs, graminoids, and deciduous shrubs and 4.8 kcal/g for evergreen shrubs (Cook et al. 2016). We then averaged across phenological stage-specific DE values to estimate mean summer DE of forage. For forage taxa that were not collected in the field, we used DE or DMD values reported in previous studies conducted in either southwest Montana (Proffitt et al. 2016), northeast Washington (Hull 2018), or northeast Oregon, USA (Wagoner 2011; Peterson et al. In press).

We combined our DE estimates with species-specific biomass estimates to calculate kcal of forage/m<sup>2</sup> at each quadrat, then took the average of quadrat-level forage estimates to characterize site-level forage. We used site-level data to develop generalized linear models with remotely sensed covariates for predicting mean kcal/m<sup>2</sup> during summer (Figure 6.4).



**Figure 6.1.** *Vegetation plot and transect sampling for estimating plant community composition, summer forage biomass and digestible energy.*

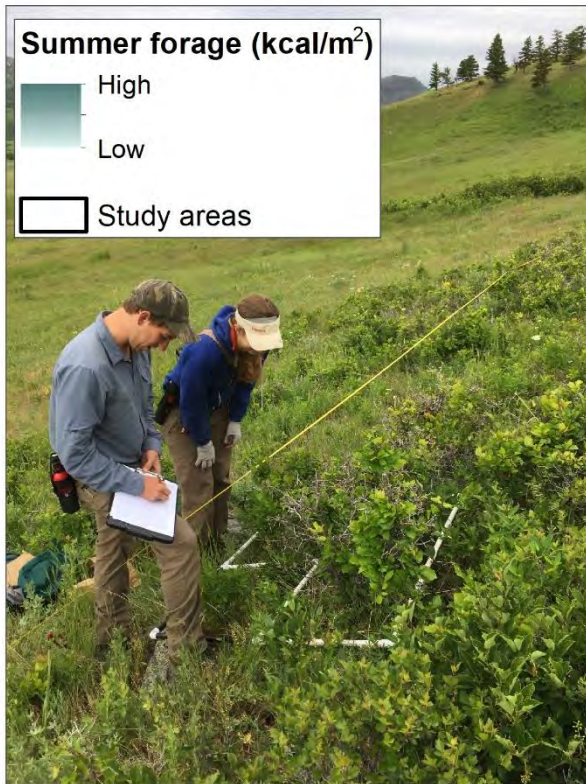
We field-sampled vegetation communities and biomass at 884 points (286 in the Rocky Mountain Front, 325 in the Cabinet-Salish Mountains, and 273 in the Whitefish Range) and made predictions of forage digestible energy (kcal/m<sup>2</sup>) per study area (Figure 6.4; Peterson et al. In press). For paired comparisons of disturbance and reference conifer forests, we sampled 336 points in reference conifer forest, 70 in harvest followed by prescribed fire, 135 in harvest, and 143 in wildfire and prescribed fire patches.



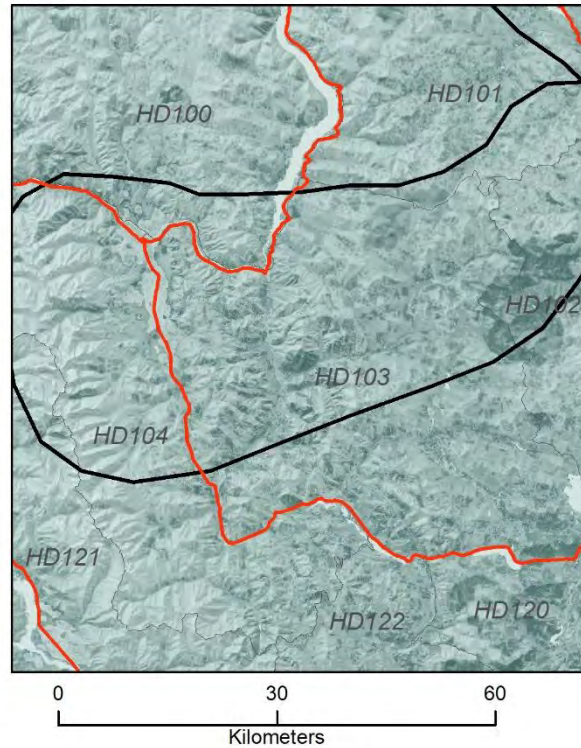
**Figure 6.2.** Annual mule deer ranges in 3 study areas (polygons), proportionate forest disturbance history within each study area (pie charts), and sampling locations of forest vegetation surveys (black points), June 1 – August 31, 2017–2019.



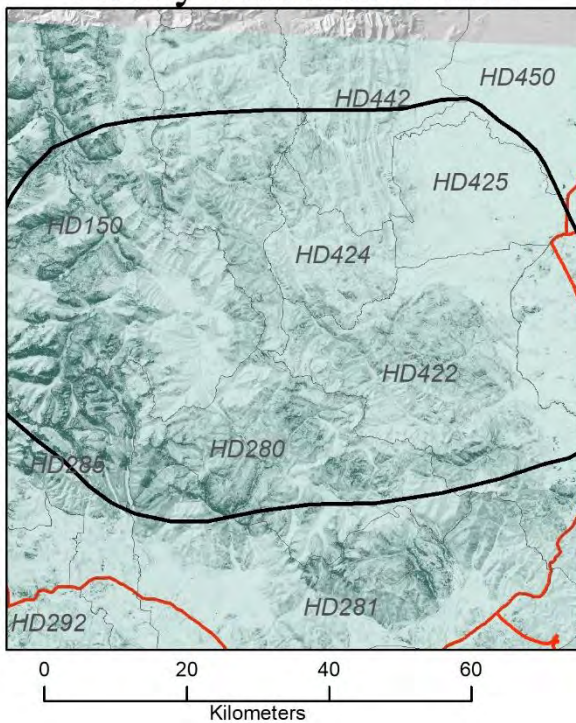
**Figure 6.3.** Example vegetation sampling site within a wildfire disturbance patch in the Pretty Prairie area of the Rocky Mountain Front study area, July 2017.



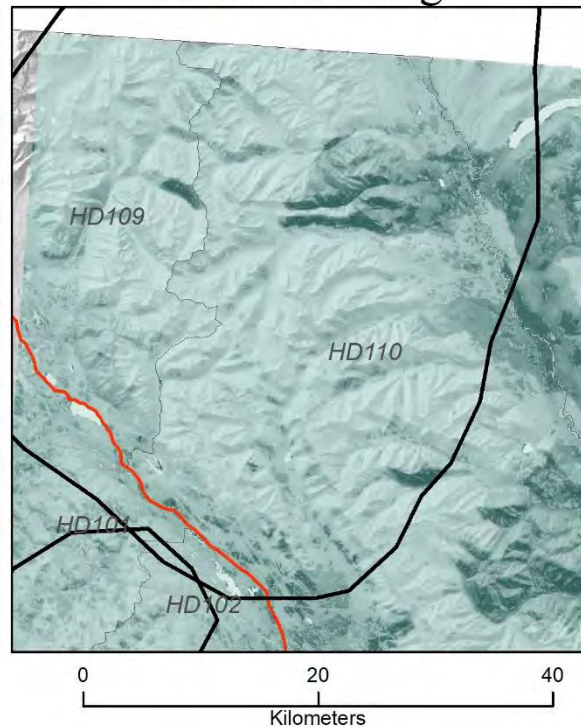
### Cabinet-Salish Mountains



### Rocky Mountain Front



### Whitefish Range



**Figure 6.4.** Predicted summer forage quality (digestible energy in kcal/m<sup>2</sup>) across three study areas in western Montana. Note color ramps are scaled differently in each panel, so relative quality values are depicted within each area but values not comparable across panels as shown here, 2017–2019.

## 6.2. Vegetation response to forest disturbance

(Note: this portion of study has been published at a peer-reviewed journal. Below is an abridged summary; see manuscript for full details)

Hayes, T. A., N. J. DeCesare, C. J. Peterson, C. J. Bishop, and M. S. Mitchell. 2022. Trade-offs in forest disturbance management for plant communities and ungulates. *Forest Ecology and Management* 506:119972.

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**6.2.1. Background**—Forest disturbances can be a tool to meet a variety of objectives, such as increasing the prevalence of early successional stands, improving wildlife habitat (Hebblewhite et al. 2009, Rowland et al. 2018) or managing the prevalence and spread of exotic species (U.S. Forest Service 2013). Habitat management guidelines for many state and federal agencies in the western United States include forest treatment recommendations to improve mule deer forage quality and quantity (Hayden et al. 2008). Although forest disturbance has been established as an important way for managers to redistribute and enhance nutritional resources for mule deer (Hayden et al. 2008, Lehmkuhl et al. 2001), the effects of different disturbance types and subsequent succession on nutritional resources remain less clear. Site- and disturbance-specific factors, including forest type, severity and timing of disturbance, and patterns of tree regeneration after disturbance influence the response and nutritional value of understory vegetation (Sachro et al. 2005, Romme et al. 2016). Disturbance from wildfires can create a mosaic of vegetation that benefits mule deer (Patton and Gordon 1995, Roerick et al. 2019). Lower-severity prescribed fire had minimal effect on forage quality in some studies (Wood 1988) or a short-term increase in others (Keay and Peek 1980, Hobbs and Spowart 1984). Whereas forest thinning has produced mixed effects on forage responses and habitat selection by mule deer (Long et al. 2008, Kramer et al. 2015, Roerick et al. 2019), other mechanical treatments have shown some evidence for enhancing deer population performance, depending upon the response metric being measured (Bergman et al. 2014a, 2014b; 2015).

Vegetative responses to forest disturbance clearly have other management implications beyond those specific to herbivorous wildlife. Disturbances are often considered a contributing factor to successful invasion by non-native plant species and to concomitant declines in biodiversity (Parks et al. 2005, Willms et al. 2017). For example, wildfires have been associated with increases in non-native species (Rew and Johnson 2010) and greater increases have followed forest thinning compared to prescribed fire (Willms et al. 2017). Facing multiple objectives of promoting biodiversity, minimizing invasive species, and promoting wildlife habitat (among many others), managers thus encounter trade-offs when making decisions that bridge conservation objectives.

A variety of tools and practices are available to balance multiple criteria for forest management decisions (Ananda and Herath 2009), including decision analysis (Kangas and Kangas 2005). Decision analysis is an approach for selecting among actions that have uncertain outcomes, where decision makers evaluate each alternative action with the same set of criteria, then rank alternatives based on their performance across all criteria. This process can be used to evaluate consequences and trade-offs among alternatives and identify the most optimal decision while accounting for the priorities of the decision-maker.

Here, we studied the effects of forest disturbances on summer plant communities in 3 regions of Montana, each with different disturbance regimes and each occupied by mule deer. We summarized



vegetation responses according to 3 metrics with potential management relevance: 1) forage nutrition for mule deer, 2) invasive species biomass, and 3) ecological value and conservatism, as indexed by the floristic quality assessment index (FQAI; LaPaix et al. 2009). We used generalized linear modelling of vegetation metrics to predict management outcomes of different disturbance types, and evaluated trade-offs amongst outcomes using decision analysis (Kangas and Kangas 2005, Eggers et al. 2019).

**6.2.2. Methods**—We identified three types of forest disturbance (fire [predominately wildfire but also including prescribed fire], harvest, and harvest followed by prescribed fire) using a combination of LANDFIRE (LF; LANDFIRE 2012) and global forest change (GFC; Hansen et al. 2013) remotely-sensed data. We further categorized disturbances according to LF disturbance severity categories (low, medium, high), and calculated time since disturbance as the difference between the disturbance event and the year of field data collection.

We then summarized summer plant community and biomass field data (see Section 6.1) according to 3 metrics of vegetative response: 1) mule deer forage nutrition (see Section 6.1), 2) invasive species biomass, and 3) floristic quality, a metric of ecological value and conservatism indexed by FQAI (LaPaix et al. 2009). Floristic quality is calculated for each plant species encountered in vegetation field sampling, and then integrated into FQAI according to:

$$FQAI = \bar{C} (\sqrt{N}), \text{ (eq. 5.3)}$$

where  $\bar{C}$  represents the average coefficient of conservatism for native species according to expert opinion (Pipp 2017), and  $N$  is the total number of native plant species (La Paix et al. 2009). Values of  $\bar{C}$  for each species range from 0 to 10, where 0 represents a non-native species, species with low values have a wide range of ecological tolerances and are found in variety of plant communities, while species with high values have a narrow range of ecological tolerances, are less tolerant of disturbance, and typically reside in stable or advanced stages of community plant succession (Pipp 2017).

We used general linear models to investigate the relationships between disturbance type and three different vegetation response metrics: i) forage nutrition, ii) invasive species biomass, and iii) floristic quality. Using each metric as the response variable of 3 separate modeling exercises, we also evaluated 7 additional covariates shown previously to influence forage nutrition in previous studies (Peek et al. 2001, Sachro et al. 2005, Romme et al. 2016, Davis et al. 2019): forest type, canopy cover, aspect, elevation, time since disturbance, severity of disturbance, and water deficit. We began model selection procedures with a base model that included the interaction of disturbance type and study area. We then added individual variables in a manual, forward stepping approach according to their univariate significance according to inspection of both significance tests and Akaike Information Criteria (AIC), while ensuring variance inflation factors < 2.0 (Arnold et al. 2010, Zuur et al. 2010). We conducted exploratory analyses interacting disturbance severity with each disturbance type and study area to explore whether severity had unique implications for different disturbance types among study areas and subsequently subdivided disturbance type categories by severity category for significant combinations. We identified the best-supported models using AIC and used  $R^2$  values to assess model fit.

We conducted multi-criteria decision analysis (Kangas and Kangas 2005) to explore management decisions as a function of multiple potential management actions, study areas (reflecting different disturbance regimes), and metrics of vegetative response. We first used unstandardized coefficient estimates from each top-ranked model to predict forage nutrition, invasive species biomass, and habitat

condition across all study areas. Next, we used the simple multi-attribute rating technique (SMART; Edwards and Barron 1994, Monat 2009) to compare vegetative responses to forest management options. We populated a consequence table to list possible management objectives, here measured as vegetation metrics, and management actions in a SMART spreadsheet (Runge et al. 2011). Then, we illustrated trade-offs by normalizing predicted values between 0-1 using an experiential global scale, in which the highest possible value was remapped to 1 while the lowest possible value was remapped to 0, following Monat (2009). We defined global scales for each study area using the 5th and 95th percentiles of field data collected to define reasonable bounds for each response metric. Thus, scores for each disturbance type were normalized so that the observed level of variation in field data defines the limits on achievable values for a given management objective in a given area. Alternatives with higher scores were more likely to achieve a desired outcome than alternatives with lower scores. Lastly, we evaluated the effect of weighting among objectives using 3 weighting schemes to represent different management priorities under different local circumstances: 1) equal priority among objectives, 2) mule deer forage as priority, and 3) minimizing invasive species as priority.

**6.2.3. Results & Discussion— The best-supported model predicting forage nutrition** ( $R^2 = 0.258$ ; Table 6.1) included water deficit ( $\beta = 0.23$ ) and canopy cover ( $\beta = -0.22$ ) as well as base variables for disturbance type interacted with study area. The Whitefish Range tended to have greater forage nutrition within forested sites than other study areas, predicting that reference forests produce, on average, 184% greater forage nutrition than those at the Cabinet-Salish and 249% more than those at the Rocky Mountain Front. Disturbance generally increased nutrition in all study areas (Table 6.1, Figure 6.5). The exceptions were a lack of increase in forage associated with harvest and harvest followed by prescribed fire in the Rocky Mountain Front, where availability of such types is low and data were constrained by small sample sizes ( $n = 12, 7$ , respectively). In this study area, fire had a weakly positive effect on forage, with a mean nutrition value of 2.1 kcal/m<sup>2</sup> (95% CI: 1.36 - 3.16 kcal/m<sup>2</sup>) being 217% greater than that in reference forests. In the Cabinet-Salish, disturbance from fire had 413% greater forage nutrition (CI: 3.30 - 8.47 kcal/m<sup>2</sup>) than undisturbed forests (CI: 0.88-1.90 kcal/m<sup>2</sup>). In the Whitefish Range, high severity harvest had the greatest effect on forage nutrition with a mean value of 11.09 kcal/m<sup>2</sup> (CI: 6.88 - 16.73 kcal/m<sup>2</sup>) being 452% greater than that in undisturbed forests, followed by fire with 7.40 kcal/m<sup>2</sup> (CI: 4.70 - 10.97 kcal/m<sup>2</sup>) being 302% greater than that in reference forests.

**The best-supported model of invasive species biomass** included disturbance type interacted with study area as well as additional effects of water deficit and forest type (Table 6.1). Overall, invasive species biomass increased in harvests across all study areas (Figure 6.5). In the Cabinet-Salish and Whitefish ranges, where we sampled low- and high-severity harvests, this effect was driven by high severity harvests. High severity harvests had a mean invasive species biomass of 0.06 g/m<sup>2</sup> (95% CI: 0.01 - 0.18) in the Cabinet-Salish and a mean of 0.21 g/m<sup>2</sup> (CI: 0.07 - 0.47) in the Whitefish Range. In both areas, low-severity harvest had a weak, positive influence on biomass of invasive species. In the Cabinet-Salish, the effect of fire was strongly positive and similar to that of high-severity harvest, with a mean biomass of 0.09 g/m<sup>2</sup> (CI: 0.02- 0.23). However, fire was only weakly significant in the other study areas. We compared the occurrence of common invasive species that are of high concern for land and wildlife managers (Fig. 6.6). Annual bromes were most prevalent in fires and harvests in the Cabinet-Salish, a result that was driven primarily by cheatgrass, due to the relatively limited occurrence of other annual bromes. Thistles (*Cirsium* spp.) were found primarily in harvests and harvest combined with fire in the Whitefish Range. Less mobile invaders, including knapweed, hawkweed (*Hieracium* spp.), prickly lettuce (*Lactuca serriola*), and mullein (*Verbascum thapsus*) tended to be most common in harvests, harvests followed by prescribed fire, and with intermediate occurrence in fires. Generally, annual bromes and

knapweed were much more abundant in the Rocky Mountain Front and Cabinet-Salish areas than in the Whitefish Range.

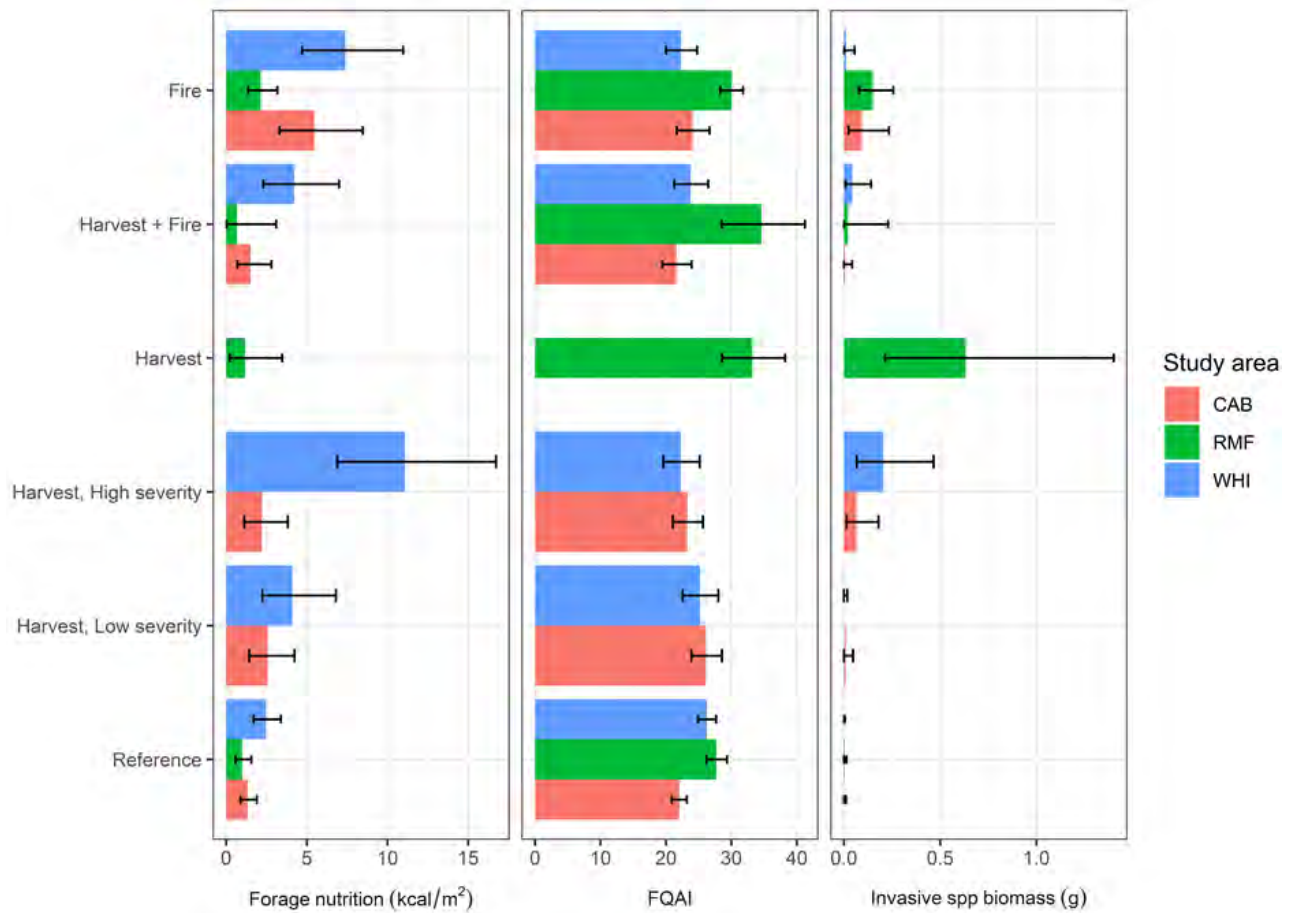
**Table 6.1.** Standardized coefficient estimates, standard errors, and significance for the best-supported models of forage nutrition, invasive species biomass, and floristic quality for mule deer during summer, 2017–2019. Undisturbed conifer forest in the Cabinet-Salish study area served as the reference category for comparison with other included categorical combinations of study area and disturbance type.

Covariate	Forage nutrition (kcal/m <sup>2</sup> )			Invasive species biomass (g/m <sup>2</sup> )			Floristic quality (FQAI)		
	$\beta$	SE	p	$\beta$	SE	p	$\beta$	SE	p
(Intercept)	1.10	0.07	<0.001	0.28	0.06	<0.001	4.69	0.06	<0.001
Water deficit	0.23	0.03	<0.001	0.09	0.02	<0.001	0.04	0.03	0.20
Canopy cover	-0.22	0.04	<0.001						
CAB*Fire	0.67	0.16	<0.001	0.33	0.09	<0.001	0.21	0.14	0.14
CAB*Harvest, Low Severity	0.27	0.14	0.06	0.08	0.08	0.33	0.42	0.13	0.00
CAB*Harvest, High Severity	0.20	0.15	0.19	0.28	0.08	0.00	0.13	0.14	0.34
CAB*Harvest + Fire	0.05	0.16	0.76	0.06	0.08	0.46	-0.04	0.14	0.75
RMF*Conifer	-0.11	0.11	0.33	0.02	0.07	0.81	0.57	0.10	<0.001
RMF*Fire	0.19	0.12	0.12	0.41	0.07	<0.001	0.79	0.10	<0.001
RMF*Harvest	-0.04	0.25	0.86	0.74	0.14	<0.001	1.07	0.22	<0.001
RMF*Harvest + Fire	-0.23	0.31	0.46	0.16	0.17	0.37	1.19	0.28	<0.001
WHI*Conifer	0.25	0.10	0.01	-0.05	0.06	0.40	0.43	0.09	<0.001
WHI*Fire	0.85	0.16	<0.001	0.10	0.09	0.25	0.03	0.14	0.84
WHI*Harvest, Low Severity	0.50	0.17	<0.001	-0.04	0.09	0.69	0.33	0.15	0.03
WHI*Harvest, High Severity	1.13	0.19	<0.001	0.47	0.10	<0.001	0.03	0.16	0.87
WHI*Harvest + Fire	0.52	0.17	<0.001	0.23	0.09	0.01	0.18	0.15	0.22
Dry Forest				-0.13	0.05	0.02			
Mesic Forest				-0.16	0.06	0.01			

The best-supported model of floristic quality included disturbance type interacted with study area and an additional effect of water deficit ( $R^2 = 0.16$ ; Table 6.1). Floristic quality values for surveyed locations ranged from 4.0 to 60.9, with a mean value of 25.8. Mean floristic quality values were greater in harvests compared to reference conifer forests (Figure 6.5). Overall, disturbance had a positive effect in the Rocky Mountain Front and the Cabinet-Salish Mountains. Values for reference forests were less variable than any disturbance type. Reference forests in the Rocky Mountain Front area had the greatest mean floristic quality among study areas, with 27.7 (95% CI: 26.2 – 29.3), followed by the Whitefish Range (26.3, CI: 24.9 – 27.7), with the lowest and most consistent values in the reference area, the Cabinet-Salish Mountains with 22.0 in reference forests (CI: 20.9 – 23.2).

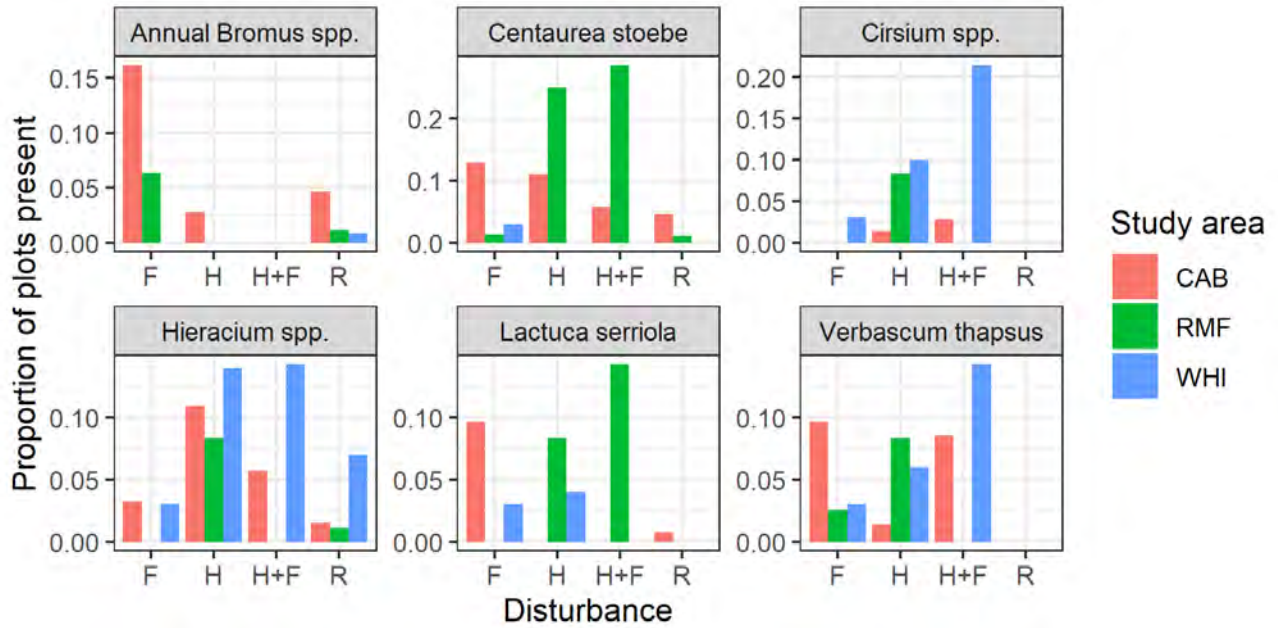
We used best-supported models to predict responses of forage nutrition, invasive species biomass, and floristic quality in each study area, and we used 5th and 95th percentile values from field data to rescale predictions to normalized values within each study area (Table 6.2). Comparison of normalized vegetative responses revealed differences in the outcomes of disturbance types between study areas. With all management objectives weighted equally, low-severity harvests had the highest total score in the Cabinet-Salish (1.781, reference = 1.513) and in the Whitefish Range (1.649, reference = 1.633). In the Rocky Mountain Front, harvest combined with fire had the highest score (1.661) compared to reference forest (1.439). The same management alternatives received the highest scores when control of invasive species is the highest priority. When prioritizing forage however, optimal outcomes changed

in all areas. Fire in the Cabinet-Salish and Rocky Mountain Front produced the greatest increase in forage nutrition, whereas high-severity harvest maximized forage predictions in the Whitefish Range.



**Figure 6.5.** Predicted forage nutrition ( $\text{kcal}/\text{m}^2$ ), invasive species biomass, and FQAI in fire, harvest with prescribed fire, harvest, and reference forests in northwest Montana, USA, during summer, 2017–2019.





**Figure 6.6.** Proportion of vegetation plots where particular invasive species were recorded in reference conifer forest (R) and 3 disturbance types: fire (F), harvest (H), and harvest with prescribed fire (H+F) in 3 study areas, 2017–2019.

**Table 6.2.** Decision analysis results showing normalized predicted outcomes for each of three vegetation response metrics (forage nutrition, invasive species biomass, and floristic quality) according to study area and disturbance type, and total scores under three weighting scenarios prioritizing the vegetation metrics in different ways, western Montana, 2017–2019.

Disturbance	Forage nutrition	Invasive sp. biomass	Floristic quality	Total scores, by weighting scheme			
				Equal	Maximize forage	Minimize invasive spp.	
CAB	Fire	0.28	0.95	0.55	1.775	<b>1.397</b>	2.204
	Harvest, Low severity	0.13	1.00	0.65	<b>1.781</b>	1.225	<b>2.265</b>
	Harvest, High severity	0.11	0.96	0.51	1.585	1.084	2.108
	Harvest + Fire	0.08	1.00	0.43	1.499	0.990	2.096
	Reference	0.07	1.00	0.45	1.513	0.988	2.108
RMF	Fire	0.11	0.98	0.47	1.557	<b>1.069</b>	2.106
	Harvest	0.06	0.90	0.58	1.542	0.999	2.003
	Harvest + Fire	0.04	1.00	0.63	<b>1.661</b>	1.039	<b>2.193</b>
	Reference	0.05	1.00	0.39	1.439	0.925	2.063
WHI	Fire	0.30	0.99	0.34	1.633	1.339	2.171
	Harvest, Low severity	0.17	1.00	0.48	<b>1.649</b>	1.188	<b>2.189</b>
	Harvest, High severity	0.45	0.85	0.34	1.641	<b>1.523</b>	2.007
	Harvest + Fire	0.17	0.97	0.41	1.553	1.136	2.095
	Reference	0.10	1.00	0.53	1.633	1.099	2.180

Our results suggest that several mechanisms are likely driving forage availability, invasive species, and floristic quality: 1) the pre-existing abiotic conditions and composition of plant communities in the absence of disturbance, 2) study area-level factors and disturbance frequency, and 3) disturbance-specific effects on vegetative responses.

This study revealed that no single management action is likely to yield optimal results across regions for every objective. However, applying models to field-collected data allowed us to predict outcomes in multiple settings and to account for some of the uncertainty in vegetative responses to disturbance. Generally, disturbances tended to increase all measured vegetation responses: forage nutrition, invasive species biomass, and floristic quality, so that the benefits of management actions come with less optimal outcomes for other objectives. Our results add to other work that suggests that increased canopy openings, particularly in areas with limited disturbance regimes, will likely increase forage availability. For all study areas, we found that low-severity harvest is a management option that may balance increases in forage nutrition while limiting invasive species and maintaining floristic quality. Vegetative responses to fire varied, with the greatest increases in forage nutrition occurring in the Whitefish range, followed by the Cabinet-Salish Mountains. Dry sites and open woodland, particularly after fire, may benefit from restoration management to help improve resiliency to subsequent disturbance and reduce invasive species biomass and spread. Most forest sites show minimal changes or slight increases in average floristic quality with disturbance, but for those that support high floristic quality, management that minimizes disturbance frequency and severity will allow for the persistence of plants with high site-fidelity.

Through SMART analysis, managers can define their own priorities to weigh the relative merits of management actions in differing disturbance regimes. The use of decision analysis provides managers more information to develop strategies for land management and to identify treatments to balance objectives for management of mule deer. Decision analysis tools can improve the interpretability of complicated information and thus have potential for wide application in forest and other natural-resource management. These tools can be used in similar ways to provide a reproducible process for decision-making, inform planning efforts, manage risks, and make comprehensive use of different kinds of information from multiple sources.



### 6.3. Risk-forage trade-offs

(Note: this portion of study has been peer-reviewed and published within 2 manuscripts, available at the links below. Below is an abridged summary; see manuscripts for full details).

Peterson, C. J., M. S. Mitchell, N. J. DeCesare, C. J. Bishop, and S. S. Sells. 2021. Habitat selection by wolves and mountain lions during summer in western Montana. *PLoS One* 16:e0254827. <https://doi.org/10.1371/journal.pone.0254827>

Peterson, C. J., N. J. DeCesare, T. A. Hayes, C. J. Bishop, and M. S. Mitchell. In press. Consequences of migratory strategy on habitat selection by mule deer. *Journal of Wildlife Management*.

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**6.3.1. Background**—Forage and predation risk are important factors that influence ungulate behavior, distribution, and demography (Bowyer et al. 2005, Bergman et al. 2015, Winnie and Creel 2017). In highly seasonal environments, ungulate migration has traditionally been viewed as a strategy that increases access to forage or reduces exposure to predation risk during summer (Fryxell and Sinclair 1988). Partially migratory populations, in which some individuals migrate seasonally and others remain resident in the same range year-round (Chapman et al. 2011), offer the opportunity to study the relative benefits of migratory versus non-migratory behavior. Migration influences the levels of forage and predation risk individuals are exposed to at broad spatial scales (Dingle and Drake 2007), which can affect selection for forage and avoidance of predators at finer scales (e.g., the home range [second order] and within-home range [third order] scales; Johnson 1980, Bastille-Rousseau et al. 2017).

Within the northern Rocky Mountains of the United States, grey wolves (*Canis lupus*) and mountain lions (*Puma concolor*) have undergone range expansion and population growth concurrently with changes in forage availability and mule deer declines (Russell et al. 2012, Robinson et al. 2014, Proffitt et al. 2015, MFWP 2018, 2020). Forage and predation risk are often positively correlated, imposing tradeoffs on ungulates (Hebblewhite and Merrill 2009), and detailed studies are needed to parse out the relative effects of forage, predation risk, and their effects on mule deer behavior and distribution.



We proposed 3 complementary hypotheses regarding how forage and predation risk shape the behavior of migrant and resident mule deer at different spatial scales. First, we hypothesized that mule deer face an extrinsic tradeoff between forage and predation risk. We predicted forage would be positively correlated with wolf and mountain lion predation risk, and deer that selected forage when locating their individual home ranges (second order scale) or when selecting fine-scale locations within their home ranges (third order) would exhibit tolerance of risk at respective scales. Second, we hypothesized that migration and residency would pose contrasting availability of forage at a broad (summer range) spatial scale. Because migratory ungulates in the Rocky Mountains often track shifting spatiotemporal patterns in plant emergence (Fryxell and Sinclair 1988, Hebblewhite et al. 2008, Aikens et al. 2017), we predicted the availability of forage would be higher for migrants than residents. Third, we hypothesized that the availability of forage at a given spatial scale would affect selection for forage and avoidance of predation risk at that scale, indicative of a functional response in selection driven by forage availability. We predicted that among migrant and resident groups in different study areas, those with higher forage availability in their summer range would exhibit weaker second-order selection for forage and lower tolerance of predation risk. Among individuals, we predicted that those with higher forage availability in their home ranges would show weak third-order selection for forage and low third-order tolerance of risk.

**6.3.2. Methods**—We developed second-order (home range scale) and third-order (within-home range scale) RSFs for mule deer during summer. For every individual, we estimated year-specific summer home ranges using a 90% kernel density estimate (KDE) with smoothing parameter  $h = 0.01$  (Kie et al. 2010), which we merged to create a single, multi-year summer home range per deer (Hebblewhite and Merrill 2009). We defined used locations at the second order as random points within individual home ranges equal to the number of GPS points uploaded per individual (DeCesare et al. 2012) and sampled available locations randomly within landscape-scale summer ranges of westward migrants, eastward migrants, and residents equal to 10 times the number of GPS points within each summer range (Meyer and Thuiller 2006, Northrup et al. 2013). We defined used locations at the third order as GPS-collar locations within individual home ranges and sampled available points randomly within home ranges equal to 10 times the number of used points per individual. Sample sizes of used locations for second- and third-order analyses were equal ( $n = 4,081$  [Cabinet-Salish migrants];  $n = 642$  [Cabinet-Salish residents];  $n = 6,589$  [Rocky Mountain Front migrants];  $n = 2,312$  [Rocky Mountain Front residents];  $n = 3,217$  [Whitefish migrants];  $n = 410$  [Whitefish residents]). This resulted in an average of 1,800 available points per individual, and 57,600 available points per study area.

At each spatial scale, we developed RSFs that included predicted forage quality (see Section 6.1) and predicted mountain lion and wolf predation risk (see Peterson et al. 2021) as covariates using hierarchical mixed-effects RSFs in a Bayesian framework (Manly et al. 2002, Thomas et al. 2006, Peterson et al. In press). We corrected for fix success and transmission biases by developing a spatial model to predict the probability of a collar transmitting fixes ( $P_{\text{fix}}$ ) as a function of topography and tree canopy cover, which commonly affect collar to satellite communications (Frair et al. 2010). We modeled  $P_{\text{fix}}$  using store-on-board location data from GPS collars recovered from mule deer that had died across our 3 study areas (Peterson et al. In press), and weighted the log-likelihood of each used location  $j$  by  $1/P_{\text{fix},j}$ , such that the likelihood of the data depended on the relative probability of selection of a location and the probability of a GPS-collar successfully acquiring a fix at a location.



**6.3.3. Results & Discussion**—Positive correlations between forage quality and predation risk by both wolves and mountain lions suggested that mule deer do indeed face extrinsic trade-offs in these study areas. In the Cabinet-Salish, mean availability of forage was 1.32 kcal/m<sup>2</sup> higher for residents than migrants, whereas on the Rocky Mountain Front and the Whitefish Range, forage availability was similar between migrants and residents with overlapping 95% confidence intervals (Table 6.3). Wolf predation risk was similar among migrants and residents in the Whitefish Range, higher for migrants in the Cabinet-Salish, and lower for migrants on the Rocky Mountain Front (Table 6.3). Mountain lion predation risk was 8% and 32% higher for migrants than residents in the Cabinet-Salish and Rocky Mountain Front areas, respectively, but it was 4% lower for migrants in the Whitefish Range (Table 6.3).

Resource selection results suggested a high degree of local variation among study areas. We lacked strong inference on resource selection coefficients when pooling animals across study areas according to migratory strategy alone, as all 95% credible intervals substantially overlapped zero (Figure 6.7A). At the second-order of selecting home ranges, point estimates were generally neutral for both forage and wolf risk, and weakly negative for mountain lion risk for both migratory strategies (Figure 6.7A). At the third-order of selecting locations within home ranges, point estimates were weakly positive for forage, weakly negative for mountain lion risk, and significantly negative for wolf risk (Figure 6.7A).

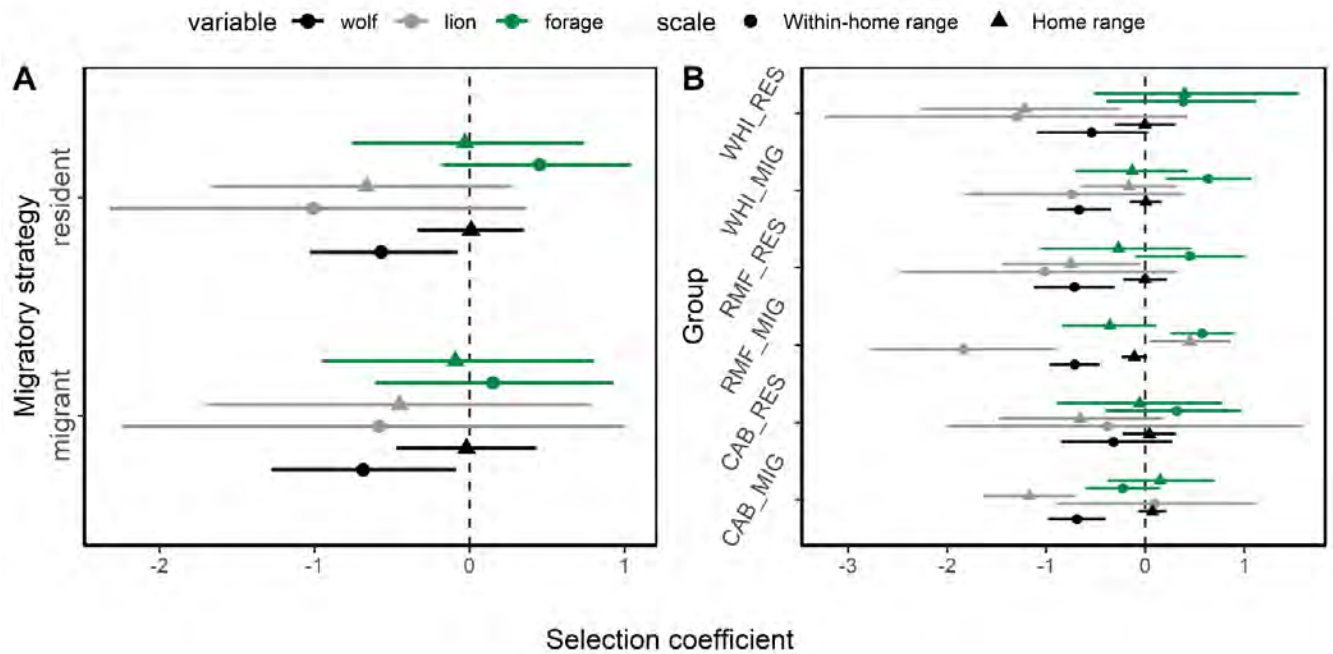
However, when estimating selection patterns distinctly among both study areas and migratory strategies, second-order selection coefficients for mountain lion risk were significantly negative for migrants in Cabinet-Salish and residents in Rocky Mountain Front and Whitefish Range (Figure 6.7B). At the third order, selection coefficients for forage were significantly positive for Whitefish and Rocky Mountain Front migrants and weakly positive for all other groups besides Cabinet-Salish migrants. Third-order selection coefficients for wolf risk were significantly negative for all migrant groups and Rocky Mountain Front residents, and weakly negative for Cabinet-Salish and Whitefish Range residents (Figure 6.7B). Third-order selection coefficients for mountain lion risk were significantly negative for Rocky Mountain Front migrants and weakly negative for all other groups besides Cabinet-Salish migrants (Figure 6.7B).

Resource selection analysis results were clarified when put in the context of forage availability for individual deer. When selecting home ranges (second-order), selection for forage decreased as landscape-scale availability of forage in summer ranges increased, ( $P = 0.052$ ), whereas avoidance of mountain lion ( $P = 0.495$ ) and wolf risk ( $P = 0.804$ ) did not change (Figure 6.8A). At the finer scale of selection within home ranges, we found marginal evidence that as forage availability increased within home ranges, individuals showed weaker selection of forage during local movements ( $P = 0.081$ ; Figure 6.8B). We did not find evidence of changes in third order avoidance of mountain lions ( $P = 0.134$ ) or wolves ( $P = 0.40$ ) by individual mule deer as forage increased within home ranges (Figure 6.8B).

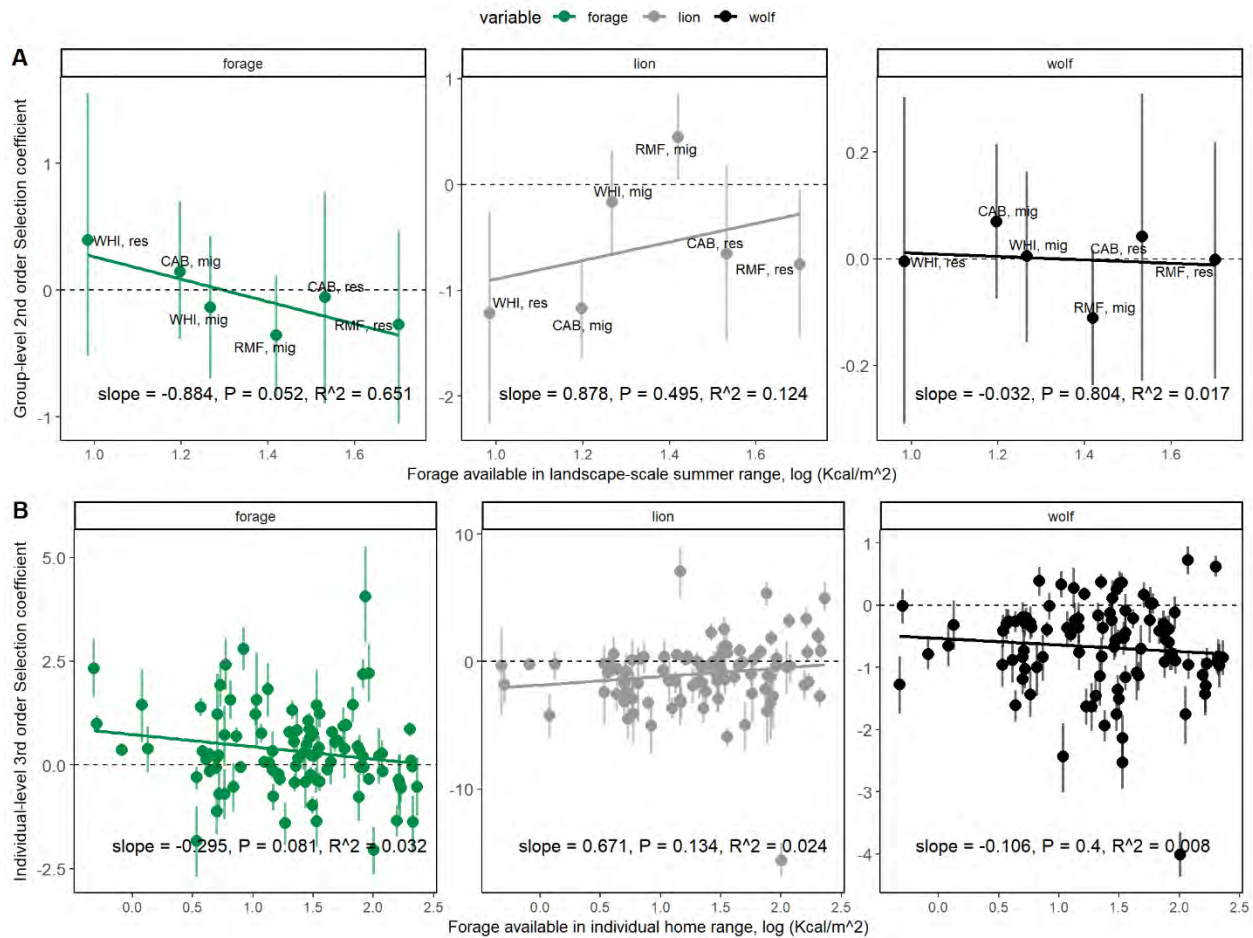


**Table 6.3.** Mean availability of forage (kcal/m<sup>2</sup>) and values from wolf and mountain lion resource selection functions (RSFs; percentile scale) within summer ranges of migrant (mig) and resident (res) mule deer in 3 study areas, 2017–2019. Mig - Res is the difference between variable means in migrant and resident summer ranges, and Prob > 0 is the probability that migrant means are less than resident means.

Variable	Study area	Strategy	$\bar{x}$	2.50%	97.50%	Mig -Res	2.50%	97.50%	Prob > 0
Forage	CAB	mig	3.311	2.612	4.088	-1.318	-2.657	-0.059	0.020
		res	4.629	3.610	5.767				
	RMF	mig	4.134	3.286	5.080	-1.347	-3.156	0.332	0.059
		res	5.481	4.081	7.067				
	WHI	mig	3.551	2.751	4.446	0.873	-0.298	2.068	0.928
		res	2.677	1.931	3.536				
Wolf	CAB	mig	52.845	51.09	54.606	4.686	2.200	7.173	0.999
		res	48.159	46.374	49.926				
	RMF	mig	41.267	39.504	43.042	-18.470	-20.970	-15.976	0.000
		res	59.736	57.983	61.491				
	WHI	mig	49.724	47.976	51.472	-1.533	-4.063	0.930	0.112
		res	51.258	49.509	53.020				
Lion	CAB	mig	54.684	52.992	56.361	8.371	5.964	10.795	1.000
		res	46.312	44.611	48.008				
	RMF	mig	66.329	64.611	68.008	31.690	29.339	34.042	1.000
		res	34.639	32.987	36.324				
	WHI	mig	48.537	46.853	50.225	-3.914	-6.285	-1.546	0.000
		res	52.451	50.752	54.129				



**Figure 6.7.** Selection coefficients and 95% credible intervals by A) migratory (MIG) vs. resident (RES) behavioral strategy and B) study area, 2017–2019.



**Figure 6.8.** A) Group-level selection coefficients with 95% credible intervals from second-order resource selection functions (RSFs) and B) Individual-level selection coefficients from third-order RSFs plotted against forage availability (log-transformed) at each scale, 2017–2019.

Our research yielded several key findings in relation to our hypotheses regarding forage-risk trade-offs in the context of multiple spatial scales and migratory strategies. First, we hypothesized that mule deer would face a tradeoff between selection for forage and avoidance of predation risk and that selection for forage would correspond with increased tolerance of risk. While forage and risk were positively correlated in most situations, there were no instances where selection for forage corresponded with selection for riskier areas among any group of deer, at either spatial scale (Figure 6.7B). Rather, our results suggested that mule deer exhibiting selection for forage were also able to avoid wolf and mountain lion risk at both scales (Figure 6.7). Our findings are consistent with research showing mule deer, elk, and caribou (*Rangifer tarandus*) may select high-forage, low-risk areas (Pierce et al. 2004, DeVoe et al. 2019) sometimes in the face of positive forage-risk correlations (Bastille-Rousseau et al. 2015), but our results contradict results of others showing selection of forage by ungulates increases exposure to predation risk (Bowyer et al. 1998, Creel et al. 2005, Fortin et al. 2005, Winnie and Creel 2017). The paucity of results showing significantly positive selection for forage at the second order was counterintuitive given the absence of forage-risk tradeoffs. Within the summer ranges of these groups,

the availability of forage may have been high enough for deer to meet nutritional needs through random home range placement and third-order selection (Beyer et al. 2010, Merems et al. 2020). Second, we hypothesized that migrants would have more forage available to them than residents on their summer ranges within each study area. However, migration did not predictably result in exposure to higher forage availability at a summer range scale, for in some study areas, migrants were exposed to similar or lower forage and higher risk than residents, and vice versa.

Third, we hypothesized that the availability of forage at a given scale would affect selection for forage and avoidance of risk at that scale. In summer ranges with greater forage availability, mule deer exhibited weaker second-order selection for forage, indicative of a functional response to forage, which supports our prediction (Figure 6.8A). This pattern held true, though was statistically weaker, among individuals at the third order too (Figure 6.8B). These findings corroborate Anderson et al. (2012) and Godvik et al. (2009) who reported selection of foraging habitat by mule deer and red deer (*Cervus elaphus*), respectively, increases as availability decreases. The effects of food availability may transcend forage selection outcomes alone, influencing animal tolerance of risky areas when forage-risk tradeoffs are present (Mysterud and Ims 1998, Hebblewhite and Merrill 2009, Muhly et al. 2019). Accordingly, we predicted deer in areas with low forage availability would be forced to select riskier areas than deer with high forage, though we found that decreased availability of forage did not correspond with greater tolerance of risk at either scale (Figure 6.68).



Our index of mountain lion predation risk was related to home range placement by mule deer, and mule deer avoided mountain lion risk at the second order to some degree (except Rocky Mountain Front migrants). In contrast, mule deer did not avoid wolves when selecting home ranges, perhaps because of the lower predation rates of wolves versus mountain lions we documented (see Section 4.2.1). The influence of mountain lions, with their higher predation rates, on home range selection may have overridden that of wolves, which is a common behavioral response of prey in multi-predator systems (Relyea 2003, Morosinotto et al. 2010, Kohl et al. 2019).

Though we did not detect consistent exposure to enhanced nutrition or reduced risk among migrants, the proportion of migrants sampled was  $\geq 3.5$  times greater than that of residents in every study area. So, why do mule deer in western Montana migrate? First, migrants may have received nutritional benefits that we did not account for, such as exposure to delayed plant phenology in higher elevation summer range, which can improve mule deer survival (Hurley et al. 2014). Second, environmental stochasticity may alter the relative benefits of migrant versus resident strategies over multi-year time scales (Lack 1968, Schindler et al. 2010, Riotte-Lambert and Matthiopoulos 2020). Multiple large fires have occurred in our study areas in the past decade, potentially resulting in short-term improvements in summer forage conditions for migrants in those areas (see Section 6.2). Finally, our estimates of predation risk may have inaccurately portrayed differences in risk between migrants and residents. As in all studies of habitat selection, methodologies used in predator RSF modeling may have resulted in inaccurate estimates of the relative probability of selection by predators at any point on the landscape (Peterson et al. 2021). Furthermore, these models do not account for underlying differences in absolute abundance of predators across study areas or species, which may have added effects on predation risk perceived by ungulates on top of the fine-scale space use of predators as predicted by our models.

Mule deer selected forage more strongly at the third order than the second order of selection in our study, and generally exhibit low plasticity in summer home range selection. Therefore, rather than attempting to expand mule deer habitat by improving forage conditions where home range selection is unlikely, focusing treatments aimed at improving forage in areas where home ranges are already likely to exist could yield the greatest benefits for populations. Wildlife managers in western Montana could use our second-order RSFs to identify where mule deer home ranges are likely to be, which could indicate where habitat treatments could be most effective. Because mule deer generally avoided mountain lion predation risk when selecting home ranges, conducting habitat treatments in areas with lower mountain lion risk (like ridgelines and areas with low hiding cover) could be most effective for improving mule deer habitat, especially in portions of western Montana that are outside the extent of our RSF predictions. Because the majority of mule deer in our study system were migratory, but migration does not predictably yield nutritional benefits, focusing habitat improvements in higher elevation summer range of migrants could be the most efficient way for improving mule deer habitat at a population scale.

## 7. WINTER HABITAT RELATIONSHIPS

*Note: this portion of study is currently in revision at a peer-reviewed journal [Anton et al. In revision. Climate and habitat interactions shape mule deer resource selection on dynamic winter landscapes. Journal of Wildlife Management]. Some re-analyses are underway and results here are preliminary and subject to change. Below is an abridged summary; see manuscript for full details, when finalized.*

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**7.3.1. Background**—Seasonally limited resources pose challenges as animals must adapt behavior over spatially and temporally varying scales (Senft et al. 1987). For large herbivores, plant senescence in winter can lead to nutritional deficits that affect behavior (Gilbert et al. 2017), vital rates (Kucera 1988, Hobbs 1989, Bishop et al. 2005, 2009, Hurley et al. 2014), and ultimately population demography (Patterson and Power 2002, Monteith et al. 2011). Beyond the reduced nutritional quality of forage, climatic shifts can impose added constraints to deer attempting to reach forage under snow while minimizing energetic expenditures from thermoregulation and travel (Halsey 2016, Withers et al. 2016).

Parker et al. (1984) quantified a nearly 500% relative increase of the energetic cost of locomotion for a 66.5 kg mule deer (*Odocoileus hemionus*) sinking 50 cm into snow when compared to bare ground. Moreover, greater snowfall has been linked to increased predation susceptibility (Nelson and Mech 1986, Fuller 1991, DelGiudice et al. 2002) and declines in fawn survival (White et al. 1987, Bartmann et al. 1992, Bishop et al. 2005, Hurley et al. 2011). Characteristically low winter temperatures can modify animal behavior and space use (Elmore et al. 2017) and reduce survival (Forrester and Wittmer 2019). Thermal conditions are also affected by local landscape features such as increased direct solar radiation in open areas or improved heat-retention in areas with thick vegetation (Mysterud and Østbye 1999). While thermoregulation costs alone can be relatively small, when combined with increased costs of travel through snow and reduced energy intake from plant senescence, winter conditions significantly impact an animal's energy balance (Hobbs 1989, Withers et al. 2016).



**Figure 7.1.** Collared mule deer doe, Rocky Mountain Front study area, winter 2017–2018.

In the northern forest ecoregion, winter conditions are viewed as a predominate constraint to mule deer population dynamics (Hayden et al. 2008). Here, we apply resource selection functions (RSFs) to understand mule deer habitat selection patterns when confronted with variable winter conditions in northwest Montana. We focused on three covariates and their influences on mule deer resource selection in winter: (1) snow accumulation; (2) forage biomass availability; and (3) canopy cover. We predicted that mule deer would generally select areas to maximize forage, with interacting effects of snow and canopy as conditions varied over space and time, and we studied deer in 3 different populations facing a gradient of climatic conditions.

**7.3.2. Methods**— We studied mule deer habitat selection using collared adult female mule deer (Figure 7.1), resource selection functions, and a use-availability sampling design (Manly et al. 2002). We sampled habitat use with location data collected from GPS collars. To focus our studies on the winter season, we used individual- and population-level migration patterns to estimate start and end dates of winter. We then defined availability within winter ranges according to 99% kernel density polygons, estimated separately for each of the three study areas. We buffered this kernel by 1km and randomly sampled 10 locations for every used location within this buffered polygon (Fieberg et al. 2021).

To characterize resources of potential importance to mule deer winter habitat selection, we extracted covariate data at each used and available location for a suite of habitat variables found to be important in previous ungulate resource selection studies. Because some resource covariates varied temporally, we assigned a date to all available locations using random draws from the distribution of dates in the used dataset. Resource covariates included slope angle, percent forest canopy cover, landcover type (6 categorical levels: conifer forest, grassland, shrubland, wet areas, disturbance, and developed land), solar radiation index, daily snow water equivalent (SWE), and a predictive model of herbaceous and shrub forage biomass, excluding conifers, across each study area.

The forage biomass model was developed following Peterson et al. (In press) adjusted for winter conditions, according to 3 steps: 1) estimating species-specific biomass (in g/m<sup>2</sup>) of forage through ground-based sampling (see Section 6.1); 2) identifying winter forage species (see Section 5.2); and 3) developing generalized linear models (GLMs) for predicting spatial variation in forage biomass across each study area. Vegetation field sampling for this model was conducted during summer, in support of other summer-focused nutrition studies (Peterson et al. In press). For this study, we restricted the spatial extent of vegetation data to our defined winter ranges, used winter-specific estimates of diet to identify forage species, and developed new winter-focused GLMs. Because we sampled vegetation during summer, our biomass data included plant parts that are not always present during winter, such as flowers, fruits, and leaves of deciduous plants. Therefore, model predictions likely overestimate the biomass of forage present during winter. Furthermore, our summer field data did not include biomass of conifer species, which were important components of winter diets in these deer populations. We also accounted for variation in fix upload success using a spatial model that predicted the probability of a successful fix upload ( $P_{\text{fix}}$ ), given a location's canopy cover and topographic characteristics, to weight cases in our analyses (Frair et al. 2010; Peterson et al. In press).

We fit study area-specific RSFs using generalized linear mixed effects models (GLMMs) using the `glmer` function in the `lme4` package in R (Bates et al. 2015). Models were structured using individual deer as random effects to account for the inherent autocorrelation present in animal relocation data (Fieberg et al. 2010). We tested both linear and quadratic forms of canopy cover and also evaluated a small set of interactions regarding the effect of snow on selection of other variables. We calculated odds ratios for

most continuous and categorical terms within top models to assess effect sizes, including corrections of categorical land cover type predictors for their relative availabilities (Fieberg et al. 2021).

We validated multivariate models using k-fold cross validation (CV) to iteratively withhold 20% of animals and re-estimate model coefficients (Boyce et al. 2002). Validation of each fold was then estimated as the Spearman rank correlation between 10 equal-area ranked bins of model predicted values and the frequency of withheld GPS data within each bin (Boyce et al. 2002). We also tested the broader applicability of study-area-specific RSF's by applying each top model to out-of-sample data from the other two study areas (DeCesare and Pletscher 2006).

***7.3.3. Results & Discussion***—Winter season start and end dates varied according to migration timing of each deer, but averaged December 6 to April 18, respectively. After screening techniques, the data used for winter habitat selection modeling included 30,810 GPS locations (RMF: 11,726; WF: 8,347; CS: 10,737) from 241 deer-winters (RMF: 100; WF: 72; CS: 69).

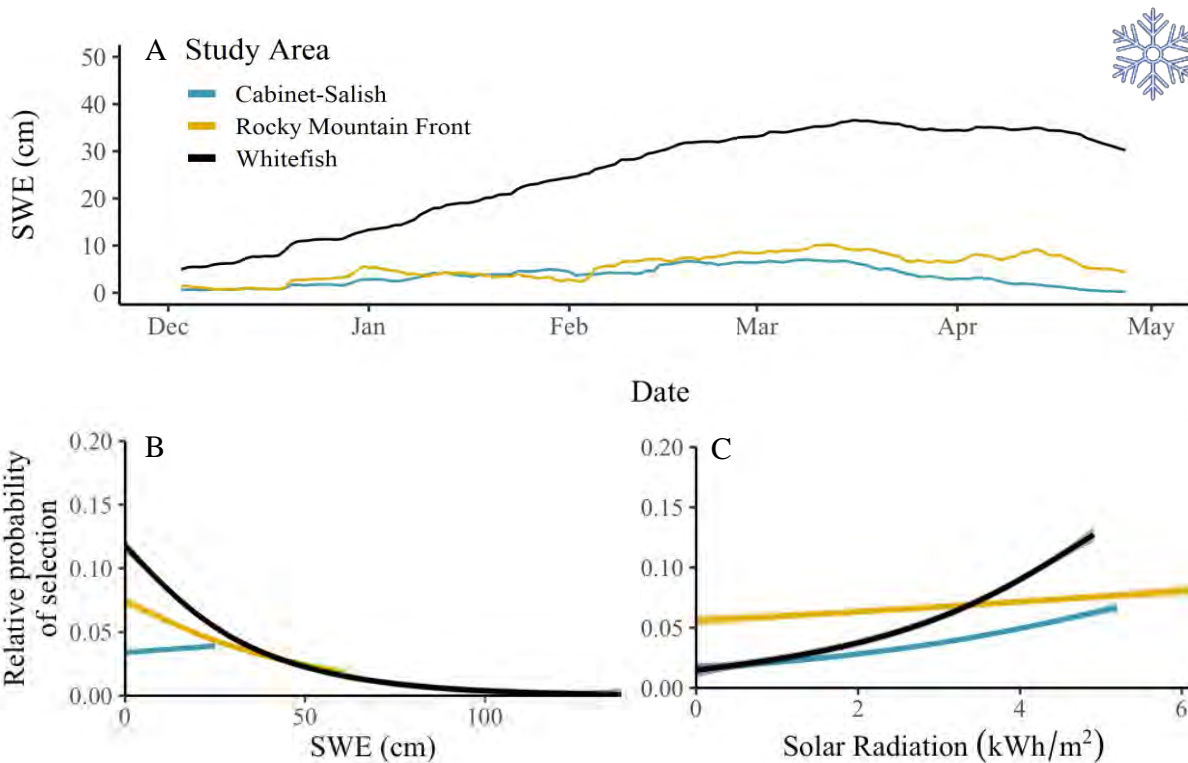
For winter forage modeling, we included summer vegetation plot surveys at 477 sites in mule deer winter range: 146 in Cabinet-Salish, 124 on the Rocky Mountain Front, and 177 in the Whitefish Range. On average, herbaceous and shrub forage biomass was highest in grasslands and lowest in conifer forests. Our top model for predicting winter herbaceous and shrub forage in the Cabinet-Salish showed positive effects of perennial plant cover, wildfires, timber harvests, and grass/shrublands, and negative effects of canopy cover, with an  $R^2$  value of 0.306. On the Rocky Mountain Front, we found positive effects of perennial plant cover and moderate slopes, and negative effects of conifer forests, shrub cover, and wildfire on herbaceous and shrub forage ( $R^2 = 0.547$ ), and in the Whitefish Range, our top model showed positive effects of grass/shrublands, shrub cover, southern aspects, and moderate slopes, and negative effects of prescribed fires and canopy cover ( $R^2 = 0.41$ ).

Resource covariates in our top models for deer habitat selection varied between the three study areas (Figures 7.2, 7.3), and top models validated well using both in and out of sample data. For RMF, the top model included continuous variables for slope angle, TPI, SWE, solar radiation and herbaceous and shrub forage biomass, and also a categorical variable for land cover type and an interaction term between SWE and herbaceous and shrub forage biomass. Deer in the RMF study area were 2.43 times more likely to select a patch with 24 g/m<sup>2</sup> of herbaceous and shrub forage (the 95<sup>th</sup> percentile of available values in this area) versus a patch with 12 g/m<sup>2</sup> (the 5<sup>th</sup> percentile). Top models in CS and WF also included slope angle, TPI, solar radiation, land cover type and SWE but contained canopy cover and not herbaceous and shrub forage, due to collinearity between canopy cover and forage. CS and WF top models also included an interaction between canopy cover and SWE (Figure 7.3). In the CS study area, deer preferred areas with more open canopies and were 16.01 times more likely to select area with 15% canopy cover (5<sup>th</sup> percentile value) over those with 65% cover (95<sup>th</sup> percentile). However, in WF, deer favored closed canopy forests and were twice as likely to use a patch with 65% canopy cover instead of those with 15%. Mule deer were 2.68 and 1.72 times more likely to select a disturbed forest compared to an undisturbed conifer forest patch in the CS and WF study areas, respectively.

Results suggested mule deer avoid patches with greater snow accumulation as measured by SWE, but the level of avoidance varied across the study areas (Figure 7.2). We used 0.05 and 0.95 quantile values for each study area to characterize low and high values of SWE, respectively, and used odds ratios to evaluate selection relative to snow. Deer in WF experienced significantly more snowfall on average (Figure 7.2A), which led to greater avoidance of deeper snow levels; these deer were 15.69 times more likely to select a patch with 1 cm versus 78 cm SWE (Figure 7.2B). In contrast, CS experienced the least



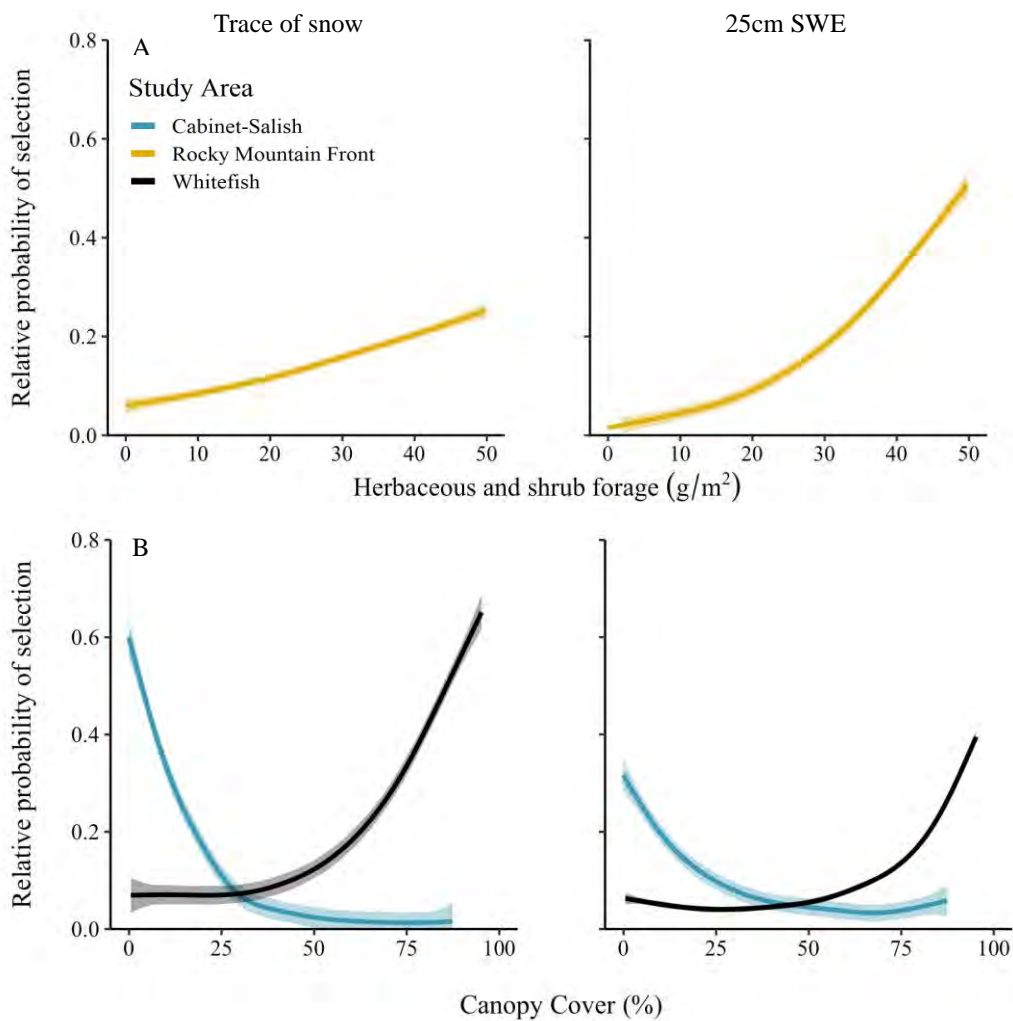
snow accumulation, which likely dampened and reversed the effect of SWE such that deer were 1.09 times more likely to select a patch with 12 cm instead of 0 cm SWE (Figure 7.2B). Lastly, RMF deer were 1.87 times more likely to select an area with 0 cm compared to those with 26 cm SWE (Figure 7.2B). Deer in all three study areas sought areas with higher solar radiation values. We also found evidence of interactions between snow and deer selection for herbaceous and shrub forage (RMF study area) and canopy cover (CS and WF study areas; Figure 7.3). Preference for lower snow depths has been found in many studies and could be attributed to reducing susceptibility to predation (Nelson and Mech 1986, Fuller 1991), reducing energetic expenditure associated with travel through deep snow (Parker et al. 1984), or minimizing snow substrate covering possible forage (Gilbert et al. 1970). As a demographic consequence of all of these mechanisms, snow depth can be a primary determinant of deer body condition as they enter the final period of gestation (Garroway and Broders 2005).



**Figure 7.2.** The three study areas experienced different climatic conditions and corresponding differences in mule deer habitat selection patterns, as demonstrated by A) the daily SWE value for each study area averaged across all years, 2017-2020, and B) relative probability of selection for snow water equivalent and C) relative probability of selection for solar radiation.

In addition to the direct effects of snow on habitat selection (Figure 7.2), snow indirectly mediated mule deer selection for forage resources and canopy cover (Figure 7.3). Furthermore, our diet analysis revealed a prominence of coniferous species across all 3 study areas (see Section 5, Figure 5.1). Mule deer diets often change seasonally as available resources fluctuate (Gill et al. 1983, Hobbs 1989), typically shifting from nitrogen-rich forbs and graminoids to browse species as the former senesce and become buried by snow (Hobbs et al. 1983, Nordengren et al. 2003, Nicholson et al. 2006, Frisina et al. 2008). For example, mule deer diets in the Cabinet-Salish study area displayed higher diversity and

greater reliance on forbs and graminoids compared to the other areas, which may be attributed to lower snow accumulation allowing these species to remain available (Hobbs 1989). To the contrary, mule deer in the Whitefish area faced considerably deeper snow conditions (Figure 7.2A), which had multiple effects. Deer using deep-snow winter ranges generally used a great proportion of conifer species in their diets (see Section 5, Figure 5.2), and the interaction between SWE and canopy cover in WF deer showed higher affinity for dense forests as snow levels increased (Figure 7.3). Conceivably, these 2 results are indicative of the same general phenomenon, that deer avoiding snow accumulation seek snow-intercept refuge offered by forest canopy (Parker et al. 1984, Kirchhoff and Schoen 1987, D’Eon and Serrouya 2005) as well as accessible conifer forage resources in closed canopy forests (Poole and Mowat 2005, Serrouya and D’Eon 2008).



**Figure 7.3.** Snow (indexed with SWE) had interacting effects on deer habitat selection for other habitat covariates, such as A) herbaceous and shrub forage, in the Rocky Mountain Front study area, and B) canopy cover in the Cabinet-Salish and Whitefish Range study areas.



**Figure 7.4.** A collared mule deer doe in the Cabinet-Salish study area, February, 2018.

Studies of mule deer in other deep-snow environments have suggested a “deep” snow threshold to occur at 40–50 cm, above which deer avoid open habitats and increase selection of closed canopy forests (Gilbert et al. 1970, Armleder et al. 1994, Poole and Mowat 2005, Serrouya and D’Eon 2008). Putting our SWE results in the context of snow depth, 40-50 cm of snow depth would translate to 8.4–15.5 cm of SWE on average, highlighting that conditions on all study areas, but the WF study area in particular, often exceeded levels expected to affect mule deer behavior (Figure 7.2A).

Animal-habitat relationships can provide important insight for identifying priority management actions to improve population performance (Johnson et al. 2004, Heinrichs et al. 2017). Our findings emphasize the importance of climatic conditions and landscape heterogeneity when managing mule deer habitat (Serrouya and D’Eon 2008, Gilbert et al. 2017). The variation in snow conditions across our three study areas was a primary driver of variation in mule deer ecology. In the deepest snow environments such as in the Whitefish Range, conifer forests appear important for snow-intercept and for an accessible source of winter forage, more so as snow increased over space and time (Rea et al. 2017). In such environments, management to reduce forest canopy might offer additional forage (e.g., shrub) resources but only to the spatiotemporal extent under which snow conditions permit access. While winter conditions were also at times severe in our other two study areas (enough so to impact spring recruitment; see Section 4.2.3), mixed foraging on both shrubs, conifers, and other taxa showed lesser impact of snow on access to forage. Habitat management to promote shrubs in these environments may be less costly to energy expenditure and forage accessibility.

## 8. FALL MIGRATION: TIMING AND INITIATING FACTORS

### 8.1. Evaluating drivers of fall migration timing

*(Note: this portion of study is preliminary and still in preparation for internal review and submission to a peer-reviewed journal; primary author of manuscript will be C. Anton).*

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**8.1.1. Background**— Seasonal migration is a behavioral strategy that animals have evolved to exploit seasonally changing resources through short or long-distance movements. A predictable pattern for ungulates in northern temperate landscapes is to seasonally migrate from low-elevation winter ranges to higher-elevation summer ranges in spring and then back to winter range in autumn (Myserud et al. 2011, Jones et al. 2014). Thus far, spring migration has been thoroughly examined with its timing primarily attributed to tracking phenological greenup (Bischof et al. 2012) and gaining access to parturition areas (Barten et al. 2001). In contrast, snow depth and temperature changes have been identified as the main drivers of autumn migration timing (Monteith et al. 2011, Jones et al. 2014), but the deterioration of forage quality (Rivrud et al. 2016) and predation risk may also play roles in cueing autumn migration (Mikle et al. 2019).

Mule deer are an important game species in Montana with roughly 150,000 hunters annually pursuing mule deer each autumn. Archery and rifle hunting by humans can induce spatiotemporal patterns of mortality risk, which can lead to behavioral alterations for some animals (Proffitt et al. 2010, Rivrud et al. 2016). This period of increased human-related risk coincides with mule deer autumn migration, leading to the possibility that animals could alter their migration timing to exploit landscape refugia and reduce their exposure to hunting risk (Rivrud et al. 2016, Mikle et al. 2019). As migratory behavior declines worldwide (Berger 2004), autumnal climate patterns change (Gallinat et al. 2015), and hunting remains an important recreational and subsistence activity, it is important to quantify the relative impacts of these variables as triggers of autumn mule deer migration.

We specifically studied the initiation of autumn migration, and developed five hypotheses to explain the timing of animals leaving summer range. First, we hypothesized that snow depth could reduce access to forage and increase energetic expenditure, such that mule deer would need to start migration prior to significant snow accumulation. We predicted a positive correlation between precipitation and the probability of beginning migration with large storm events increasing this probability (Monteith et al. 2011). Second, we hypothesized minimum temperatures could provide a separate cue that winter is approaching, and predicted temperature to be negatively correlated to the probability to initiating migration. Third, plant forage quality can shape ungulate landscape use (Hebblewhite et al. 2008), guiding seasonal movements to track higher quality forage as it changes through phenological stages (Bischoff et al. 2012). We predicted migrations would start when plant forage quality had decreased and plants had fully senesced on summer range. Fourth, human hunting pressure can alter habitat selection of ungulates and induce movements away from disturbances (Doherty et al. 2021). We predicted a positive correlation between hunting pressure in deer summer ranges and probability of initiating migration. Lastly, we hypothesized that individuals would vary in their total distance travelled during migration. We predicted that mule deer with longer distance migrations would begin autumn movements earlier (Rivrud et al. 2016).



**8.1.2. Methods**— We identified migration events using the Migration Mapper application (Wyoming Migration Initiative 2020), which uses net squared displacement curves to aid in the classification of migration timing (Bunnefeld et al. 2011). We excluded outlier animals that left summer range before July 31 or after December 31, and we used a subset of GPS data for each mule deer that began on August 26<sup>th</sup> of each year and ended on each animal’s first day of migration. We chose August 26<sup>th</sup> to include at least 2 weeks of location data prior to their initiation of migration for all animals.

We monitored environmental conditions by summarizing daily climatic and anthropogenic variables across multiple time scales. Recognizing that mule deer may respond to both instantaneous and cumulative changes in the environment (e.g., a single snowstorm vs. a gradual accumulation of snow), we assessed conditions experienced by each deer according to weekly, two-day and daily time scales. We downloaded daily 1-km resolution precipitation, snow water equivalence (SWE), and minimum temperature rasters from the Daymet database (Thornton et al. 2020), and calculated weekly and two-day averages of each. Additionally, we subtracted these weekly averages from daily values as a metric of change and for both precipitation and SWE we also calculated a weekly cumulative sum.

To capture changes in plant phenology, we used daily 250-m resolution normalized difference vegetation index (NDVI) from the MODIS MOD09GQ database. Similar to the climatic variables, we calculated the difference between daily NDVI values and the average of the previous week. We also downloaded annual summary metrics calculated from sequences of NDVI data, including the day of year associated with the end of measurable photosynthesis and NDVI value at that moment, available from the USGS Remote Sensing Phenology database (<https://doi.org//10.5066/F7PC30G1>). To make these USGS layers relevant, we subtracted the end of season values from either the MODIS NDVI rasters or from the day of the year to measure the photosynthetic decay or time that had occurred since the measured end of the season.

Autumn in Montana brings an influx of archery and rifle hunters into mule deer habitat. We attempted to measure hunting pressure by combining available statistics on hunter effort within our study areas. Every two years, MFWP personnel measure deer (or elk on alternate years) hunter effort by conducting phone surveys that produce estimates of the number of hunters in each hunting district pursuing elk and deer, separately for archery and rifle hunters. We used these data to estimate the sum of hunter days spent during both archery and general seasons in each hunting district in our study areas. To distribute hunter day totals across daily and weekly time sequences we used an independent set of data collected from moose hunters which included daily hunter effort across every day of the season and were assumed to be proportional to those for deer and elk hunters in terms of the relative differences in hunting pressure across days of the week and weeks of the season. Similar to climatic and NDVI variables we also calculated two-day and weekly averages, and subtracted the weekly average from the daily value. We also included a categorical hunting season variable to indicate when hunting seasons occurred. Lastly, for each deer we also calculated migration distances and the duration of migrations, measured in days.

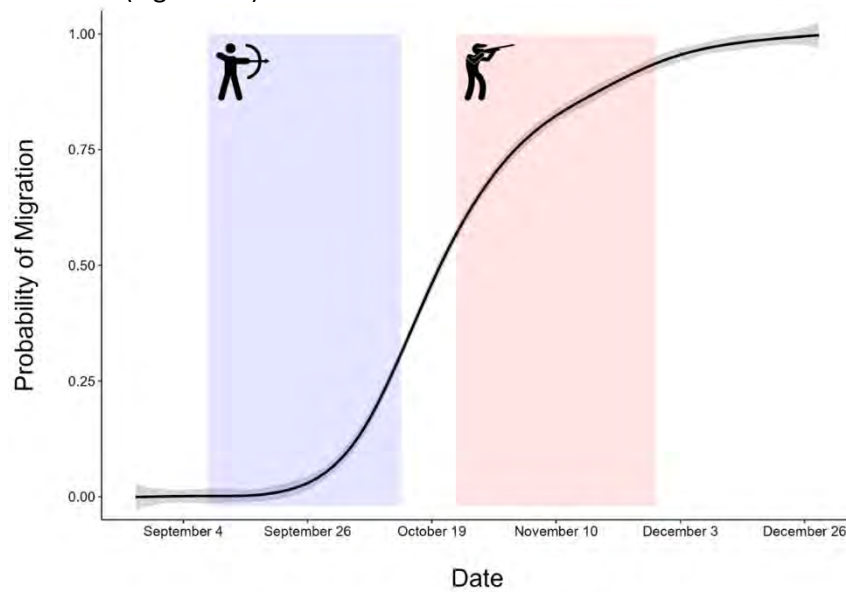
We used a time-to-event analysis framework to assess the impacts of the aforementioned variables on autumn migration timing. Most time-to-event, typically related to survival, analyses assume continuous measurement of time, whereas our data were formatted in discrete days and included many instances of ties in migration timing, wherein multiple animals migrated on the same day. Thus, we employed discrete-time survival analysis models in software R using generalized linear mixed models (GLMM) with a complimentary log-log link function (Singer and Willett 1993). These GLMM models are comparable to Cox proportional hazards models with log-normal frailty terms but specifically include one or more variables that account for the effect of time itself on the probability of an event occurring. The coefficient(s) for this parameterization of time effectively establishes the baseline hazard function akin to that in continuous-time proportional hazards models (Singer and Willett 1993).

We employed an information-theoretic model selection approach (Burnham and Anderson 2002) to avoid overfitting our models (Schwartz et al. 2013). We first scaled and centered continuous variables and then grouped our individual and landscape variables into classes and explored within-class combinations of variables. We conducted AIC-based model selection within each class of variables and carried forward variables that were included in best supported for each class. We grouped variables into five classes: precipitation (precipitation and SWE), temperature, NDVI, hunting pressure, and individual migration characteristics. We checked for collinearity among variables using Pearson correlation coefficients and removed variables from models when correlation coefficients were  $> 0.6$ . We then conducted final modelling across classes by combining these variables into a global model and applying a second stage of model selection. Following Arnold (2010), we discounted models where new variable additions did not improve AIC scores by  $\geq 2$ . After AIC model selection, we used receiver operator characteristic curves (ROC) and the likelihood ratio chi-squared tests to assess goodness of fit and predictive performance.



**8.1.3. Results & Discussion**— Mule deer autumn migration displayed considerably more variation in timing and duration in all three study areas compared to similar metrics for spring migration (See Section 3, Figure 3.4). After screening procedures, we included 102 fall migrations (34 in Cabinet-Salish, 40 in Rocky Mountain Front, and 28 in Whitefish) from 68 individuals (23 in Cabinet-Salish, 26 in Rocky Mountain Front, and 19 in Whitefish). The mean migration day for all mule deer was October 19 (SD:22 days, September 17 – December 29). There was no significant difference between study areas. Mule deer travelled an average of 26.3 km during fall migration (SD: 11.5km, 3.9 – 58.2km).

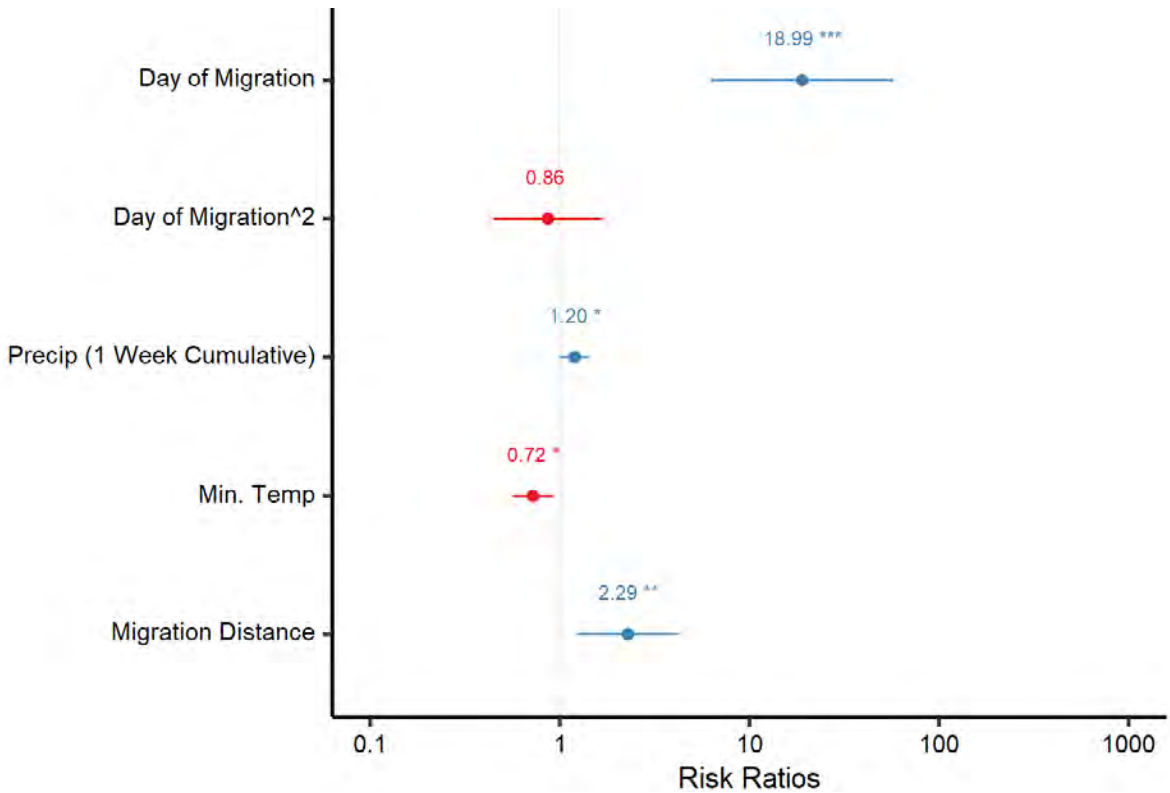
Our initial base model described the probability of migration as a function of time according to the day since August 26 (referred to as day to migration from here forward), and we evaluated multiple treatments of time and mixed effect structures. The most parsimonious base model included both a linear and polynomial term for the day to migration, random intercepts for each deer in the study, and random slopes for the day to migration term. Specifically, model predicted values demonstrated that mule deer migration probability began to steeply increase in early October before levelling out in late November and December (Figure 8.1).



**Figure 8.1.** Predicted probability of fall migration given date, daily minimum temperature, hunting pressure, weekly precipitation, and migration distance for mule deer in northwest Montana. The shaded blue region displays the archery hunting season, and the red region shows the rifle hunting season.

Initial modeling of covariates to migration initiation showed support for all classes of covariates, including those related to precipitation, temperature, forage, hunting pressure, and migration distance. For climatic variables, there were seven precipitation-focused models with support, including variables for daily precipitation, two-day average SWE, 1-week cumulative sum of precipitation, 1-week precipitation average, and the difference between daily SWE and the average of the previous week. A model including daily minimum temperature was also supported. We subsequently tested NDVI variables to explain the change in plant phenological state. The top model for plant phenology included a term describing the relative difference between current daily NDVI and the end of the season NDVI value. We also tested several temporal variations of hunting pressure and found only negative correlations between hunting pressure and migration probability, which did not correspond with our predictions and were thus not considered further. Finally, a model for the linear distance (km) of migration was supported.

When combining variables across all classes, the top model included variables quantifying the weekly cumulative sum of precipitation, daily minimum temperature, daily hunting pressure, the distance travelled during migration, and the underlying curvilinear effect of time (Figure 8.2). Deer were more likely to migrate as precipitation during the prior week increased ( $\beta = 0.18, P = 0.046$ ) and when daily minimum temperature decreased ( $\beta = -0.33, P = 0.011$ ). Probability of migration increased as migration distance increased ( $\beta = 0.83, P = 0.009$ ). The top model demonstrated excellent predictive power with a pseudo-  $R^2$  of 0.68 that increased to 0.88 when including the mixed effect structure. The model scored well with an ROC= 0.94 and a significant likelihood ratio chi-squared = 18.23.



**Figure 8.2.** Discrete-time survival analysis results displaying risk of migrating based on landscape, anthropogenic, and individual variables. Risk ratios of these standardized covariates represent the relative difference (e.g., 2.29 times more likely, for migration distance) in daily probability of initiating migration for each SD-level change in the covariate.

Applying discrete-time survival analyses to our data revealed several key relationships guiding the timing of mule deer autumn migration. First, the inclusion of time itself in these models is done in recognition that there is a baseline relationship between migration initiation and time for which we must account before statistically assessing additional effects of things like weather that vary from year to year. Biologically speaking, we interpret this as akin to the evolved relationship between migration and photoperiod, and the significance of other covariates in the model shows added effects of locally varying conditions affecting the migrations of individual deer and years above the effect of photoperiod alone.

Following our first and second hypotheses, our results demonstrate that plunging temperatures and increasing precipitation in autumn provide important cues for mule deer to begin their migration back to winter range. Mule deer likely use these two cues in order to avoid having to undertake their large



migration movements through deeper snow and colder temperatures associated with their higher elevation summer ranges, both contributing to greater energy expenditures (Parker et al 1984, Hobbs 1989). These findings are consistent with previous studies relating autumn migration timing to both snow and temperature (Monteith et al. 2011, Jones et al. 2014).

Following our third hypothesis, univariate parameter estimates did show some support for the idea that mule deer responded to plant senescence. Specifically, mule deer were more likely to migrate when NDVI had dipped below the threshold indicating the end of the season, signifying forage quality had bottomed out at post-summer levels. However, this parameter was not retained in the top model when competing with other climate and hunting-related metrics. While ultimate drivers of ungulate migration can include access to improved forage quality (Albon and Langvatn 1992), our results suggest other factors may be more important in the timing at which animals initiate their return to winter ranges.

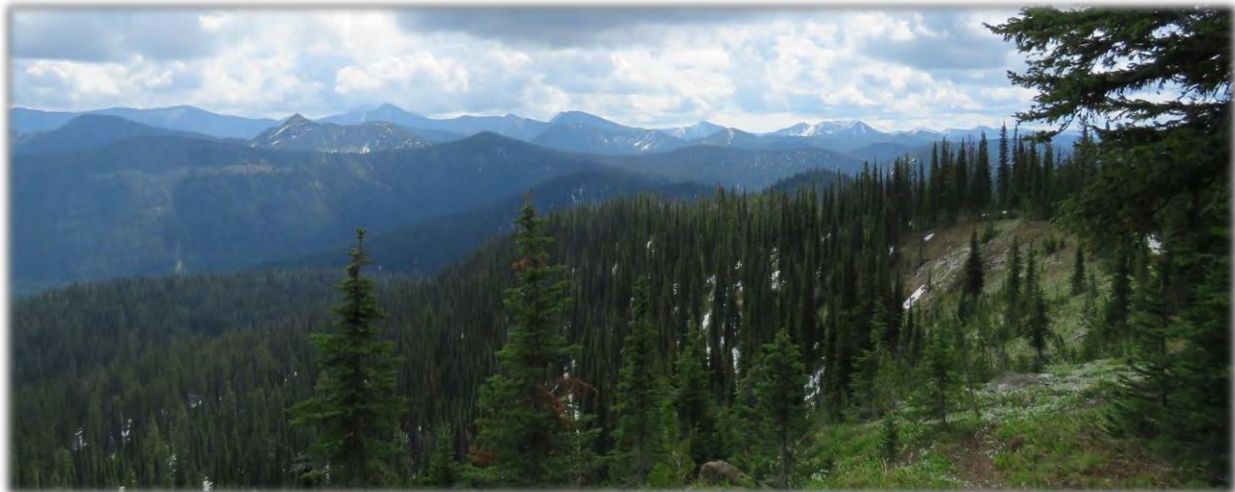
We did not find support for instantaneous or time-lagged effects of hunting pressure increasing the initiation of migrations. However, it is important to acknowledge that our study of hunting pressure effects on migration comes with 2 important caveats. First, we were studying the effect of hunting pressure in areas where harvest of these particular animals (adult female mule deer) was closed (Cabinet-Salish and Whitefish Range) or limited (Rocky Mountain Front). Thus, our study addressed whether added presence of hunters on the landscape impacted animal movements even when those animals were not direct targets of hunters during this study period. Second, our measurement of hunting pressure was spatially coarse, at the HD-scale, which likely does not translate directly to the pressure experienced by individual deer in local home ranges. Further evaluation of spatial correlates to fine-scale variation in hunting pressure, such as distances from roads or trails, might offer alternatives to address this covariate. Finally, we addressed our fifth hypothesis by including individual mule deer migration distances and confirmed our predictions that individuals with longer migrations would start earlier in the season. This head start likely provides individuals enough time to get back to winter range before unfavorable climatic conditions associated with winter fully set in.

Mule deer plasticity in migration timing allows individuals to respond to locally-varying environmental cues like precipitation, temperature, or distance from summer range. Our results highlight the overlap of autumn migration with hunting seasons and the complexity of autumn migration timing, which varies considerably more than spring migrations (see also Figure 3.4). In combination with results showing how migrations span multiple HDs (Section 8.2, below), these results suggest that coordination of hunting regulations across multiple HDs may be necessary to apply deer management prescriptions equally across migratory and resident segments of mule deer populations. Results are specific to adult female mule deer but should also have implications for antlered bucks given their migrations can be driven by similar phenomena (Rodgers et al. 2021), and should facilitate overlap with females during the rut.



## 8.2. Migration across hunting district boundaries

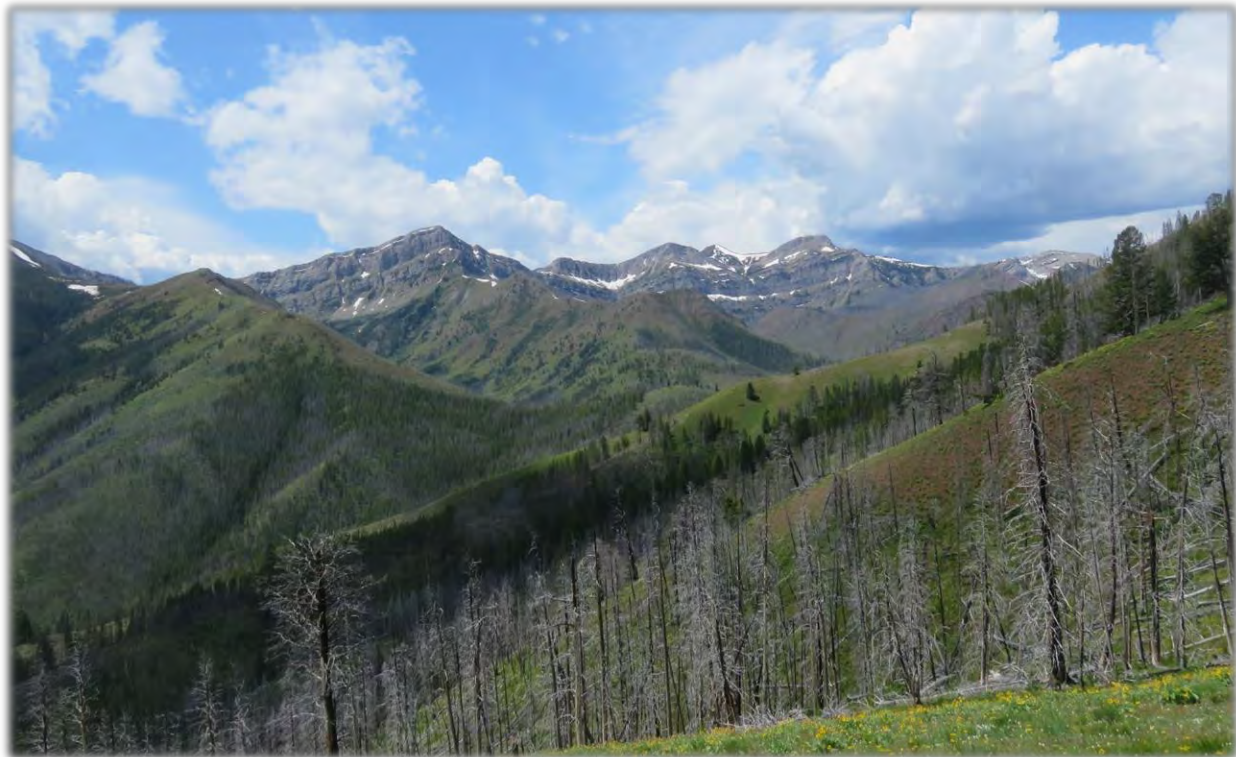
To complement the mechanistic look at factors driving the initiation of fall migrations (see Section 8.1), we also conducted a descriptive summary of where and when adult female mule deer are located across the hunting season, with specific attention to hunting district (HD) boundaries. Within each study area, we grouped deer according to subsets of the winter range in which they were captured. In the Cabinet-Salish, all deer were captured within a winter range encompassed by HD103, but we categorized deer into 2 groups according to whether they were captured east or west of the Fisher River. In the Rocky Mountain Front, we captured deer in winter range habitats that spanned 3 hunting districts and categorized deer into 3 groups according to whether they were captured in HD422, HD424, or HD425. It is important to note that some deer were captured near the district boundaries and in those cases individual home ranges often spanned multiple districts. Thus, alternate groupings based on different terrain features might improve the resolution in this study area. In the Whitefish Range, deer were captured on winter range that spanned 2 districts, HD109 and HD110, and we categorized deer according to the district in which they were captured. We included both resident and migratory mule deer in this exercise, and then estimated the proportion of GPS data within each hunting district per day of the hunting season, beginning with the first day of archery season and ending on the last day of general rifle season each year.

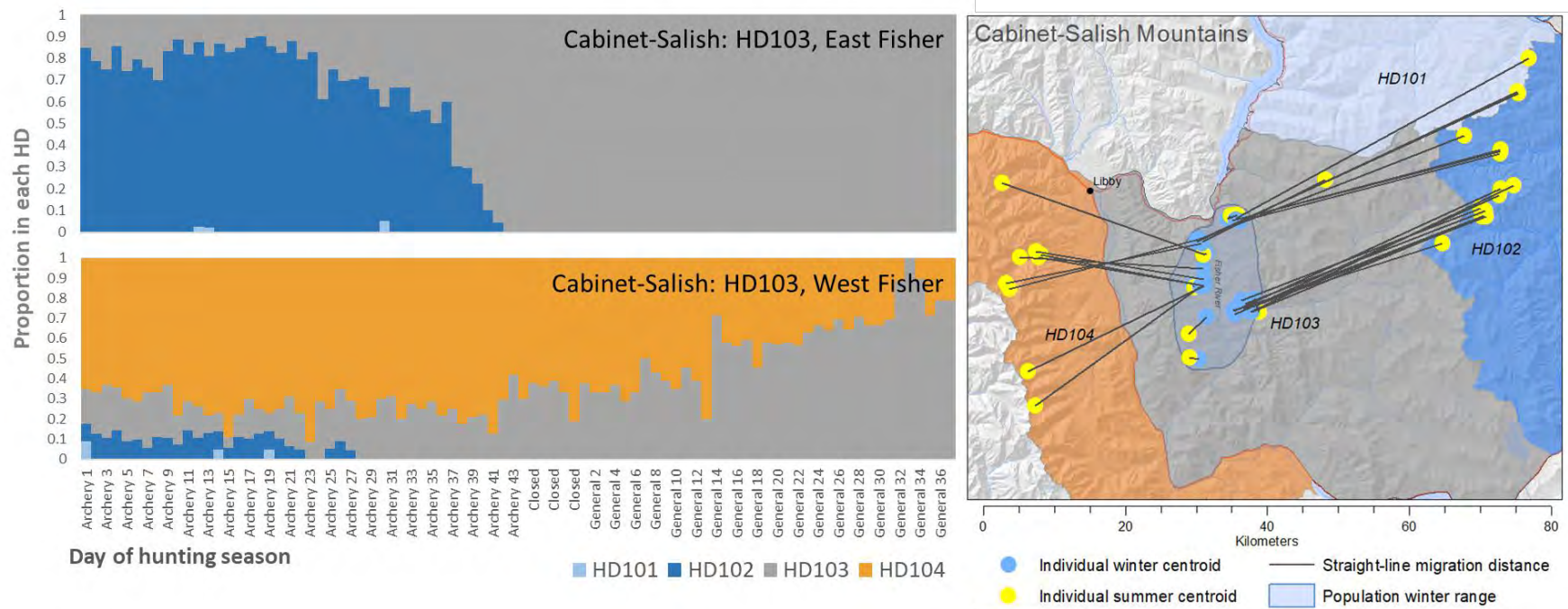


*Cabinet-Salish:* The timing of return migrations varied considerably across individual deer, and in some cases across winter range groupings. In the Cabinet-Salish, most deer that were captured east of the Fisher River (Mt. Sterling and Butler Creek areas of HD103) migrated eastward into summer ranges in HD102 and remained there until the beginning of archery season. Return migrations began roughly 3 weeks later and essentially all of these deer were located within HD103 by the end of archery season (Figure 8.3). Regarding deer that were captured west of the Fisher River, the small sample of animals captured to the south in Vian and Harris Creeks remained resident in the Fisher River drainage of HD103 year-round. To the north, some deer from Buck Creek migrated eastward into HD102, but most deer from the Buck and Doe Creek winter ranges migrated westward into the Cabinet Mountains of HD104 for the summer (Figure 8.3). These deer were slower to return to HD103; when the general rifle season began more than half were still to the west in HD104, and some remained in HD104 even when the rifle season ended at the end of November (Figure 8.3).

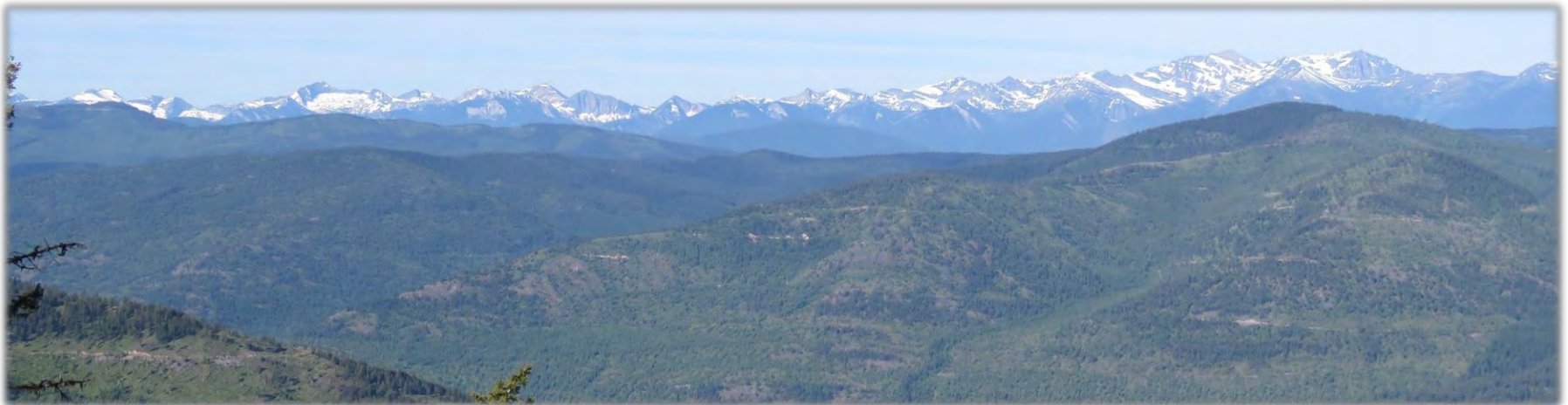
*Rocky Mountain Front:* Many of the deer captured in HD422 (Ford, Smith, Goss, and Elk Creek drainages) remained within the district year-round, while some migrants began the archery season in the wilderness districts of HD150, 280, 281, and the Sun River Game Preserve (SRGP; Figure 8.4). Most of these deer returned to HD422 late in the archery season, though some remained in wilderness into, or throughout the general rifle season. Deer captured in HD424 (McCarty Hill area and upper portions of Ford Creek) were divided between wilderness (HD150 and SRGP) and front-country (HDs 422, 424, 425) summer ranges, with some wilderness deer returning to HD424 during archery season but others remaining in wilderness districts until midway through the general rifle season (Figure 8.4). Lastly, the majority of deer captured in HD425 (Sun River WMA and lower portions of Willow Creek) were not in HD425 at the start of archery season, but included wilderness deer to the west in HD150 and the SRGP as well as deer that summered to the east in HD444 (Figure 8.4). Most of these deer did not return to HD425 until after the archery season was closed, and some remained in both HD444 and the SRGP through all or most of the general rifle season.

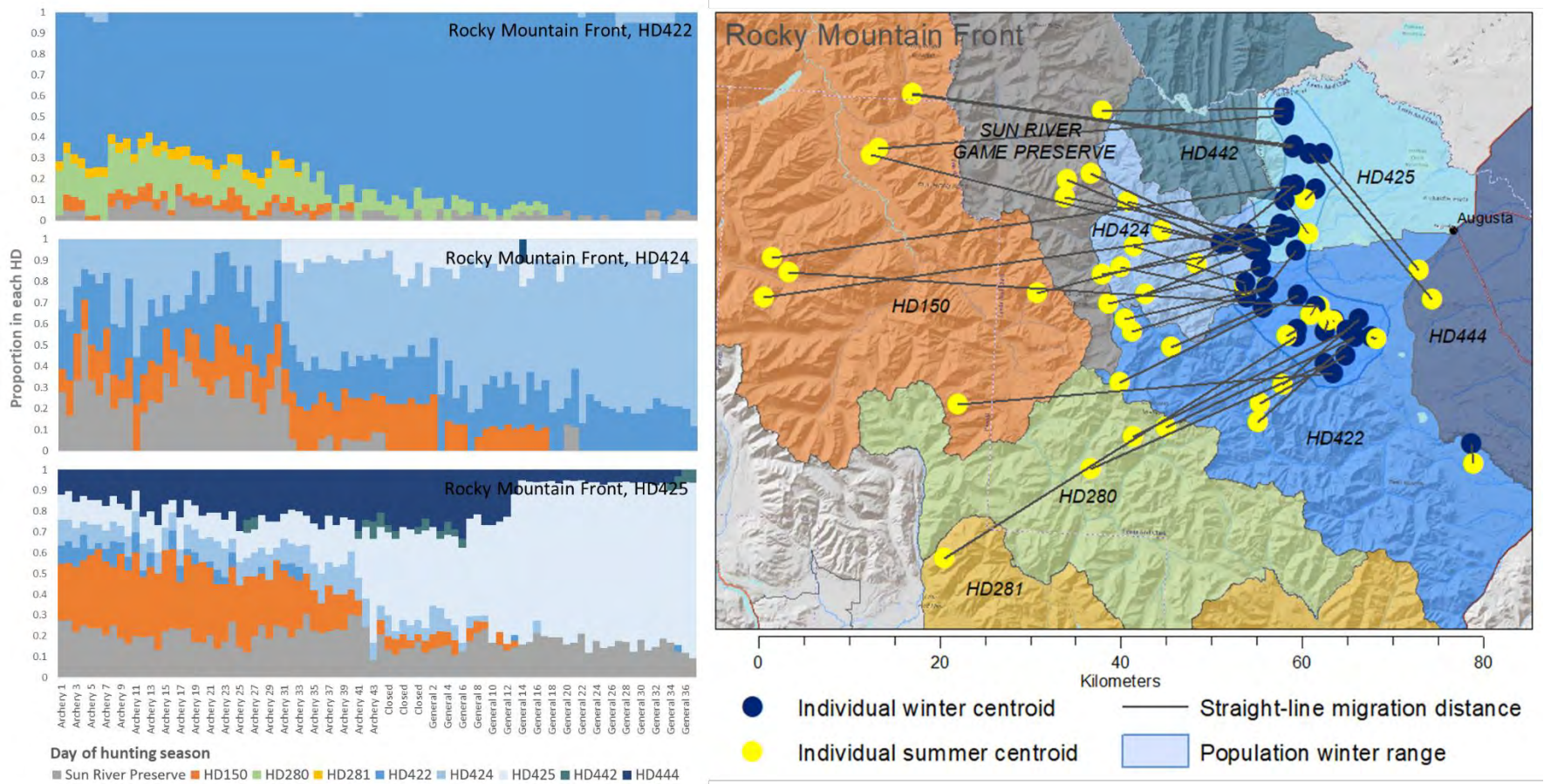
*Whitefish Range:* Deer captured in the HD109 portion of the Whitefish Range (Gibraltar Ridge, Deep Creek and Dickey Lake areas) predominately migrated into high elevation portions of HD110 and into British Columbia (BC; Figure 8.5). Deer in BC largely returned near the end of archery season, while some deer in HD110 did not return to HD109 until the last week of general rifle season. Deer captured in HD110 (Bull Lake and Point of Rocks areas) largely remained resident within the same area year-round, with the exception of some animals that migrated to high elevations predominately still within HD110. Also of note, 2 deer captured on the east-side of HD110 (Demers Ridge) included 1 that remained resident on Demers Ridge year-round and another that migrated into Glacier National Park; this migrant was in the National Park until the last week of the general rifle season, when it had started moving westward but was killed by a mountain lion.



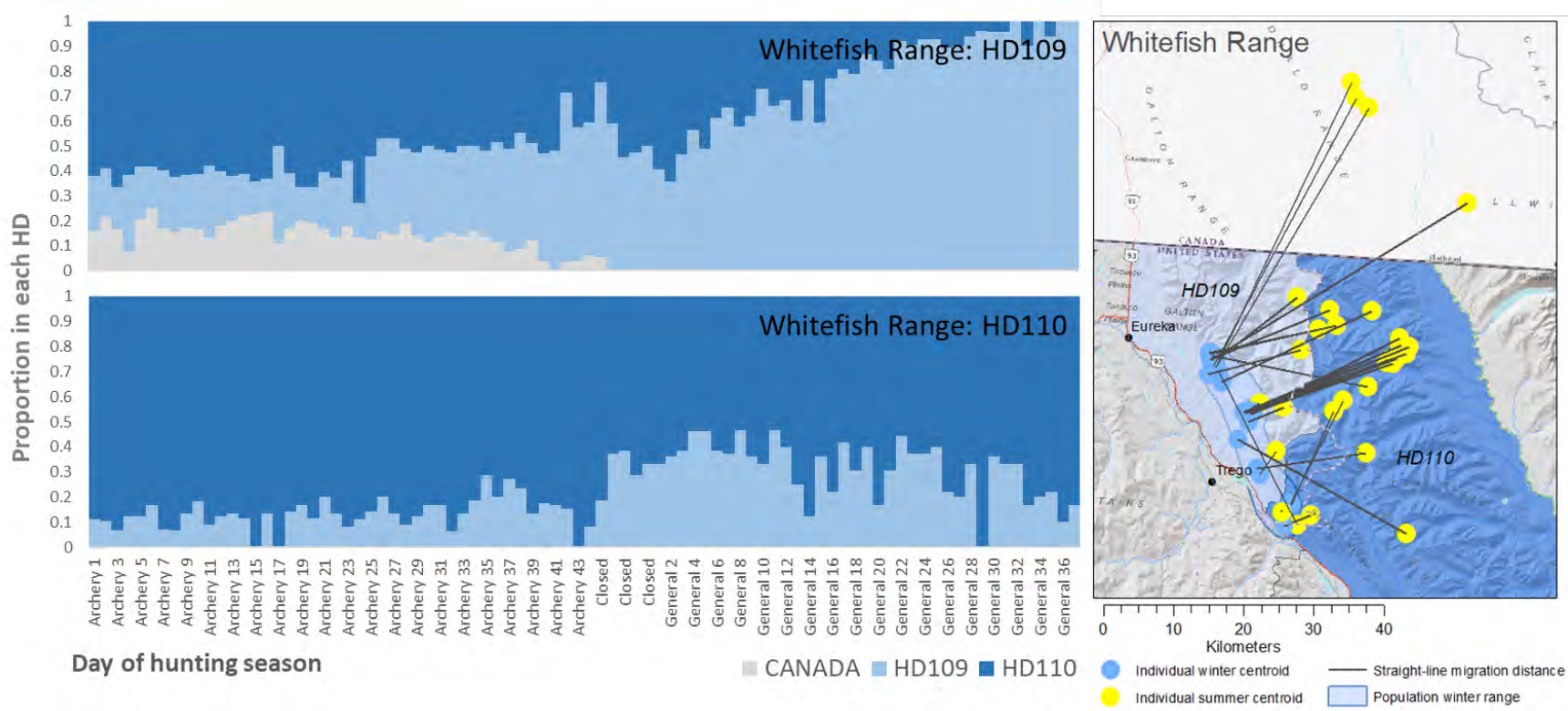


**Figure 8.3.** Proportion of adult female mule deer locations within each hunting district or administrative region per day of the fall hunting season, according to deer captured east vs. west of the Fisher River, Cabinet-Salish study area, 2018–2020.

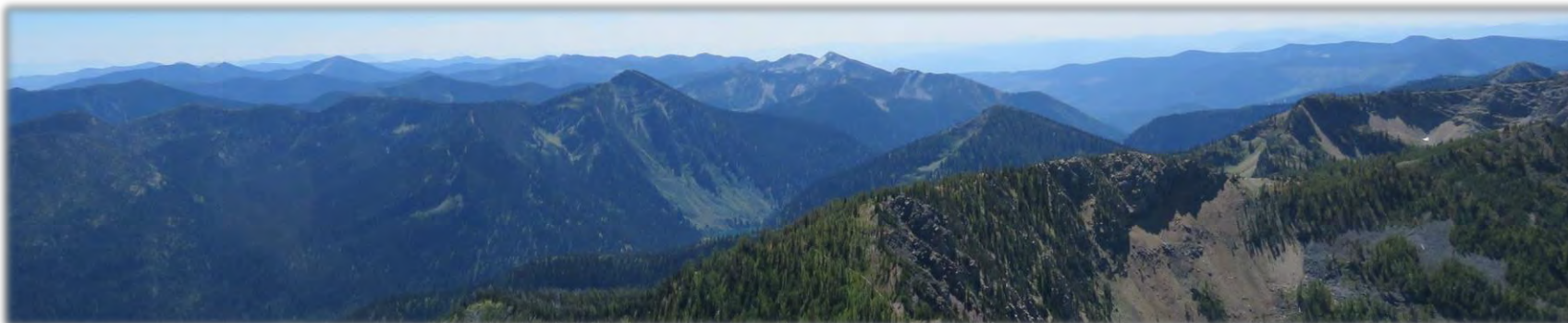




**Figure 8.4.** Proportion of adult female mule deer locations within each hunting district or administrative region per day of the fall hunting season, according to deer captured in HDs 422, 424, and 425, Rocky Mountain Front study area, 2017–2020.



**Figure 8.5.** Proportion of adult female mule deer locations within each hunting district or administrative region per day of the fall hunting season, according to deer captured in HD109 or HD110 portions of the winter range, Whitefish Range study area, 2018–2020.



## 9. INTEGRATED POPULATION MODELING: PRAIRIE-BREAKS

*(Note: these portions of study [9.1–9.2], are preliminary and still in preparation for internal review and submission to a peer-reviewed journal; primary author of manuscript(s) will be D. Messmer).*

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### 9.1. Hunting-district scale population estimates

**9.1.1. Background**— MFWP staff propose biennial mule deer hunting regulations at the HD scale using a combination of HD hunter harvest estimates, field observations, check station data, hunter and landowner input, and population parameters from trend monitoring survey areas. While MFWP hunter harvest sampling yields robust and precise harvest estimates for each HD (Lukacs et al. 2011), trend area polygons delimiting aerial survey boundaries occur in a subsets of HDs and areas within those HDs. Given gaps in aerial survey coverage and unmeasured spatial heterogeneity in deer densities, trend areas do not necessarily yield estimates of deer density or other population parameters at the same HD-scale. Additionally, data collected in trend areas are minimum counts, sufficient for unbiased estimation of population trend, but insufficient for estimating absolute abundance without correction for imperfect sightability (Samuel et al. 1987, Humbert et al. 2009). Thus, there is a disconnect in population sampling between harvest and population survey data which complicates the combined interpretation of both information sources.

As part of the 2001 AHM document, attempts were made to incorporate a modeling component that could predict, with reasonable certainty, future trends in mule deer population numbers. However, MFWP biologists had little success in modeling mule deer populations in a reliable and predictive sense. Therefore, the modeling component of AHM was removed from this plan (2021) and moved into a research and development function. Here we apply a new approach to statistical population modeling, integrated population models (IPMs), to combine HD harvest estimates with population parameters inferred at larger scales from trend areas to derive HD-scale population estimates (Schaub and Abadi 2011). We combined IPMs with a simple population reconstruction method to estimate HD population abundance based on existing data sources and vital rate information in the literature.

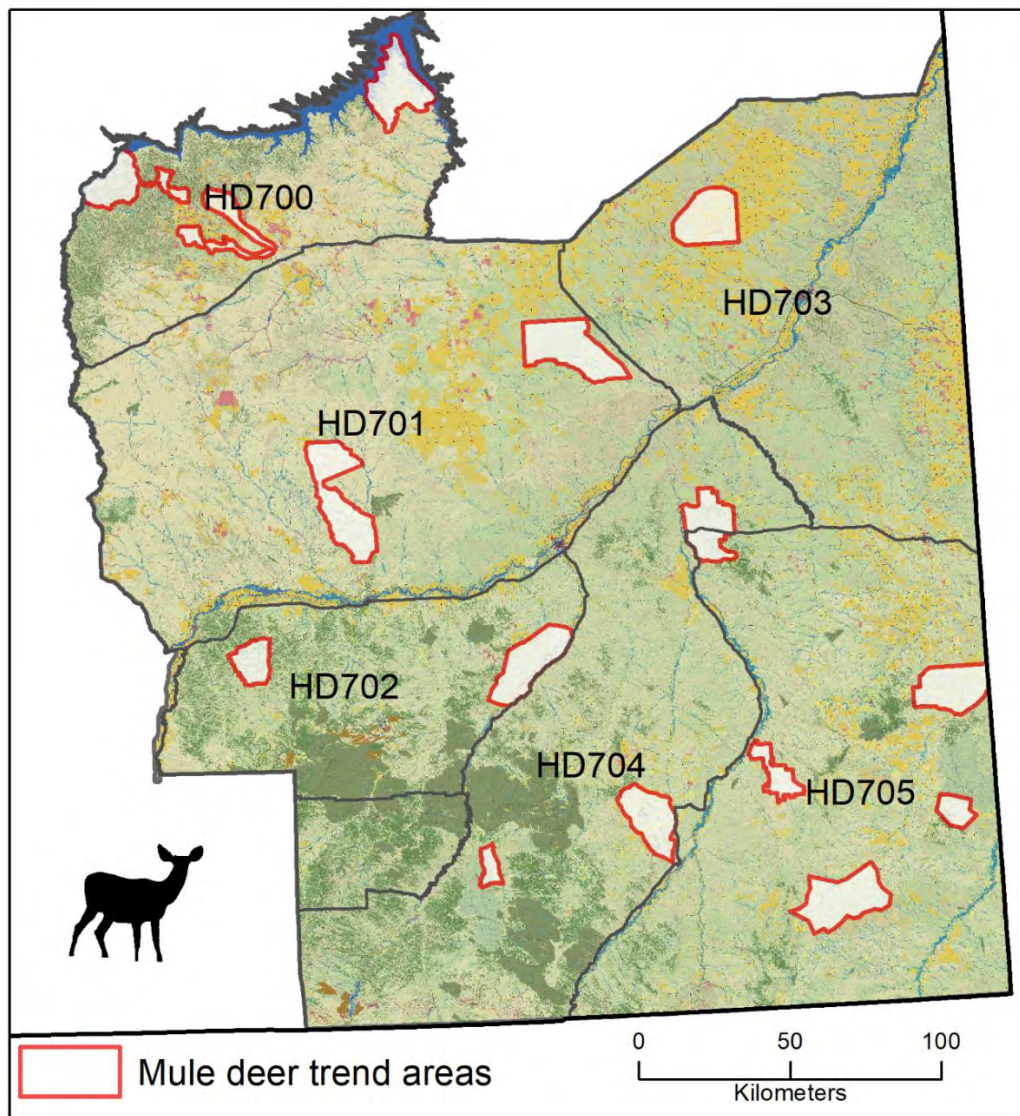
We consider 2 ways to infer HD-scale deer abundance from trend area data. First, a current informal approach is to assume density estimates from trend areas are representative of the surrounding HDs and to extrapolate these densities to the full HD-scale area. The alternative investigated in this study is to assume instead that harvest mortality rates (i.e., proportion of deer harvested) within trend areas are representative of rates in the surrounding HDs. With this approach, harvest rates can be estimated and aligned with the HD-scale harvest data to estimate HD-scale abundance using a population reconstruction method (Skalski 2010):

$$N = (\text{Harvest} / \text{Harvest Rate}) - \text{Harvest}$$

The first method would be most accurate where density is relatively spatially homogenous across HDs, whereas the second method would be most accurate where harvest rate could be treated as spatially homogeneous. Neither assumption is entirely accurate, but previous research on Montana mule deer

populations suggest that harvest mortality rates may be more spatially consistent than densities (Mackie et al. 1998). Our objective was to apply a population reconstruction method by first developing a trend area-scale IPM to estimate the latent annual harvest mortality rates according to observed count and composition data recorded during aerial surveys. Next, we combined these estimates of harvest rate with existing HD-scale harvest estimates to infer annual HD population size. Included in this approach are uncertainty estimates for abundance which account for spatial variability in the harvest mortality rate (among trend areas) and uncertainty due to sampling error (i.e., related to sample size).

**9.1.2. Methods**— We modeled population dynamics of mule deer in trend areas ( $n = 14$ ) of MFWP administrative Region 7 for the years 1999 – 2017 (Figure 9.1). The Region lies within the Prairie-Breaks mule deer PMU (MFWP 2021) and is broadly characterized by prairie and river breaks landscapes with a semiarid continental climate. Prairie land use is a mix of grazed grassland and dry-land farming. Land use in river break landscapes include grazing and some irrigated cropland adjacent to large rivers.



**Figure 9.1.** Mule deer trend survey areas and hunting districts in MFWP’s administrative Region 7, southeastern Montana.



Trend areas are surveyed from fixed-wing aircraft twice each year following protocols established previously (MFWP 2021). Counts are conducted after the general hunting season during early winter (i.e., Dec–Jan) and again in April before new fawns are born. The post-season count provides adult male:female and fawn:female ratios, whereas the spring count (during which sex is indistinguishable from aircraft) provides fawn:adult ratios (an index of fawn-to-yearling recruitment, 10 to 11 months after births in the previous year). The spring count is also considered the best index of abundance on the trend areas due to the tendency for deer to be congregated on spring vegetation green-up locations and relatively easier to count. Trend areas are distributed throughout the Region (Figure 9.1), however sampling intensity does not generally allow HD-level estimates of population parameters. Additionally, trend area locations were not randomly selected, but instead were systematically distributed among HDs. Estimates of hunter harvest are conducted via live-caller phone surveys with a statistically robust sampling design and produce relatively precise HD-level estimates of hunter harvest (Lukacs et al. 2011).

We built a full life cycle integrated population model (IPM) for pre-parturition spring populations based on trend area data for abundance, age, and sex ratios (Hatter et al. 2017; Figure 9.2).

The **process model** describes population dynamics:

$$N \text{ fawns}_{i,t} \sim \text{Poisson}(N \text{ females}_{i,t-1} \times \text{Recruitment}_{i,t-1} \times \text{Winter survival}_{\text{fawn } i,t-1})$$

$$N \text{ females}_{i,t} \sim \text{Binomial}(\text{Survival}_{\text{female } i,t-1}, N \text{ females}_{i,t-1} + N \text{ fawns}_{i,t-1} \times 0.5)$$

$$N \text{ males}_{i,t} \sim \text{Binomial}(\text{Survival}_{\text{male } i,t-1}, N \text{ males}_{i,t-1} + N \text{ fawns}_{i,t-1} \times 0.5)$$

$$\text{Survival}_{\text{male } i,t} = 1 - (\text{Harvest mortality rate}_{\text{male } i,t} + \text{Natural mortality rate}_{\text{male } i,t})$$

$$\log(\text{Harvest rate}_{\text{male } i,t}) = \mu + \text{year}_t + \text{site}_i + \text{harvest intensity}_{\text{male } i,t} \times \beta$$

$$\text{year}_t \sim \text{Normal}(0, \sigma_{\text{year}})$$

$$\text{site}_i \sim \text{Normal}(0, \sigma_{\text{year}})$$

where subscripts *i* and *t* refer to site and year, respectively. For the terms estimated in the population models, we specified weakly informed priors based primarily on the ranges of Montana mule deer vital rate estimates compiled in Mackie et al. (1998).

$$\text{Natural mortality rate}_{\text{male } i,t} \sim \text{Uniform}(0.01, 0.10)$$

$$\text{Harvest rate}_{\text{male } i,t} \sim \text{Normal}(0.40, 0.20)$$

$$\text{Winter survival}_{\text{fawn } i,t} \sim \text{Uniform}(0.4, 1.0)$$

$$\text{Survival}_{\text{female } i,t} \sim \text{Uniform}(0.05, 1.0)$$

$$\text{Recruitment}_{i,t} \sim \text{Uniform}(0.01, 4.0)$$

The distributions of mortality and survival rate priors above were truncated between 0 and 1. HD harvest estimates are not directly informative of harvest on trend areas because harvest is not evenly distributed across HDs. However, we assumed that harvest intensity (harvest estimate/HD area) in each HD would be proportional to harvest in the trend area. Therefore, we used harvest intensity as a covariate in the model estimating harvest rate. We only attempted to differentiate natural vs hunting mortality rates for adult males. Harvest of males is likely to be correlated with their harvest mortality rate because regulations in Region 7 have not restricted buck harvest and harvest accounts for most buck mortality (33–59% versus 4–9% from natural causes [statewide]; Mackie et al. 1998).

The **observation model** describes how trend area data (left sides of equations) relate to process model parameters (right sides of equations):

$$\text{Spring adults}_{i,t} \sim \log \text{Normal}(\log(N \text{ female}_{i,t} + N \text{ male}_{i,t}), \sigma_{\text{observation error}})$$

$$\text{Spring fawns}_{i,t} \sim \log \text{Normal}(\log(N \text{ fawn}_{i,t}), \sigma_{\text{observation error}})$$

$$\text{Post-season male:female}_{i,t} \sim \log \text{Normal}\left(\log\left(\frac{N \text{ male}_{i,t}}{N \text{ female}_{i,t}}\right), \sigma_{\text{male:female observation error}}\right)$$

$$\text{Post-season fawn:female}_{i,t} \sim \text{Normal}(R_{i,t}, \sigma_{\text{recruitment observation error}})$$

Adults and fawns were counted during spring surveys, while the sex and age ratios are observed during the post-hunting seasons survey. Our model assumes: 1) fawns counted during spring surveys are evenly split between male and female, b) yearlings have the same survival rates as adults, and c) natural mortality for male and female fawns after the hunting season are equal.

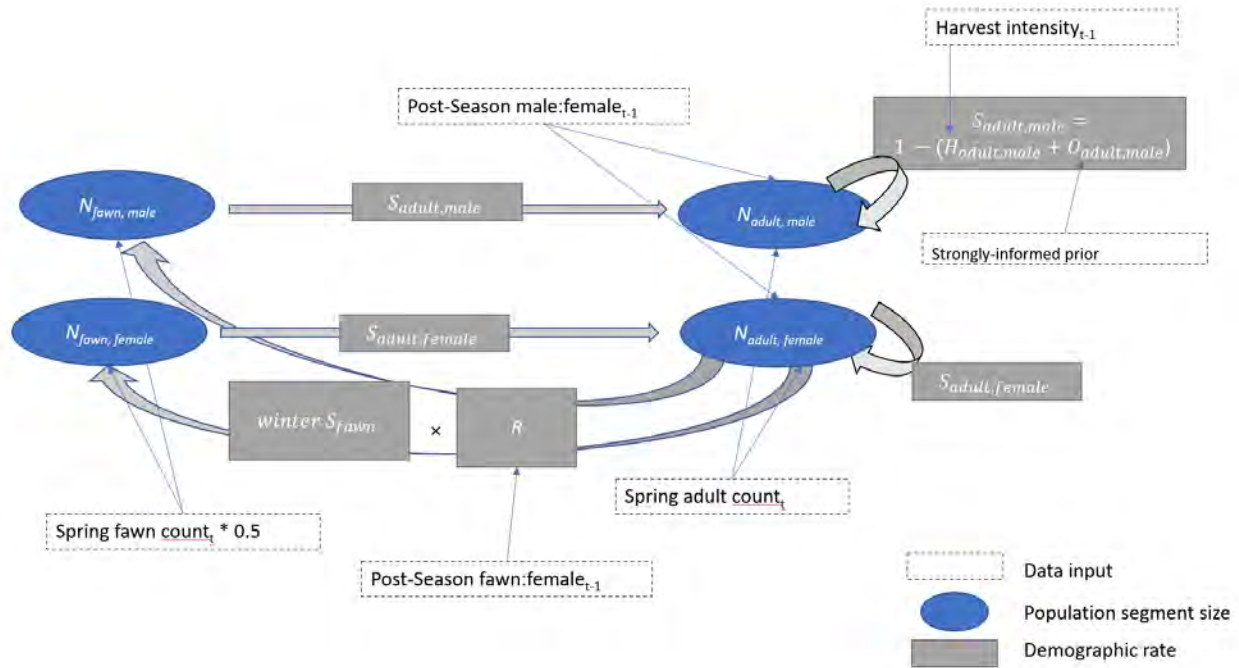
We fit the model in a Bayesian statistical estimation framework using JAGS software (4.3.0; Plummer 2003) executed from R via the package jagsUI (Kellner and Meredith 2021), a wrapper to the package rjags (Plummer et al. 2021). We generated 3 chains with 200,000 iterations, a burn-in of 40,000, and a thinning rate of 5. We assessed convergence by ensuring Gelman-Rubin convergence statistic for each parameter was <1.1 (Brooks and Gelman 1998) and that chains were well-mixed.

From the parameter estimates in this model, we combined the harvest mortality rate parameters with HD harvest estimates to estimate spring HD adult male abundance and subsequently female and fawn abundance according to:

$$\text{Spring male } N_{i,t} = \left( \frac{\text{male harvest}_{i,t}}{\text{Harvest rate}_{i,t}} \right) - \text{male harvest}_{i,t} \times (1 - \text{Natural mortality rate}_{i,t})$$

$$\text{Spring female } N_{i,t} = \text{Spring male } N_{i,t} \times \left( 1 / \text{Spring male:female}_{i,t} \right)$$

$$\text{Spring fawn } N_{i,t} = (\text{Spring female } N_{i,t} + \text{Spring male } N_{i,t}) \times \text{Spring fawn:adult}_{i,t}$$



**Figure 9.2.** Full life cycle spring (pre-parturition) integrated population model for mule deer in FWP Region 7, southeast Montana. Thin blue arrows represent the parameters which the data inputs most directly inform. Data inputs also indirectly inform other parameters through links (grey arrows) in the population model.  $H$  and  $O$  represents harvest and natural mortality rates for bucks, respectively.  $R$  represents fawn recruitment to 10 months old and  $S$  represents various survival rates.

We compared these results with regional mule deer population estimates that are currently reported by MFWP for Region 7. The current method treats each trend area as a sample of density from the overall Region and calculates an annual regional abundance as:

$$R7 \text{ mule deer abundance}_t = \text{mean}(\text{density}_{i,t}) \times \text{total area of mule deer habitat in R7}$$

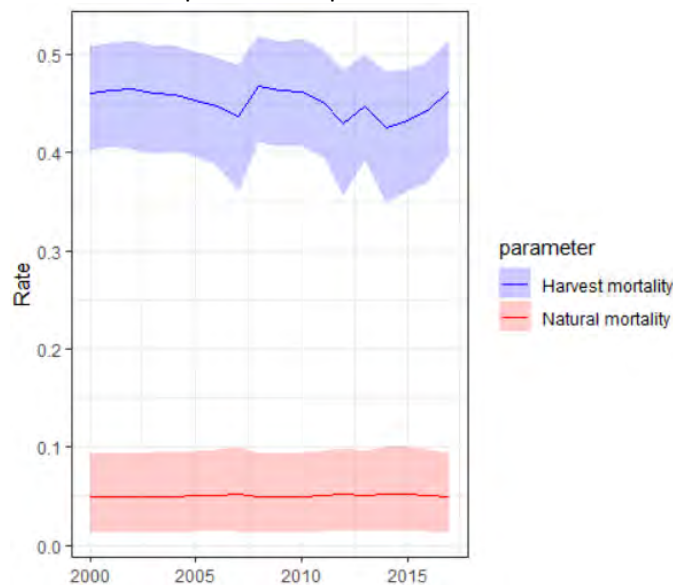
HD-level abundance estimates are also sometimes used informally by extrapolating the trend area densities to the HD which contains them. We compared these estimates to our HD-level population reconstruction method as well.



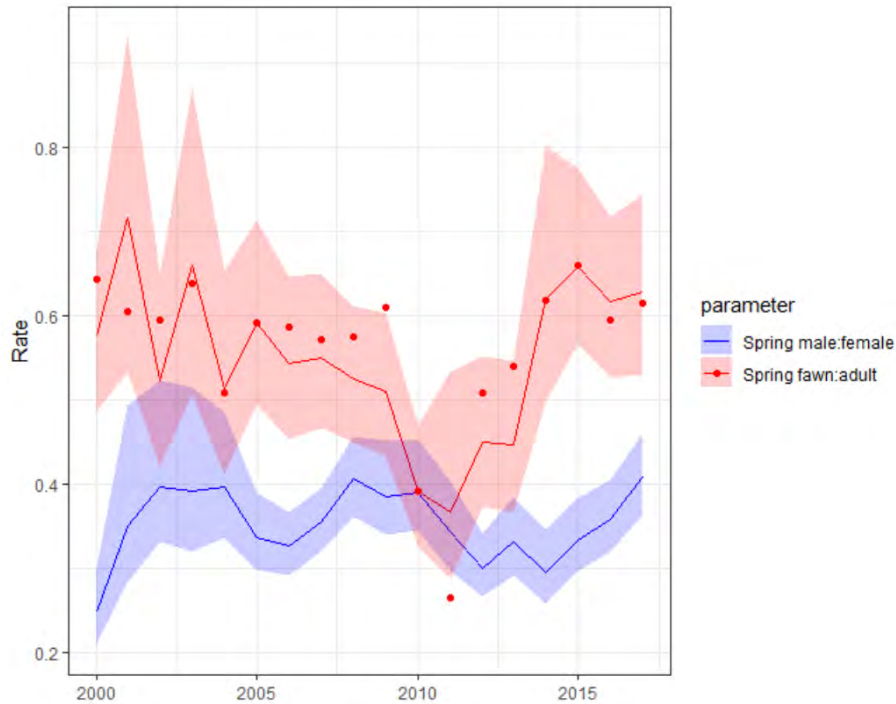
**9.1.3. Results**—Our model estimated adult male harvest and natural mortality rates of 0.46 (95% CrI: 0.39–0.53) and 0.04 (95% CrI: 0.02–0.07), respectively (Figure 9.3), averaged across trend areas over the entire study period. Despite these rates being unobserved variables based on count data from trend areas alone, the estimates fall in the general range observed in past studies of prairie-breaks deer populations in Montana (Mackie et al. 1998). Similarly, spring fawn:adult (observed variable) and spring adult male:female ratio (unobserved variable) fall within historical ranges for this ecoregion (Figure 9.4; Mackie et al. 1998).

Regional population estimates based on the IPM-based population reconstruction method and the density extrapolation method for Region 7 are of similar absolute values during some parts of the study period (e.g., 2000–2005 and 2011–2015; Figure 9.5) but differ greatly at other times (2006–2010 and 2016–2017). Where estimates differ substantially, the density extrapolation method produced larger estimates. The overall correlation of the 2 methods when aggregated at the regional scale was  $r = 0.39$ . When extrapolating trend area densities to their surrounding HD (Figure 9.6), it was apparent that the estimates in HDs 703, 704, and 705 drove the periods of major differences between the 2 methods. Focusing on the 2016–2017 period where regional estimates from the density extrapolation method greatly exceeded those from IPM-based population reconstruction, these estimates were strongly influenced by the Boxelder creek (HD 705) and Olive (HD 704) trend areas which averaged 4.2 and 2.8 mule deer/km<sup>2</sup>, respectively. The regional average was 1.2 mule deer/km<sup>2</sup> without these trend areas, whereas it was 1.6 mule deer/km<sup>2</sup> with them - a 33% increase.

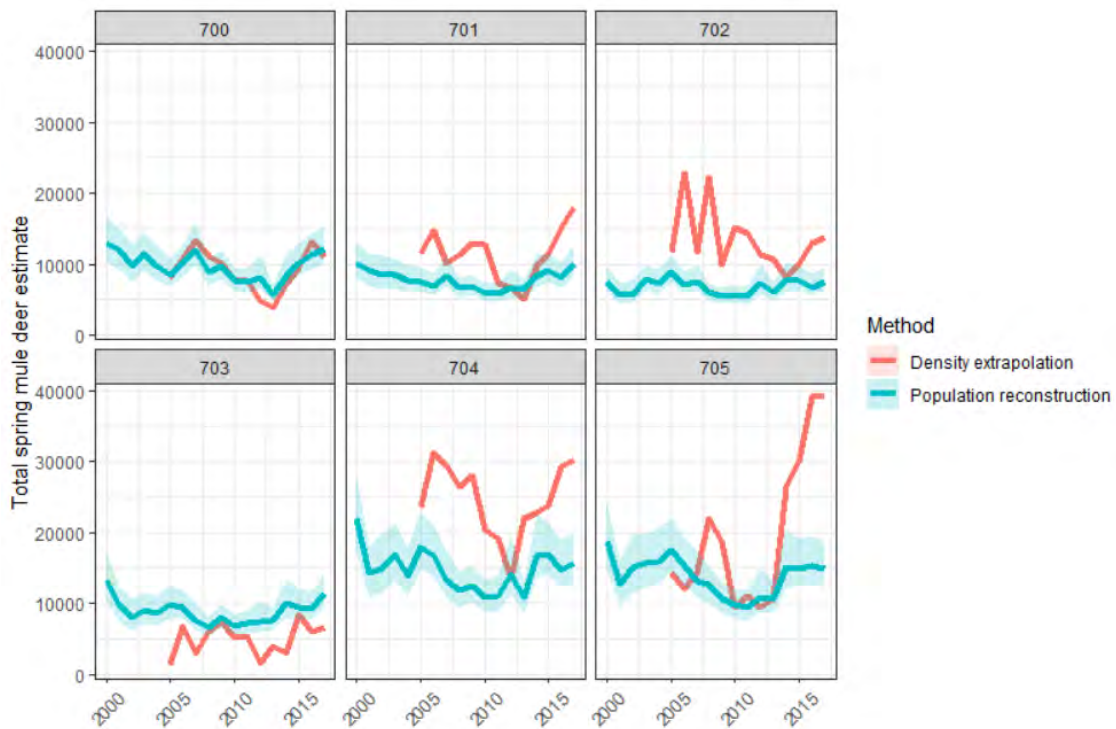
While this comparison between methods does not imply the IPM-based population reconstruction method is superior, it points out how density extrapolation could be biased or less precise over time if trend area sites are not randomly selected or consistently representative of the outlying area. Biological variation in the proportion of deer using trend areas, such as might occur with variation in migration timing (see Section 8) or facultative movements in response to weather (Jakes et al. 2018), might also induce additional error. Similar problems could impact accurate harvest rate estimation, though our random intercepts model reduced the potential impact of extreme values.



**Figure 9.3.** Mean male mule deer harvest and natural mortality rates and 95% CrI estimated across trend areas ( $n=14$ ) in Region 7 Montana, 1999–2017. Neither rate is directly observed and both are estimated indirectly based on other population data and weakly informed priors.



**Figure 9.4.** Mean spring adult male:female and fawn:adult ratios and 95% CrI estimated across trend areas ( $n=14$ ) in Region 7 Montana, 1999–2017. Red dots represent raw regional mean fawn:adult data. Spring adult male:female ratios are unobserved and are estimated indirectly from other population data.



**Figure 9.5.** Estimated total mule deer and 95% CrI based on the population reconstruction and density extrapolation methods in each of the Montana Region 7 hunting districts, spring 2000–2017. Density extrapolation method estimates were not yet available before 2005 at this scale.



**Figure 9.6.** Comparison of density extrapolation method versus the population reconstruction method (95% CrI ribbon) for estimating the regional total spring mule deer in Montana Region 7, 2000–2017.

**9.1.4. Discussion**—MFWP biologists are charged with managing hunting regulations at hunting district scales yet, aside from harvest estimates, they lack population data sampled at this scale. Most recently, concerns with the spread of chronic wasting disease have increased desire for HD-scale mule deer abundance estimates. Here, we used IPMs to evaluate deer monitoring data within the framework of biological models of deer population growth and allow estimation of an important, but previously unavailable metric: harvest rate. With the assumption that harvest rates (but not necessarily density) of deer within trend areas are representative at the HD-scale, our approach allows estimation of HD-scale abundance and sex-age composition of mule deer.

Absolute Region-scale estimates of N from both density extrapolation and IPM-population reconstruction methods corresponded well in some periods but deviated greatly in others. Investigating the greatest deviations, it was apparent that a few trend area density estimates had substantial leverage on the regional estimates. For instance, in 2015-2017 we found that 2 of 14 trend areas seemed to be outliers with densities 2.3 and 3.5 times larger than the overall mean. Their values resulted in a 33% larger estimate of regional abundance than if they had been excluded. While this does not necessarily imply those densities are unrepresentative, it does point to further evaluation being necessary. During this same period, the reconstruction method suggested a less pronounced trend of population growth, and population trends from this approach were more strongly correlated to the Region’s total buck

harvest ( $r = 0.54$ ) than those estimated from density alone ( $r = 0.37$ ) during the 2000–2017 study period.

Our study took place in FWP Region 7 which, by virtue of its relatively large HDs, had a greater number of trend monitoring areas per HD (1-3 trend areas per HD, whereas other Regions average <1 per HD given higher numbers of HDs themselves). In Regions with fewer trend areas per HD, the prospect of being able to utilize the HD-resolution harvest data to aid in population estimation is particularly attractive. As we explored here, nesting HD-level harvest and trend area survey data within broader regional or other population units may allow us to share information across districts and yield estimates in HDs currently lacking trend area survey data.

Differences in harvest management, hunter access, deer populations, and other factors may lead to substantial variation in harvest rate that is not adequately represented by nearby trend areas. Prescriptive differences in buck harvest management are known to be a primary driver of variation in harvest rate, with male:female ratios varying substantially between over-the-counter general license hunting and limited entry hunting in special management districts (Newell and Lukacs 2011). Most districts managed with over-the-counter opportunity for antlered buck mule deer have potential to fit this approach, but limited entry regulations for antlered bucks may present additional challenges. Central to our models is the tenet that harvest-based mortality can be distinguished from baseline natural mortality through the lens of deer dynamics in trend areas, as fit within the IPM. Where harvest-based mortality becomes low in limited entry scenarios, estimation of harvest rate may become imprecise with similar implications for population estimates. It is possible that additional parameters, assumptions, or extrapolation from areas with over-the-counter hunting may yet facilitate estimates in such districts, but additional work on this topic is needed.

Other important questions for the applicability of our approach will be the extent to which harvest rates over spatial scales within HDs, or whether it would be possible to model harvest rates themselves (e.g., as a function of landscape features such as road-access, land ownership, topography, and human population density) to account for this heterogeneity in the reconstruction model. An analogous approach to improve the density extrapolation method would be modeling mule deer density in relation to a broad-scale resource selection function estimated at a regional or statewide scale (Russell et al. 2015). Investigating either of these ideas could potentially improve our ability to infer from trend areas to larger scales and either approach could take advantage of the IPM developed in this study to make predictions about how future harvest will impact HD-level deer abundance.



Migration in some mule deer populations may add additional nuance to this IPM-based link between harvest and trend area survey data as described earlier in this report. Migration of mule deer across hunting districts during the hunting season (see Section 8.2) may cause changes in population segments being sampled per HD when comparing harvest and trend survey data. Extrapolation of HD-scale harvest estimates in migratory systems would produce HD-scale abundance estimates during the hunting season specifically, which may not align with winter and spring population boundaries during which survey data are collected. In the context of those migrations, we have recommended multi-HD coordination of hunting regulations where possible (Section 8), and similar multi-HD nesting of harvest and survey data is likely to improve population modelling under our approach.

Available evidence suggests natural mortality rates may be higher currently in some populations than found previously in Montana study areas (Mackie et al. 1998). In northern forests study areas, we observed relatively higher rates of natural mortality (21–25%) with an emphasis of high predation by mountain lions, and these values exceed those used in our prior distribution here for Region 7 (0–10%). The expanding distribution and prevalence of chronic wasting disease within mule deer of Montana (Almberg et al. 2021) may also have implications for the dynamics of natural mortality in mule deer populations of Region 7 or elsewhere (DeVivo et al. 2017). While the IPM is designed to distinguish natural and harvest mortality from survey data, the natural mortality rates observed in field studies reported in this report (21–25%; Section 4) are notably higher than the distribution of natural mortality rates found previously and used in this modelling exercise (Mackie et al. 1998). While further evaluation is necessary, harvest rates (and subsequent population estimates) may come with decreased precision in such scenarios where the prior distribution of natural mortality is wider than considered here. Additional information regarding spatial variation in cause-specific mortality may guide model prior distributions in local areas.

Selection of the method applied here over the extrapolation of trend area densities implies a belief that harvest rates of deer subpopulations sampled by trend areas are more representative of HD-scale patterns than mule deer densities. The approach demonstrates a plausible way to infer HD -scale population dynamics with limited direct data, although statewide application of this approach for monitoring mule deer dynamics will require additional analysis and exploration.

Possible extensions of this approach include re-incorporation of population models into MFWP's deer adaptive management program and exploration of the forecasting function of models in this framework. A primary components of the 2001 AHM plan was predictive population modeling given a suite of harvest and weather scenarios (MFWP 2001). Despite being founded upon very powerful data sets, Pac and Stewart (2007) found the AHM population models achieved mixed results and subsequently recommended they remain in an experimental phase rather than be implemented as a management tool (AHM 2021). Since that time have come improved weather data products, additional years of data, and recent advances in population modeling tools such as integrated population models (IPMs). Further evidence has also mounted concerning relationships between broad-scale weather patterns and mule deer dynamics (Hurley et al. 2014, 2017; Monteith et al. 2014; Ciuti et al. 2015; Stoner et al. 2016). Thus, we have also begun to revisit this topic of incorporating population modeling and weather data into an adaptive management framework for mule deer management.

The IPM developed above could facilitate iterative forecasting of dynamics and harvest impacts with potential to be refined via adaptive management. While precision of annual vital rate estimates from the IPM are lower than those that can be obtained with extensive radio-collar studies, the large number of trend areas and 22 years of counts in this R7 case study provide a good sample size for estimating



annual weather impacts. We have assembled weather station and satellite-observed covariate data describing fall and winter snow conditions and temperatures, timing of spring green-up, estimates of rangeland forage biomass, and spring and summer temperatures. Specifically, we are evaluating vital rate-specific effects of weather metrics such as snow cover, plant phenology and biomass, and seasonal temperature minima and maxima found to occur for mule deer in other western jurisdictions (Hurley et al. 2014, 2017; Monteith et al. 2014; Ciuti et al. 2015; Stoner et al. 2016). Starting within the framework of this R7-focused IPM, we will examine how these covariates impact recruitment, adult survival, and ultimately, population growth rates.

#### 9.1.5 Management Recommendations

The current mule deer monitoring platform used by MFWP samples mule deer population performance and hunter harvest at different spatial scales. While suitable for mule deer management under AHM (MFWP 2021), these data were not designed to provide HD-scale population estimates. The approach we have pioneered here may facilitate such estimates without needing any additional data. We recommend further evaluation and validation of this methodology, including special attention to the effects of buck management and predation- or disease-influenced variation in natural mortality on harvest rate estimation, as well as parsimonious incorporation of weather covariates to potentially improve or smooth predictions (Hurley et al. 2017). Further investigation of fine-scale spatial variation in harvest rates may also improve the precision and utility of this approach. An alternative approach is to improve the density extrapolation method by developing a resource selection model and extrapolating trend area deer densities to the HD as a function of habitat quality. Either approach could take advantage of the IPM developed in this study to make predictions about how future harvest will impact HD-level deer abundance and potentially provide an additional tool to further guide mule deer management in Montana.



## 10. MANAGEMENT RECOMMENDATIONS

*Mule deer migration (Sections 3, 8)*—The majority of female mule deer were migratory in all 3 study areas in northwest Montana, and were spread across multiple hunting district (or other administrative boundaries) throughout the hunting season. In these cases migration may impose a disconnect between population units managed and sampled during the hunting season (via harvest regulations and harvest survey data) and population units monitored during the winter (via post-season and spring surveys). This cross-boundary movement of animals may emphasize broad-scale, multi-district coordination of mule deer harvest management and interpretation of harvest and survey data.

Drivers of the timing of animal migrations during the fall hunting season are multi-factorial, including annual variation in the onset of winter weather (precipitation and temperature), but also characteristics of individual deer (i.e., migration distance). Comparison of migration timing among different groups of deer also suggests subgroupings within populations that migrate at different times, such as the relatively early return of deer to the eastern Fiver River drainage of HD103 vs. the relatively late return of deer to the western Fisher River (Figure 8.3). In these cases, season structures that increase harvest opportunity during early vs. late season may have unequal effects on subgroups of deer, depending upon migration timing and the spatial continuity of hunting regulations. For migratory deer, recognizing the practical challenges of applying broad scale hunting regulations over a large landscape, it may be necessary to further consider mirroring regulations in both summer and winter ranges over time to avoid undue impacts on those that return early vs. late. These results are specific to adult females but should have implications for antlered bucks given their migrations can be driven by similar phenomena and should facilitate overlap with females during the rut.

*Survival and recruitment (Section 4)*—Rates of natural (non-hunting) mortality were relatively high in our study populations (21–25%) compared to previous studies of female mule deer in eastern Montana (5–7%), with mountain lion predation being the leading cause of mortality. The high natural mortality rates observed here leave little to no room for additional hunting opportunity of antlerless deer, if mortality from hunting is even partially additive to other natural causes. Our results suggest reduction of mountain lion populations may have direct implications for mule deer given the paramount importance of adult female survival driving population dynamics in ungulate populations. However, we qualify this conclusion with evidence from previous studies elsewhere showing changes in population trend may still be marginal or short-term where such predator management is applied. Where combined predation rates approach 10–15% such as observed here, reduced capacity for antlerless human hunting may be a consequence of intact predator communities. Pulses of mortality of animals in poor nutritional condition early spring indicate the potential that some antlerless harvest could be compensatory with winter mortality. However, such harvest would only be recommended in scenarios where deer are assumed to be at or near nutritional carrying capacity and where reducing deer density would reliably be expected to improve average nutritional condition.

The effects of winter severity on both adult and fawn survival were also apparent. The relatively severe winter of 2018 was particularly associated with higher mortality of collared deer in the Whitefish Range. Relatively low fawn recruitment was also apparent in the Cabinet-Salish (15–28 fawns/100 adults) and the Rocky Mountain Front (17–18 fawns/100 adults) following winters that saw notably high snowfall relative to long-term averages. This mirrors results elsewhere showing the importance of winter conditions on fawn survival and implies a complex and interacting network of factors affecting mule deer dynamics that includes predator communities, population density, and annual weather conditions.

Summer habitat management (Sections 5,6) — Mule deer diets during summer consisted largely of forbs and shrubs, and the availability of forage nutrition in forested environments generally increased with forest disturbance, both fire and timber harvest. That said, the responses of plant communities to disturbance were highly variable both within and among study areas, and less desirable outcomes such as increased invasive species biomass and decreased floristic quality were also associated with some disturbances. Decision analyses such as that presented here may help managers weigh outcomes and management priorities to make decision when faced with such trade-offs. For example, in our case low-severity timber harvest was an appealing forest management action in that it best balanced increased forage nutrition while limiting invasive species and maintaining floristic quality.

Regarding the placement of targeted forest management for mule deer habitat, the high fidelity of mule deer summer ranges (Section 3) and more consistent selection for forage at fine- than broad-scales (Section 6) may suggest limited utility of management-directed forage improvements to individual deer unless placed within existing home ranges. Our broad-scale habitat models may be used to predict home range habitat where treatments could be effective. Where mule deer populations are largely migratory, such as we studied in northwest Montana, summer habitat management for mule deer may necessitate disturbance management in higher-elevation summer ranges. Wilderness designation and limited access in such ranges may limit options for management-driven changes to summer nutrition.

Winter habitat management (Sections 5,7) — The variation in snow conditions across our three study areas was a primary driver of variation in mule deer winter resource selection. In the deepest snow environments such as in the Whitefish Range, conifer forests appear important for snow-intercept and for an accessible source of winter forage, more so as snow increased over space and time. In such environments, management to reduce forest canopy might create additional forage (e.g., shrub) resources but those resources appear to become inaccessible when and where snow is deep enough to inhibit movement or bury plants. While winter conditions were also at times severe in our other two study areas (enough so to impact spring recruitment), mixed foraging on both shrubs, conifers, and other taxa showed lesser impact of snow on access to forage. Habitat management to promote shrubs in these areas may be less costly to energy expenditure and increase the biomass of accessible forage, with favorable implications for deer population dynamics.

Population monitoring and modeling (Section 9) — The current mule deer monitoring platform used by MFWP samples mule deer population performance and hunter harvest at different spatial scales. While suitable for mule deer management under AHM (MFWP 2021), these data do not allow HD-scale population estimates. The approach we have pioneered here allows novel estimation of a previously unavailable and management-relevant metric: the harvest rate of antlered buck mule deer. Furthermore, it facilitates HD-scale population estimates without needing any additional data, though broader-scale fitting and interpretation of these models may be required in other portions of Montana. We recommend further evaluation and validation of this methodology, including special attention to the effects of buck management and predation- or disease-influenced variation in natural mortality on harvest rate estimation, as well as parsimonious incorporation of weather covariates to potentially improve or smooth predictions. Refinement of density extrapolation approaches with spatial habitat models is an alternate means of estimating deer populations within the biological underpinnings of the IPM developed here. A project to develop statewide winter habitat models for mule deer has been recently prioritized by MFWP, and products from that effort could be integrated within the IPM we developed for such a purpose.

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