




RESEARCH ARTICLE

Interactive effects of wildfires, season and predator activity shape mule deer movements

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Abstract

1. Wildfires are increasing in size, frequency and severity due to climate change and fire suppression, but the direct and indirect effects on wildlife remain largely unresolved.
2. Fire removes forest canopy, which can improve forage for ungulates but also reduce snow interception, leading to a deeper snowpack and potentially increased vulnerability to predation in winter. If ungulates exhibit predator-mediated foraging, burns should generally be selected for in summer to access high-quality forage and avoided in winter to reduce predation risk in deep snow. Fires also typically increase the amount of deadfall and initiate the growth of dense understory vegetation, creating obstacles that may confer a hunting advantage to stalking predators and a disadvantage to coursing predators. To minimize risk, ungulates may therefore avoid burns when and where stalking predators are most active, and use burns when and where coursing predators are most active.
3. We used telemetry data from GPS-collared mule deer (*Odocoileus hemionus*), cougars (*Puma concolor*) and wolves (*Canis lupus*) to develop step selection functions to examine how mule deer navigated species-specific predation risk across a landscape in northern Washington, USA, that has experienced substantial wildfire activity during the past several decades. We considered a diverse array of wildfire impacts, accounting for both the severity of the fire and time since the burn (1–35 years) in our analyses.
4. We observed support for the predator mediating foraging hypothesis: mule deer generally selected for burned areas in summer and avoided burns in winter. In addition, deer increased use of burned areas when and where wolf activity was high and avoided burns when and where cougar use was high in winter, suggesting the hunting mode of resident predators mediated the seasonal response of deer to burns. Deer were not more likely to die by predation in burned than in unburned areas, indicating that they adequately manage fire-induced changes to predation risk.

5. As fire activity increases with climate change, our findings indicate the impact on ungulates will depend on trade-offs between enhanced summer forage and functionally reduced winter range, mediated by characteristics of the predator community.

KEYWORDS

Canis lupus, magnet effect, *Odocoileus hemionus*, predator–prey interactions, *Puma concolor*, step selection function, ungulate, wildfire

1 | INTRODUCTION

Across the globe, climate change, a history of fire suppression and loss of indigenous burning practices have increased the frequency, size and severity of wildfires, with the risk of catastrophic fires predicted to rise into the future (Abatzoglou & Williams, 2016; Jolly et al., 2015; Kimmerer & Lake, 2001; Stavros et al., 2014). Such changes in fire regime alter the distribution, structure and composition of vegetation, with cascading impacts on the wildlife those habitats support (Geary et al., 2020; Hessburg et al., 2005). The impacts may be direct, by altering the food resources available to herbivores (Raynor et al., 2015; Westlake et al., 2020) or indirect, by influencing predation rates (Leahy et al., 2015), predator distributions (Jorge et al., 2020) or driving a behavioural response to changing predation risk (Cherry et al., 2017). The impacts of wildfire depend on both the time since the fire and the severity of the fire, although rarely are the diversity of the impacts considered simultaneously, leading to a variety of observed effects on wildlife (Volkman et al., 2020). For instance, ungulates have been shown to avoid burned areas (Eckrich et al., 2019; Konkolics et al., 2021), select for burned areas (Keay & Peek, 1980; Pearson et al., 1995; Westlake et al., 2020) and show no response or a mixed response to burned areas (Eckrich et al., 2020; Gogan et al., 2019; Long et al., 2008; Roerick et al., 2019). To understand how herbivores respond to burns, it is necessary to consider both the spectrum of fire characteristics and the potential direct and indirect pathways of their effects.

Historically, low- and mixed-severity fires of western North America burned frequently, reducing canopy cover and surface fuels while increasing light to the understory, facilitating the growth of the herbaceous understory (Arno & Fiedler, 2005; Hessburg et al., 2005). In xeric landscapes of western North America, the nutritional value of the understory improves immediately following a fire, although peak abundance of forage for ungulates occurs 6–15 years post fire before returning to near pre-fire levels after ~20 years (Hayes et al., 2022; Hull et al., 2020; Proffitt et al., 2019). Improved forage in burned areas often attracts herbivores, termed the magnet effect (Archibald et al., 2005). Such attraction to fire-affected areas can persist up to 20 years (Raynor et al., 2015; Wan et al., 2014; Westlake et al., 2020). Wildfire can also impact predation risk through structural changes in the landscape. Homogeneous burns can reduce hiding cover for prey

(Germaine et al., 2004) and stalking predators, whereas heterogeneous burns can create patchy refugia for prey (Skatter et al., 2017) and provide cover for stalking predators (Doherty et al., 2022). Fire may increase structural complexity through accumulation of deadfall and initiating regeneration of serotinous vegetation, which could impact predator detection and evasion abilities for ungulates (Metsaranta et al., 2003). Predation risk management by ungulates in heterogeneous landscapes, such as those impacted by wildfire, may depend on the hunting mode of the predator (Kohl et al., 2019; Preisser et al., 2007). Stalking predators such as cougars (*Puma concolor*) exploit complex landscapes where it is easier to approach prey undetected (Ruth et al., 2019), which may cause ungulates to avoid burned areas if fires increase deadfall and initiate the growth of dense understory vegetation. Alternatively, cursorial predators such as wolves (*Canis lupus*) favour open areas to hunt (Kauffman et al., 2007) and ungulates may use burned areas to minimize wolf predation risk. Thus, it may be necessary to account for characteristics of the predator community to predict how ungulates will respond to wildfires (Doherty et al., 2022).

Predation risk effects, particularly as related to wildfire, may also be seasonally dependent. Fire can increase snow depth by allowing falling snow that would have been intercepted by the canopy to accumulate to deeper levels (Maxwell et al., 2019; Musselman et al., 2008; Varhola et al., 2010). Studies from Isle Royale, USA (Post et al., 1999) and Banff National Park, Canada (Hebblewhite, 2005) have shown that snowpack strongly influences an ungulate's ability to evade predators, favouring predators over prey in deep, low-density snow that may accumulate in recent burns. For example, deeper snow increased rates of predation from wolves and coyotes (*Canis latrans*) on white-tailed deer (*Odocoileus virginianus*) because the higher ungulate foot load caused deer to sink deeper into the snow than carnivores, impeding escape from predators (Nelson & Mech, 1986; Olson et al., 2021). Because adult ungulates suffer the highest rates of predation mortality in winter relative to other seasons, snowpack characteristics could strongly influence their populations (Brodie et al., 2013; Cosgrove et al., 2021; Forrester & Wittmer, 2013). Deeper snowpack also increases energetic output for ungulates and can hinder their ability to access key nutritional resources when forage is buried under deep or crusty snow (Gilbert et al., 2017; Parker et al., 1984; Penczykowski et al., 2017).

In navigating these complex, fire-affected landscapes, ungulates must balance the need to secure high-quality nutrition

while minimizing the risk of predation (i.e. risk sensitive foraging; Brown, 1988). Fear of predators can drive prey away from the highest quality food resources, with potential consequences for prey survival and distribution (Brown et al., 1999; Hernández & Laundré, 2005). For instance, white-tailed deer avoided burned areas with high-quality forage to minimize predation risk when rearing fawns in Georgia, USA (Cherry et al., 2017). Understanding the responses of ungulates to wildfires therefore requires considering food resources, shifting predation risk and the trade-offs therein (Doherty et al., 2022).

Here, we examine the movement and survival of adult female mule deer (*O. hemionus*) in northern Washington, USA, from summer 2017 to winter 2020–2021 to determine how they respond to a diverse history of wildfire while being subject to cougar and wolf predation risk. We also used remotely sensed data to determine if fire reduced canopy cover, improved forage quality and led to a deeper snowpack. This region experienced major wildfires in 2001, 2003, 2006, 2014, 2015, 2017 and 2018, creating a complex landscape to study the impacts of fire on predator–prey dynamics (MTBS Project, 2021). Wolves began to naturally recolonize this region in 2008 after nearly a century of extirpation and some areas remain unoccupied, providing a unique opportunity to examine predator–prey dynamics in areas with and without wolves.

We used global positioning system (GPS) telemetry data to model wolf, cougar and mule deer activity to test three primary hypotheses of how ungulates could respond to a gradient of wildfire impacts and predator use. Under the *magnet effect hypothesis* (H1), ungulates should be attracted to the high-quality forage of low and moderate recent burns (<20 years after fire) independent of predator use in the summer, selecting for these burns irrespective of predation risk. Under the *two-component predation risk hypothesis* (H2), ungulate movement in response to burns should reflect the traits of the predator (*predation risk effect – predator traits hypothesis*, H2a); that is, in periods with no or low snow, ungulates should avoid burned areas where stalking predators are more active and prefer burned areas where coursing predators are more active. In the winter, ungulates may increase avoidance of burned areas where both stalking and coursing predators have movement advantages in deep low-density snow and forage is harder to access (*predation risk effect – winter vulnerability hypothesis*, H2b). Finally, we hypothesized that ungulates could display *predator-mediated foraging* (H3) whereby they balance access to improved forage post fire (*magnet effect*, H1) with predation risk (*predation risk effect*, H2) such that they are no more likely to die by predation in burned areas than in unburned areas. We expected *predator-mediated foraging* (H3) to be supported based on risk-sensitive foraging theory and empirical evidence (Altendorf et al., 2001; Brown, 1988), but the dynamic nature of wildfire impacts could preclude an optimal response by ungulates and lead to either a strong forage-attraction or predator-avoidance response. Collectively, our analysis offers a comprehensive examination of a diversity of fire impacts on predator–prey interactions.

2 | MATERIALS AND METHODS

2.1 | Study area

Our study encompassed the northern half of the Washington Department of Fish and Wildlife's East Slope Cascades Mule Deer Management Zone within Okanogan County, Washington, USA (11,040 km²; latitude: c. 48.050° to 49.150°; longitude: c. -120.900° to -119.700°; Figure 1). Rolling shrub-steppe foothills at lower elevations (min: 230 m) transition to conifer forests at mid elevations, while the terrain becomes steep and rocky at high elevations (max: 2830 m). The region has a relatively low human population density (mean: 0.006 ± 0.173 people per km², min: 0, max: 59) that is primarily concentrated around valley bottoms. Cold winters (average low of -7°C, average high of 1°C from December to March) and hot summers (average low of 9°C to average high of 26°C from June to September) are typical, with 57 cm of rain and 292 cm of snow estimated annually in Mazama, Washington, USA (based on data collected from 1981 to 2010; <https://www.usclimatedata.com/climate/mazama/washington/united-states/uswa0264>).

Historically, low-severity fires occurred every 1–25 years and mixed-severity fires occurred every 25–100 years, but fires in this region are becoming increasingly severe and frequent (Arno & Allison-Bunnell, 2013; Hessburg et al., 2005). Since the Monitoring Trends in Burn Severity (MTBS) program began mapping fire perimeters in 1984, 38% of the region has burned, over half of which occurred since 2014 (MTBS Project, 2021). Prior to the start of the study, extreme fire years occurred in 2006 with the Tripod Complex (70,753 ha) and Farewell (31,340 ha) fires and in 2014 with the Carlton Complex (111,730 ha) and Upper Falls (3580 ha) fires. These were followed by two major fire years during the study; the Canyon Creek (499 ha), Diamond Creek (47,561 ha) and Uno Peak (3593 ha) fires burned in 2017, and the Crescent Mountain (21,553 ha) and McLeod (10,011 ha) fires burned in 2018. No major fires occurred in the region from 2019 through the end of our study.

The study area supported a wide array of both predators and prey. In addition to mule deer, white-tailed deer were common in the region, while elk (*Cervus canadensis*) and moose (*Alces alces*) were present but rare. Cougars occurred across the study area and preyed on mule deer, as did black bears (*Ursus americanus*), bobcats (*Lynx rufus*) and coyotes, although these predators primarily prey on neonatal deer. Since 2008, wolves have naturally recolonized portions of the region, creating areas of presence and absence for comparison. The Lookout and Loup Loup packs occupied the southwest and northeast regions of the study area (Figure 1c) for the duration of the project (Washington Department of Fish and Wildlife et al., 2018, 2019, 2020, 2021). Over the study, the Loup Loup pack varied from 2 to 6 wolves (mean = 4.0) and the Lookout pack varied from 3 to 8 wolves (mean = 5.2). The Sullivan Creek pack formed along the eastern edge of the study area in 2019, and the Navarre pack established in the southern region of the study area in 2020.

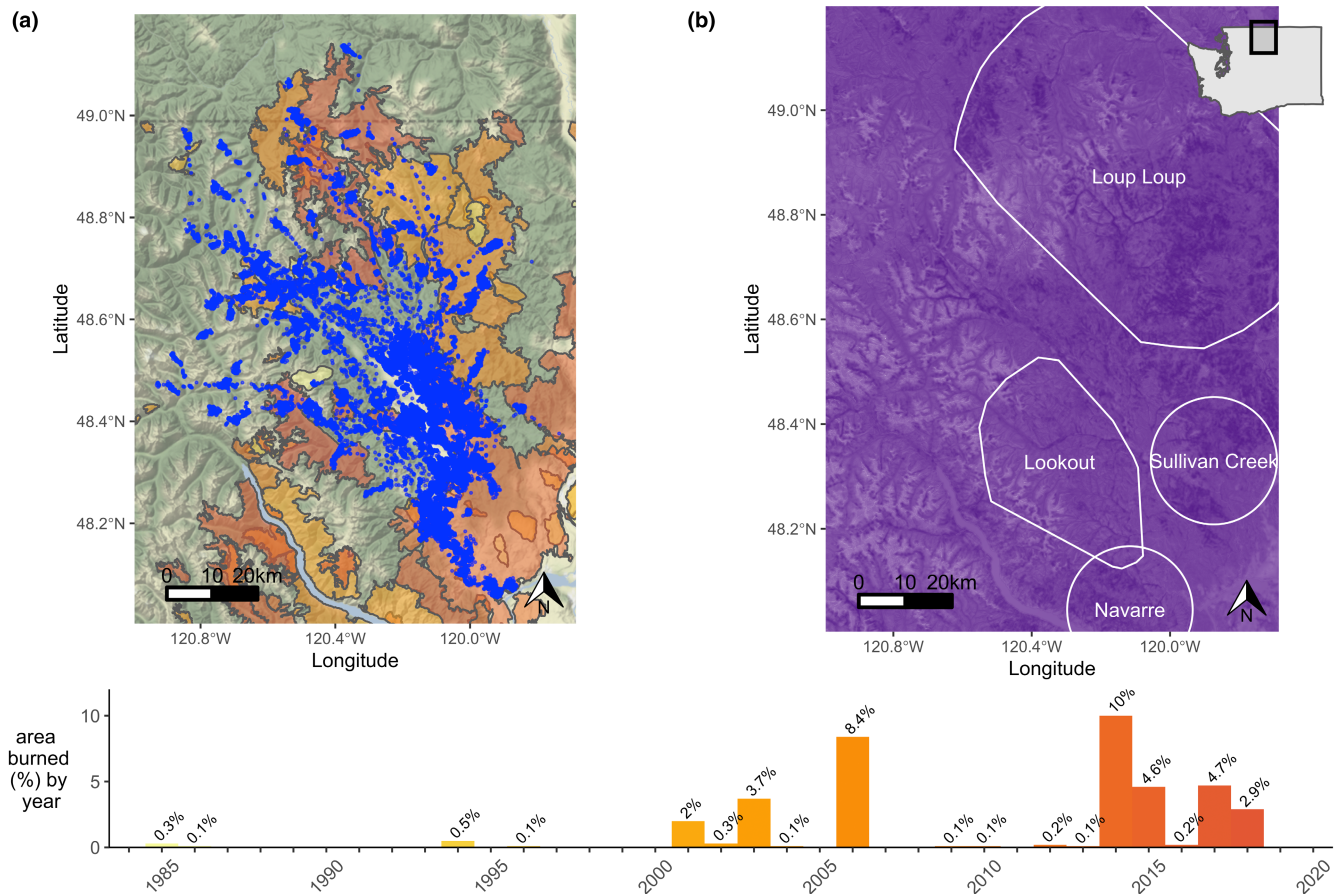


FIGURE 1 Mule deer (GPS locations from collared individuals shown in blue) in Okanogan County, Washington, USA (a) encounter a range of fire histories through their annual migrations. Orange shading in (a) illustrates the extent of the burn perimeter and corresponds to the year of the burn (c). Since collection of fire data began in 1984, (c) 38.4% of the 11,040 km² region burned, over half of which has occurred since 2014 (MTBS Project, 2021). (b) Predicted cougar use (summer 2019 displayed as example) is higher where colours are darker. Wolf pack territories during the study, shown as 95% minimum convex polygons, are overlaid. The Sullivan Creek (est. 2019) and Navarre (est. 2020) packs did not have collared wolves during our study, so their approximate territories are represented with circles.

Aerial and in-field surveys as well as camera trap monitoring indicate that the Sullivan Creek and Navarre packs did not substantially overlap with the collared mule deer, although wolves from these packs were not collared so their precise range was unknown (Washington Department of Fish and Wildlife et al., 2020, 2021). Based on the reported minimum count of wolves from these packs from 2016 to 2020 (Washington Department of Fish and Wildlife et al., 2018, 2019, 2020, 2021), we estimated an averaged minimum density of 0.103 wolves per 100 km² (SD = 0.053, range: 0.045–0.190) during the study.

2.2 | Landscape change

We used linear regression to test if fire reduced canopy cover, increased forage quality and increased snow depth. Methods, results and interpretation of the investigation are presented in Supplementary Material S1. For all analyses, fire timing and severity were sourced from MTBS, which maps the size and severity of fires >1000 acres across the United States from 1984 to the present

(MTBS Project, 2021). MTBS classifies six categories of fire impacts based on a composite burn index at 30-m resolution: unburned to low, increased greenness, low severity, moderate severity, high severity and mask (Key & Benson, 2006). We reclassified MTBS's 'unburned to low' (unburned within a burned perimeter or visible fire impacts affecting <4.5 m² out of the 90m² pixel) as 'unburned', and pooled 'increased greenness post fire' with 'low-severity' burns (hereafter low severity), leaving us with unburned, low-, moderate- and high-severity burn classifications for analysis. Masked values (burn severity unobtainable due to atmospheric or terrain factors) were removed from the analysis. In the MTBS classification system, low-severity burns are characterized by significant consumption of vegetation <1 m and up to 25% mortality of overstory trees, whereas high-severity burns are characterized by near complete consumption of the understory vegetation and >75% tree mortality and moderate-severity burns either display characteristics between low- and high-severity burns or contain a mix of low- and high-severity burns (Key & Benson, 2006; <https://burnseverity.cr.usgs.gov/glossary>). We treated fire impact as a categorical covariate in the regression models with all combinations of time class (0–4 years,

5–9 years, 10–20 years, and 21–35 years) and the three severity classes (low, moderate, high), such that there were 13 categories including an unburned class. Time classes were selected based on the post fire stages of forest succession relevant to mammals (Fisher & Wilkinson, 2005), which aligned well with the distribution of our fire impacts across the study area.

2.3 | Animal captures

We captured cougars using wire-mesh cage traps or by ground-darting after treeing them with trained pursuit hounds (Hornocker, 1970; Kertson et al., 2011). We fit cougars with either an Iridium GPS-radio collar (Model Vertex Lite, Vectronic Aerospace, Berlin, Germany) or GPS-enabled accelerometer collar (Model G5-AL, Advanced Telemetry Systems, Inc.). Wolves were captured with padded leg-hold traps and by aerial darting (Frame & Meier, 2007; Jessup, 1982), and they were fit with GPS radio-collars (Models Vertex Lite and GPS Plus, Vectronic Aerospace). Adult female mule deer were captured on their wintering grounds in the Methow Valley, Washington, USA (c. 48.329°, -120.066°) using drive nets in 2017, and by aerial net-gunning from 2018 onward (Jessup, 1982) and fitted with GPS-radio collars (Model Vertex Plus, Vectronic Aerospace). All animal collars were programmed to record a GPS fix every 4 h. Wolves were captured as part of existing management and conservation activities (Washington Department of Fish and Wildlife et al., 2021) by Washington Department of Fish and Wildlife personnel in accordance with their agency-approved wolf capture and handling protocols (Washington Department of Fish and Wildlife, 2019) and the guidelines of the American Society of Mammalogists for the use of live animals in research (Sikes et al., 2016). Cougar and mule deer captures and handling followed protocols approved by the University of Washington Institutional Animal Care and Use Committee (IACUC Protocol #4226-01).

Mule deer collars transmitted mortality signals that triggered after 9 hours of inactivity, and mortalities were investigated as soon as possible to determine cause of death. Our investigations included the following: (1) an evaluation of the scene, (2) examination of predator tracks and signs where relevant (Elbroch & McFarland, 2019), (3) DNA swabbing of lethal bites in the event of predation (Caniglia et al., 2013; Mumma et al., 2014) and (4) necropsy with sample collection and testing when necessary. We recorded the location of the mortality using a handheld GPS receiver and confirmed the time of death with the telemetry data. Predation was confirmed at mortality sites if the carcass had lethal bite marks with haemorrhage or clear signs of a chase or a struggle. In cases where there were no clear signs of haemorrhage due to consumption of the carcass, but all evidence clearly indicated a single species of predator responsible for the mortality, we classified the cause of death as 'unknown - likely predation'. If there were no clear signs of haemorrhage due to consumption of the carcass and the evidence weakly indicated a single species of predator, we classified the cause of death as 'unknown - possible predation'.

2.4 | Movement models

Our analyses included four summer seasons (2017, 2018, 2019 and 2020) and four winter seasons (2017–2018, 2018–2019, 2019–2020 and 2020–2021). Summer was defined as June 15–September 30 and winter as December 1–March 15 based on the seasonal range use of mule deer, which were identified using net squared displacement (Bunnefeld et al., 2011; Sawyer et al., 2009) in Migration Mapper (Merkle et al., 2017). We used resource selection functions (RSFs; Manly et al., 2002; Johnson et al., 2006) to describe cougar use and used localized density distributions (LDDs; Kittle et al., 2016) to describe wolf use, reflecting the different distributions and densities of these predator species. We used these predator layers to parameterize the mule deer step selection function. All analyses were performed in Program R version 4.1.0 (R Core Team, 2021).

2.5 | Cougars: Resource selection functions

Beausoleil et al. (2021) recently estimated cougar density as 1.55 ± 0.44 cougars per 100 km² in this study system. We used the CTMM package in R (Calabrese et al., 2016) to calculate 95% autocorrelated kernel density home ranges (Fleming et al., 2015) of collared adult cougars (≥ 2 years old and with >3 months of data; Beausoleil et al., 2013) and found that home ranges varied from 102 to 7792 km² with a median of 836 km² ($n = 14$). As such, we assumed that the area was fully occupied by cougars and focused on modelling the probability of use within the home range (third-order selection; Johnson, 1980) to describe cougar activity. We randomly selected 20 points for each telemetry location from within the 100% seasonal minimum convex polygon for each cougar with an individual's data pooled across years using R package AMT (Signer et al., 2019). We then combined the used and available locations for each cougar into a single dataset and used logistic regression in an RSF framework to model cougar use across the study area (Keating & Cherry, 2004). Because we were interested in producing the model with the best predictive fit rather than interpreting the effect of predictors, we did not eliminate predictive covariates based on correlation between them, nor did we use model selection to choose the most parsimonious model. We evaluated predictive performance of our models using leave one individual out cross validation (Boyce et al., 2002; Mahoney et al., 2018).

We modelled cougar space use with measures of terrain, landcover and human impacts (Kertson et al., 2011; Knopff et al., 2014). Specifically, we used elevation, elevation², heat load index, topographic position index, terrain roughness index, percent forest, percent shrub, percent open, distance to water, percent developed, human population density, distance to minor roads (logging and residential roads) and distance to major roads (freeways, highways and secondary highways) as covariates. Continuous covariates were standardized to have a mean of zero and standard deviation of one. Elevation, heat load, topographic position index, terrain roughness index and landcover were available at 30-m resolution. Heat load incorporates slope, aspect and

latitude to estimate potential direct incident radiation at a location (McCune, 2007; McCune & Keon, 2002). Topographic position index identifies ridges and valleys by their difference in elevation from neighbouring terrain and can be important for cougar movement (Peterson et al., 2021). Terrain roughness measures heterogeneity of the elevation and cougars generally select rougher terrain over gentler terrain (Riley et al., 1999; Riley & Malecki, 2001). We obtained landcover from Terradapt:Cascadia (<https://www.cascadiapartnerforum.org/terradapt>), which provides spatial layers covering the entire annual range of the collared mule deer, including southern British Columbia. Simplified cover types were ground-truthed during vegetation surveys for a related study in northeastern Washington (T.R. Ganz et al., unpublished data) and resulted in open, shrub, forest and developed categories. Each landcover type was represented as percent cover (unstandardized) within a 250m moving window at 30m resolution. We selected a 250m buffer because this approximated the mean step-length taken by deer for our focal periods (summer: mean = 253m, SD = 281m; winter: mean = 251m, SD = 265m) and thus represented the resources available to deer at each step.

2.6 | Wolves: Localized density distributions

To describe wolf pack activity while accounting for areas outside of known wolf pack territories, we created LDDs for summer and winter. LDDs are analogous to utilization distributions but incorporate multiple animals for social species such as wolves, representing a spatial distribution of pack use weighted by the number of individuals in the group (Kittle et al., 2016, 2017). Wolf pack size was based on aerial and in-field track surveys and camera trap monitoring (Washington Department of Fish and Wildlife et al., 2018, 2019, 2020, 2021). To create pack-level distributions, we first used an autocorrelated kernel density estimator to generate separate utilization distributions for each collared individual for each winter and summer. If more than one wolf was collared in a pack in a season of a year, we averaged the layers to describe pack use. For periods when a wolf was not collared within a pack, we used the average of that pack's layers from other years to approximate use in that season. For each season-year-pack combination, we set values <0.05 in the distribution layer to 0.00 to approximate the 95% home range, then scaled the layer such that all values summed to one to account for variable intensity of use between different size home ranges (Kittle et al., 2016; Klauder et al., 2021). Finally, we multiplied the layer by minimum pack size for the year (Washington Department of Fish and Wildlife et al., 2018, 2019, 2020, 2021) and summed pack layers for the relevant period to create seasonal landscape level use layers for each season-year combination (Kittle et al., 2016).

2.7 | Mule deer: Step selection functions

Mule deer exhibit strong fidelity to their home ranges and movement corridors relative to other ungulates (Kreling et al., 2021; Morrison et al., 2021; Sawyer et al., 2018), so we expected that changes in

selection owing to fire would be most evident at the finest spatial-temporal scale available in our GPS data (i.e. fixes collected every 4 hours). To validate this assumption, we calculated kernel density estimates (KDEs) of the 90% isopleth (Börger et al., 2006) using R package *AMT* (Signer et al., 2019; Signer & Fieberg, 2021) for each deer with at least 200 locations on each seasonal range, corresponding to a minimum of about 1 month of data. We censored locations 3 weeks post-capture for all deer to minimize potential effects of capture on movement and survival (Northrup et al., 2014; van de Kerk et al., 2020). From these KDEs, we determined overlap of seasonal home ranges between subsequent years for individual deer by calculating the Bhattacharyya coefficient (Bhattacharyya, 1943) in R package *AMT* (Signer et al., 2019). The Bhattacharyya coefficient is a measure of overlap between two distributions that is well suited to comparing the volumetric overlap between home ranges and spans from 0 for no overlap to 1 for complete overlap (Fieberg & Kochanny, 2005). Only three deer in our study had fires burn within their home range between study seasons while they were monitored, so we were unable to statistically compare home range characteristics before and after fire. Each of these deer returned to the same summer home range after the fires that they had used before.

We used step selection functions (Fortin et al., 2005) to examine how mule deer responded to recent burns and predator use while accounting for other potentially important factors such as terrain, human impacts and land cover. Step selection functions are a form of conditional logistic regression that compare landscape characteristics at the end of a taken step (the transition between two consecutive GPS points) to characteristics at the end of randomly generated steps that an animal could have accessed at that time (Thurfjell et al., 2014). We created separate population-level models for deer on summer and winter ranges (i.e. not while migrating) and restricted dates to match those used in modelling predator distributions. For each seasonal dataset, we removed any individual with fewer than 50 fixes after the 3-week post-capture censor. Based on the seasonal movement characteristics of the deer, we generated 5 random steps with the turn angle drawn from a von Mises distribution and step-length drawn from a gamma distribution (Northrup et al., 2013; Thurfjell et al., 2014) using the *AMT* package in R (Signer et al., 2019). Random steps were compared to taken steps with conditional logistic regression using the R package *MLOGIT* (Elff, 2016).

We developed a set of 11 candidate models to test our hypotheses that deer would respond to past fires, wolves and cougars subject to additional influences from landscape factors. The candidate models were as follows: (1) null, (2) null+wolf, (3) null+cougar, (4) null+wolf+cougar, (5) null+burn, (6) null+burn+wolf, (7) null+burn+cougar, (8) null+burn+wolf+cougar, (9) null+burn×wolf, (10) null+burn×cougar and (11) null+burn×wolf+burn×cougar. As a null model, we used elevation, heat load index, terrain roughness index, percent open, percent forest, percent shrub and percent developed to explain mule deer selection. Elevation, heat load index, terrain roughness index, percent open, percent forest, percent shrub and percent developed covariates were used as previously described.

Wolf and cougar distributions were both standardized so covariate effects could be estimated at the mean level of predator use intensity. Because of the high density of cougars across the area, deer may not have been able to avoid cougars but might have been able to avoid the areas with the highest cougar activity. To account for this possible nonlinear effect of cougar use, we included an additive effect of cougar² in the models with cougar. A negative coefficient estimate for the cougar² covariate would indicate that deer increased avoidance (if the response to cougars was negative) or reduced the strength of selection (if the response to cougars was positive) for areas where cougar activity was more intense. In the summer, deer were not exposed to wolves in the 21–35 years since fire for low-, moderate- or high-severity burns, so this component of the burn × wolf interaction was excluded. We removed the 10–20 year burn classes from the winter wolf × burn interaction for the same reason.

Before running models, we checked Pearson's correlation between the covariates and eliminated covariates with $|r| > 0.7$ (Dormann et al., 2013). If correlation exceeded 0.7, we retained the covariate of primary interest and excluded the other. If the correlated covariates were of equal interest (e.g. landcover type), we used AIC to compare the null models excluding each of the correlated covariates and retained the covariate producing a better model fit (Anderson & Burnham, 2002). We selected the most parsimonious model for each season based on AIC (Burnham & Anderson, 2002) and evaluated predictive performance of the best models with leave one individual out cross validation (Boyce et al., 2002; Mahoney et al., 2018).

2.8 | Spatial predictors of mortality

We used a general linear model to test if deer were more likely to die from predation in burns relative to unburned areas. We coded each deer mortality location as ones and paired these with 20 locations randomly selected from their used telemetry points, which were coded as zeros following Olson et al. (2021). Locations were excluded for the first 3 weeks post capture so any deer dying in this window were likewise excluded. We constructed two separate models to account for uncertainty in cause of death: (1) confirmed predations only and (2) confirmed, likely, and possible predation mortalities. Because of the small sample size, we treated burn as a binary predictor, where burns included low-, moderate- and high-severity burns since 1984. All burned locations in this dataset were < 20 years after fire.

3 | RESULTS

3.1 | Movement models

We captured 24 cougars (16 females, 8 males) of which 20 were adults (≥ 2 years), and 4 were subadults (1.5 to < 2 years) at first capture (Beausoleil et al., 2013). All cougars contributed to the winter

model and 17 cougars informed the summer model (Supplementary Material S2, Tables S2.1 and S2.2, Figure S2.1). Both winter and summer models had good predictive performance ($r_{s,winter} = 0.99$, $r_{s,summer} = 0.95$; Supplementary Material S2, Figure S2.2). We used telemetry data from the five wolves that were GPS-collared during the project to model their distribution for each season of each year (Supplementary Material S2, Figure S2.4). Three wolves were from the Loup Loup pack (1 female, 2 males) and two were from the Lookout pack (2 males; Supplementary Material S2, Table S2.3). We captured and collared 149 adult female mule deer during our study. After censoring post-capture data and removing deer with < 50 locations per season from the step selection function, 143 deer informed the winter model and 116 deer informed the summer model (Supplementary Material S3, Table S3.1). We quantified 586 seasonal KDEs and found strong fidelity to seasonal ranges, with a median Bhattacharyya coefficient of 0.89 (range: 0.03–0.99).

Predicted cougar use and percent shrub were highly correlated in the summer (Pearson's correlation of 0.75), so we removed percent shrub from mule deer step selection summer models because we were more interested in interpreting the effect of cougar presence on deer than land cover per se. Likewise, terrain roughness and cougar use were highly correlated in the winter (Pearson's correlation of 0.72), so we removed terrain roughness from all winter models. Shrub and open were correlated by 0.76 in the winter, so we used AIC to compare the null models excluding shrub and excluding open. The model with open received 100% of model weight and an AIC score 259.44 points lower than the model with shrub, so we removed shrub from all winter models. In both summer and winter, the most complex mule deer model received 100% of the model weight (Supplementary Material S3, Table S3.2), indicating fire history, predator activity and the interactions therein were important drivers of deer selection. Both the highest ranked summer and winter models performed well ($r_{s,winter} = 1$, $r_{s,summer} = 0.988$; Supplementary Material S3 Figure S3.1).

Deer showed significant responses to nearly all the 'null' habitat covariates with no difference in the direction of the effect by season (Table 1). Mule deer selected for areas with higher elevation, greater heat load, more open habitat and greater terrain roughness (summer only) relative to what was available to them. We did not detect a significant relationship with percent forest cover in the summer, but areas of greater forest cover were avoided during winter (Table 1). The summer model revealed strong selection for developed areas by deer, but the population-level pattern appeared to be driven by 48 individuals that did not migrate into remote, wilderness areas in the summer where there was no exposure to development. We did not detect a significant relationship between deer use and development in the winter. Counterintuitively, both our summer and winter models revealed deer selection increased with greater predicted use by cougars. However, deer reduced selection of areas with the highest levels of predicted cougar use, particularly during the summer, as evidenced by the negative coefficient of the cougar² covariate. Deer avoided wolves throughout the year, and the effect was stronger in the winter than in the summer (Table 1).

TABLE 1 Non-burn-related coefficient estimates for the seasonal step selection functions for mule deer with 95% confidence intervals. Terrain roughness was not considered in the winter model. Coefficient estimates for fire effects are provided in Supplementary Material S3, Table S3.3

Covariate	Summer			Winter		
	$\hat{\beta}$	Lower CI (2.5%)	Upper CI (97.5%)	$\hat{\beta}$	Lower CI (2.5%)	Upper CI (97.5%)
Elevation	0.15	0.11	0.20	0.36	0.33	0.39
Heat load	0.08	0.07	0.08	0.08	0.07	0.09
Terrain roughness	0.08	0.06	0.09			
Open	0.19	0.13	0.26	0.61	0.55	0.68
Forest	-0.04	-0.11	0.02	-0.68	-0.81	-0.56
Developed	1.20	0.91	1.50	0.19	-0.10	0.48
Cougar	0.26	0.25	0.28	0.33	0.32	0.34
Cougar ²	-0.052	-0.059	-0.045	-0.012	-0.018	-0.007
Wolf	-0.07	-0.12	-0.03	-0.29	-0.36	-0.22

Deer responses to wildfire strongly depended on season, species-specific predator use and the characteristics of the burned area. In the summer, deer primarily selected for burns, although not in all cases (Figure 2a). Cougar activity had little effect on use of low- and high-severity burns 0–4 years old, low-severity burns 5–9 years old and moderate-severity burns 10–20 years old in the summer (Figure 2b). As cougar activity increased in moderate-severity burns 0–4 and 5–9 years old, deer increasingly selected for these areas, but avoided high-severity burns 5–9 years old. Responses to cougars were mixed in 10–20 year old burns, but deer avoided the oldest burns (21–35 years) with increased cougar activity. Unlike the mixed response to cougars, deer consistently increased their use of post fire areas where wolf activity was higher in the summer, except for high-severity burns 5–9 years post fire, which had no effect (Figure 2c).

The winter season presented more consistent trends as deer mostly avoided all burn classes at the mean levels of predator exposure (Figure 2a). With increasing levels of cougar activity, deer consistently strengthened their avoidance of all burn classes <21 years old, while the oldest burn classes had nonsignificant effects (Figure 2b). Conversely, deer reduced avoidance of burns up to 9 years after fire with higher wolf activity but increased avoidance of the oldest burns (Figure 2c).

3.2 | Spatial predictors of mortality

We documented 52 deer mortalities over the course of the study, excluding three deer that were censored from analysis due to a mortality in the first 3 weeks post capture. In some cases, the cause of mortality was indeterminate owing to insufficient evidence remaining at the mortality site, severe autolysis of tissues and contamination of the mortality site by scavengers. Of the 52 mortalities, 22 were confirmed to be the result of predation, nine resulted from an unknown cause of death that was likely to be predation, and one resulted from an unknown cause of death where predation was possible ($n = 32$; Table 2).

Deer were not more likely to die at burned sites than unburned sites throughout the year (confirmed predations: $z_{460} = -0.65$, $p = 0.52$; confirmed, likely and possible predations: $z_{670} = -0.03$, $p = 0.97$), nor in the winter (confirmed predations: $z_{165} = -0.53$, $p = 0.59$; confirmed, likely and possible predations: $z_{268} = -0.14$, $p = 0.89$; Table 3). We conducted a post hoc analysis focused on deer mortality from cougars as these were their primary predator, and likewise did not detect differences in the predation risk with respect to burns (confirmed predations: $z_{313} = -0.51$, $p = 0.61$; confirmed, likely and possible predations: $z_{418} = 0.47$, $p = 0.64$).

4 | DISCUSSION

As wildfires become more frequent, burn at higher intensity and grow in size, it becomes increasingly important to understand their direct and indirect effects on wildlife populations (McKenzie et al., 2004; Volkmann et al., 2020). We found that mule deer response to burned areas depended on the season, predator activity and predator species, subject to the characteristics of the fire that had burned there. We observed the most support for the *predator mediated foraging hypothesis* (H3), which predicted that mule deer would be attracted to burned areas in the summer due to the forage-enhancing effects of fire, while also responding to predator exposure such that the likelihood of dying by predation did not increase in burned areas. In the winter, deer consistently avoided burned areas that we predicted would result from the accumulation of deeper, fluffier snow rendering deer more vulnerable to predators (*predation risk effect - winter vulnerability hypothesis*, H2b). However, the avoidance of burned areas in the winter was mediated by the traits of the predator (*predation risk effect - predator traits hypothesis*, H2a). Burned areas were avoided more in winter where activity from stalking predators (cougars) was higher, whereas the avoidance of burned areas was weakened under exposure to coursing predators (wolves). In the summer, deer increased use of burns where wolf activity increased but had a

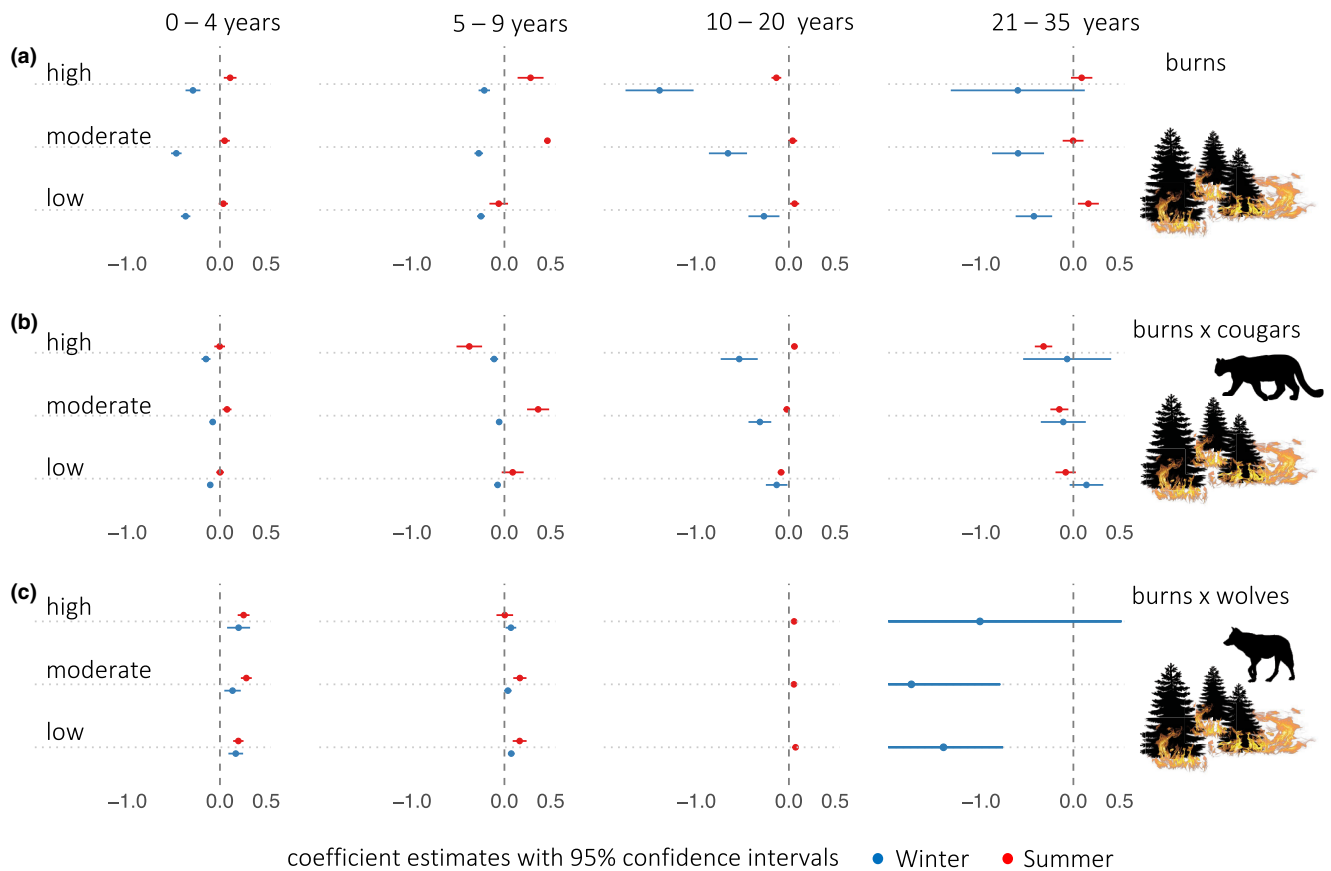


FIGURE 2 Coefficient estimates for deer selection for burned areas across fire severity and time since fire for (a) the main effect of burns and the additive effect of burns with a standard deviation increase in (b) cougar and (c) wolf activity above the mean. The net response of deer to a particular burn class with a standard deviation increase in wolf or cougar activity above the mean is the sum of the coefficient for the burn class at mean predator exposure plus the coefficient estimate representing the interaction with wolves or cougars in that burn class and the independent response to the predator. Dots indicate the estimated coefficient value, and corresponding lines display the 95% confidence intervals. Blue represents the winter model, and red represents the summer model. Negative coefficients show avoidance of the burn class, whereas positive coefficients indicate selection for the burn class at mean predator exposure (a), and interactions with the predator (b) and (c) indicate the degree to which the main effects of burns are strengthened or weakened by predator exposure. For instance, in the winter, deer avoided moderate-severity burns 0–4 years after fire (a) and avoided these areas even more strongly when cougars were present because the interactive effect of cougars and moderate-severity burns 0–4 years after fire was negative (b). Deer avoidance of these areas was weakened when wolves were present because the interactive effect of wolves and moderate-severity burns 0–4 years after fire was positive (b). Effects of wolf activity interacting with burn class could not be estimated in the winter for the period 10–20 years since fire or in the summer for the period 21–35 years since fire due to lack of exposure. In (c), the confidence intervals for all burns 21–35 years after fire extended beyond the lower x-axis limit, and beyond the upper x-axis limit for high-severity fire. They have been cropped to improve the resolution of the figure.

TABLE 2 Predation mortalities where the cause of death was confirmed, likely to be or possibly predation. The likely predation from the unknown predator was due to a canid, but we could not distinguish between coyote or wolf

	Black bear	Bobcat	Cougar	Coyote	Wolf	Unknown
Confirmed	1	2	15	3	1	0
Likely	1	0	5	2	0	1
Possible	0	0	0	0	0	1
Total	2	2	20	5	1	2

mixed response to burns where cougar activity was more intense. Collectively, our findings reveal an important context dependency of predator–prey interactions that has been previously unexplored and highlight the importance of accounting for the indirect effects of wildfires via predation risk to predict impacts on herbivores.

Fire effects on understory vegetation quality and abundance are a primary direct pathway through which wildfires impact herbivores, as has been documented in numerous studies of ungulates, forage quality and fire (Allred et al., 2011; Eby et al., 2014). Deer were generally attracted to burned areas in the summer, as we predicted

packs in 2019 and 2020) and the size of the packs increase, effects of wolves on deer will likely intensify. It is also important to consider that we represented cougar activity with RSFs, which represent third-order selection (Johnson, 1980), whereas we used LDDs (Kittle et al., 2016) to describe wolf pack territories, which are inherently a second-order process (Johnson, 1980). These different approaches could influence our interpretation of deer responses to each predator. Given the patchy nature of wolf presence across the study area relative to the high density of cougars, we felt this approach best represented mule deer exposure to predators, although it may have oversimplified use within a wolf pack territory. It is also possible that we did not capture some wolf activity due to uncollared wolves, although movement from individual wolves in a pack tends to reliably describe pack level use (Benson & Patterson, 2014) and track and camera surveys indicate that transient wolves were rare. We believe this framework represents a reasonable approach for considering the interactive effects of these two predators and fire.

Mule deer response to wildfires was contingent on predator exposure therein, an important indirect effect of wildfires on mule deer. We found support for the *predation risk effect – predator traits hypothesis* (H2a), although our predictions were upheld more consistently for wolves compared to cougars and in winter compared to summer. Deer were more likely to use burned areas up to 20 years after fire with increased wolf activity in both the summer and the winter, likely because the regrowth of the understory could provide suitable hiding from wolves, and the coursing hunting style of wolves (Kauffman et al., 2007) would be impeded by obstacles such as deadfall in burns while the stotting gait of mule deer should facilitate escape (Dellinger et al., 2019). In contrast, deer avoided burns as cougar activity increased in the winter. Deadfall and early-seral vegetation may enhance the hunting success of stalking predators like cougars by providing hiding cover for an ambush attack (Metsaranta et al., 2003; Ruth et al., 2019). Thus, our findings indicate the composition of the resident predator community may strongly affect how ungulates respond to wildfires and the resulting magnitude of predation risk effects (i.e. foregone foraging opportunities; Brown et al., 1999). In systems like ours, the presence of stalking predators like felids should lead to strong risk effects from prey avoiding recent burns that contain high-quality forage. In contrast, the presence of coursing predators like canids in fire-affected landscapes may induce negligible risk effects in the summer given that recent burns likely confer both food and relative safety rather than a trade-off between the two.

The direction of predation risk effects should depend on the structural changes to the landscape induced by fire, which may differ by system. For instance, fires in shrub- and grass-land dominated systems can decrease cover, which should cause herbivores to select for burns to reduce risk from stalking predators (Eby et al., 2013; Jennings et al., 2016). In this study, mule deer in the summer did not respond to low-severity burns 0–9 years post fire or moderate-severity burns 10–20 years after fire both independent of predator exposure and with cougars. Fire may not have driven sufficient change in these areas to alter forage quality or perceived risk from

cougars. Deer selected for moderate-severity burns 0–9 years after fire when cougar activity increased, so it may be that the primary effect of fire in these burn classes was to reduce stalking cover for cougars. Deer avoided older burns (10–35 years after burn) more consistently with increased cougar activity, when early successional habitat favoured by cougars may have improved stalking cover (Kertson et al., 2011). Thus, the effects of burns on the hunting efficacy of predators via habitat alterations needs to be considered to predict impacts of fires on ungulates.

In the winter, we suspect that snow depth relative to the height of both forage plants and mule deer themselves played an important role in mule deer avoidance of burned areas. One reason for this was likely the movement advantages of both cougars and wolves in deep, low-density snow (*predation risk effect – winter vulnerability hypothesis*, H2b), although deer weakened their avoidance of burns with increased wolf exposure, indicating that habitat structure and predator hunting mode were still important in the winter (*predation risk effect – predator hunting mode*, H2a). Ungulates prefer areas of shallower snow when the depth of low density, fluffy snow exceeds half their chest height (Mahoney et al., 2018; Sweeney & Sweeney, 1984), and movement becomes severely impeded when snow depth exceeds 2/3 of chest height (Gilbert et al., 1970; Kelsall, 1969). Winter snow depth in Winthrop, Washington, USA, (station ID: 9376, c. 48.47°, –120.18°, elevation 533 m) averaged 30–52 cm over the course of the study (USDA Natural Resources Conservation Service, 2021). Jones (1975) recorded an average chest height of 57 cm for mule deer, indicating that snow depths reported during our study could have driven the observed response, particularly if snow was deeper in burned areas. However, effects may have been conflated if lower elevations of the system had less snow, which may also explain why deer did not select for forests in the winter (Table 2). Shrubs up to 60 cm tall may be rendered 75% to 100% unavailable to deer at the snow depths estimated during our study, substantially limiting nutrient availability and further driving avoidance of burned areas if snow is deeper within them (Gilbert et al., 2017; Hanley et al., 2012; White et al., 2009). Most ungulates in snow dominated systems occupy a restricted range in the winter (including the mule deer in this study), so avoidance of burns in winter could functionally reduce the habitat available and thus the carrying capacity of the landscape, akin to avoidance of anthropogenic impacts (Dwinnell et al., 2019; Sawyer et al., 2006).

In systems like ours where mule deer were able to manage predation risk relative to burned areas (i.e. they were no more likely to die by predation in burned areas compared to unburned areas), the primary effects of wildfire should result from changes to the nutritional landscape and the risk effects influencing the use of those nutritional resources. In regions where snow is rare, fire may primarily improve the forage landscape for herbivores. However, at more northerly latitudes and higher elevations, deeper and more persistent snowpacks may reduce winter forage availability to an even greater extent, both by impeding access to forage and influencing predation risk for a longer duration. Future work examining how the use of burned areas influences body condition (Kreling et al., 2021),

fetal rates and survival could help to quantify the importance of the changing nutritional landscape and the impact of risk effects induced by the predator community (Volkman et al., 2020).

We demonstrated that the response of mule deer to fire depended greatly on the season of consideration, the severity of fire impacts and stage of succession and species-specific patterns of exposure to predators, highlighting key sources of context-dependency in predator–prey interactions. As researchers continue to investigate how prey such as herbivores respond to wildfire and climate change, direct measures of forage quality, snow depth and subsequent demographic impacts will improve our knowledge of wildlife dynamics in a changing world (Boelman et al., 2019; Penczykowski et al., 2017; Volkman et al., 2020). Importantly, predicting impacts of wildfires on prey species depends not only on understanding changes to forage quality but also understanding changes to landscape structure and risk effects from the predator community (Doherty et al., 2022).

AUTHOR CONTRIBUTIONS

Taylor Ganz, Laura Prugh and Melia DeVivo conceived of this study. Taylor Ganz conducted data analyses and led the writing of the manuscript. Melia DeVivo, Brian Kertson, Trent Roussin, Taylor Ganz and Lauren Satterfield collected and managed the data. Aaron Wirsing provided conceptual guidance. Taylor Ganz, Melia DeVivo, Brian Kertson, Lauren Satterfield, Aaron Wirsing and Laura Prugh edited the manuscript.

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CONFLICT OF INTEREST

We have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

Data available from the Digital Dryad Repository <https://doi.org/10.5061/dryad.jsxksn0d2> (Ganz et al., 2022). Due to the sensitive nature of these data, the locations have been withheld, but covariates are retained to allow for reproduction of the analyses. Deer, cougar and wolf GPS locations are available by request from the Wildlife Chief Scientist, Washington Department of Fish and Wildlife, 1111 Washington Street SE, Olympia, Washington 98501, USA. Phone: +1 (360) 902-2515.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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