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Climate, habitat interactions, and mule deer resource selection on winter landscapes

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Abstract

Mule deer (*Odocoileus hemionus*) are a valued game species across their range in North America. At higher latitudes mule deer inhabit the Northern Forests ecoregion, where the winter season poses challenging conditions. We studied resource selection during winter by mule deer in northwest Montana, USA, focused on the effects of snow and canopy cover on deer behavior. Specifically, we assessed the effects of land cover type, terrain characteristics, snow accumulation, percent canopy cover, solar radiation, and forage biomass on resource selection by 126 mule deer captured during 2017–2019 in 3 partially migratory subpopulations. We collected pellet samples and conducted diet analyses to assess forage species by individual and study area. Deer displayed a shift from nitrogen-rich forbs and shrubs in summer to nutrient-poor evergreens like conifers in winter. Deer avoided areas with deeper snow and sought more closed canopy forests for their snow-intercept advantages. Weather and vegetative variation among and within study areas resulted in disparities in selection for attributes such as land cover. Similarly, mule deer diets varied spatiotemporally as a function of snow, with some deer favoring coniferous species in deep snow, whereas others less constrained by snow had more diverse diets with more shrub species. Additional analyses revealed annual individual survival correlated with changes in snow depth, suggesting fitness consequences as snow accumulated. These differences suggest locally adapted behaviors as mule deer reflect energetic constraints of winter landscapes.

Seasonally limited resources pose challenges as animals adapt behavior over spatially and temporally varying scales (Senft et al. 1987). Shifts in movement patterns can respond to temporal fluctuations in food quality and quantity, affecting local and long-distance movements (Merkle et al. 2016). Seasonal habitat selection should similarly reflect how animals prioritize habitat patches that maximize fitness (Fretwell and Lucas 1969, Douhard et al. 2014). For large herbivores, plant senescence and reductions in food digestibility in winter can lead to nutritional deficits that affect habitat selection patterns (Gilbert et al. 2017), vital rates (Kucera 1988; Hobbs 1989; Bishop et al. 2005, 2009; Hurley et al. 2014), and population demography (Patterson and Power 2002, Monteith et al. 2011). Beyond nutritional quality impacts, deep snow buries most preferred foods such as nitrogen-rich graminoids and forbs, reducing forage availability and promoting a switch to browse like shrubs and conifers (Hobbs et al. 1983, Hanley and McKendrick 1985, Frisina et al. 2008). Extreme cold temperatures (e.g., <−19°C; Parker and Gillingham 1990) and increased cloud cover can impose added constraints on deer attempting to reach forage through deep snow while minimizing expenditures for thermoregulation and travel (Hanley and McKendrick 1985, Parker et al. 1999, White et al. 2009). Overall, winter may produce cascading effects on animal behavior, energetics, and demography.

Winter landscapes in northern latitudes experience significant snow accumulation, which is an important factor affecting mammalian movements (Telfer 1970, Crête and Larivière 2003, Halsey 2016). Deep snow can exclude mule deer (*Odocoileus hemionus*) or other ungulates from large swaths of potential winter habitat (Gilbert et al. 1970). Snow characteristics that affect the depth an animal sinks will strongly influence energetic expenditures (Verme 1968, Parker et al. 1984). Parker et al. (1984) estimated a nearly 5-fold increase in energetic costs for a 66.5-kg mule deer sinking 50 cm into snow compared to bare ground. Greater snowfall has been linked to increased predation vulnerability (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). Consequently, as snow accumulates, mule deer habitat selection can transform. For example, deer may select patches with greater canopy closure for snow-intercept advantages regardless of the presence of higher quality patches with more shrubs and forbs or lower solar radiation potential (Kirchhoff and Schoen 1987, Schwab et al. 1987, Parker et al. 1999, Visscher et al. 2006, Serrouya and D'Eon 2008). Thus, mule deer can display seasonal shifts from open- to closed-canopy patches as snow depths increase (Schoen and Kirchhoff 1990).

Energetics of wild animals can be difficult to quantify (Halsey 2016, Withers et al. 2016). Behavior patterns coupled with habitat associations can be important surrogates for understanding factors that affect individual performance. Animal–habitat relationships can provide important insight for identifying priority management actions to improve population performance (Johnson et al. 2004, Heinrichs et al. 2017). Habitat selection studies may be most useful when analyses consider the variation of local resource abundance (Morrison 2001), especially those that vary temporally (Gilbert et al. 2017). For example, the timing and severity of snow accumulation can affect distribution (Sawyer et al. 2006, Coe et al. 2018), which reflects changes in selection.

Shifts in resource quantity and quality have led many deer populations to seasonally migrate to optimize time spent in more favorable habitat (Nicholson et al. 1997). In the Northern Forests ecoregion, winter conditions strongly affect deer population dynamics (Hayden et al. 2008). We developed resource selection functions (RSFs) to understand mule deer habitat selection patterns under variable winter conditions in northwest Montana, USA. We focused on 3 covariates and their influences on mule deer resource selection in winter: snow accumulation, forage biomass availability, and canopy cover. We predicted that mule deer would select areas to maximize access to forage, with interacting effects of snow and canopy as conditions varied over space and time. We studied deer in 3 different populations across a gradient of conditions.
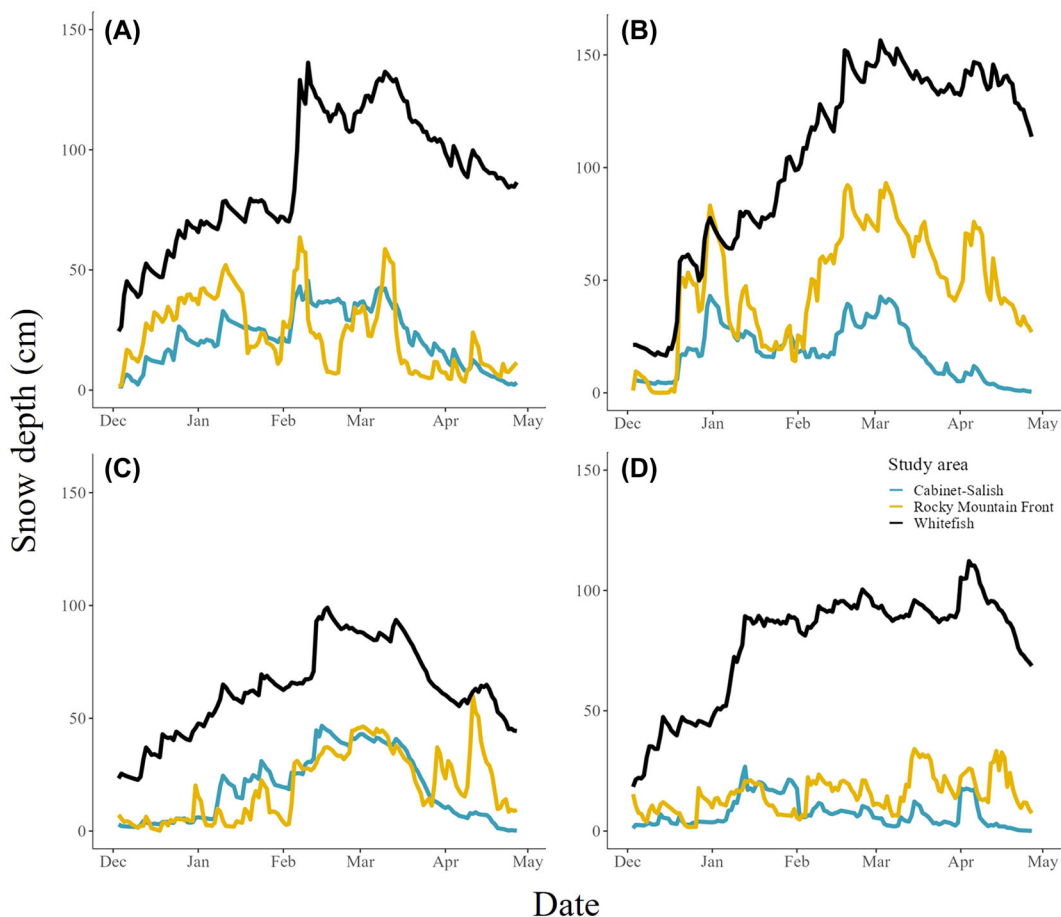
STUDY AREA

We studied mule deer in 3 study areas in northwest Montana (Figure 1). The Cabinet-Salish study area was a 549-km^2 region near the northern terminus of the Fisher River with elevations from 630–1,760 m. Mule deer in the Cabinet-Salish were partially migratory, including both eastward summer migrations into the Salish Mountains and westward migrations to the Cabinet Mountains. The area was primarily composed of conifer forest with open shrub and grassland on south-facing slopes. The study area also included a substantial footprint of past logging and wildfires. Winter (Dec–Apr) temperatures ranged from −20°C to 26°C and average daily snow depth for each winter during the study period (2017–2020) ranged from 1.58–4.52 cm. Except for the low snowfall observed in 2020, snow depth was comparable to the average, 4.43 cm, from 2004–2020 (Figure 2; Figure S1, available in Supporting Information). The annual range of mule deer in the Cabinet-Salish study area overlapped that of 4 other native ungulates: moose (*Alces alces*), elk (*Cervus canadensis*), mountain goat (*Oreamnos americanus*), and white-tailed deer (*Odocoileus virginianus*). Predators in this area included mountain lions (*Puma concolor*), coyotes (*Canis latrans*), wolves (*Canis lupus*), black bears (*Ursus americanus*), and grizzly bears (*U. arctos*).

The Rocky Mountain Front study area was a 1,357-km^2 area on the western ecotone between prairie habitat and mountainous terrain (Figure 1). The Sun River delineated the northern end and the Dearborn River the southern end of the study area. Elevations ranged 1,280–2,510 m with much of the lower elevations dominated by montane grasslands. Deciduous shrubland interrupted larger swaths of grasslands as elevations increased into the foothills of the Rocky Mountains and dry-mesic conifer forests became the dominant land cover type. This area included substantial privately owned agricultural lands abutting national forests. The herd was partially migratory with most migrations trending westward into the Bob Marshall Wilderness. During the winters of this study, temperatures ranged from −27°C to 24°C and snow depth varied from 3.65–10.4 cm. Except for 2020, average snow depths were higher than the average of 3.55 cm from 2004–2020 (Figures 2, S1). The annual range of mule deer in the Rocky Mountain Front overlapped a similar suite of ungulate and predator species to that of the Cabinet-Salish, with the addition of pronghorn (*Antilocapra americana*) and bighorn sheep (*Ovis canadensis*).

The Whitefish study area was a 794-km^2 area on the west side of the Whitefish Mountain range, where elevations ranged 850–2,280 m (Figure 1). Whitefish was dominated by wet and mesic conifer forests mixed with regenerating forest patches resulting from past fire and logging. The west end of this study area included human
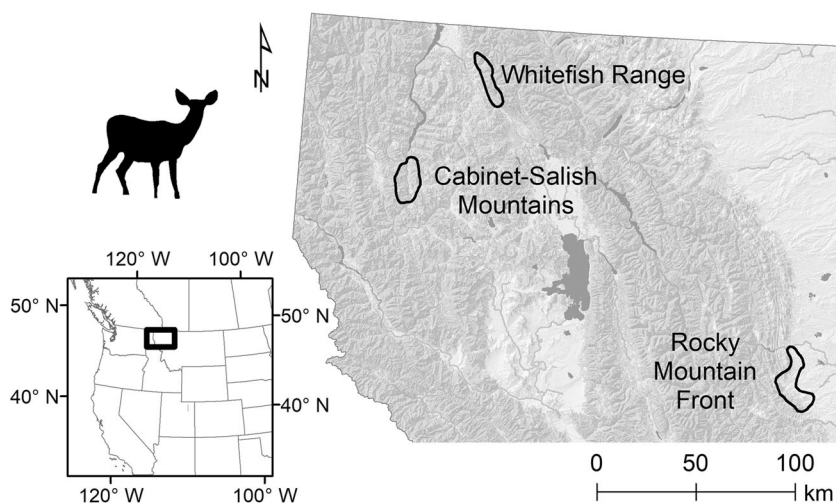
FIGURE 1 Overview map of 3 study areas in northwest Montana (Cabinet-Salish, Rocky Mountain Front, and Whitefish), USA. We computed resource selection functions from 136 mule deer captured from 2017–2020.

FIGURE 2 The 3 study areas in northwest Montana, USA, experienced different levels of snow accumulation. We present average daily snow depth data (cm) from 2017 (A), 2018 (B), 2019 (C), and 2020 (D), demonstrating that the Whitefish study area (black line) can receive significantly more snow accumulation than the other study areas. The Cabinet-Salish (blue) and Rocky Mountain Front (yellow) receive comparable snowfall with some interannual variation.

development and a 2-lane highway. The Whitefish herd was also partially migratory with most animals migrating to summer ranges to the east into the Whitefish Mountains and some animals migrating farther to the northeast across the Canadian border. Temperatures ranged from −20°C to 22°C and yearly snow depths averaged 19.59–28.81 cm. Snow depths during 2017, 2018, and 2020 were greater than the average, 20.9 cm from 2004–2020 (Figures 2, S1). The annual range of mule deer in Whitefish overlapped a similar suite of ungulate and predator species compared to deer in the Rocky Mountain Front, with the exceptions of pronghorn and mountain goats.

METHODS

Use and availability sampling

We studied mule deer habitat selection using RSFs and a use–availability design (Manly et al. 2002). We sampled habitat using location data collected from global positioning system (GPS) telemetry collars. During December to

March 2017–2019, we deployed GPS collars (LifeCycle 330, Lotek Wireless, Newmarket, Ontario, Canada) on 126 female mule deer captured across the 3 study areas (38 in Cabinet-Salish, 39 in Whitefish, 49 in Rocky Mountain Front). Deer captures covered the entirety of study areas (Figure 1). We captured deer by helicopter net gunning (Gerlach et al. 1986), clover trapping (Thompson et al. 1989), and ground darting according to capture and handling protocols approved by Animal Care and Use Committees at the University of Montana (protocols 001-17CBWB-011017) and Montana Fish, Wildlife and Parks (FWP03-2016). Collars were programmed to collect GPS locations every 13 hours. We also collected fecal samples from each deer at the time of capture for subsequent diet analyses.

We used individual- and population-level migration patterns to estimate start and end dates of mule deer occupancy on winter range. We used the R application Migration Mapper version 2.3 (Wyoming Migration Initiative 2020) to examine net-squared displacement curves for individual deer winters, which allowed us to identify migration dates for migratory deer (Bunnefeld et al. 2011). We then delineated a starting date for winter for each deer according to the later of 2 dates: 1) the date they arrived on winter range following fall migration, if migratory; or 2) the 0.95 quantile value of dates characterizing the end of fall migration for all migratory deer in that study area. Similarly, we delineated the end date of winter as the earlier of 2 dates: 1) the date the animal left winter range during spring migration, if migratory; or 2) the 0.05 quantile value of dates characterizing the start of spring migration for all migratory deer in the study area. We applied these cutoff dates to resident and migratory deer. For example, locations for a deer that migrated back to winter range after the start of a season cutoff date (e.g., Jan) would include only GPS locations after migration had concluded. In contrast, a deer that migrated back to winter range in September would include only GPS locations after the start of a season cutoff date.

We included animals with partial and full winter seasons of locations and omitted individuals with <30 locations. After compiling location data characterizing winter habitat use, we then defined availability within winter home ranges using 99% kernel density polygons, estimated separately for each deer (Calenge 2006). We buffered each home range kernel by 1 km and randomly sampled 10 locations for every used location within these buffered polygons (Fieberg et al. 2021).

Winter diet

We estimated mule deer diet composition from individual-level analysis of fecal samples collected during winter captures of each deer. We reconstructed diets from samples using DNA metabarcoding (Jonah Ventures Laboratory, Boulder, CO, USA; Taberlet et al. 2007). We determined the proportion of distinct taxa in each individual's diet and aggregated results by study area to determine the relative proportion of each taxon at the population level.

To explore the relationship between snow depth and forage selection, we conducted a *post hoc* analysis exploring proportionate use of conifer as a function of the snow conditions for each deer. We used daily snow depth (Barrett 2003) raster layers with 1-km resolution to quantify snow conditions over time and space in each study area. We then summarized the average snow depth for each deer using individual deer home ranges and according to 2 timeframes: using snow depth on the date the deer was captured and using mean snow depth 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 snow depth during modeling.

Resource covariates and forage modeling

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 previously important in deer 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, ensuring the distribution was proportional temporally to the used dataset. We extracted slope angle from a 30-m resolution digital elevation model and estimated percent forest canopy cover at the same resolution using LANDFIRE data (LANDFIRE 2019). We reduced available land cover data (Montana Natural Heritage Program 2017) to 6 classes: conifer forest, grassland (included agricultural land), shrubland, wet areas (wetlands, marshes, and riparian zones), disturbance (burned forests and timber harvests), and developed land (human developments, roads, and train tracks). We calculated a solar radiation index using the Area Solar Radiation tool in ArcMap 10.2 (Esri, Redlands, CA, USA). In addition, we obtained daily snow depth estimates at 1-km resolution from the Snow Data Assimilation System (SNODAS; Barrett 2003). To explore variation in snowfall, we calculated average daily snow depth for each winter within each study area.

We also used field sampling and available spatial data to develop a predictive model of herbaceous and shrub forage biomass, excluding conifers, across each study area. This approach followed 3 steps: estimating species-specific biomass (g/m^2) of forage on the landscape through ground-based vegetation sampling, identifying forage species that were either highly used or preferred during winter, and developing generalized linear models (GLMs) for predicting spatial variation in biomass of forage species across each study area. We conducted vegetation field sampling for this model during summer, in support of other summer-focused nutrition studies (Peterson et al. 2022). 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 available and selected by mule deer, and developed new winter-focused GLMs.

We conducted field sampling of species-specific forage biomass during summers 2017–2019 (Peterson et al. 2022). We stratified sampling according to land cover type, and at each site we sampled percent cover for each forage type within 3 1-m^2 quadrats and clipped biomass within 3 0.5-m^2 clip plots, each spaced along 40-m transects (Peterson et al. 2022). We then used diet data in combination with field plot data to identify forage species that were used or preferred relative to availability. We estimated how deer selected forage taxa relative to their availability on the landscape by dividing the proportion of each taxon in deer diets by the proportion of total biomass each taxon made up on the landscape. We classified taxa that made ≥1% of deer diets in a study area, or that were consumed in greater proportion than their availability on the landscape, as forage taxa in that study area for subsequent predictive modeling of herbaceous and shrub forage (Table S1, available in Supporting Information).

Because we conducted vegetation surveys during summer, our initial estimates of biomass included plant parts that are not always present during winter, including flowers, fruits, and leaves of deciduous plants. For evergreen species that retained foliage into winter (e.g., conifer species and some shrubs including ceanothus [*Ceanothus* spp.] and Oregon grape [*Mahonia repens*]), we assumed summer biomass estimates were equivalent to biomass available in winter. For deciduous plants that did not retain leaves or remain green, we accounted for the reduction in forage biomass that occurs during winter (Hanley et al. 2012) by adapting an algorithm developed by Poorter et al. (2015) for estimating the amount of biomass allocated to stems of plants, and used predicted stem biomass values to represent available winter biomass of non-evergreen forage. Poorter et al. (2015) used 11,000 records of leaf and stem biomass from 1,200 herbaceous and woody plant species and reported that the relationship between dry leaf and stem biomass of plants can be described by the equation:

$$log_{10}(leaf\ biomass) = 0.113 + 0.740 \times log_{10}(stem\ biomass) \tag{1}$$

Poorter et al. (2015) reported that the residuals of Equation 1 were skewed; however, they demonstrated that the function has very high predictive ability ($R^2 = 0.978$). Therefore, we considered this function to be useful for estimating the amount of biomass allocated to leaves and stems in our dataset. Because we did not weigh plant parts separately, we needed to adapt Equation 1 to estimate stem biomass from stem and leaf biomass combined. To do this, we simulated values of stem biomass ranging from 10^{-7} g to 10^3 g, which encompassed the range of individual-plant biomass values we observed in the field, then used Equation 1 to predict values of associated leaf biomass. We summed those simulated leaf and stem biomass values to obtain total biomass values and following

Poorter et al. (2015), we log_{10}-transformed the estimated values (Table S2, available in Supporting Information). We then used linear regression to develop a revised equation for predicting stem biomass from total biomass:

$$log_{10}(stem\ biomass) = -0.312 + 1.076 \times log_{10}(stem + leaf\ biomass) \tag{2}$$

We used this equation to estimate the biomass of stems of non-evergreen plants in our dataset.

We developed GLMs for predicting spatial variation in the relative quantity (g/m^2) of herbaceous and shrub forage taxa across winter study areas. We square-root transformed estimates of forage biomass at each site and tested the effects of 8 variables: vegetation cover type, slope, southern aspects (coded categorically), canopy cover, climatic water deficit (deficit; Hoylman et al. 2019), percent cover of annual forbs and graminoids (Jones et al. 2018), percent cover of perennial forbs and graminoids (Jones et al. 2018), and time since most-recent disturbance. We also tested the interaction between southern aspects and canopy cover and tested for a quadratic effect of slope. Because perennial and annual forb and graminoid cover predictions were significantly lower under high canopy cover (Jones et al. 2018), we masked out values in areas with >40% tree canopy. We estimated forb cover for each season; for all other variables, we estimated averages across seasons. We used Pearson's correlation coefficient ($r > 0.5$) and variance inflation factors (>5) to screen for multicollinearity among variables. We then used a manual backward stepping model selection approach to values of β/standard error and Akaike's Information Criterion (AIC; Arnold 2010). We calculated the coefficient of determination (R^2) values for top models. For each study area, we used coefficients from the top-ranked model to predict herbaceous and shrub forage biomass across mule deer winter range at a 30-m resolution. To keep from extrapolating our models beyond the range of resource values we sampled, we capped resource values used for predictions to their maximum value sampled in each study area.

Resource selection function and survival analyses

Broad-scale variation in the availability of resources (Holbrook et al. 2019) and consequent plasticity in habitat selection among local populations of species like mule deer (Mackie 1998) influence variation in habitat selection across mule deer populations. Thus, we fit Bayesian hierarchical mixed effects RSFs that simultaneously estimated individual deer and study area-specific selection coefficients. This approach accounted for unbalanced samples of used locations among individuals and inherent variation among individuals when calculating study area-level parameters (Thomas and Taylor 2006, Muff et al. 2020). The model included 3 elements: a data (likelihood) model, an individual parameter model, and a hyperparameter model (study area-level parameters). We employed hierarchical centering to ensure identifiability of mixed effect parameters (Ogle and Barber 2020). We assigned uninformed hyperprior distributions for all study area-level hyperparameter means and variances (Equations 3 and 4, respectively). These study area-level hyperparameters informed individual-level mixed effect parameters (Equation 5), which we used in the likelihood model to estimate relative probabilities of selection for all resource covariates outlined above (Equation 6).

$$\mu_{Covariate_S} \sim Normal\ (\mu = 0, \sigma = 1,000) \tag{3}$$

$$\sigma^2_{Covariate_S} \sim Inverse\ Gamma\ (1,1) \tag{4}$$

$$\beta_{Covariate_{i,S}} \sim Normal\ (\mu_{Covariate_S}, \sigma_{Covariate_S}) \tag{5}$$

$$log\ (p_{j,i}) = (\beta_{0_{i,S}} + \beta_{1_{i,S}} Covariate_{1_{j,i}} + \cdots + \beta_{N_{i,S}} Covariate_{N_{j,i}}), \tag{6}$$

where observations $j = 1...n$ are clustered by individuals $i = 1...k$ within study area S; $\beta_{0_{i,S}}$ are the random intercepts and $\beta_{N_{i,S}}$ are random slope coefficients for covariate N for individual i within study area S. We calculated marginal posterior distributions of RSF parameters using JAGS 4.3.0 (Plummer 2003) through the jagsUI

package in program R. We retained 3,000 iterations from each of the 3 chains, after discarding 6,000 for adaptation and burn in and thinning by 2. We assessed post-model performance by inspecting Gelman-Rubin convergence diagnostics ($\hat{R}$) to ensure values were <1.1 (Brooks and Gelman 1998) and by visually inspecting trace plots of posterior parameter distributions.

The GPS collars we used had variable success in uploading location data to Globalstar satellites, with an average success of 72% and ranging from 30% to 100%. These data upload rates were likely affected by location-specific habitat differences that can introduce bias into resource selection studies (Frair et al. 2010). We accounted for this variation in fix upload success using a spatial model that predicted the probability of a successful fix upload (*Pfix*), given a location's canopy cover and topographic characteristics, to weight cases in our analyses (Frair et al. 2010, Peterson et al. 2022). The *Pfix* model used store-on-board collar data from 23 GPS collars recovered from 22 mule deer mortalities and 1 slipped collar from all 3 study areas. We then weighted our samples by 1/*Pfix*, thereby boosting the influence of samples in locations with low probabilities of fix success (Frair et al. 2010). We incorporated sample weighting by non-integer values into the binomial likelihood using the ones trick (Ntzoufras 2009).

Prior to model fitting procedures, we examined the correlation among variables using the Pearson correlation coefficient and only included variables together in a model if their correlation coefficient was <0.50. We scaled and centered all continuous covariates prior to analysis (Schielzeth 2010). We tested linear and quadratic forms of canopy cover and evaluated a small set of interactions regarding the effect of snow on selection of other variables. We calculated odds ratios for most categorical terms to assess effect sizes. We corrected odds ratios for categorical land cover type predictors using their relative availabilities within study areas (Fieberg et al. 2021).

To further explore the relationship between snow and canopy cover, we conducted another *post hoc* analysis summarizing canopy cover and snow depth within each individual's home range. For each animal year in the dataset, we obtained the average snow depth and used each animal's random slope estimate to calculate relative predicted probabilities of selection across the range of available canopy cover percentages within their home range. We then obtained the percent canopy cover related to the maximum predicted probability of selection for each animal (preferred canopy cover) and ran a simple linear regression analysis using preferred canopy as the response and average snow depth within the home range as the singular covariate.

To examine the potential causal mechanisms for mule deer survival, we conducted another *post hoc* analysis associating known fate data from collared mule deer to snow depth and percent canopy cover metrics. To maximize the available data, we started survival monitoring on 21 December and ended on 21 June. We calculated average available snow depth and percent canopy cover to each animal's year-specific home range. We incorporated these data into Cox proportional hazards models that estimated shared frailty for each study area using the coxme function from the R package coxme (Therneau 2012).

RESULTS

During 2017–2020, we captured 126 deer and fitted them with GPS collars (Rocky Mountain Front: 49, Whitefish: 39, Cabinet-Salish: 38). Most deer migrated 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. Winter start and end dates varied by study area according to migration timing of each deer but averaged 6 December to 18 April, respectively. After screening techniques, the data we used for winter habitat selection modeling included 30,810 GPS locations (Rocky Mountain Front: 11,726, Whitefish: 8,347, Cabinet-Salish: 10,737) from 241 deer-winters (Rocky Mountain Front: 100, Whitefish: 72, Cabinet-Salish: 69).

Winter diet and forage quality modeling

We collected winter fecal samples from all captured deer plus 10 additional samples 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 (17.9% of diet), followed by ceanothus (14.8%) and poa (*Poa* spp.; 11.8%; Table S1). On the Rocky Mountain Front, mule deer consumed Douglas-fir more than other taxa (30.4%) followed by juniper (*Juniperus* spp.; 11.9%) and ceanothus (10.4%), and in the Whitefish Range, mule deer consumed Douglas-fir (46.4%) the most, followed by Oregon grape (4.0%) and western red cedar (*Thuja plicata*; 3.5%; Table S1). After grouping species by functional type, conifer and shrub forage species were most used in all study areas, with their ranking differing among areas (Figure S2, available in Supporting Information).

There was strong evidence for a relationship ($F_{1,71}$ = 22.92, P < 0.001) between the amount of conifer species in an individual's diet and the average snow depth the individual experienced in their home range on the day of capture, and an R^2 of 0.27 (Figure 3A). The relationship was stronger when measuring snow at the time of capture compared to the average snow depth across the entire winter of capture, suggesting this relationship may vary over time within each winter season.

We surveyed vegetation at 477 sites in mule deer winter range: 146 in Cabinet-Salish, 124 on the Rocky Mountain Front, and 177 in the Whitefish Range (Table 1). On average, herbaceous and shrub forage biomass was highest in grasslands and lowest in conifer forests (Table 1). Our top model predicting winter forage biomass in the Cabinet-Salish showed positive effects of wildfires and logging, and negative effects of tree canopy cover (Table S3, available in Supporting Information), with an R^2 value of 0.298. On the Rocky Mountain Front, we found positive effects of annual plant cover and moderate slopes, and negative effects of tree canopy cover, shrub cover, and wildfire on forage biomass (R^2 = 0.548; Table S4, available in Supporting Information). In the Whitefish Range, our top model showed positive effects of grass and shrublands, southern aspects, and moderate slopes, and negative effects of prescribed fires and canopy cover on winter forage biomass (R^2 = 0.364; Table S5, available in Supporting Information).

Resource selection and survival

Resource covariate significance in the generalized linear mixed model for deer habitat selection varied among the 3 study areas, identified by parameter estimate 95% credible intervals in relation to zero (Table 2). For Rocky Mountain Front, significant variables included continuous variables for elevation, slope angle, topographic position index (TPI), snow depth, solar radiation, linear and quadratic percent canopy cover terms, and a categorical variable for land cover. The interaction term between snow depth and canopy cover was significant, with a marginal shift towards more closed canopy forests when snow depth increased (Figure 4). Significant variables in Cabinet-Salish also included slope angle, TPI, solar radiation, land cover, the quadratic canopy cover term, and an interaction term between snow depth and canopy cover. As in Rocky Mountain Front, deer in Cabinet-Salish displayed a shift to slightly more closed canopy cover forests as snow depths increased (Figure 4). Significant variables for deer in Whitefish included elevation, slope angle, TPI, solar radiation, the linear percent canopy cover term, herbaceous and shrub forage, and a categorical variable for land cover.

Evaluation of available snow conditions revealed considerable variation in snow in each study area (Figure 2). Thus, snow had different effects on selection patterns by study area. Contrary to our hypothesis, deer in the Rocky Mountain Front selected areas with greater snow depths. Deer in Whitefish experienced more snowfall on average (Figure 2), which led to greater avoidance of deeper snow; however, the parameter estimate for snow depth was not significant (95% CI included zero; Table 2). The Cabinet-Salish study area experienced the least snowfall and deer displayed no consistent response to snow in selection patterns (Table 2). There was also evidence of interactions between snow and deer selection for canopy cover (Cabinet-Salish and Rocky Mountain Front study areas; Table 2; Figure 4). To evaluate snow depth impact on deer canopy cover selection, we fixed snow depth
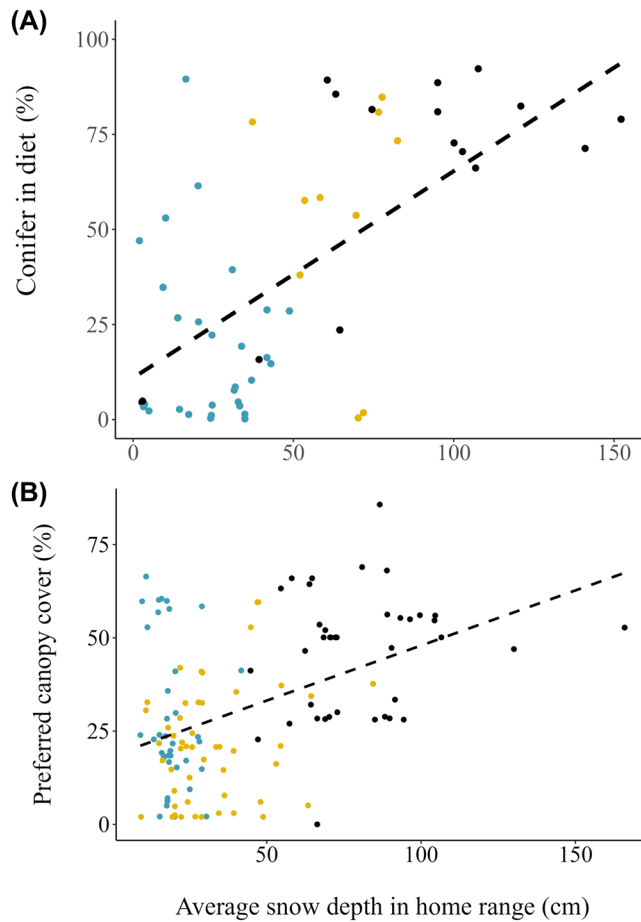
FIGURE 3 The relationship between an individual mule deer's browse selection for coniferous species and the average snow accumulation (cm) in their home range (A) in Montana, USA, 2017–2020. Additional analyses revealed individuals shifted preferred percent canopy cover in response to snow depths (cm) in their home range (B). Colored points refer to individuals within each study area with Cabinet-Salish deer plotted in blue, Rocky Mountain Front in yellow, and Whitefish in black.

TABLE 1 Sample sizes, means, and standard deviations of forage biomass (grams/m^2) from vegetation survey plots in 3 study areas in northwest Montana, USA, 2017–2020.

| Land cover	Cabinet-Salish			Rocky Mountain Front			Whitefish		
	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
Conifer	56	8.087	4.971	34	5.956	4.713	79	7.408	6.659
Deciduous shrubland	11	14.382	7.197	11	26.181	18.632	10	13.659	9.020
Grassland	19	13.772	7.600	44	27.572	21.147	13	27.647	10.968
Timber harvest	31	15.362	6.865	3	8.085	1.627	26	12.193	5.027
Prescribed fire	15	12.097	5.200	5	12.385	10.620	22	8.555	4.257
Thin	5	7.470	3.418	1	13.120		14	11.071	6.213
Burn	9	15.244	9.668	25	10.780	7.457	12	11.249	11.032

TABLE 2 Parameter estimates from top resource selection function models for mule deer in each of the 3 study areas in northwest Montana, USA, 2017–2020. We used Bayesian generalized linear mixed models with random intercepts and slopes estimated for individual mule deer.

	Cabinet-Salish			Rocky Mountain Front			Whitefish		
	β	SD	95% CI	β	SD	95% CI	β	SD	95% CI
Intercept	-3.09	0.138	-3.370, -2.828	-2.67	0.271	-3.209, -2.147	-3.58	0.275	-4.146, -3.081
Elevation	-0.03	0.087	-0.201, 0.142	-0.35	0.145	-0.624, -0.056	-0.34	0.069	-0.483, -0.207
Slope	0.33	0.054	0.228, 0.438	0.48	0.054	0.372, 0.586	0.40	0.055	0.287, 0.506
Solar radiation	0.23	0.063	0.105, 0.356	0.21	0.046	0.126, 0.305	0.33	0.068	0.197, 0.463
Canopy cover	-0.07	0.340	-0.737, 0.589	-2.78	0.450	-3.674, -1.930	0.79	0.336	0.110, 1.434
Canopy cover^2	-0.87	0.213	-1.296, -0.448	-1.74	0.303	-2.347, -1.156	-0.30	0.187	-0.667, 0.071
TPI[a]	0.24	0.047	0.154, 0.337	0.48	0.075	0.330, 0.623	0.24	0.064	0.109, 0.362
Snow depth	-0.04	0.221	-0.477, 0.392	0.77	0.193	0.400, 1.161	-0.16	0.128	-0.412, 0.094
Snow × canopy cover	1.26	0.211	0.849, 1.678	0.79	0.204	0.389, 1.196	0.06	0.107	-0.151, 0.270
Forage biomass	-0.05	0.171	-0.382, 0.298	0.04	0.057	-0.066, 0.158	0.26	0.084	0.096, 0.423
Snow × forage[b]	-0.25	0.225	-0.684, 0.203	-0.06	0.047	-0.153, 0.030	0.05	0.051	-0.049, 0.153
Disturbance[c]	-0.13	0.124	-0.384, 0.106	-1.65	0.605	-2.955, -0.558	-0.35	0.091	-0.537, -0.179
Grassland	-0.23	0.070	-0.366, -0.090	-0.27	0.085	-0.443, -0.107	-4.93	3.096	-12.847, -1.545
Shrubland	-0.28	0.064	-0.409, -0.157	-0.35	0.084	-0.520, -0.189	-1.42	0.465	-2.409, -0.579
Anthropogenic	-1.08	0.226	-1.560, -0.679	-2.63	0.764	-4.552, -1.581	-1.39	0.214	-1.864, -1.017
Wetland and riparian				-0.59	0.139	-0.883, -0.338	-0.95	0.219	-1.427, -0.567

[a]Topographic position index.

[b]Herbaceous and shrub forage biomass.

[c]Conifer forest land cover type used as reference category.
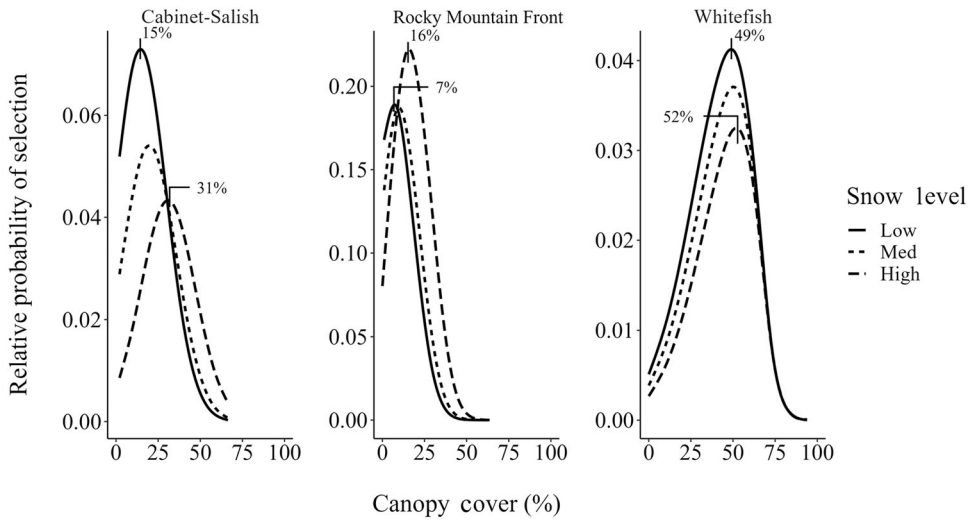
FIGURE 4 The 3 study areas in northwest Montana, USA, 2017–2020, where we collared mule deer experienced different climatic conditions and forest cover. Deer avoided areas with greater snow accumulation and snow displayed a mediating effect with how mule deer selected for canopy cover. Mule deer were more likely to select areas with higher canopy cover as snow depth increased. We fixed snow depth values at study area-specific 0.1, 0.5, and 0.9 quantiles to represent changing snow conditions as it increased from low, medium (med), and high depths, respectively. In the Cabinet-Salish, deer shifted preferred canopy cover from 15% to 31% as snow depth increased from low (0.004 cm) to high (43.35 cm), respectively. Similarly, deer in the Rocky Mountain Front shifted from 7% to 16% canopy cover as snow depth increased from low (0.004 cm) to high (71.98 cm), respectively. Deer in the Whitefish study area displayed a smaller shift with deer moving from 49% to 52% canopy cover as snow depth increased from low (27.73 cm) to high (124.23 cm), respectively.

values at the study area-specific 0.10, 0.50, and 0.90 quantiles of the dataset to represent low, medium, and high snow depth conditions, respectively (Figure 4). Deer selected for higher percent canopy cover as snow depth increased. In the Cabinet-Salish, deer shifted preferred canopy cover from 15% to 31% as snow depth increased from low (0.004 cm) to high (43.35 cm), respectively. Similarly, deer in the Rocky Mountain Front shifted selection from 7% to 16% canopy cover as snow depth increased from low (0.004 cm) to high (71.98 cm), respectively. Deer in Whitefish selected higher levels of canopy overall all but did not shift in response to snow (Table 2); preferred canopy changed only from 49% to 52% canopy cover as snow depth increased from low (27.73 cm) to high (124.23 cm), respectively. There was further evidence of the impact of snow depth on canopy cover selection when we calculated preferred percent canopy cover for each individual deer and compared it to the average snow depth in their home range (Figure 3B). This resulted in a positive relationship ($R^2 = 0.27$, $F_{1,124} = 46.5$, $P < 0.001$) demonstrating that when snow depth increases, individuals selected for increased canopy cover.

Deer in all study areas selected for patches with greater solar radiation potential (Table 2). Deer in all 3 study areas also were similar relative to selection for topography, with deer preferring lower elevations, somewhat steeper slopes, and ridgelines instead of valleys (Table 2). Selection responses to our predictions of herbaceous and shrub forage biomass were only significant in the Whitefish study area, with deer selecting for patches with higher forage biomass. Our modeling did not support an interaction between snow depth and forage biomass.

Categorical variables for land cover were included in the model for all study areas (Table 2). In Rocky Mountain Front, deer were most likely to select grasslands, the dominant land cover (Figure S3, available in Supporting Information). Deer were 2.18 times more likely to select grasslands than conifer forests, the second most abundant land cover. In Cabinet-Salish and Whitefish, conifer forests were the most abundant land cover, which contributed to contrasting changes in odds of selection compared to Rocky Mountain Front (Figure S3). Mule deer were 3.19

and 139.07 times more likely to select conifer forests instead of grasslands in the Cabinet-Salish and Whitefish areas, respectively. Disturbance from logging and wildfire events were more common in both Cabinet-Salish and Whitefish winter ranges. Regardless, mule deer were 4.75 and 125.10 times more likely to select undisturbed forest compared to a disturbed conifer forest in the Cabinet-Salish and Whitefish study areas, respectively.

We detected 36 deer mortalities (11 in Cabinet-Salish, 11 on the Rocky Mountain Front, and 14 in the Whitefish Range) from GPS-collared animals. Three quarters of these mortalities occurred in April and May, and 50% occurred in 2018, which experienced the highest snow accumulation (Figure 2). We tested 3 Cox proportional hazards models with a shared frailty term for study area using mule deer home range metrics of average snow depth, percent canopy cover, and both average snow depth and percent canopy cover (Tables S6 and S7, available in Supporting Information). Model selection with AIC identified the top model, which included a single covariate for snow depth indicating that mule deer with higher average snow depths within their home range likely had lower in survival (Figure 5). The model estimated a
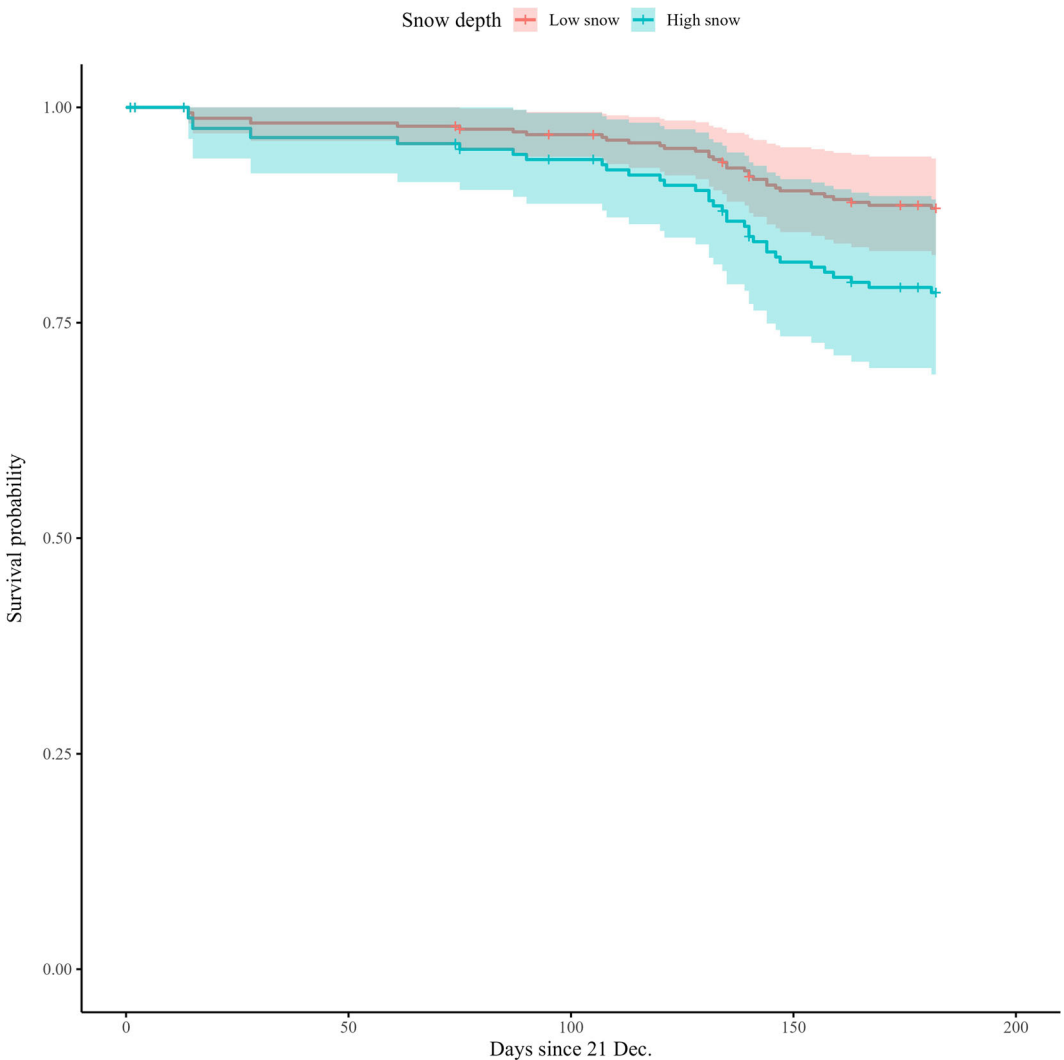
FIGURE 5 The impact of snow depth on survival probability for mule deer in Montana, USA, 2017–2020, where average home range snow depths at low values (9.5 cm) lead to higher survival probability compared to those experiencing high values (94.2 cm).

2.19 (95% CI = 0.88–5.46) increase in the hazard ratio as snow depth increased and there was weak evidence for a relationship ($\chi^2_{1,239}$ = 2.56, P = 0.11).

DISCUSSION

Landscapes with temporal changes in resources present challenges to deer, often reshaping their relationship with less dynamic resources. Although mule deer responded to snow accumulation differently across the 3 study areas, our results indicated snow conditions likely affect how deer select for canopy cover and consequently dietary items and affect their survival (Figures 3A,B, 4, and 5). Deer in Cabinet-Salish and Whitefish areas preferred patches with less snow (Gilbert et al. 1970, 2017). The magnitude of avoidance of deeper snow was much more pronounced in Whitefish, where deer experience more snowfall (Figure 2). This preference for lower snow depths has been reported in many studies and could be attributed to predator avoidance (Nelson and Mech 1986, Fuller 1991), reducing energetic expenditure associated with travel through deep snow (Parker et al. 1984), or avoidance of areas where forage is buried by snow (Gilbert et al. 1970, White et al. 2009). Deer in Cabinet-Salish and Whitefish likely avoided areas with snow because the increased energy expenditures and reduced forage availability associated with deep snow can contribute to reduced body condition as deer enter the final months of gestation (Garroway and Broders 2005). In Cabinet-Salish, deer experienced far less snow accumulation (Figure 2), thereby reducing the magnitude of its impact on deer resource selection. Thermal environments can be affected by local landscape features such as direct solar radiation in open areas or improved heat-retention in areas with thick vegetation (Parker and Gillingham 1990, Mysterud and Østbye 1999). Thermoregulation costs can be relatively small unless extreme conditions persist (Parker and Robbins 1984, Parker and Gillingham 1990), but when combined with increased costs of travel through snow and reduced availability of the highest quality forages after plant senescence and burial under snow, winter conditions likely affect an animal's energy balance (Hobbs 1989, Jenkins et al. 1990, White et al. 2009, Withers et al. 2016).

Researchers of mule deer in other deep-snow environments have suggested a snow depth threshold of 40–50 cm, above which deer avoid open areas and increase selection of closed canopy forests (Gilbert et al. 1970, Armleder et al. 1994, Poole and Mowat 2005, Serrouya and D'Eon 2008); however, snow conditions on all of our study areas, and the Whitefish study area in particular, often exceeded levels expected to preclude mule deer use. While the snow depth parameter estimate was not significant for mule deer in Whitefish, the pervasive deep snow may have presented deer with limited options for areas with better conditions. The resolution of our snow depth raster data (1 km × 1 km) may also have been too coarse to depict fine-scale heterogeneity in snow depth within individual deer home ranges. The choice to move to patches with lower snow can have pronounced impacts on individuals as winter progresses and mortality risk increases towards the end of winter (Apr–May; Figure 5; Nicholson et al. 1997, Unsworth et al. 1999). Most of the mule deer mortalities that occurred in this study were in late winter 2018, which was characterized by record snow accumulation (Figure 2).

Our diet analysis revealed a prominence of coniferous species across all 3 study areas (Figure S2, Table S1). 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). Mule deer diets in the Cabinet-Salish study area had higher diversity and deer had greater reliance on forbs and graminoids compared to the other areas, which may be attributed to lower snow accumulation and subsequently higher accessibility to such species (Hobbs 1989, White et al. 2009). Mule deer in the Whitefish area faced deeper snow, which had multiple effects. Deer using deep-snow winter ranges generally must forage heavily on conifer species (Figure 3A), despite its relatively lower nutritional quality (White et al. 2009). Additional analysis of individual canopy cover preferences and average snow depths within home ranges demonstrated a positive relationship (Figure 3B). Conceivably, these 2 results suggest the same general phenomenon, that deer avoiding snow accumulation seek snow-intercept

refugia offered by forest canopy (Parker et al. 1984, Kirchhoff and Schoen 1987, D'Eon and Serrouya 2005) and accessible conifer forage in closed canopy stands when other forages are buried under snow (Poole and Mowat 2005, Serrouya and D'Eon 2008). The Cabinet-Salish and Whitefish study areas had more closed canopy forests compared to the Rocky Mountain Front (Figure S3). This difference in dominant land cover led to differences in which variables were important in top models and their parameter estimates (Table 2). Both Cabinet-Salish and Whitefish had been previously logged and sustained periodic wildfires (Hayes 2020). In contrast, the Rocky Mountain Front area experienced relatively little forest disturbance on winter range, specifically. Low- to moderate-severity forest disturbance can create landscape heterogeneity and improve mule deer forage conditions (Hayden et al. 2008, Proffitt et al. 2016). Hayes (2020) used analogous forage and GPS data from these 3 study areas and reported increases in forage quality and mule deer selection in disturbed areas, specific to the summer season. Within winter, mule deer preferred undisturbed habitat.

Our results were affected by our choices of spatial scale and measured covariates. We explored selection behaviors at both second- and third-order scales (Johnson 1980). Decomposing selection at each spatial scale may have revealed more nuanced, scale-specific patterns (Kie et al. 2002, DeCesare et al. 2012). For example, Peterson et al. (2022) reported that mule deer in these study areas selected for forage quantity at the third order but not at the second order. We did not incorporate variability in timing or severity of landscape disturbances. Plant succession following disturbance can occur at different rates depending on the intensity and type of disturbance, ultimately leading to nonequivalent selection patterns by deer (Gilbert et al. 2017, Hayes 2020). Our forage layer predicted availability of forage biomass specific to non-coniferous food resources and their availability during the preceding summer season. Future research could directly measure available forage in winter, including conifer species and accounting for more precise measures of the time-varying effects of seasonality and snow depth. Lastly, we did not incorporate any direct measure of predation risk. Multiple researchers have reported ungulates alter resource selection in response to perceived predation risk (Brown and Kotler 2004, Frair et al. 2005, Peterson et al. 2022). Peterson et al. (2022) reported that mule deer in these same study areas responded differently to predation risk depending on the study area, spatial scale of inference, and migratory strategy. Nonetheless, predation risk is best incorporated along with temporal processes and ungulate behavioral states (Abrahms et al. 2016, Kohl et al. 2018), which were beyond the scope of this study.

MANAGEMENT IMPLICATIONS

Our results demonstrated the importance of canopy cover to deer, depending on local snow conditions. Forest disturbance regimes in these areas included regulated harvests, prescribed burns, and wildfires, all of which can decrease canopy cover. While these methods may increase shorter term production of valuable forbs and graminoids, it can also reduce the snow-intercept capabilities of the canopy leading to greater snow burial of possible forage and detering deer travel as snow accumulates. We recommend managers find preferred percent canopy cover based on the prevalent snow conditions in their area (Figure 4). Finally, we emphasize the potential importance of non-deciduous forage species, like conifers and shrubs, to mule deer habitat management, especially in the northern ecoregion where deer diets display a higher dependence on evergreen tree and shrub species.

CONFLICTS OF INTEREST

The authors acknowledge that there are no conflicts of interest to report for this study.

ETHICS STATEMENT

All deer used in our study were handled using protocols approved by the Animal Care and Use Committees at the University of Montana (protocols 001-17CBWB-011017) and Montana Fish, Wildlife and Parks (FWP03-2016).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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