

Integrating statewide research and monitoring data for mule deer in Montana



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Project Personnel

Nick DeCesare, Research Biologist
Tonya Chilton-Radandt, Area Biologist - Libby
Brent Lonner, Area Biologist – Fairfield
Ethan Lula, Area Biologist - Eureka



**MONTANA FISH,
WILDLIFE & PARKS**

Teagan Hayes, MS Student
Collin Peterson, MS Student
Chad Bishop, Director, Wildlife Biology Program
Mike Mitchell, Unit Leader, MCWRU



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Background and summary

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 dynamics is of relevance across Montana. The methods by which Montana Fish, Wildlife and Parks (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.

MFWP currently collects multiple sources of monitoring data to guide management decisions under the AHM system, and distinct from this current process are other vital rate data collected as part of research studies. With this project, we seek to leverage existing monitoring and research data together for an integrated quantitative assessment of mule deer dynamics for guiding management. Additionally, we aim to collect novel field data in portions of northwest Montana and along the Rocky Mountain Front where biologists are faced with reduced mule deer numbers yet lack basic ecological and population information to manage with strong confidence.

Location

Field studies are focused in Lincoln, Flathead, and Lewis and Clark counties, where mule deer use 3 different and less understood habitat types. Population modeling involves utilization of research and monitoring mule deer data from across their statewide distribution.

Study Objectives (2018-2019)

During the 2019 calendar year, the primary objectives were to;

- 1) Integrated population modeling: data compilation and preliminary analysis
- 2) Mule deer field studies in 3 study areas of Montana
 - 2.1 Winter deer captures across 3 study areas
 - 2.2 Vital rate monitoring of adult female mule deer
 - 2.3 Monitor seasonal space use and migration of adult female mule deer.
- 3) Mule deer habitat selection and foraging in 3 study areas
 - 3.1 DNA-based diet sampling of mule deer
 - 3.2 Conduct field work to assess forage species composition, biomass and quality
 - 3.3 Assessment of mule deer response to predation risk
 - 3.4 Assessment of vegetation and mule deer response to landscape disturbance

Objective #1: *Integrated population modelling*

Integrated population models (IPMs) are growing in use by management agencies seeking to accommodate multiple data streams that characterize populations (Cooper et al. 2003, Schaub et al. 2007, Johnson et al. 2010, McCaffery and Lukacs 2016). One advantage of this approach is that it aligns multiple data streams into a single model of the population, while weighting the contribution of each data set according to its relative precision. A second advantage is that it formalizes the level of uncertainty surrounding any given point estimate, such that estimates of population trend or recruitment ratios come with explicit attention to precision. Third, one can incorporate links to environmental covariates into population models, which show particular potential for mule deer given links between remotely-sensed metrics of climate and vegetation and concurrent deer population dynamics (Mackie et al. 1998, Hurley et al. 2014, Ciuti et al. 2015, Stoner et al. 2016). Lastly, these models could conceivably facilitate the extrapolation of patterns from data-rich portions of the state to those without comparable monitoring data.

Our mule deer IPM will begin with a simple mathematical construction of annual mule deer dynamics, requiring input data for animal abundance and vital rates. Models can initially be informed by prior values derived from the literature, and then the fit adjusted according to input data from local populations. For example, Hurley et al. (2017) presented models that predicted 70-80% of the variation in over-winter fawn survival with 3 weather covariates (% snow cover winter, weeks of snow cover in Nov/Dec, and fall plant productivity). Applying such models to weather data across various management units in Montana may be one means to set meaningful prior values in an IPM framework.

Population data specific to Montana will start with 3 sources of annual monitoring data: 1) deer harvest data, 2) trend area minimum counts, and 3) trend area sex/age composition data. These data each come with variable levels of precision each year, and levels of agreement amongst them may vary over time and space (Figures 1, 2). Thus, the role of the IPM will be to balance all available information into a single depiction of dynamics per spatial unit. In order to provide the most robust results, it is likely that such spatial units will be more broad than single hunting districts.

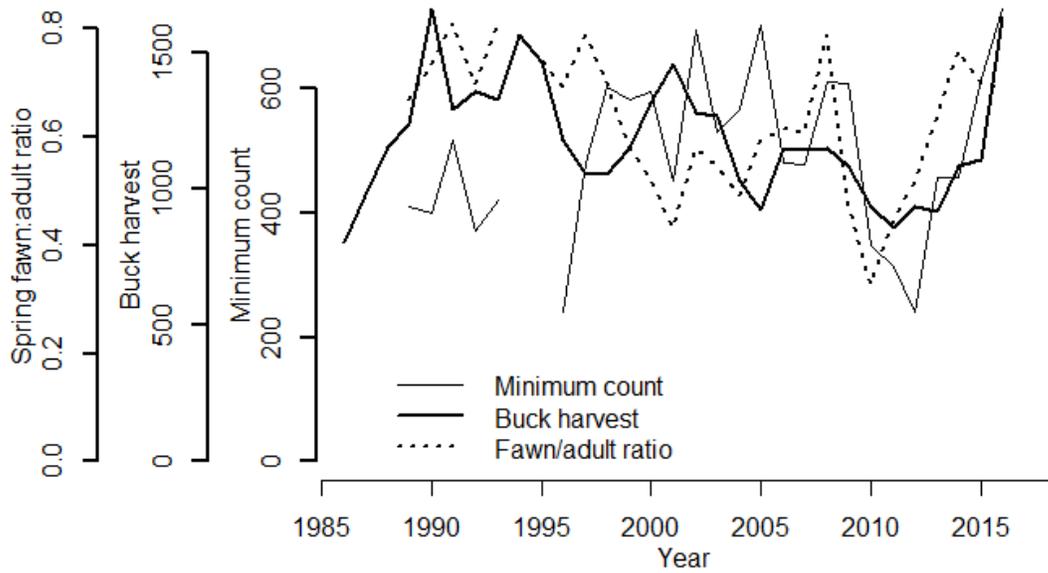


Figure 1. Example time series of mule deer monitoring data for deer hunting district HD701, including combined minimum counts and spring fawn:adult ratios from 2 trend areas as well as buck harvest estimates for the entire district, 1986-2016.

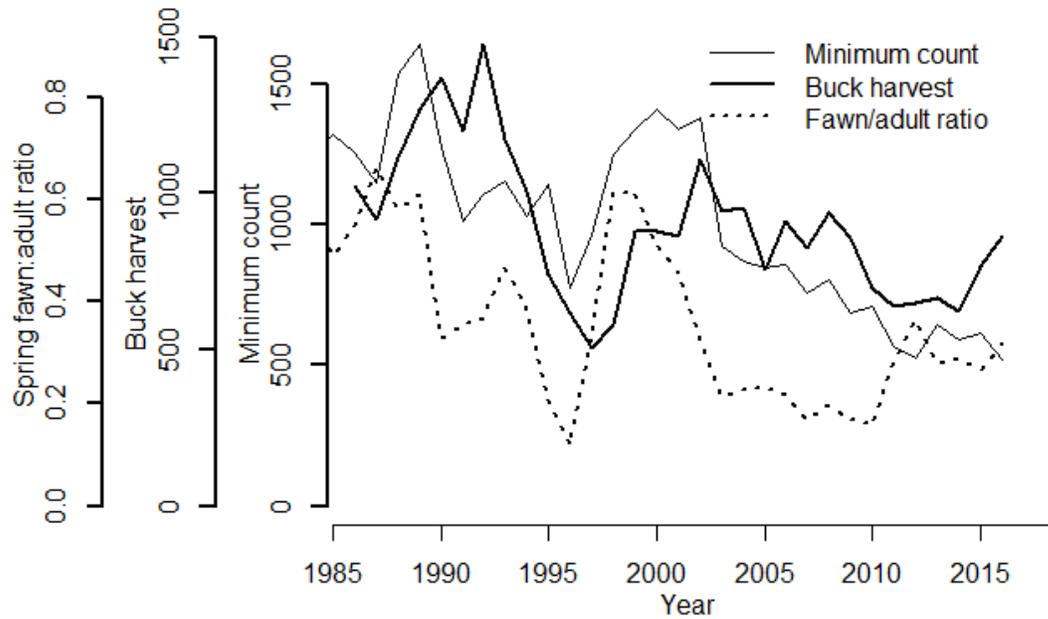


Figure 2. Example time series of mule deer monitoring data for deer hunting district HD575, including minimum counts and spring fawn:adult ratios from 1 census area as well as buck harvest estimates for the entire district, 1985-2016.

Input data may also include adult female survival rates estimated from multiple study areas across the state. To date, we have compiled such data from 9 studies completed across the state since the year 2000. Kaplan-Meier analysis of adult female survival (excluding hunter harvest mortality) estimated a range of average annual survival rates from 0.70–0.87 across study areas (Figure 3).

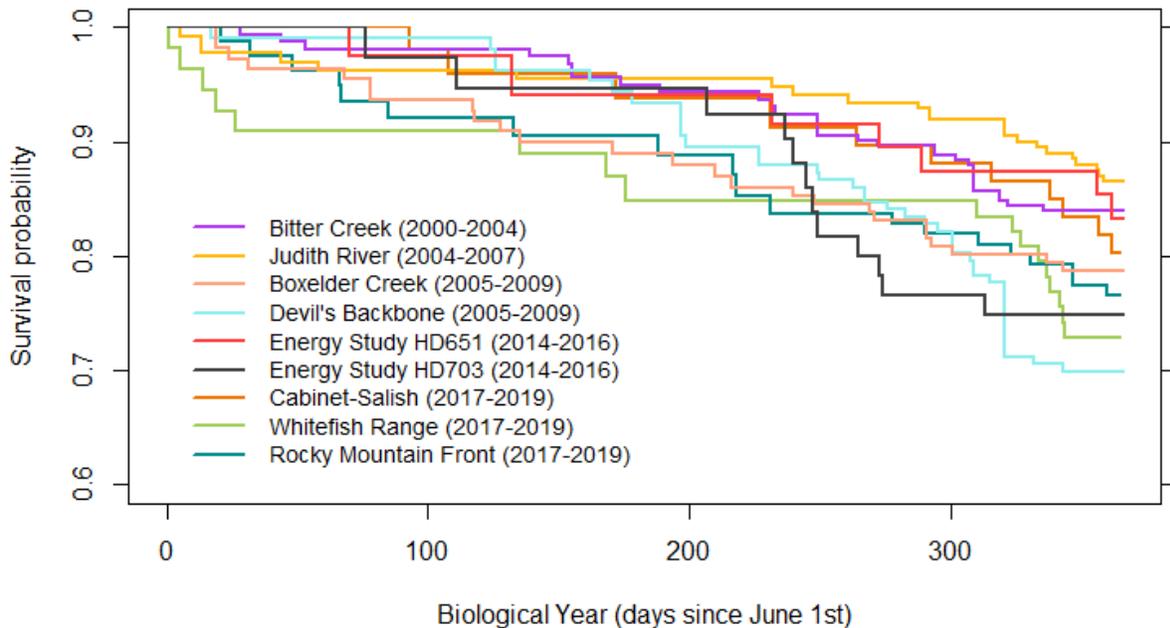


Figure 3. Annual survival estimates for adult female mule deer, excluding hunter harvest mortality, across 9 study areas in Montana, 2000–2019.

Objective #2: Field studies in 3 study areas of Montana

2.1. Animal capture and handling

Capture work is now completed for monitoring mule deer vital rates, seasonal space use and migration, habitat selection, and summer forage across 3 study areas. In total, we captured and radio-collared 134 adult female mule deer for these purposes. All deer were fit with GPS radio-collars (Lotek LifeCycle330), and deer were caught using a combination of helicopter net-gunning, ground trapping with alfalfa-baited Clover traps and ground darting (Figure 4; Table 1). With captures beginning in 2017, some collars have begun to reach the end of their battery lives at this stage of the study. To date the median collar life has been 1.8 years, though some have lasted up to 2.5 years.

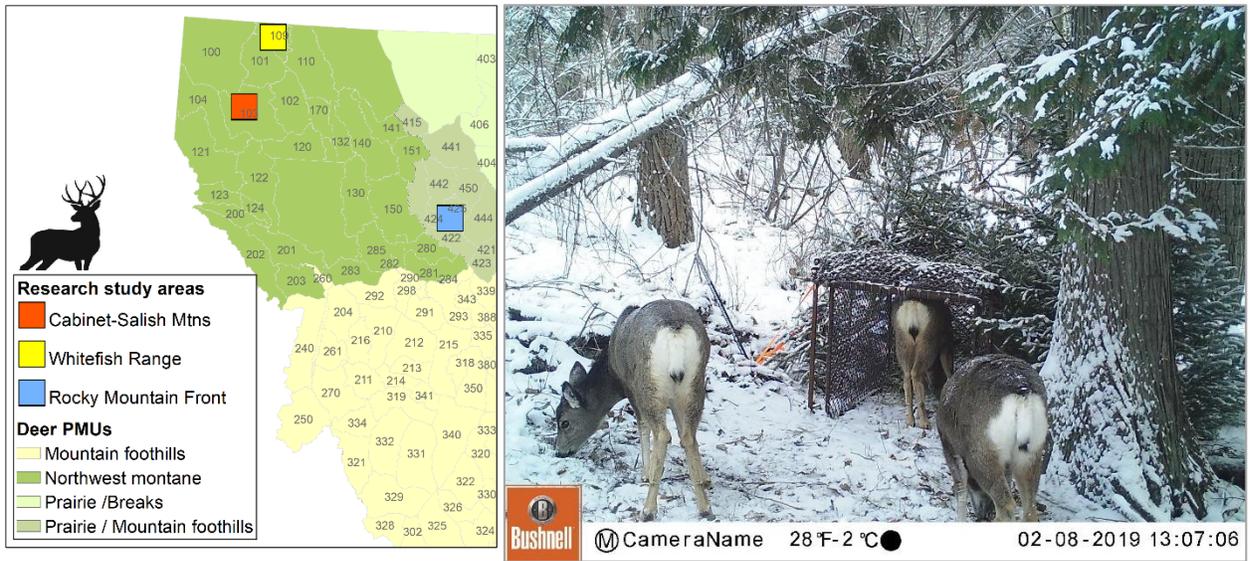


Figure 4. Mule deer field research study area locations (map also showing deer population management units [PMUs] and hunting districts), and a remote camera photo of deer approaching a baited Clover trap site in the Whitefish Range study area, February 2019.

Table 1. Numbers of adult female mule deer captured and radio-collared across 3 study areas, 2 winter seasons, and 3 capture techniques, Montana, 2017–2019.

	<u>Rocky Mtn Front</u>		<u>Cabinet-Salish</u>		<u>Whitefish Range</u>	
	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
<i>Total</i>	49		41		44	
<i>Currently on-air, December, 2019</i>	3		21		20	

2.2 Vital rate monitoring

Capture and collaring of adult female deer in 3 study areas facilitates the monitoring of adult female survival and pregnancy rates. Preliminary estimates of annual adult female survival in each study area are 0.802 (95% CI: [0.704, 0.915]) in the Cabinet-Salish study area, 0.766 (95% CI: [0.677, 0.866]) in the Rocky Mountain Front study area, and 0.729 (95% CI: [0.626, 0.848]) in the Whitefish Range study area. We have documented probable causes of death for a number of mortalities by inspecting carcasses following collar notification of mortality events (Table 2). Remote locations of some mortality sites have prevented us from determining causes in all cases.

Table 2. Causes of mortality as determined from inspection of carcasses of GPS-collared adult female mule deer across 3 study areas in western Montana, 2017–2019. Note these data exclude capture-related mortalities and are the result of 3 years of survival monitoring on the Rocky Mtn Front study area and 2 years of monitoring in the Fisher River and Whitefish Range study areas.

Cause of mortality	Rocky Mtn Front	Fisher River	Whitefish Range	Total
Health related	2	1	3	6
Human, caught in fence			1	1
Infected wound	1			1
Predation, coyote		1		1
Predation, lion	5	7	8	20
Predation, wolf	3	1	1	5
Predation, unknown spp.	1			1
Unknown	7		3	10
Total	19	10	16	45

At the time of capture, blood samples are collected for pregnancy determination via lab analysis of pregnancy-specific protein B (PSPB) levels in deer serum (Wood et al. 1986). This assay is most effective ≥ 40 days following conception. The peak period of breeding for mule deer in Montana is estimated to occur in mid-November; thus, we censored samples collected in December from our pregnancy analyses, because PSPB results were not yet reliable.

Pregnancy rate data are incomplete as some samples are still awaiting lab analyses. Pregnancy rates thus far have been estimated as 76% in the Fisher River ($N=21$), 100% ($N=46$) in the Rocky Mountain Front, and 100% ($N=30$) in the Whitefish Range. Just 5 females, all from the Fisher River study area, were estimated as non-pregnant. Of these 5, 3 were aged in the field as yearlings, and age was unknown for the other 2. Pregnancy of yearling mule deer has been shown to be more sensitive to a population’s average nutritional status than that of adult does (Julander et al. 1961, Monteith et al. 2014). Thus, it is possible that lower yearling pregnancy in this population is indicative of a limiting role of nutrition in overall population-level dynamics. However, pregnancy rate for this population in particular is founded upon a relatively low sample size of individuals ($N=21$), and testing may have missed late-estrus pregnancies as well. Additional pregnancy analyses of samples collected during the winter of 2018–2019 will improve our understanding of this vital rate across all populations.

2.3. Space use and seasonal migrations

We used net-squared displacement (NSD) to classify individual mule deer summer movement 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 migrateR package (Spitz, Hebblewhite, and Stephenson 2017) in Program R version 3.6.1 (R Core Team 2019) to classify movement behaviors. Deer populations in all 3 study areas exhibited some degree of partial-migration behavior, in which some individuals remained resident in an annual range, whereas others migrated various distances from winter to summer range. The Rocky Mountain Front had the largest proportion of residents, and the Whitefish Range had the largest proportion of migrants.

Rocky Mountain Front

From 2017-2019, 49 deer were collared on the Rocky Mountain Front. Of these, some either died before summer began or their GPS collar failed, so we were able to assess migratory behavior of 44 deer. During summers 2017-2019, 10 deer were considered residents and 34 deer migrated. Mean migration distance (the distance between the winter and summer home ranges) was 24.1 km (SD=19.42, range=7.43-58.3). Of the deer that migrated, the majority moved westward into the Bob Marshall Wilderness Complex; however, 2 deer migrated southeast along the Rocky Mountain Front and remained in plains habitat yearlong. Across study areas, individuals exhibited fidelity to a single strategy from year to year, but one deer on the Rocky Mountain Front switched behaviors during our study. In spring of 2017, this deer travelled 31.5 km from its winter home range to a new home range in plains habitat and remained in this home range when monitoring ended in Fall 2019, so we classified this deer as a resident.

Cabinet/Salish Mountains

Of the 41 deer collared in the Cabinet/Salish from 2018-2019, we were able to assess migratory behavior of 34. 7 deer were considered residents and 27 were migrants. Mean migration distance was 33km (SD=8.02, range = 20.87-49.07). The direction deer migrated appeared dependent on which side of the Fisher River they over-wintered on. Of the 12 migrant deer collared on the west side of the Fisher, most migrated west and eventually summered in the Cabinet Mountains. Of the 15 migrant deer collared on the east side, most migrated east into the Salish Mountains.

Whitefish Range

Of the 44 deer collared in the Whitefish Range from 2017-2019, we were able to assess migratory behaviors of 32. Five deer were considered residents and 27 were migrants. Mean migration distance was 23.24km (SD=21.71, range=11.49-44.95). Four deer crossed the Canadian border and spent their summers in British Columbia, and the majority of the remaining deer migrated east into the Whitefish Range.

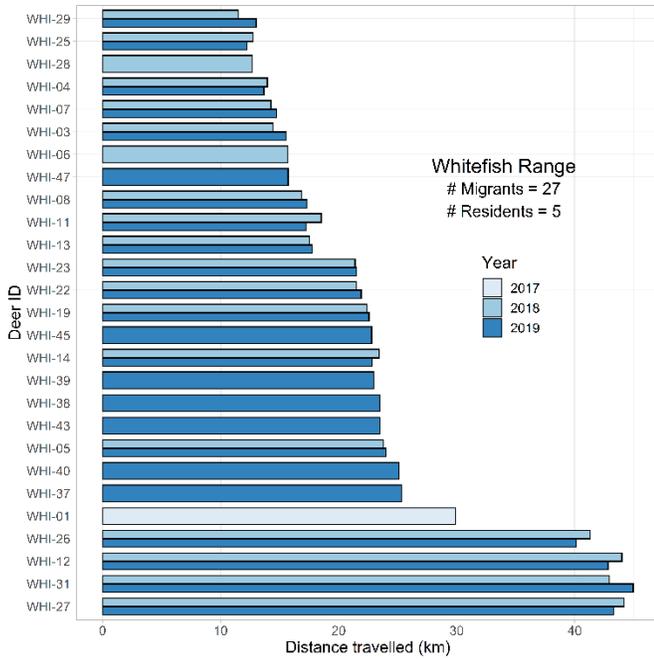
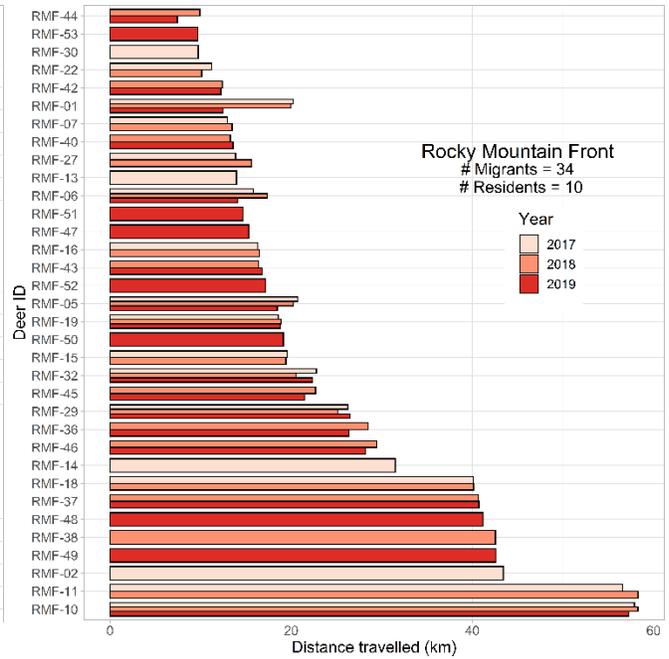
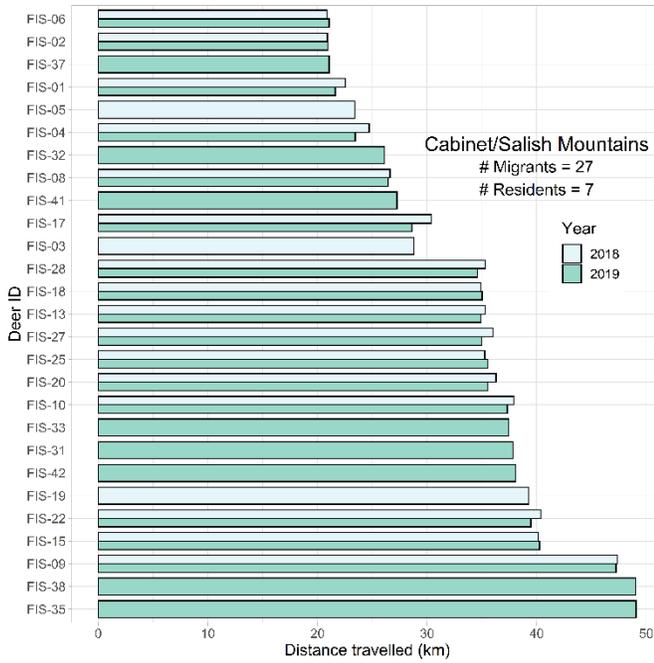


Figure 5. Migration distances (km) per individual adult female mule deer, shown only for the subset of deer that were deemed to be migratory according to analysis of net displacement data, and distinguished across 3 study areas and 3 years of monitoring, western Montana, 2017–2019.

Objective #3. Mule deer habitat selection and forage studies

3.1 Seasonal diet sampling

Diet and nutrition have been consistently shown to be important drivers of mule deer survival, reproduction and overall population stability (Bishop et al. 2009, Monteith et al. 2014). Therefore, understanding mule deer diet helps to inform population and habitat management. During winter captures, we collected fecal pellets from newly collared mule deer, including samples from 29 captures in 2019. In addition, we directed additional effort during the 2019 summer field season to collect 104 fecal pellets from both collared and un-collared mule deer during in all 3 study areas. Through the length of the study, we have collected a total of 221 fecal samples to estimate both individual- and population-level diets across seasons and study areas.

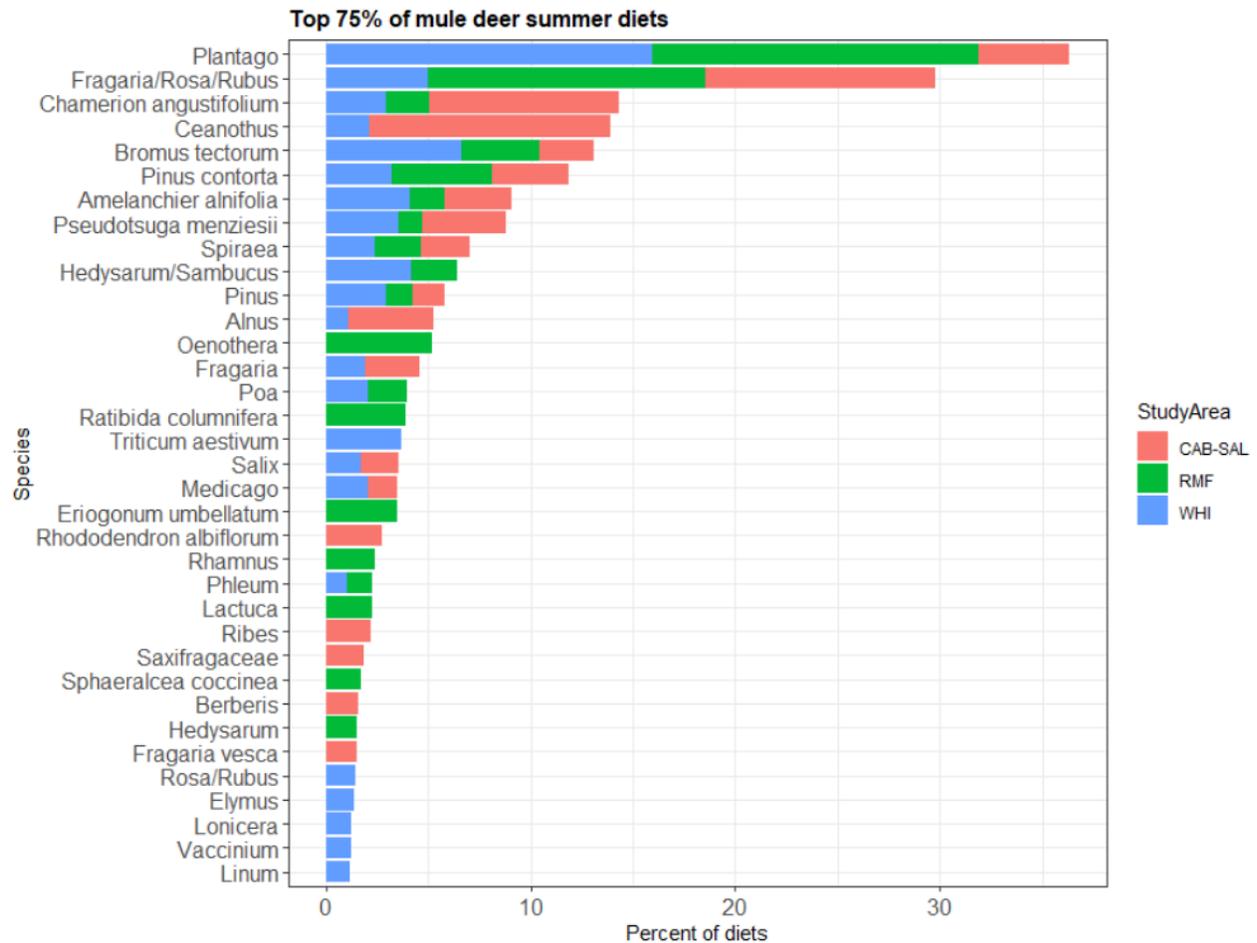


Figure 6. Forage species that make up the top 75% of mule deer summer diets from fecal collections during 2017-2019. Values represent the cumulative proportion of individual diets for a given study area

Traditional methods of microhistology assess diet composition based on fecal plant fragments; however, this method can underestimate the importance of forage plants with higher digestibility or faster decomposition (Alipayo et al. 1992). DNA-based approaches isolate a standardized region (DNA barcode) from DNA in fecal samples and compare it to a reference database for identification. The development of next generation sequencing (NGS) can identify up to thousands of species simultaneously (DNA metabarcoding), making DNA-based methods more accessible, faster, and more accurate than ever before (Pompanon et al. 2012). NGS returns the relative quantities of plant species in mule deer diets. Most DNA barcodes matched with an existing plant in the database at 98% similarity. 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).

Summer diets include a diverse assemblage of plant species and the amount of forage species in individual diets varied widely. To estimate importance of diet species, we calculated the proportion of diet species for individuals and then the cumulative proportion for the whole study area (Figure 6). Several species make up more than 5% of the study area diet, including *Plantago* (plantain) species, *Fragaria* (strawberry), *Rosa* (rose), *Rubus* (raspberry), *Chamerion angustifolium* (fireweed), *Ceanothus* (buckbrush), and *Bromus tectorum* (cheatgrass). The prevalence of species in study area diets falls off quickly, so that many of the remaining species in the top 95% of diets consist of less than 1% of total diet in the study area.

3.2 Summer forage species composition, biomass and quality

University of Montana MS students Teagan Hayes and Collin Peterson led a crew of 8 technicians conducting field work in all three study areas from June to August 2019 during the third and final summer field season on this project. They collected fecal samples to characterize mule deer diets and completed vegetation surveys to quantify how vegetation and nutrition is distributed on the landscape.

During vegetation surveys, field technicians identified and estimated the cover of all forbs, graminoids, and shrubs in three 1-meter² quadrats at each surveyed point. They also recorded clipped herbaceous plants and shrubs in a subsection of each quadrat to estimate biomass of the plots. Biomass was dried, then weighed after the field season. Throughout the summer, technicians also collected samples of forage plants to estimate forage quality of the most important species in mule deer diets. Plant composition, biomass, and nutritional data will be combined to estimate the available forage in sampled areas. Field crews sampled grassland, deciduous shrubland, and conifer forest. Crew members also completed surveys in disturbances that included wildfire, prescribed fire, and timber harvest from 1-20 years post-disturbance. Each disturbance point was paired with a matched control point to better estimate the effects of disturbance on the plant communities and forage availability.



Figure 7. University of Montana graduate students Collin Peterson and Teagan Hayes recording vegetation survey data at a site in the Rocky Mountain Front study area, 2017.

In 2019, crews completed 401 vegetation survey plots. Over three field seasons, field crews conducted 873 total vegetation plots – 283 in the Rocky Mountain Front, 322 in the Cabinet-Salish Mountains, and 267 in the Whitefish Range.

3.3. Predation risk and mule deer habitat selection

Exposure to predation risk is a major cost shaping ungulate behavior and distribution (Lima and Dill 1990; Winnie and Creel 2017). Understanding how ungulates, like mule deer, avoid risk facilitates investigation of phenomena like predator-prey interactions (Merems 2018; Harvey and Fortin 2013), tradeoffs between security from predators and forage quality and quantity (Pierce et al. 2004; Hebblewhite and Merrill 2009), and how these processes scale up to indirectly shape populations of other animal species and vegetation communities in an ecosystem (Creel et al. 2005; Cooley et al. 2008). Moreover, predicting deer response to risk helps researchers and managers determine the ultimate factors shaping deer behavior, forecast how they may respond to changing environmental conditions, and predict deer distribution on a landscape (Rosenwieg 1991; Mcloughlin et al. 2010). These predictions aid in conservation and management of mule deer (and other ungulates), their predators, and the resources that both predators and prey rely on.

In seeking to characterize how ungulates respond to predation risk on a landscape, spatial scale is a crucial consideration, as predator avoidance strategies may vary with spatial scale (Boyce 2006). Johnson (1980) outlined some hierarchically-nested “orders” of selection associated with spatial scales relevant to an animal’s life history: first-order selection – a population’s selection of a population range within their species’ range, second-order selection - an individual’s selection of a home range within its population range, and third-order selection - an individual’s selection of locations within its home range. Considering multiple scales of selection to

determine how deer avoid predators is necessary to accurately assess behavior because selection strategies can switch with scale. For example, deer may be indifferent to predators while selecting a summer home range, prioritizing other resources like forage, but may then strongly avoid predators on a day to day basis within their home range. The migratory strategy of individuals may also shape their predator avoidance behaviors (Hebblewhite and Merrill 2009). Within partially migratory populations, or populations where some individuals migrate seasonally and others remain resident in the same range year-round, migrants may be exposed to vastly different resource conditions than residents. Accordingly, migrants and residents may adopt alternate strategies for avoiding risk.

To understand how predation risk shapes mule deer behavior, we estimated the spatial distribution of risk by developing resource selection functions (RSFs) for wolves and mountain lions in three study areas. We then analyzed GPS-collared mule deer locations relative to these wolf and lion RSFs and asked:

How does selection for security from predators vary between migrant versus resident mule deer at the second- and third-order selection scale (home range and within-home range, respectively)?

To address this question, we tested multiple alternate hypotheses:

Consistent selection hypothesis: mule deer will select for security from predators in a similar manner across both spatial scales. Under this hypothesis, we predicted that if wolves or lions were avoided at the second order, they would also be avoided at the third order.

Compensatory selection hypothesis: mule deer will sacrifice security from predators at one spatial scale, then compensate for that sacrifice by selecting for security at a different spatial scale. Under this hypothesis, we predicted that if deer didn't avoid predators at the second order, they would strongly avoid predators at the third order, and vice versa.

To test these hypotheses, we used fixed-effect logistic regression models to develop separate RSFs for migrant and resident mule deer in each study area (Figure 8). We used wolf and lion predation risk estimates as covariates affecting mule deer resource selection.

Predation risk – preliminary results. Mule deer tactics for selecting security from predators varied according to predator species, study area, migratory status, and the scale of resource selection under consideration.

Wolves

Across study areas and migratory strategies, mule deer avoided wolves more strongly at the third order (while selecting locations within their home ranges) than at the second order (while selecting home ranges) (Figure 9A). Across all study areas, migrants exhibited compensatory selection for security from wolves: they were indifferent to wolves at the second order but avoided wolves at the third order. On the Rocky Mountain Front, residents exhibited compensatory selection for security from wolves too. However, in the Whitefish Range and Cabinet/Salish mountains, residents exhibited consistent selection for security from wolves, avoiding them at both the second and third order (Figure 9A).

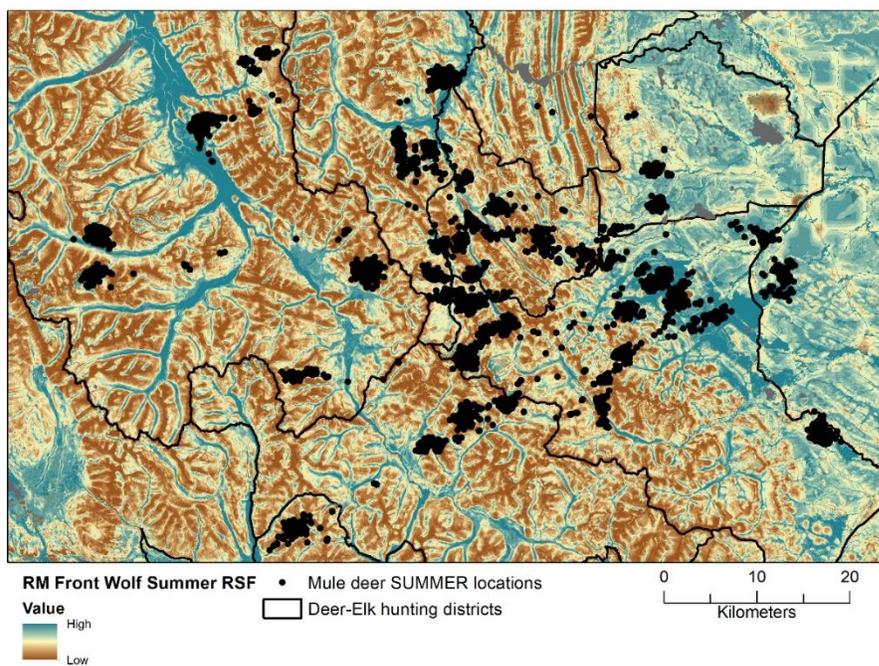


Figure 8. An example summer wolf resource selection function from the Rocky Mountain Front study area, with summer adult female mule deer GPS locations overlaid, 2015-2019.

Lions

Patterns of selection for security from lions were less consistent with regard to spatial scale or migratory strategy. On the Rocky Mountain Front and in the Cabinet/Salish mountains, both migrants and residents exhibited consistent selection for security from lion, avoiding them at the second and third order (Figure 9B). In the Whitefish Range, migrants and residents both exhibited compensatory selection for security from lions, but adopted opposite scale-specific means of selection: migrants avoided lions at the second order and were indifferent at the third order, whereas residents were indifferent at the second order and avoided lions at the third order (Figure 9B).

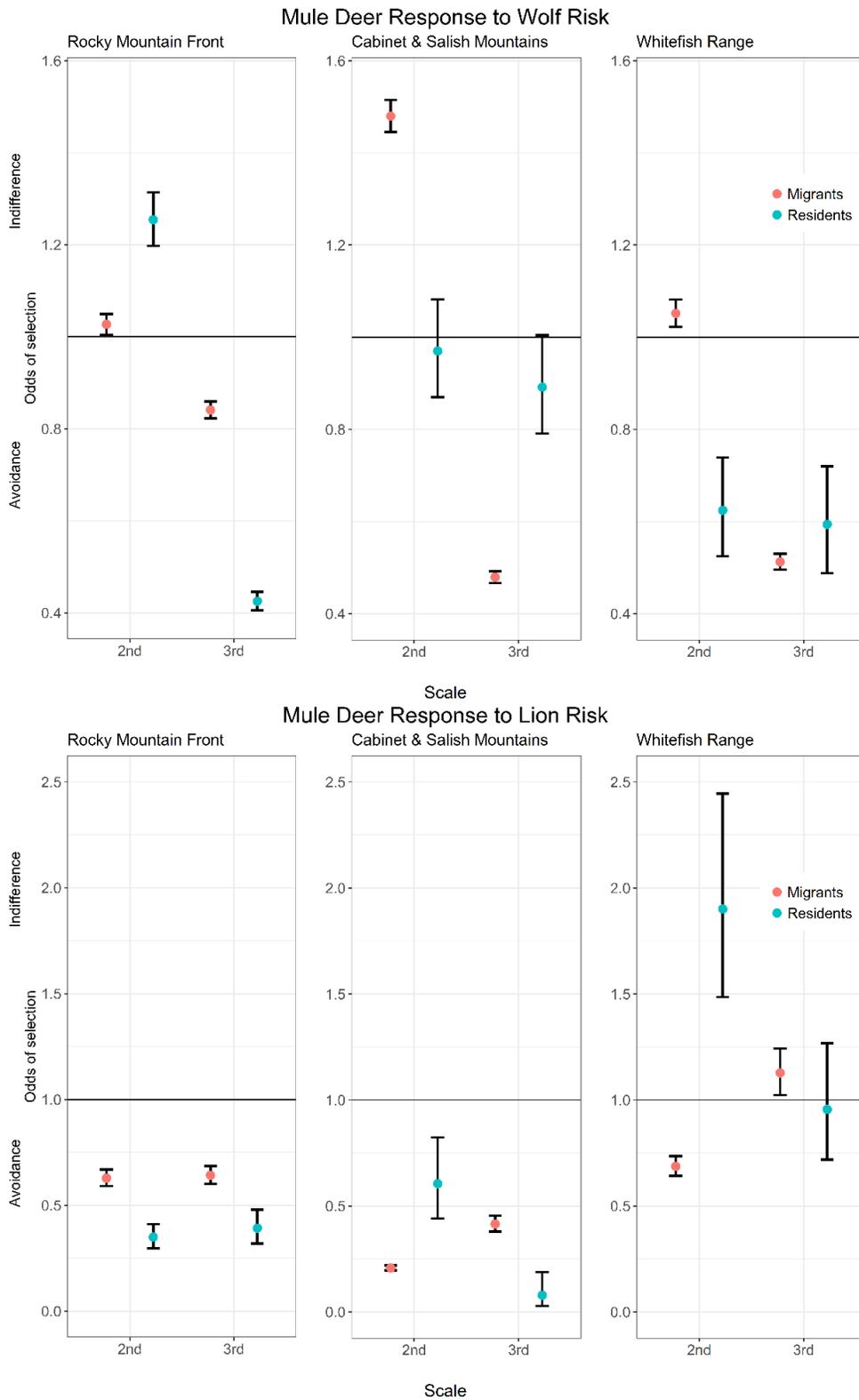


Figure 9. Odds ratios and 95% confidence intervals for mule deer selection of security from A) wolves and B) mountain lions across 2 spatial scales (2nd and 3rd order selection) and 2 migratory strategies (migrant and resident) in 3 study areas of western Montana. Values less than 1 indicate avoidance of predation risk, values greater than 0 indicate indifference to risk.

3.4 Forest disturbance and mule deer habitat selection

In much of northwest Montana, disturbance is an important driver of landscape heterogeneity and the distribution of nutritional resources. Disturbances alter the characteristics and configuration of the nutritional landscape in space by altering forest structure and reducing canopy cover of mature trees. Reduced overstory cover can increase the amount of light that reaches the understory, and this can contribute to changes in the distribution and composition of forage. With increasing time since disturbance, the overstory canopy often fills in. Forest succession typically results in decreased light and reduced forage biomass for deer in the understory. Anthropogenic disturbance has increasingly replaced wildfire disturbance in the western U.S. (Frelich 2002), and wildfires differ from timber harvests in their effects on understory vegetation and forage. If we assume that mule deer are likely to spend more time in and near habitat that offers the greatest benefit for the least cost, GPS collar location data can offer information about deer selection of habitat features.

To estimate mule deer selection of disturbance, we developed two a priori hypotheses that predict selection as 1) a function of time since disturbance and 2) spatial distribution of habitat and disturbance. First, if successional phase and available nutrition drive deer selection of forest disturbance (Visscher and Merrill 2009, Proffitt et al. 2019), the age of disturbance and canopy cover will be strongly correlated with mule deer selection. Second, if the availability of nutritional resources differs between wildfire and timber harvest (Monteith et al. 2014), mule deer will select habitat that is closest to the most beneficial disturbances.

We used an RSF to predict the relative probability of selection of resource units compared to availability based on measured covariates (Manly et al. 2002). We used GPS location data from collared mule deer does to understand resource selection in each study area. Location data were collected during 2018-2019 summer seasons (June 1 – August 31) from all three study areas, with additional data in summer 2017 on the Rocky Mountain Front. With these locations we calculated kernel density estimate (KDE) home ranges, defining the KDE of collared deer as areas inside the 95% fixed kernel estimates for each individual. For each used location, we created 5 random points to represent available points within the home range estimate.

To understand the influence of disturbance on selection, we conducted multiple logistic regression. The amount of time since disturbance and the amount of canopy describe the successional stage of a forest, and the frequency of harvest describes how much time has been between successive disturbances. Proximity to forest disturbances described the spatial distribution of disturbance across the landscape. We scaled continuous variables so that the effects of all covariates on mule deer resource selection can be directly compared (Figure 10).

Mule deer spatial selection of disturbance was mixed for each study area (Figure 10). Deer in the Whitefish and Rocky Mountain Front areas showed negative selection with increasing distance to harvest, while selection was positive for deer in the Cabinet-Salish ranges. Deer in the both Cabinet-Salish Mountains and the Rocky Mountain Front showed negative selection with increasing distance to wildfire. Conversely, deer in the Whitefish Range selection increased with increasing distance to wildfire. Selection patterns for temporal variables of disturbance were generally similar in all study areas. Regardless of study area, deer selection increased with increasing harvest frequency. Selection decreased with increasing canopy cover and tended to decrease with increasing time since disturbance. However, deer in the Cabinet-Salish Mountains showed slightly positive selection with increasing time since disturbance.

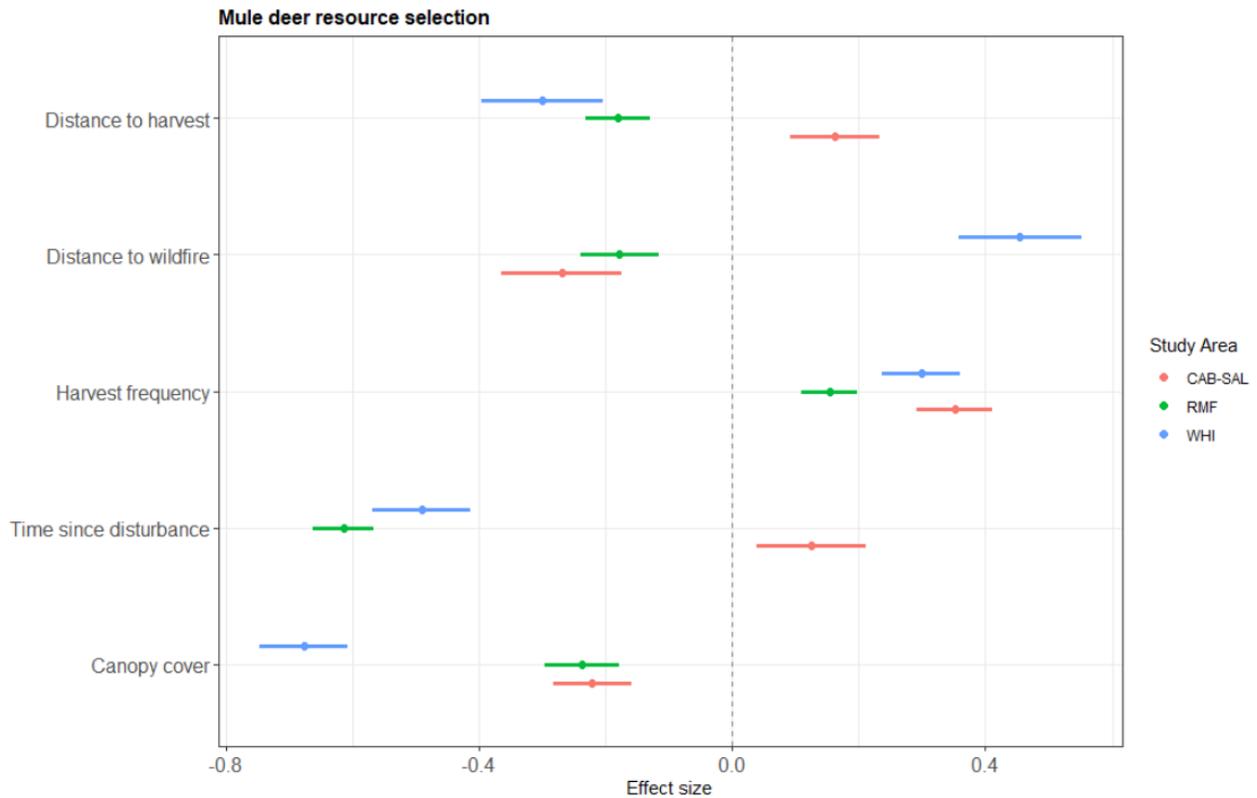


Figure 10. Beta (β) coefficients from logistic regression models of mule deer resource selection in three study areas: the Cabinet-Salish Mountains (CAB-SAL), Rocky Mountain Front (RMF), and Whitefish Range (WHI). The dotted vertical line marks the level of neutral selection. Error bars represent 95% confidence intervals.

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