

## ARTICLE

## Animal Ecology

# Forest disturbance shapes habitat selection but not migratory tendency for partially migratory ungulates

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**Abstract**

In forest management settings, disturbance resets forests to earlier successional stages, typically improving forage conditions for mule deer. Examining how forest disturbance influences mule deer behavior is important for guiding forest and wildlife management. We used GPS collar data collected between 2017 and 2019 from 136 adult female mule deer in three populations throughout western Montana, United States, to investigate how disturbance from burns (wildfire and prescribed fire) and timber harvest influenced three aspects of space-use behaviors: (1) probability of migration from winter range to summer range, (2) home range (second-order) selection by migrants on summer range, and (3) within-home range (third-order) selection. We hypothesized that deer would maximize use of disturbances during summer for nutritional benefits, predicting that deer with higher proportionate disturbance in their winter home range would be less likely to migrate away from those disturbances during summer. We predicted that migrants would select disturbances at the second and third orders. We found that proportionate disturbance in winter home ranges had no effect on the probability of migration. Among migrants, deer generally selected burns, timber harvests, and open-canopy habitat at the second order in all study areas, with particularly strong selection for 6- to 15-year-old disturbances. At population levels, selection for disturbances ceased at the third order. At individual levels, however, third-order selection for burns increased with availability, whereas selection for harvests decreased, suggesting burns may satisfy more resource needs than harvests. Our results emphasize how space-use fidelity constrains mule deer habitat selection. During summer, adherence to migratory strategies constrains the habitat available for second-order selection, preventing deer from exploiting disturbances that would otherwise be available had they remained resident in wintering areas. Second-order selection then determines disturbance availability within home ranges, affecting third-order behaviors. Although variance in selection

Teagan A. Hayes and Collin J. Peterson contributed equally to the work reported here.

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behaviors among individuals was high, population-level patterns were remarkably similar among study areas, suggesting these responses may be generalizable to mule deer throughout the northern Rocky Mountains. Forest management practices like timber harvest, prescribed burns, and wildfire management within higher elevation areas of summer range used by migrants could yield the greatest nutritional benefits for mule deer.

#### KEYWORDS

fire, forest management, habitat selection, migration, mule deer, partial migration, site fidelity, timber harvest

## INTRODUCTION

Forest management practices, including prescribed fire, timber harvest, and management of wildfires, can drive the composition, abundance, and quality of nutritional resources for wildlife (Lyon et al., 2000). Vegetation responses to forest disturbance can alter the behavior, distribution, and demography of animal populations (Palm et al., 2022; Proffitt et al., 2016; Rahman & Candolin, 2022). For North American herbivorous ungulates, opening of the forest canopy via disturbance can increase forage production, yielding nutritional benefits that vary with disturbance type and over time (Allred et al., 2011; Noss et al., 2006; Proffitt et al., 2019; Rowland et al., 2018; Snobl et al., 2022). Contrary to these benefits, disturbances can also impose costs to wildlife, such as increased exposure to human presence or predation risk with timber harvest (Francis et al., 2021; Hebblewhite et al., 2009), and deleterious effects on forage and movement energetics with severe wildfires (Kreling et al., 2021; Roerick et al., 2019; Severson & Medina, 1983; Taber, 1973). Understanding the behavioral responses of wildlife to different types of forest disturbances can inform how forests can be managed to promote nutritional resources over time for healthy wildlife populations.

In the western United States, mule deer (*Odocoileus hemionus*) populations have undergone major fluctuations and notable declines throughout much of their range over recent decades (Bergman et al., 2015; Heffelfinger & Messmer, 2003). Nutritional conditions during both winter and summer are a foundational component driving population dynamics across systems (Bishop et al., 2009; Monteith et al., 2014). Summer nutrition, in particular, can drive the fecundity of adult deer and the masses and subsequent survival of fawns (Bender et al., 2007; Tollefson et al., 2010, 2011). Past research has found that prescribed fire (Dills, 1970), timber harvest and thinning, and wildfires (Hayes et al., 2021) can increase the quality or quantity of forage for mule deer on summer range. Studies of mule deer

habitat selection have shown mixed results between deer selection and avoidance of disturbed habitats with respect to season, time since disturbance, and disturbance type (Roerick et al., 2019; Sorensen et al., 2020). Ultimately, habitat selection patterns represent an important link between management prescriptions and their intended benefits for the fitness of mule deer and other ungulates (DeCesare et al., 2014; Gaillard et al., 2010).

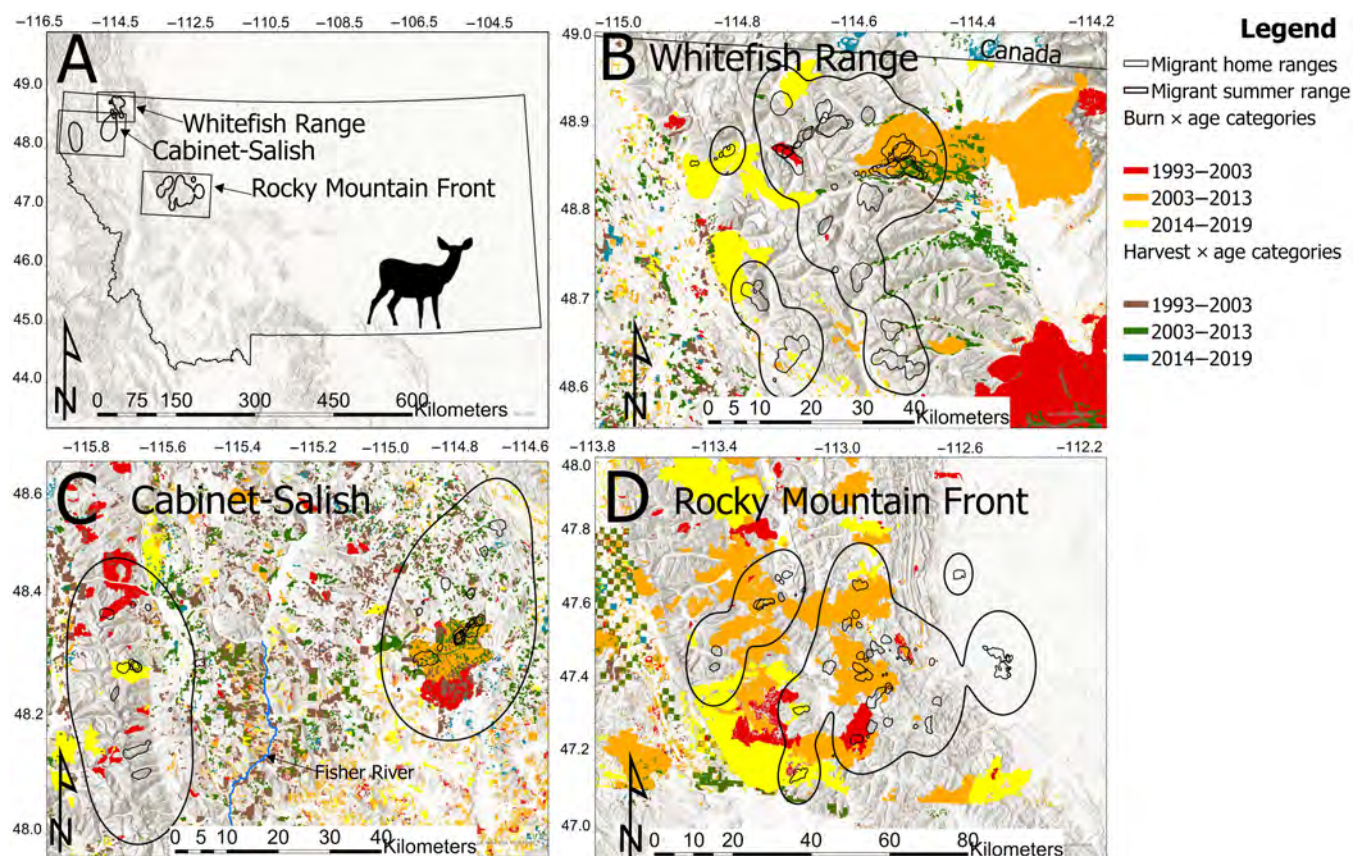
Factors like forest disturbance and associated variation in forage conditions, as well as inherent fidelity to particular movement behaviors, may affect how mule deer use habitat at multiple spatial scales. The decision of whether to migrate represents a broad-scale space-use decision that dictates the suite of resources available for finer scale habitat selection (Dingle & Drake, 2007), but precedes the habitat selection process of an animal stabilizing activity at and within a home range (Gaudry et al., 2015). Mule deer populations often exhibit partial migration, whereby some individuals migrate to summer range and others remain resident in the same range year-round (Chapman et al., 2011). The degree of migratory behavior in a population is influenced by a multitude of factors, including landscape complexity and environmental predictability (Bastille-Rousseau et al., 2017; Cagnacci et al., 2011), and the benefits of forage in high-elevation summer range relative to lower elevation winter range (Aikens et al., 2017; Lendrum et al., 2012). In forested environments, the amount of disturbance in winter range may affect this balance, potentially influencing the degree or timing of migratory behavior (Barker et al., 2019; Peterson & Messmer, 2007). Among ungulates, individual mule deer exhibit particularly high fidelity to their migratory strategy throughout their lifetime, seldom switching whether or where they migrate on an annual basis (Sawyer et al., 2019). Although behavioral fidelity could preclude the ability of mule deer to facultatively switch migratory strategies in response to conditions on winter range (McClure et al., 2005), the degree to which environmental conditions influence individual mule deer migratory strategies is poorly

understood. Ungulates may learn movement patterns from conspecifics (Jesmer et al., 2018) and adopt their mother's migratory strategy, although yearling mule deer (Jakopak et al., 2019) and white-tailed deer (Nelson, 1998) have been shown to deviate from their mother's movement and migratory strategies. Given the potential for new migratory strategies to develop across generations, the environmental drivers of different migratory behaviors within populations deserves deeper investigation (van de Kerk et al., 2021). Understanding how conditions on winter range, such as the availability of forest disturbances, influence a mule deer's probability of migration will help managers predict how deer may respond behaviorally to environmental change.

Behavioral fidelity may dampen the capacity of mule deer to make summer range decisions like home range placement (second-order selection) in response to recent disturbances (Kreling et al., 2021). At finer spatial scales, mule deer are behaviorally plastic and are able to select areas within their home range (third-order selection) with higher forage abundance (Peterson et al., 2021). Fine-scale selection of resources may vary substantially

within a population, which is often explained by differing availability of resources among individuals (i.e., a functional response; Holbrook et al., 2019). It is important to account for the influence of availability (itself the result of broad-scale selection) on the patterns of habitat selection at fine scales.

The implications of forest disturbances for mule deer forage and foraging behavior remain an important management consideration for the diverse habitats of the northern forest ecoregion of the United States (Hayden et al., 2008). As part of a multicomponent research project, we assessed the effects of forest disturbances on mule deer forage and habitat selection in three areas with differing disturbance regimes in northwestern Montana (Figure 1). Previous studies in this system have yielded several key contributions toward understanding the relationship between mule deer and disturbance. Hayes et al. (2022) showed that wildfires, prescribed fires, and timber harvests lead to increased forage nutrition (in kilocalories per square meter) for mule deer during summer, relative to undisturbed forests, in northwest Montana. However, Anton et al. (2022) found that mule deer in this system



**FIGURE 1** (A) Map overviewing distribution of study areas for radio-collared mule deer in western Montana, United States. (B–D) Maps showing forest disturbances relative to summer ranges of migratory mule deer (95% population-level kernel density estimate [KDE]) and individual summer home ranges of migratory mule deer (90% individual-level KDEs) in the (B) Whitefish Range, (C) Cabinet–Salish, and (D) Rocky Mountain Front study areas.

did not consistently prefer forest disturbances during winter habitat selection. Peterson et al. (2021) documented partially migratory behavior throughout these populations, indicating that migrants are the only group of deer making novel second-order selection choices during summer, as residents largely use the same home range year-round. Thus, remaining questions that we address here include the effects of forest disturbance on multiscale habitat selection processes during summer, including the degree of migratory behavior as well as second- and third-order selection within summer ranges.

We investigated (1) how the amount of forest disturbance from timber harvest and fire in mule deer winter range influences an individual's probability of migration, (2) how these disturbances affect second-order selection by migratory deer, and (3) how disturbances affect third-order habitat selection by migrants, given their availability. We hypothesized that mule deer would seek out forest disturbances during summer due to forage benefits. To maximize use of areas with high-quality forage, we predicted that mule deer with a higher proportion of their winter home range consisting of disturbances would be less likely to migrate. Further, we predicted that migratory deer would select disturbances at the second order. At the third order, we predicted that mule deer would use disturbances to a large degree but that selection would decrease with increasing availability. To test these predictions, we characterized the spatial composition of disturbances in our study areas, then used data from GPS-collared mule deer to assess migratory behavior relative to disturbances, and quantified habitat selection using resource selection functions (RSFs) at multiple spatial scales.

## STUDY AREAS

The study encompassed three areas in northwest Montana, namely, the Rocky Mountain Front, Cabinet-Salish Mountains, and the Whitefish Range. The Rocky Mountain Front study area included portions of the Bob Marshall and Scapegoat Wilderness areas as well as public and private lands extending eastward. Elevation ranges from approximately 1200 to 2750 m, and yearly average temperatures range from  $-10$  to  $28^{\circ}\text{C}$ . East of the continental divide, lower elevation areas include riparian areas, agricultural land, and mixed-grass prairie dominated by bluebunch wheatgrass (*Pseudoroegneria spicata*) and fescues (*Festuca campestris* and *Festuca idahoensis*). Moving west, the foothills give way to shrub- and conifer-dominated ecosystems and then to a diverse mosaic of meadows, alpine steppe, and subalpine conifer areas at higher elevations. Forest stands are generally

mixed and composed of lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), spruce (*Picea* spp.), and subalpine fir (*Abies lasiocarpa*). Much of this region experiences a stand-replacement fire regime with fire intervals of 150–250 years (Arno, 2000), and timber harvest has been minimal within the past 30 years.

The Cabinet-Salish Mountains study area was centered within the Fisher River drainage, and extends westward into the Cabinet Range and eastward to the Salish Mountains. Elevation ranges from 600 to 2100 m. Yearly average temperatures range from 0 to  $31^{\circ}\text{C}$ . The study area offers dense- to open-conifer forests with interspersed shrubland and grassland areas. Forests are composed mainly of western larch (*Larix occidentalis*), Douglas fir, lodgepole pine, and Engelmann spruce (*Picea engelmannii*). Smaller areas of western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) occur on some aspects. This region has received consistent and widespread logging activity for decades from timber companies and Forest Service harvests. Wildfires are dispersed, although larger, more frequent burns tend to occur in the drier Salish Mountains.

The Whitefish Range is bordered to the east by Glacier National Park and extends northward into the East Kootenay region of British Columbia, Canada. Elevations range from 790 m in the Tobacco Valley to around 2440 m in the Whitefish Range. Yearly average temperatures range from  $-8$  to  $30^{\circ}\text{C}$ . Forests are generally composed of western larch, Engelmann spruce, Douglas fir, lodgepole pine, and western red cedar. Disturbance includes some areas of small United States Forest Service (USFS) forest thinning projects, and wildfires are relatively small and dispersed.

Elk (*Cervus canadensis*), white-tailed deer (*Odocoileus virginianus*), bighorn sheep (*Ovis canadensis*), and moose (*Alces alces*) are sympatric with mule deer in all study areas. Pronghorn (*Antilocapra americana*) are also present on Rocky Mountain Front foothills, and mountain goats (*Oreamnos americanus*) are present in the Rocky Mountain Front and Cabinet Mountains. Carnivore species in all study areas include mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), gray wolf (*Canis lupus*), coyote (*Canis latrans*), American black bear (*Ursus americanus*), and grizzly bear (*Ursus arctos*).

## METHODS

### Telemetry location data

We captured 136 female adult ( $\geq 1.5$  years of age) mule deer in winters 2017–2019 using helicopter net-gunning,

clover trapping, and chemical immobilization in compliance with the University of Montana institutional animal care and use committee policy number 001-17CBWB-011017 and Montana Fish, Wildlife and Parks (MFWP) animal care and use committee protocol number FWP03-2016. We collared mule deer with Lotek LifeCycle 330 GPS collars programmed to upload one location every 13 h via Globalstar satellites. We collared 42 deer in the Cabinet–Salish, 49 in the Rocky Mountain Front, and 45 in the Whitefish Range and distributed capture efforts geographically across the winter ranges of study areas.

## Migration-based season delineation

We delineated the summer and winter ranges of individual deer-years according to the timing of mule deer seasonal migrations. First, we classified individual mule deer movement strategies as migrant or resident and assessed the timing of migration using net-squared displacement (Bunnefeld et al., 2011) via the Migration Mapper Application (Wyoming Migration Initiative, 2020). We defined the summer and winter seasons for migratory deer-years as the period between their arrival and departure from these seasonal ranges, respectively. We did not assess behaviors of residents during summer but defined the start of winter for residents as the 0.95 quantile value of dates characterizing the end of fall migration for all migratory deer per study area, and the end of winter as the 0.05 quantile value of dates characterizing the start of spring migration for all migratory deer per study area. Detailed methods for this process are provided by Anton et al. (2022).

## Resource covariates

Covariates hypothesized to influence mule deer habitat selection included disturbance type, landcover types outside of disturbances, forest canopy cover, slope, and topographic position index (TPI). We identified two types of forest disturbance (burns and timber harvests) based on the most recent disturbance at a location according to remotely sensed data from LANDFIRE (2017), a Global Forest Change (GFC) dataset (Hansen et al., 2013), and a USFS timber harvest activity dataset (USFS, 2023). For burns, we combined LANDFIRE data indicating prescribed burns, harvests followed by prescribed burns, and wildfires into a single category (burns). For timber harvests, we combined clear-cuts and thins identified in the LANDFIRE and USFS datasets into a single category (harvests). We did not classify postwildfire salvage cuts as

harvests, because we considered burns to be the primary disturbance in these areas. We identified remaining harvests by locating areas with tree cover loss not attributable to other disturbances (e.g., beetle-kills or fires) using the GFC dataset. GFC uses algorithms to identify reductions in forest canopy using remote-sensed data. GFC defines tree cover as all vegetation greater than 5 m in height, and tree cover loss indicates the complete removal of tree cover canopy in a 30-m pixel. For used and available points located in disturbances, we calculated time since disturbance as the difference between the year of the disturbance event and the year that each GPS point was uploaded. We assigned a year to available points of individual deer equal to the average of years that deer were collared and calculated time since disturbance for available points based on that assignment. We further divided disturbance types into time since disturbance categories of 0–5, 6–15, and 16–25 years, because these age categories have been shown to significantly differ in abundance of forage for cervids in Montana (Proffitt et al., 2016). We considered forest disturbances older than 25 years to be undisturbed forest. We classified remaining landcover into three categories (shrubland, grassland, and forest) according to a LANDSAT-derived Montana state landcover map (Montana Natural Heritage Program, 2017). We estimated percent forest canopy cover using LANDFIRE data (LANDFIRE, 2017). We calculated slope angle (in degrees) and TPI based on a 30-m-resolution digital elevation model using the raster package (Hijmans, 2019) in R. TPI is a continuous metric of landform category that distinguishes features like ridgelines from valley bottoms by comparing the elevation of a cell in a digital elevation model with the mean elevation of a 500-m<sup>2</sup> window around that cell.

## Effects of forest disturbance on the probability of migration

Our first research question concerned whether forest disturbance on individual winter ranges affected the propensity of mule deer to stay or leave, via migration to distinct summer ranges. We filtered GPS collar locations to those that uploaded during winter and combined data from across years and then excluded animals with less than 30 GPS collar locations within this multiyear period. Then, we generated a single, multiyear winter home range for each deer using a 90% kernel density estimate (KDE) using the package *adehabitatHR* (Calenge, 2023) in R, with smoothing parameter  $h = 0.004$  (Kie et al., 2010).

We estimated the proportion of each deer's winter home range consisting of either burns, harvests, or other

landcover types using a random sample of 1000 points from within individual home ranges using the raster package (Hijmans, 2019) in R. Then, we used fixed-effects logistic regression to estimate the probability of a mule deer migrating to summer range as a function of proportionate disturbance in its winter home range. Because no mule deer switched between migrant and resident strategies throughout our study, our response variable consisted of 1s (for migrants) and 0s (for residents) and did not vary by year. As explanatory variables, we log-transformed proportionate disturbance estimates to satisfy assumptions of normality. We tested the additive effects of the study area and used the Rocky Mountain Front as the reference category, because proportionate disturbance across deer in that study area was near zero.

### Effects of disturbance on summer resource selection

We assessed second-order (home range scale) and third-order (within-home range scale) RSFs only for migratory mule deer on summer range. We removed individuals that uploaded <30 GPS collar locations across summers from analysis. For each deer, we estimated a summer home range by combining GPS collar locations across years and generating a 90% KDE with smoothing parameter  $h = 0.004$ . 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 (Meyer & Thuiller, 2006). We defined available locations at the second order using 95% KDEs of GPS collar locations from all migrants by study area (excluding deer in the Whitefish Range that migrated to Canada) and then randomly sampling points within these polygons equal to 10 times the number of GPS points within each study area (Northrup et al., 2013). At the third order, we defined used locations 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.

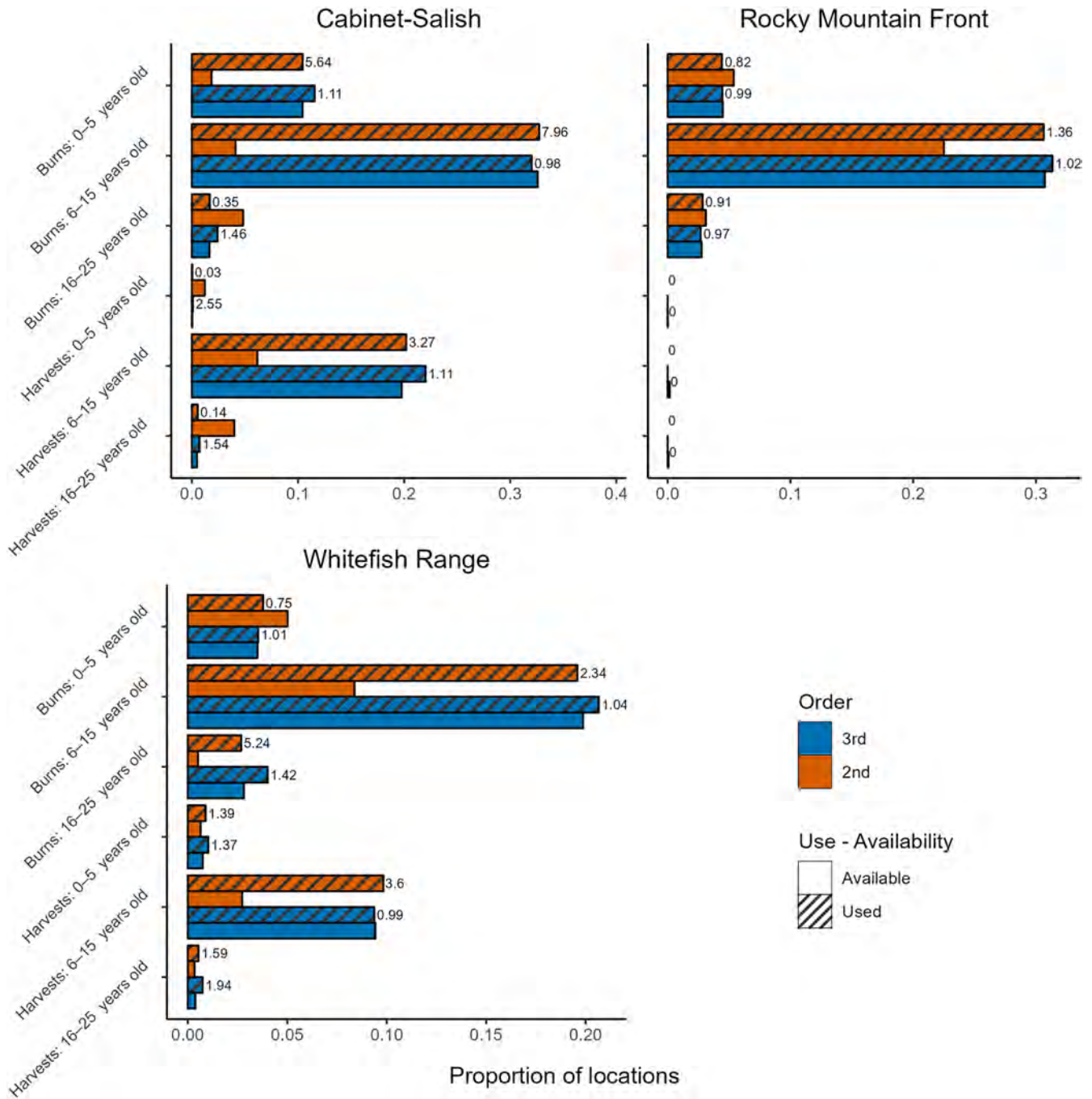
### Resource selection analysis

To accommodate inter-individual behavioral heterogeneity, avoid pseudoreplication, and account for autocorrelation and unequal sample sizes, we used a two-stage modeling approach (Fieberg et al., 2010). For each deer, we developed an individual-level RSF at both spatial scales. RSFs took the form of logistic regression, whereby we compared resources at used locations with those at

available locations using the package “glmmTMB” in R (Brooks et al., 2017). Within each study area  $\times$  spatial scale, we included the same suite of covariates in every individual-level RSF. To estimate population-level selection coefficients, we calculated a weighted mean of individual-level coefficients with weights proportional to the reciprocal of their squared SE (Murtaugh, 2007). This approach assumes that a mule deer population exhibits some underlying pattern of resource selection and individual-level selection coefficients are independent estimates of this pattern. We accounted for habitat-induced biases in the success rates of remote uploading of data from GPS collars (fixes) by using a model developed by Peterson et al. (2021) for our collared sample of deer that predicts the probability of a collar acquiring a fix (Pfix) based on topography and canopy cover at a given location. We weighted used locations in third-order RSFs by  $1/Pfix$ , such that locations in areas with low probabilities of fix success exerted more influence on selection coefficient estimates (Frair et al., 2010).

In determining which covariates to include in each study area  $\times$  scale-specific model, we assessed whether inclusion of quadratic effects of continuous covariates was justified using Akaike information criterion (AIC) on single-variable models with and without a squared term, and found that AIC improved when squared terms for canopy cover and slope were included in all models. We tested whether two-way interaction terms between canopy cover and disturbance types should be included in scale-specific models by visually assessing whether the predicted response of mule deer to canopy cover differed substantially when in or outside of disturbances. Following these procedures, we included all relevant main effects that were not correlated with Pearson's correlation coefficient ( $r$ )  $>0.4$  in each scale-specific model.

Certain disturbance  $\times$  age categories had extremely limited availability at the second order (e.g., 16- to 25-year-old harvests; Figure 2), which can lead to biased coefficient estimates (Fieberg et al., 2010; Silk et al., 2020). Therefore, we combined disturbances across age categories in our RSFs, which obfuscated the potential effects of time since disturbance on mule deer habitat selection. We confronted this issue by conducting preliminary analyses comparing the proportion of used versus available locations with selection ratios (Figure 2; Manly et al., 2002) for each disturbance  $\times$  age category. This exercise revealed a potentially strong preference for 6- to 15-year-old disturbances: Among used locations in burns, a large majority occurred in the 6- to 15-year-old age category (Cabinet–Salish: 72.9%; Rocky Mountain Front: 80.8%; Whitefish Range: 75.2%; Figure 2), and among used locations in harvests, 97.2% and 87.3% occurred in



**FIGURE 2** Proportion of used (dashed) versus available (solid) migratory mule deer GPS collar locations in multiple disturbance × age categories at two spatial scales in three study areas throughout western Montana, United States. Selection ratios (proportion used/proportion available) for each disturbance × age category × spatial scale are depicted at the ends of bars.

this age category in Cabinet-Salish and Whitefish Range, respectively (there was no use of harvests on the Rocky Mountain Front). To clarify the potentially important influence of 6- to 15-year-old disturbances on second-order habitat selection, we developed an additional model in each study area containing the same suite of covariates as original models but included only disturbance covariates for the 6- to 15-year-old category. In total, we developed two second-order RSFs per study area: an

“all-disturbances model” including the disturbances of all age categories and a “6- to 15-year old disturbances model” including the same covariates but only 6- to 15-year-old disturbances (Table 1).

At the third order, certain individuals lacked burns or harvests within their home range, rendering individual-level third-order selection coefficients inestimable for those covariates (Fieberg et al., 2010). To surmount this issue, we developed multiple third-order RSFs per

**TABLE 1** Population-level second-order resource selection covariates with coefficients ( $\beta$ ), 95% CIs (in parentheses), and sample sizes of mule deer ( $N$ ) used to develop each model for migratory deer in three study areas in western Montana, United States.

Study area	Covariate	All-disturbances model		6- to 15-year-old disturbances model	
		$\beta$ and 95% CI	$N$	$\beta$ and 95% CI	$N$
Cabinet–Salish	Intercept	<b>−2.37 (−2.90, −1.84)</b>	27	<b>−2.39 (−2.85, −1.93)</b>	27
	Burn	<b>2.38 (1.83, 2.92)</b>		...	
	Harvest	0.22 (−0.16, 0.60)		...	
	Burn 6–15	...		<b>3.47 (2.89, 4.04)</b>	
	Harvest 6–15	...		<b>0.90 (0.39, 1.41)</b>	
	Cancov	−0.28 (−0.72, 0.15)		<b>−0.38 (−0.74, −0.01)</b>	
	Cancov × harvest	<b>−1.56 (−1.97, −1.15)</b>		...	
	Cancov × harvest 6–15	...		<b>−1.37 (−1.91, −0.82)</b>	
	Cancov <sup>2</sup>	<b>−0.33 (−0.61, −0.05)</b>		<b>−0.31 (−0.58, −0.05)</b>	
	Grass	0.37 (−0.05, 0.78)		0.13 (−0.28, 0.54)	
	Shrub	<b>1.11 (0.65, 1.57)</b>		0.21 (−0.31, 0.73)	
	Slope	0.29 (−0.08, 0.66)		<b>0.55 (0.21, 0.90)</b>	
	Slope <sup>2</sup>	<b>−0.54 (−0.72, −0.36)</b>		<b>−0.46 (−0.61, −0.32)</b>	
	TPI	−0.04 (−0.14, 0.07)		−0.03 (−0.14, 0.08)	
Rocky Mountain Front	Intercept	<b>−1.86 (−2.27, −1.45)</b>	35	<b>−1.75 (−2.16, −1.34)</b>	35
	Burn	<b>0.78 (0.08, 1.48)</b>		...	
	Burn 6–15	...		<b>0.88 (0.17, 1.58)</b>	
	Cancov	0.04 (−0.45, 0.53)		0.07 (−0.42, 0.56)	
	Cancov <sup>2</sup>	<b>−0.62 (−0.88, −0.36)</b>		<b>−0.57 (−0.84, −0.30)</b>	
	Shrub	0.27 (−0.08, 0.62)		<b>0.39 (0.03, 0.76)</b>	
	Slope	<b>0.33 (0.12, 0.55)</b>		<b>0.33 (0.11, 0.56)</b>	
	Slope <sup>2</sup>	<b>−0.21 (−0.34, −0.08)</b>		<b>−0.20 (−0.34, −0.07)</b>	
	TPI	0.04 (−0.06, 0.13)		0.03 (−0.06, 0.13)	
Whitefish Range	Intercept	<b>−1.95 (−2.31, −1.60)</b>	28	<b>−1.96 (−2.29, −1.64)</b>	28
	Burn	<b>1.23 (0.66, 1.81)</b>		...	
	Harvest	0.51 (−0.12, 1.15)		...	
	Harvest 6–15	...		<b>2.13 (1.55, 2.71)</b>	
	Burn 6–15	...		<b>1.54 (0.75, 2.33)</b>	
	Cancov	<b>−0.38 (−0.68, −0.09)</b>		<b>−0.46 (−0.73, −0.18)</b>	
	Cancov × harvest	<b>−0.65 (−0.97, −0.32)</b>		...	
	Cancov × harvest 6–15	...		0.01 (−0.00, 0.02)	
	Cancov <sup>2</sup>	−0.17 (−0.36, 0.01)		−0.15 (−0.34, 0.04)	
	Grass	<b>0.66 (0.31, 1.01)</b>		<b>0.49 (0.11, 0.87)</b>	
	Shrub	<b>1.07 (0.63, 1.50)</b>		<b>0.82 (0.31, 1.32)</b>	
	Slope	<b>0.24 (0.07, 0.41)</b>		<b>0.22 (0.05, 0.40)</b>	
	Slope <sup>2</sup>	<b>−0.10 (−0.20, −0.01)</b>		<b>−0.14 (−0.23, −0.04)</b>	
	TPI	−0.06 (−0.17, 0.05)		−0.05 (−0.17, 0.06)	

Note: “Burn 6–15” and “harvest 6–15” are disturbances in the 6- to 15-year-old age category, and “cancov” is % canopy cover. Coefficients in bold have 95% CIs not overlapping zero.

Abbreviation: TPI, topographic position index.



study area, which were trained on varying samples of deer (Table 2). These were (1) a “base model” that included all covariates unrelated to disturbances and was trained on the full sample of deer; (2) a “burn model” that included the base model covariates and a covariate for burns of all age classes, trained only on deer with burns available to them at the third order; (3) a “6- to 15-year-old burn model” that included the base model covariates and a covariate for burns aged 6–15 years, trained only on deer with burns of this age available to them at the third order; (4) a “harvest model” that included the base model covariates and a covariate for harvests of all age classes, trained only on deer with harvests available to them at the third order; and (5) a “6- to 15-year-old harvest model” that included the base model covariates and a covariate for harvests aged 6–15 years, trained only on deer with harvests of this age available to them at the third order. At the third order, we developed 13 RSFs total: 5 in Cabinet–Salish, 3 in Rocky Mountain Front, and 5 in Whitefish Range (Table 2). Importantly, the selection coefficients of different disturbance types reported from separate third-order models cannot be interpreted as components of a single predictive model and instead reflect the most accurate effect sizes of disturbance types available to deer included in each model. We considered variables with CIs that did not overlap zero to be significant.

We did not perform formal model selection procedures because our goal was to understand the effects of our covariates on mule deer resource selection and not to generate the most parsimonious predictive model. It is common in two-stage RSF modeling to begin by selecting a parsimonious model from a suite of models applied to data pooled across all individuals using AIC and then using covariates from that model to develop subsequent individual- and population-level models (Burkholder et al., 2022; Fieberg et al., 2010). Given the limited availability of certain disturbance  $\times$  age categories to some individuals in our data, this process would have eliminated covariates with minor effects at the population level but major effects at the individual level immediately, and we were interested in these individual-level effects. We justified including all disturbance and landcover covariates in final models because our goal was specifically to understand how selection for nutritional resources through the lens of forest disturbance and landcover varies among individuals and across scales. Further, it was prudent to include canopy cover, slope, and TPI in all models to account for their effects, as those variables have previously been shown to have a major influence on mule deer selection in this region (Anton et al., 2022).

## Functional responses to disturbance

Under use-availability resource selection designs, interpreting an animal’s preference for a resource is contingent on the sample defining the availability of that resource (Beyer et al., 2010). Selection patterns that vary with resource availability are defined as functional responses (Holbrook et al., 2019). We tested for functional responses in third-order, individual selection for burns and harvests using the equation

$$\beta_x = \theta_0 + \theta_1 (\log(x^A)), \quad (1)$$

where  $\beta_x$  is a vector of weighted individual-level third-order selection coefficients for disturbance variable  $x$  (burns or harvests),  $\theta_0$  is the  $y$  intercept,  $\theta_1$  is the slope for the effect of the availability of disturbances on selection, and  $x^A$  is a vector of proportions of disturbance variable  $x$  in individual home ranges, by area (Holbrook et al., 2019). Functional responses were indicated if the slope  $\theta_1$  differed significantly from zero. Because we used weighted coefficients in this regression, individual coefficients in the vector  $\beta_x$  with large SEs exerted less influence on the slope  $\theta_1$  than more precise coefficients.

## RESULTS

We had sufficient data to classify 90 deer as migrants ( $n = 27$  in Cabinet–Salish,  $n = 35$  in Rocky Mountain Front,  $n = 28$  in Whitefish Range) and 18 as residents ( $n = 6$  in Cabinet–Salish,  $n = 9$  in Rocky Mountain Front,  $n = 3$  in Whitefish Range). Across all study areas, seasonal start and end dates averaged 6 December to 18 April, respectively, for winter, and 18 May to 19 October, respectively, for summer. We collected an average of 369 telemetry locations per deer during winter (range: 36–620) and 384 locations per deer during summer (range: 43–682). We monitored individuals for 516 days per deer, on average (range: 35–1037).

### Probability of migration

Across all study areas, burns, harvests, and undisturbed landcover types comprised  $17.6\% \pm 28.1\%$  (mean  $\pm$  SD),  $11\% \pm 16.8\%$ , and  $71.4\% \pm 30.3\%$  of the area of migrant winter home ranges, respectively, and  $10.8\% \pm 24.2\%$ ,  $14.7\% \pm 20.5\%$ , and  $74.6\% \pm 30.3\%$  of resident winter home ranges, respectively (Figure 3). These percentages varied by study area, and there was very little disturbance within winter home ranges on the Rocky Mountain Front, where undisturbed landcover comprised  $98.4\% \pm 2.82\%$  and

**TABLE 2** Population-level third-order resource selection covariates with coefficients ( $\beta$ ), 95% CIs (in parentheses), and sample sizes of mule deer ( $N$ ) used to develop each model for migratory deer in three study areas in western Montana, United States.

Covariate	Base model		Burn model		Harvest model		6- to 15-year-old burn model		6- to 15-year-old harvest model	
	$\beta$ (95% CI)	$N$	$\beta$ (95% CI)	$N$	$\beta$ (95% CI)	$N$	$\beta$ (95% CI)	$N$	$\beta$ (95% CI)	$N$
Cabinet-Salish		27		16		19		11		16
Intercept	<b>-2.26</b> (-2.48, -2.04) <sup>a</sup>		<b>-2.44</b> (-2.66, -2.22)		<b>-2.27</b> (-2.50, -2.04)		<b>-2.41</b> (-2.62, -2.19)		<b>-2.26</b> (-2.49, -2.03)	
Cancov	-0.26 (-0.67, 0.15) <sup>a</sup>		-0.24 (-0.77, 0.29)		-0.28 (-0.69, 0.14)		-0.27 (-1.01, 0.46)		-0.27 (-0.68, 0.15)	
Cancov <sup>2</sup>	-0.26 (-0.54, 0.02) <sup>a</sup>		-0.31 (-0.69, 0.06)		-0.25 (-0.53, 0.03)		<b>-0.70</b> (-1.14, -0.25)		-0.25 (-0.53, 0.03)	
Slope	<b>0.36</b> (0.14, 0.58) <sup>a</sup>		<b>0.27</b> (0.10, 0.45)		<b>0.36</b> (0.13, 0.59)		<b>0.19</b> (0.01, 0.38)		<b>0.36</b> (0.14, 0.59)	
Slope <sup>2</sup>	<b>-0.22</b> (-0.35, -0.10) <sup>a</sup>		<b>-0.15</b> (-0.25, -0.05)		<b>-0.25</b> (-0.38, -0.11)		<b>-0.18</b> (-0.30, -0.06)		<b>-0.24</b> (-0.37, -0.11)	
TPI	<b>0.15</b> (0.01, 0.28) <sup>a</sup>		<b>0.22</b> (0.08, 0.36)		0.15 (-0.01, 0.30)		<b>0.30</b> (0.15, 0.46)		0.14 (-0.01, 0.29)	
Grass	-0.04 (-0.23, 0.15) <sup>a</sup>		0.28 (-0.01, 0.56)		-0.04 (-0.19, 0.12)		<b>0.20</b> (0.05, 0.34)		-0.04 (-0.20, 0.12)	
Shrub	-0.06 (-0.22, 0.11) <sup>a</sup>		-0.02 (-0.33, 0.29)		-0.03 (-0.17, 0.12)		-0.07 (-0.23, 0.10)		-0.03 (-0.18, 0.12)	
Burn	...		0.05 (-0.17, 0.27) <sup>a</sup>		...		...		...	
Harvest	...		...		0.04 (-0.20, 0.28) <sup>a</sup>		...		...	
Burn 6-15	...		...		...		0.01 (-0.19, 0.21) <sup>a</sup>		...	
Harvest 6-15	...		...		...		...		0.03 (-0.19, 0.25) <sup>a</sup>	
Rocky Mountain Front		35		18		0		16		0
Intercept	<b>-1.92</b> (-2.08, -1.76) <sup>a</sup>		<b>-1.87</b> (-2.04, -1.69)		...		<b>-1.87</b> (-1.95, -1.78)		...	
Cancov	-0.11 (-0.38, 0.15) <sup>a</sup>		0.07 (-0.16, 0.30)		...		0.12 (-0.04, 0.28)		...	
Cancov <sup>2</sup>	<b>-0.30</b> (-0.50, -0.09) <sup>a</sup>		<b>-0.42</b> (-0.58, -0.26)		...		<b>-0.39</b> (-0.48, -0.30)		...	
Slope	0.12 (-0.05, 0.29) <sup>a</sup>		0.06 (-0.10, 0.21)		...		0.00 (-0.15, 0.16)		...	
Slope <sup>2</sup>	<b>-0.15</b> (-0.23, -0.07) <sup>a</sup>		<b>-0.11</b> (-0.16, -0.05)		...		<b>-0.13</b> (-0.18, -0.08)		...	
TPI	0.04 (-0.10, 0.18) <sup>a</sup>		0.05 (-0.04, 0.14)		...		0.06 (-0.05, 0.16)		...	
Shrub	<b>0.21</b> (0.08, 0.34) <sup>a</sup>		<b>0.13</b> (0.01, 0.25)		...		<b>0.16</b> (0.02, 0.30)		...	
Burn	...		-0.19 (-0.50, 0.12) <sup>a</sup>		...		...		...	
Burn 6-15	...		...		...		<b>-0.22</b> (-0.33, -0.10) <sup>a</sup>		...	

TABLE 2 (Continued)

Covariate	Base model		Burn model		Harvest model		6- to 15-year-old burn model		6- to 15-year-old harvest model	
	$\beta$ (95% CI)	<i>N</i>	$\beta$ (95% CI)	<i>N</i>	$\beta$ (95% CI)	<i>N</i>	$\beta$ (95% CI)	<i>N</i>	$\beta$ (95% CI)	<i>N</i>
Whitefish Range		28		11		16		13		13
Intercept	<b>-2.19</b> (-2.38, -2.01) <sup>a</sup>		<b>-2.32</b> (-2.47, -2.16)		<b>-2.17</b> (-2.32, -2.02)		<b>-2.60</b> (-2.71, -2.49)		<b>-2.15</b> (-2.32, -1.99)	
Cancov	0.13 (-0.05, 0.32) <sup>a</sup>		0.14 (-0.04, 0.32)		0.15 (-0.04, 0.33)		<b>0.51</b> ( <b>0.32, 0.69</b> )		0.16 (-0.03, 0.35)	
Cancov <sup>2</sup>	-0.14 (-0.34, 0.05) <sup>a</sup>		-0.06 (-0.27, 0.14)		-0.13 (-0.33, 0.07)		<b>0.44</b> ( <b>0.32, 0.56</b> )		-0.01 (-0.21, 0.19)	
Slope	<b>0.22</b> ( <b>0.10, 0.35</b> ) <sup>a</sup>		<b>0.22</b> ( <b>0.09, 0.34</b> )		<b>0.24</b> ( <b>0.13, 0.35</b> )		<b>0.13</b> ( <b>0.04, 0.22</b> )		<b>0.17</b> ( <b>0.08, 0.27</b> )	
Slope <sup>2</sup>	-0.04 (-0.12, 0.04) <sup>a</sup>		0.01 (-0.05, 0.07)		-0.03 (-0.11, 0.04)		<b>0.04</b> ( <b>0.00, 0.09</b> )		-0.05 (-0.13, 0.03)	
TPI	0.13 (-0.05, 0.30) <sup>a</sup>		0.12 (-0.04, 0.29)		0.11 (-0.05, 0.27)		<b>0.36</b> ( <b>0.26, 0.47</b> )		<b>0.18</b> ( <b>0.03, 0.34</b> )	
Grass	0.18 (-0.07, 0.43) <sup>a</sup>		-0.01 (-0.13, 0.10)		0.08 (-0.11, 0.27)		<b>0.52</b> ( <b>0.25, 0.78</b> )		-0.04 (-0.27, 0.20)	
Shrub	<b>0.40</b> ( <b>0.19, 0.60</b> ) <sup>a</sup>		<b>0.17</b> ( <b>0.04, 0.29</b> )		<b>0.34</b> ( <b>0.17, 0.51</b> )		0.06 (-0.15, 0.26)		<b>0.29</b> ( <b>0.10, 0.49</b> )	
Burn	...		0.05 (-0.13, 0.24) <sup>a</sup>		...		...		...	
Harvest	...		...		<b>0.20</b> ( <b>0.03, 0.37</b> ) <sup>a</sup>		...		...	
Burn 6-15	...		...		...		-0.02 (-0.16, 0.13) <sup>a</sup>		...	
Harvest 6-15	...		...		...		...		0.12 (-0.06, 0.29) <sup>a</sup>	

Note: "Burn 6-15" and "harvest 6-15" are disturbances in the 6- to 15-year-old age category, and "cancov" is percent canopy cover. Descriptions of each model are provided in Table 1. Sample sizes of deer vary among third-order models within study areas to accommodate the constraints of two-stage RSF modeling, because coefficients were inestimable for individuals with zero availability of a given covariate. Coefficients followed by a superscript letter "a" should be interpreted as estimations of the most accurate effect sizes of covariates available to deer included in each model. Coefficients in boldface have 95% CIs not overlapping zero.

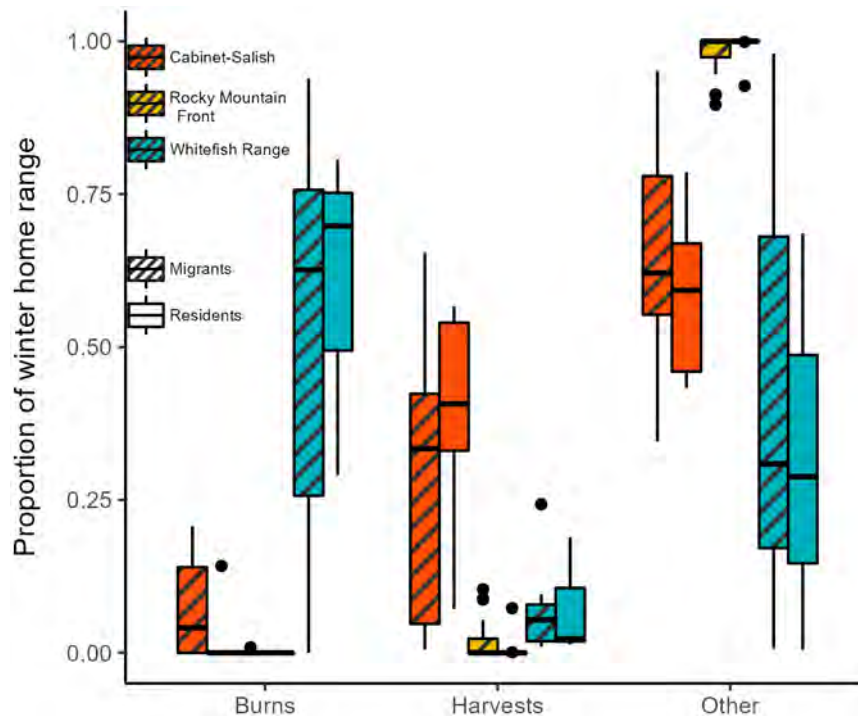
Abbreviations: RSF, resource selection function; TPI, topographic position index.

99.2%  $\pm$  2.43% of migrant and resident winter home ranges, respectively. We found no effect of proportionate disturbance on the probability of a mule deer migrating ( $\beta_{\text{harvests}} = -2.475$ ,  $p = 0.275$ ;  $\beta_{\text{burns}} = -0.601$ ,  $p = 0.778$ ) and no effect of study area ( $\beta_{\text{Cabinet-Salish}} = 0.970$ ,  $p = 0.337$ ;  $\beta_{\text{Whitefish}} = 1.28$ ,  $p = 0.368$ ).

## Resource selection

Across all study areas, we found a consistent trend whereby selection coefficients for landcover types and disturbances were greater in magnitude at the second order than the third order (Tables 1 and 2; Figure 4). Furthermore, mule deer generally selected for open-canopy landcover types

like burns, harvests, shrubs, and grasslands at the second order (Table 1) in all study areas (although we did not test the effects of grasslands on the Rocky Mountain Front because that covariate was strongly correlated [ $r = -0.479$ ] with canopy cover). Regarding burns, mule deer exhibited positive selection in all study areas at the second order (Table 1, Figure 4). Restricting our analysis to the most abundant age category of burns (6-15 years old) yielded larger positive and significant selection coefficients at the second order in all study areas (Table 1, Figure 4). The effects of burns diminished to nearly zero at the third order in all study areas (Table 2, Figure 4). Harvests had similar effects as burns on mule deer resource selection in the Cabinet-Salish and Whitefish Range. Selection coefficients for harvest were positive



**FIGURE 3** Proportions of individual winter home ranges (estimated as 90% kernel density estimates) consisting of either burns, timber harvests, or other undisturbed landcover types for migrant (dashed) and resident (solid) mule deer in three study areas throughout western Montana, United States. Box plots show median values (solid horizontal lines), 25% and 75% quantile values (shaded areas), and interquartile range (whiskers) with outliers shown as solid circles.

(although CIs overlapped zero) at the second order in both study areas (Table 1, Figure 4). However, when we considered 6- to 15-year-old harvests only, second-order selection was positive and significant (Table 1). Much like burns, the effects of harvests were nearly zero at the third order (Figure 4). Harvests were very sparsely available ( $<0.003$  proportionate availability at second order) and not used by any migratory deer on summer range in the Rocky Mountain Front, so we did not consider that covariate in that study area.

We found significant quadratic effects of canopy cover at the second order in the Cabinet-Salish and Rocky Mountain Front (Table 1), and mule deer preferred home ranges with as little canopy cover as possible in all study areas (Figure 5). At the third order, we found significant effects of canopy cover in the Rocky Mountain Front only (Table 2). At the second order, we found significant negative interactions between canopy cover and harvests of all ages in the Cabinet-Salish and the Whitefish Range (Table 1), indicating that mule deer in these study areas preferred harvests with low canopy cover (Figure 5). This interaction remained significant with 6- to 15-year-old harvests in the Cabinet-Salish but not in the Whitefish Range (Table 1). We found significant quadratic effects of slope in all study areas at the second order: Mule deer preferred  $12^\circ$  slopes in the Cabinet-Salish but preferred

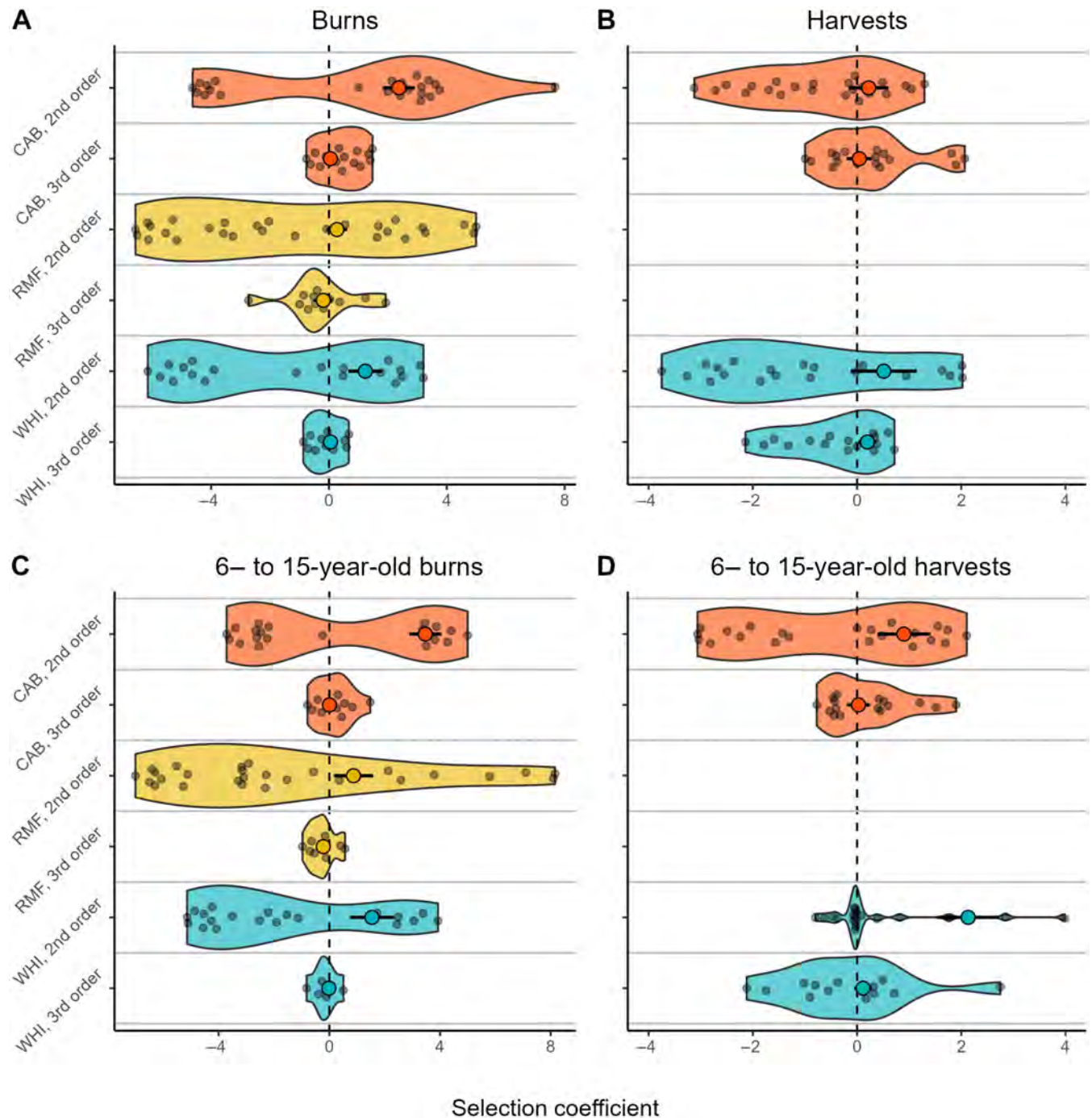
the lowest slopes available in the Rocky Mountain Front and Whitefish Range (Table 1). At the third order, mule deer selected for low slopes relative to availability within home ranges across all study areas (Table 2). TPI was significant only at the third order in Cabinet-Salish, where mule deer preferred convex (ridgelike) terrain (Table 2). Mule deer selected shrublands at the second order in all study areas and at the third order in the Rocky Mountain Front and Whitefish Range (Tables 1 and 2).

## Functional responses to disturbance

We found some evidence for a positive third-order functional response to burns, whereby individuals with greater availability of burns in their home ranges selected burns more strongly ( $p = 0.097$ ; Figure 6A). For harvests, we found evidence of a negative functional response, whereby selection for harvests decreased with increasing availability ( $p = 0.046$ ; Figure 6B).

## DISCUSSION

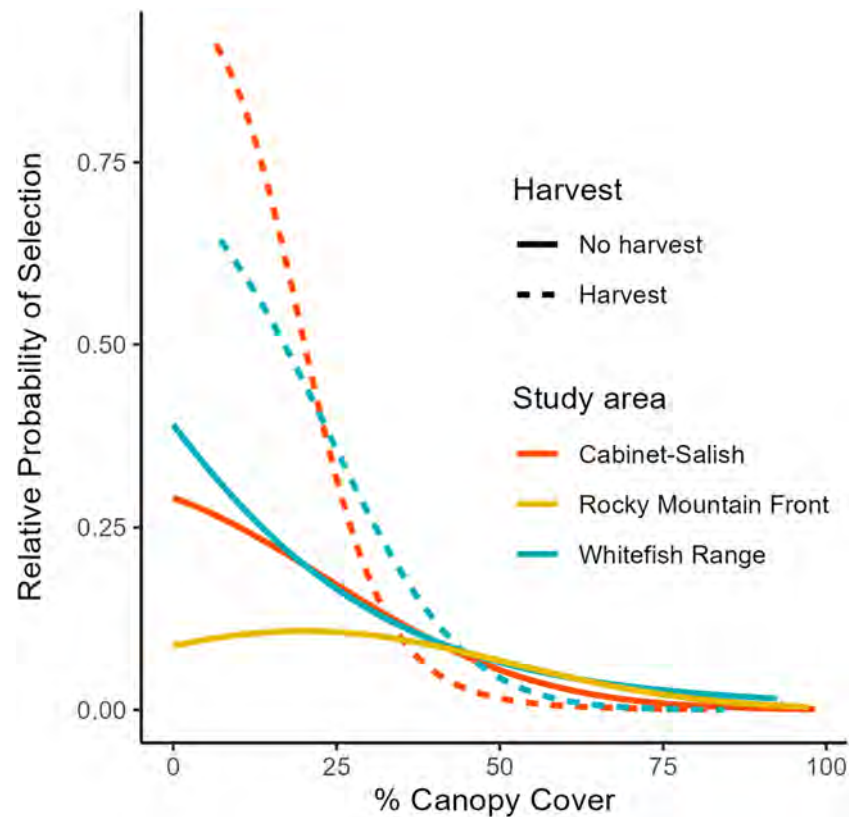
We found support for our hypothesis that mule deer seek out forest disturbances like burns and timber harvests on



**FIGURE 4** Population- (large datapoints) and individual-level (small datapoints) selection coefficients for different disturbance  $\times$  age categories from resource selection functions for migratory mule deer at two spatial scales in three study areas (CAB, Cabinet–Salish; RMF, Rocky Mountain Front; WHI, Whitefish Range) throughout western Montana, United States. Coefficients for different disturbance  $\times$  age categories were estimated using separate models, summarized in Table 2.

summer range, likely due to the nutritional benefits forest disturbances provide. At population levels, mule deer responded consistently to forest disturbances across study areas and disturbance regimes. At the second order, mule deer consistently selected for both burns and timber harvests. Furthermore, deer used burns and harvests in the 6- to 15-year-old age category more than other age

categories at this scale and showed stronger selection for this age range, which is consistent with findings that forage resources for cervids (in kilocalories per square meter) are maximized at this time since disturbance (Hull et al., 2020; Proffitt et al., 2016; Visscher & Merrill, 2009). Forest disturbances played only a minor role in third-order selection at the population level, which could

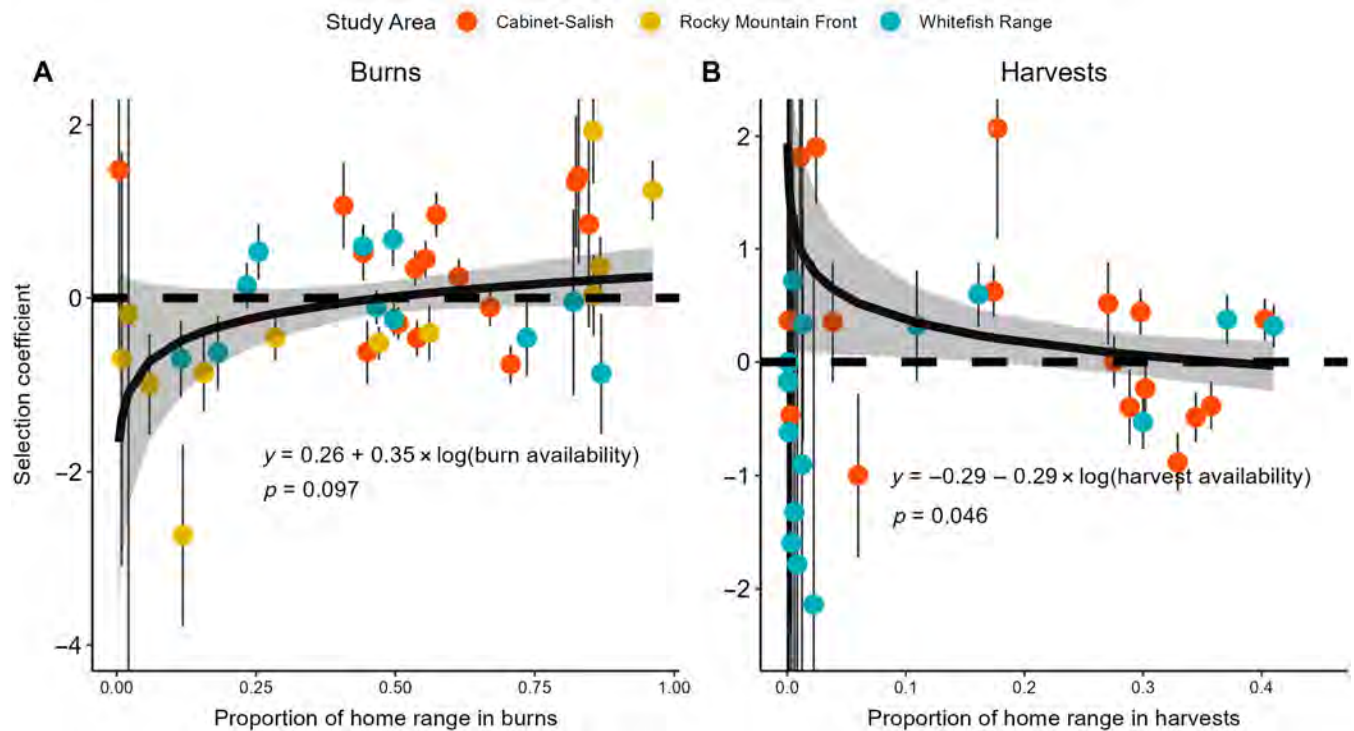


**FIGURE 5** Predicted relative probability of second-order selection by migratory mule deer for canopy cover within and outside of timber harvests, derived from a generalized linear model containing canopy cover, a quadratic effect of canopy cover, harvest, and the interaction between harvest and canopy cover in three study areas in western Montana, United States.

be attributable to several possibilities. First, via second-order selection, mule deer may satisfy resource requirements (e.g., forage) provided by forest disturbances, eliminating their need for third-order selection and allowing deer to select other resources (e.g., security) at that scale (Hebblewhite & Merrill, 2009; Rettie & Messier, 2000). Alternatively, third-order selection may be driven by resources like patches of vegetation or individual plants that vary at a finer spatial resolution than broad-scale disturbances (Long et al., 2008). Finally, we did not assess how selection behaviors vary according to time of day or behavioral state. Circadian patterns in selection, whereby animals select disturbances at certain times of day and avoid them at others, may have gone undetected in our study (Bose et al., 2018; Spitz et al., 2018).

In violation of our predictions, forest disturbances within winter ranges had no effect on the probability of an individual migrating to summer range. Our findings suggest that the degree to which environmental surroundings affect an individual mule deer's decision to migrate may be outweighed by other factors. Studies suggest that the migratory behavior of ungulates may stem from cultural transmission of strategies

(Jesmer et al., 2018), and in mule deer, there is strong fidelity to the strategy they inherit and sites they migrate to (Sawyer et al., 2019; but see Jakopak et al., 2019 for an example of novel yearling mule deer movements). Fidelity to migratory strategies and sites may ensure reliable benefits like reduced predation risk (Forrester et al., 2015; Metzgar, 1967) and competition (Kokko et al., 2006; Morrison et al., 2021) in predictable environments but are often maladaptive under changing environmental circumstances (Merkle et al., 2022). Although forest disturbances can benefit mule deer populations by enhancing forage, our findings imply that the potential to manifest these benefits is limited by the relatively rigid patterns of space use they exhibit at broad scales. These findings are relevant to other migratory ungulate species that often exhibit high site fidelity to seasonal home ranges, such as moose and bighorn sheep (Morrison et al., 2021). When animals exhibit innate site fidelity independent of variation in environmental conditions, year-long nutritional benefits are maximized when forage-enhancing disturbances occur within the seasonal range that is most limiting to population performance (Bishop et al., 2009; Monteith et al., 2014). If summer nutrition is a more limiting factor (Monteith et al., 2014),



**FIGURE 6** Third-order functional response of migratory mule deer to the availability of (A) burns and (B) timber harvests within their home ranges in three study areas throughout western Montana. Points represent individual third-order selection coefficients for burns and harvests, respectively, with associated 95% CIs. Some CIs exceed the y-axis limits of these graphs.

then forest management practices occurring on shared winter range may offer limited nutritional benefits to migrants, as migrants will likely abandon those areas during the growing season. Indeed, others have shown that habitat treatments in the form of disturbance on winter range can improve mule deer fitness (Bergman et al., 2014), and that enhancing forage conditions on winter range may delay the timing of migration to summer range (Peterson & Messmer, 2007), yielding some benefits in the growing season. However, our findings suggest that forest disturbances like burns and harvests may yield the greatest benefit for migratory mule deer when applied in higher elevation summer range. In areas where more mule deer are resident, disturbances on winter range may yield greater benefits.

Mule deer exhibit fidelity not only to a migratory strategy but also to where they migrate on an annual basis (Morrison et al., 2021; Sawyer et al., 2019), restricting the habitats available for second-order selection by individuals (Merkle et al., 2022). Despite these restrictions, we found preference for burns and timber harvests by migrants at the second order. If mule deer adhere to migrating to a given site, then how do they locate recent disturbances, which are intrinsically transient? Mule deer may possess some capacity for small shifts in home range placement to adjust to the presence of disturbances.

Certainly, other studies have documented plasticity in fine-scale space use by mule deer, like adjustments in movements during migration in response to human development (Sawyer et al., 2020) or to phenological mismatches (Ortega et al., 2023), and shifts in winter home range placement in response to competitors (Schroeder & Stewart, 2022). Furthermore, mule deer exhibited behavioral plasticity by searching for higher quality habitat within unfamiliar environments when the option for home range fidelity was eliminated entirely via translocation of individuals (Wright et al., 2020). Perhaps small shifts in home range placement permit mule deer to exploit beneficial forest disturbances when they occur on the periphery of previous summer home range areas. Moreover, use of multiple ranges may increase the likelihood of mule deer exposure to new disturbances (van de Kerk et al., 2021). However, our findings and previous research indicate that broad-scale shifts in home range placement in response to disturbance appear unlikely. For example, black-tailed deer (*O. hemionus columbianus*) exhibited low plasticity in home range placement, returning to pre-fire home ranges after catastrophic wildfire depleted forage in their summer range (Kreling et al., 2021). Long et al. (2008) also reported no change in selection patterns of mule deer before and after forest burning or thinning treatments. Indeed, we found

substantial variation in selection for disturbances among individuals, and numerous mule deer exhibited zero use of disturbances at the second order (Figure 2), several of which had migrated through disturbances en route to their summer home range (MFWP, unpublished data), suggesting limited capacity for behavioral plasticity. Constraints imposed by site fidelity may have accounted for the avoidance of disturbances by some groups of deer, which diminished the population-level effect sizes of burns and harvests at the second order. In the context of anthropogenic change, ungulate species that readily adjust to changing frequency and placement of disturbance may fare best (Wong & Candolin, 2015). To predict population responses to changing environmental conditions, more research is needed to unveil the behavioral mechanisms through which ungulates locate new forest disturbances.

We noted substantial differences in resource selection behaviors between spatial scales, with mule deer selecting forest disturbances and landcover types associated with forage (i.e., grasslands, shrublands) at the second order but exhibiting neutral selection of these variables at the third order. These results contrast with those of Peterson et al. (2021) from the same sample of migratory mule deer in this study system. They found that mule deer are generally neutral toward forage resources (measured as kilocalories per square meter) at the second order, but increase selection at the third order. Understanding how forage resources vary among and within disturbances helps reconcile this counterintuitive finding. Both Hayes et al. (2021) and Peterson et al. (2021, appendix B) noted substantially greater variance in the abundance of mule deer forage resources in harvested or burned stands than in undisturbed landcover types. Given this variation, the mean forage conditions of home ranges placed within disturbances may be similar to forage conditions in random areas on the landscape. However, patches of vegetation and individual plants within forest disturbances are often distributed in a mosaiclike pattern (Kreling et al., 2021) and of higher quality than those in undisturbed landcovers (Hayden et al., 2008; Lehmkuhl et al., 2013; Proffitt et al., 2016), allowing access to higher nutrition via third-order selection than they would in other landcover types. Our findings lend insight into the behavioral mechanisms through which mule deer seek out forage: At broad spatial scales, deer seek out areas in or near large, perceptible landscape features often associated with forage like burns, harvests, and open grasslands to place their home ranges. At finer scales, disturbance and landcover types become less relevant, and mule deer more directly seek patches of higher quality or more abundant forage (Peterson et al., 2021).

In line with our predictions, as the availability of timber harvests increased among individual home ranges, third-order selection for harvests decreased (i.e., a negative functional response; Figure 6B). This may reflect a trade-off, in which mule deer keep time spent foraging in harvests below a certain threshold due to associated costs, such as predation risk (Godvik et al., 2009; Holbrook et al., 2019). Timber harvests have been associated with increased perceived or actual mortality risk of forest-dwelling ungulates from mountain lions (Gaynor et al., 2022), wolves (DeCesare, 2012; Hebblewhite et al., 2009), and humans (Francis et al., 2021), in part due to an association with roads, which are used as travel corridors by wolves and humans. In contrast, third-order selection for burns increased with availability (a positive functional response; Figure 6A). This scenario often occurs when animals specialize on a certain habitat type that provides both forage and security (van Beest et al., 2016). Previous analyses by Peterson et al. (2021) found that predation risk from wolves and mountain lions within this study system are typically weakly correlated with forage, if at all, and that mule deer are able to circumvent forage-risk trade-offs during third-order selection. Mule deer may achieve these ends by selecting burns. In conifer forests of the western United States, fire severity and vegetation regeneration are typically highly variable within burns (Lentile et al., 2007; Snobl et al., 2022), resulting in a patchy mosaic of forage and cover resources that could provide a setting for mule deer to spatially decouple forage and risk (Pierce et al., 2004).

Through RSF modeling, we found that at the second order, selection of disturbances in the 6- to 15-year-old age category was stronger than selection of disturbances when all age categories were combined (Table 1, Figure 4). Moreover, second-order selection ratios for disturbances in each age category were largest for 6- to 15-year-old disturbances everywhere but the Whitefish Range, where selection ratios were greater for 16- to 25-year-old burns (which had very limited availability; Figure 2). In similar environments within the Rockies and northwestern United States, forage quality (average digestible energy per square meter) is highest in early stages of regeneration after disturbance (0–5 years following disturbance), whereas herbaceous biomass peaks after 6–15 years (Hull et al., 2020; Proffitt et al., 2016; Visscher & Merrill, 2009). Energy acquisition by ungulates may be optimal at intermediate timescales postdisturbance, when biomass of high-quality, early seral plant communities peak and trade-offs between forage quality and quantity are minimal (Hebblewhite et al., 2008).

In modeling resource selection, biologists can account for individual-level variation in behavior and avoid pseudoreplication in sampling designs through modeling



approaches that estimate individual-level coefficients via two-stage designs (Fieberg et al., 2010) or include random slopes for individuals (Gillies et al., 2006; Muff & Fieberg, 2020). However, these approaches present computational challenges that arise when individual animals display miniscule or zero use of categorical variables (Fieberg et al., 2010), a challenge that affected our inferences on mule deer behavior. For example, third-order selection coefficients for the “burns” variable were inestimable for individuals that did not have burns in their home ranges, necessitating us to develop separate third-order models for every disturbance  $\times$  age category we were interested in. Each submodel depended on smaller sample sizes of individuals (Table 2). For instance, only six individuals in the Whitefish Range used burns in the 6- to 15-year-old age category, leading to potential biases in third-order coefficients due to the low sample size (Leban et al., 2001; but see Street et al., 2021 for examples of robust RSFs with small samples of individuals), and coefficient estimates that do not apply to the population as a whole. Furthermore, within study areas and orders of selection, coefficients developed from separate models were not additive, precluding us from developing a predictive model for all individuals with all covariates of interest. When incorporating categorical variables into mixed-effects or two-stage RSF approaches, we strongly encourage researchers to examine selection ratios for each category and to compare population-level coefficients with individual-level coefficients to visualize potential biases.

## MANAGEMENT IMPLICATIONS

Forest disturbances like wildfires, prescribed fires, and timber harvest can improve forage conditions and are preferred during summer home range selection by migratory mule deer. Home range placement, however, is constrained by high fidelity to seasonal ranges, which further constrains nutritional resources available within home ranges. Due to these constraints, mule deer may be underutilizing the nutritional benefits of forest disturbances in western Montana. Management will have greater benefits for a greater number of deer when forest management techniques are spatially distributed in areas of summer range known to be used by migratory mule deer. Forest management actions that are applied at a rate that maintains growth of early to midseral stage vegetation can help offset declining forage in aging disturbances. Mule deer selected burns more consistently and strongly than timber harvests at the second order, and selection increased with availability at the third order. These patterns suggest that burns may satisfy more

resource needs than timber harvests. Forest management practices like prescribed fires and wildfire management, rather than suppression, may yield the greatest increase to mule deer forage. At the population level, selection patterns were remarkably similar among study areas, suggesting that these responses may be generalizable to mule deer in other populations in forested parts of the Rocky Mountains.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data (Peterson, 2024) are available from Zenodo: <https://doi.org/10.5281/zenodo.13968230>.

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