Journal of Mammalogy, 102(3):757–771, 2021
DOI:10.1093/jmammal/gyab035
Published online April 27, 2021

Fire-driven landscape heterogeneity shapes habitat selection of bighorn sheep

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Patterns in disturbance severity and time since fire can drive landscape heterogeneity that is critical to conservation; however, there is limited understanding of how wildlife interact with the spatial–temporal complexities of disturbance outcomes and at what scales. We conducted multiscale modeling of habitat selection for male and female Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) over an 8-year period. We aimed to identify the spatial scales at which bighorn sheep responded to various habitat features and determine how fire severity and time since fire can shape habitat selection by bighorn sheep over different seasons and between sexes. With the exception of litter cover, spatial scales that extended beyond the finest spatial grain (i.e., a 30-m pixel) to include the surrounding landscape were better at predicting habitat selection. Escape terrain, elevation, fire severity, year, perennial and annual forb and grass cover, and shrub cover occurred in every best-supported model. Associations with escape terrain, elevation, and perennial and annual forb and grass cover varied by sex and season. In contrast, bighorn sheep were consistently positively associated with low- and high-severity fire. Females increased use of low- and high-severity burned areas with greater time since fire, while males tended to decrease use of areas that burned at high severity with greater time since fire. Our results support the importance of landscape heterogeneity created by fire severity and time since fire for Rocky Mountain bighorn sheep and reinforces calls to integrate disturbance-driven heterogeneity into our assessments and management of wildlife.

Key words: escape terrain, fire severity, *Ovis canadensis*, prescribed fire, scale, season, sexual segregation, time since fire, ungulate, wildfire

Ecological disturbances, such as fire, are important drivers of landscape heterogeneity that can promote diversity and create species' requisite habitat structures (Hovick et al. 2015; Johnstone et al. 2016). Variation in natural disturbance severity and timing promotes landscape heterogeneity by creating unique combinations of habitat structures and functions (Hutto et al. 2020; Roberts et al. 2020). The legacies of disturbance outcomes can persist on the landscape for decades (Roberts et al. 2019). As such, there is an increased emphasis on using disturbance to maintain and restore ecosystems and wildlife (Fuhlendorf et al. 2006). For instance, prescribed fires are being combined with forest thinning to restore forest structural heterogeneity to enhance forest resilience (Knapp et al. 2017). A mixture of grazing and prescribed fire can restore vegetation structure and composition in rangelands (Ricketts and Sandercock 2016). Yet, for many disturbance processes—like fire—the spatiotemporal heterogeneity promoted by patterns in disturbance timing and severity tend to be overlooked (Geary et al. 2020; Volkmann et al. 2020).

Fire often is studied as a binary entity on the landscape (fire versus no fire—Geary et al. 2020; Volkmann et al. 2020) and used in management under a limited range of intensities

(Holling and Meffe 1996; Hutto et al. 2016, 2020). While a great deal is known about the positive outcomes of fire versus no fire for promoting biodiversity (Hovick et al. 2015; Ricketts and Sandercock 2016; Cherry et al. 2018), far fewer studies have focused on time since fire and fire severity (the degree to which a site is physically altered by fire—National Wildfire Coordinating Group 2019). Severity data have historically been difficult to quantify over adequate spatial and temporal scales for wildlife species with relatively large individual home ranges. In a global review of predator response to fire, fire severity was one of the least common fire regime variables measured across studies (Geary et al. 2020). In their review of carnivore and ungulate response to fire in conifer forests, Volkmann et al. (2020) found the majority of studies focused on recently burned areas (limited time since fire) and treated fire as a uniform disturbance (fire versus no fire) rather than a heterogeneous disturbance process. Species often display differential responses to fire (Geary et al. 2020), and understanding how time since fire and fire severity influence species response may help unravel some of this complexity. For instance, some species can select for certain fire severities more strongly than others, while another species may avoid a specific fire severity (DeCesare and Pletscher 2006; Hanson 2015; Leahy et al. 2016). With advances in remote sensing technology (Eidenshink et al. 2007), patterns in fire severity within a fire perimeter can be tracked, allowing us to better study the outcomes of disturbance (Malone et al. 2018; Roberts et al. 2020). Patterns in fire severity are increasingly recognized to promote unique ecological communities (Hutto and Patterson 2016; Roberts et al. 2019, 2020), but there is still much that we do not understand about how fire-driven landscape heterogeneity can shape complex species behaviors and movements over broad spatial scales.

Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*; hereafter bighorn sheep) have been a conservation and restoration priority across North America for the last century. Following Euro-American settlement, bighorn sheep declined from nearly 2 million in the 1800s to less than 42,000 in the 1970s (Buechner 1960; Schmidt and Gilbert 1978). Restoration efforts have had mixed success (Risenhoover et al. 1988; Cook et al. 1990), linked in part to poor habitat conditions created by disturbance suppression (Peek et al. 1979; Wakelyn 1987; Holl et al. 2012). Bighorn sheep select for large areas with high visibility, grass cover, and easily accessible escape terrain (Wakelyn 1987; Zeigenfuss et al. 2000; DeCesare and Pletscher 2006). Fire suppression has led to dense, closed-canopy forests and shrublands encroaching into large portions of bighorn sheep range, causing animals to become congregated in small isolated patches of suitable habitat (Peek et al. 1979; Wakelyn 1987; Risenhoover et al. 1988; Smith et al. 1999; Holl et al. 2012). Prescribed burning, which typically involves relatively uniform low-severity burns, has been used as a restoration technique to boost habitat quality (Singer et al. 2000; Clapp and Beck 2016). However, these practices have had mixed results in improving bighorn sheep habitat (Bentz and Woodard 1988; Smith et al. 1999; Holl and Bleich 2010; Clapp and Beck 2016), potentially because of mismatches between fire treatments and the spatiotemporal complexity and scales at which bighorn sheep respond to the heterogeneity created by fire.

Few studies have investigated the impact of fire severity on bighorn sheep behavior nor assessed spatial scales at which bighorn sheep respond to fire outcomes. The majority of studies have focused on presence or absence of fire rather than fire severity (Holl and Bleich 2010; Clapp and Beck 2016). Those that have assessed severity have focused on relatively limited time scales (1–2 years post fire) to measure wildlife response (DeCesare and Pletscher 2006). Resource selection modeling (used to evaluate how physical, chemical, and biological resources interact to affect wildlife occupancy) has long treated an organism's environment as hierarchically structured in space to capture organism-centered levels of habitat selection (i.e., geographic range versus individual home range within a geographic range—Johnson 1980; Schaefer and Messier 1995; Manly et al. 2002). However, within a single level or order of selection, animals may respond to different environmental variables at different spatial scales (grains of observation—McGarigal et al. 2016). For instance, a bighorn sheep might not respond strongly to whether the patch of ground it is standing on was burned, but the proportion of the surrounding landscape that was burned may be highly important to its habitat selection. Multiscale assessments of wildlife response to habitat are limited in relation to fire severity but might hold integral information about wildlife response to complex disturbance outcomes (McGarigal et al. 2016).

We evaluated the response of Rocky Mountain bighorn sheep to fire severity and time since fire, along with land cover and topography. We aimed to (1) identify the spatial scales at which bighorn sheep responded to fire severity and other landscape features and (2) determine how fire severity and time since fire interacted with land cover and topography to influence habitat selection of bighorn sheep. Bighorn sheep habitat selection is influenced by forage availability (Peek et al. 1979; Festa-Bianchet 1988) and predator avoidance (DeCesare and Pletscher 2006; Sappington et al. 2007; Poole et al. 2016). Fire can influence both of these factors depending on fire severity and time since fire (Holl et al. 2004, 2012; Bleich et al. 2008). Our candidate model set contained models primarily representing forage abundance, predator aversion, and a combination of the two. Past studies have identified complex interactions between habitat selection, seasons, and sex (Mooring et al. 2003; Briand et al. 2009; Schroeder et al. 2010). We integrated seasons and sex into our assessments of habitat selection. We conducted habitat selection modeling over an 8-year period (2011–2018) using remotely sensed fire severity information across four fires. Using GPS collar data collected for male and female bighorn sheep, we tracked seasonal responses of bighorn sheep to fire severity, time since fire, and several habitat variables.

Materials and Methods

*Study area.—*The Ferris and Seminoe mountain ranges are located ~50 km northeast of Rawlins, Wyoming, United States

(Fig. 1). The region is primarily federal land administered by the U.S. Department of Interior Bureau of Land Management and Bureau of Reclamation, mixed with State of Wyoming and private land holdings. Elevations are ~2,000 to 3,000 m above sea level; deep canyons and steep slopes create extreme local relief. Vegetation cover types included sagebrush (*Artemisia* spp.)-dominated shrub and grasslands along with conifer forest and woodlands. Predominant conifer tree species included rocky mountain juniper (*Juniperus scopulorum*), limber pine (*Pinus flexilis*), lodgepole pine (*Pinus contorta*), and ponderosa pine (*Pinus ponderosa*—Clapp and Beck 2016). Narrowleaf cottonwood (*Populus angustifolia*) and quaking aspen (*Populus tremuloides*) were predominant deciduous tree species (Clapp and Beck 2016). Big sagebrush (*A. tridentata*), chokecherry (*Prunus virginiana*), birchleaf mountain mahogany (*Cercocarpus montanus*), and antelope bitterbrush (*Purshia tridentata*) were predominant shrub species (Clapp and Beck 2016). Three large mixed-severity wildfires burned in the Ferris and Seminoe mountain ranges in 2011 and 2012 (MTBS Project 2019; Fig. 1). The region also received a prescribed burning treatment in 2011 (Fig. 1). A total of 6481 ha fell within fire perimeters, where 54% burned at low severity, 25% burned at moderate severity, and 5% at high severity (MTBS Project 2019).

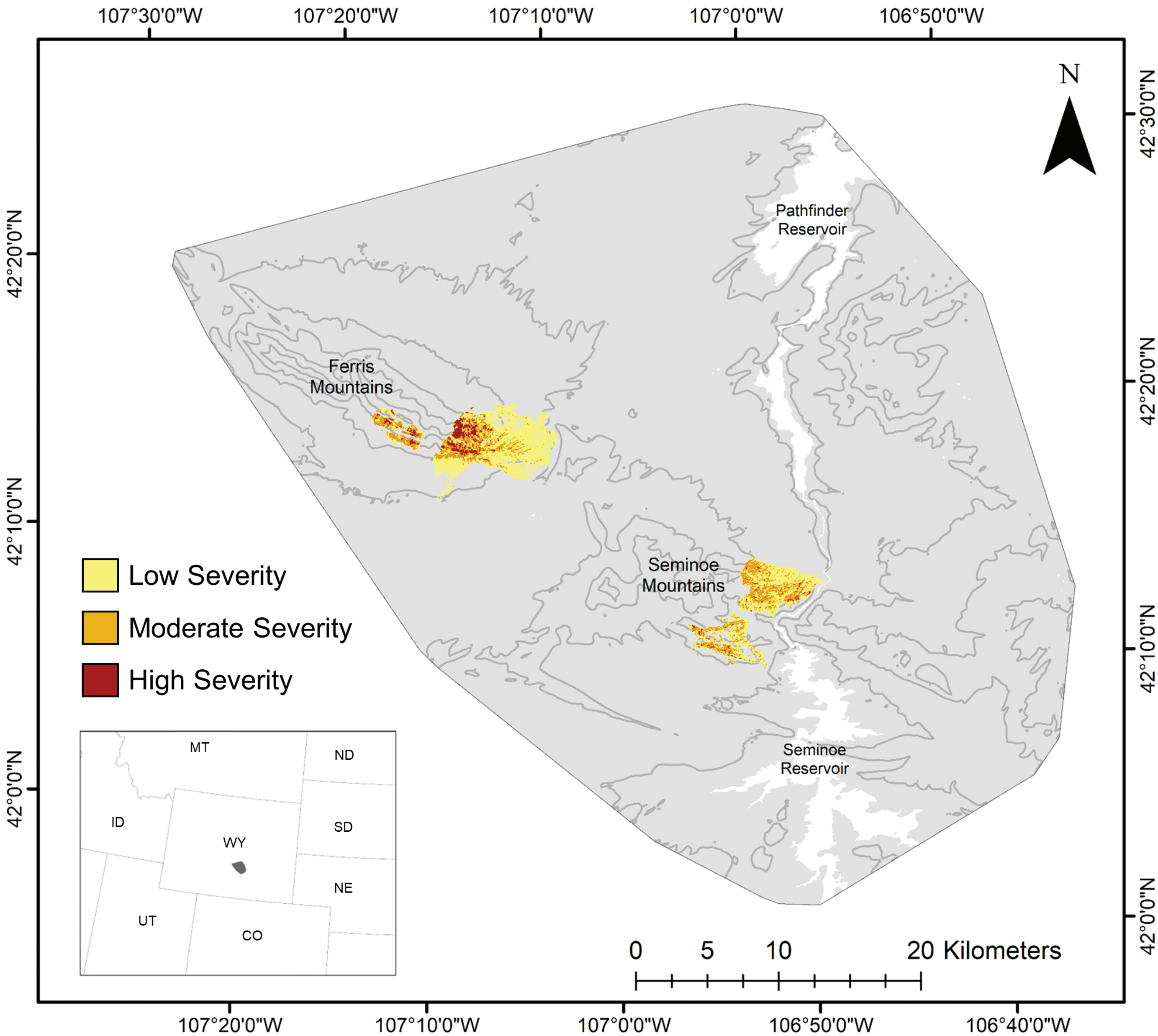

Fig. 1.—The study area, including the distribution for fire severity across four fires that burned in 2011 and 2012, in the Ferris and Seminoe mountain ranges in south-central, Wyoming, United States. The study area was defined by the 100% minimum convex polygon of 103,844 locations obtained from 18 male and 74 female adult Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) between 2011 and 2018. White areas represent water. Dark gray lines represent 200 m elevation contours. The map in the lower left corner shows the location of the study area (gray) within the state of Wyoming, United States.

The Ferris and Seminoe mountain ranges were active sites for bighorn sheep restoration by the Wyoming Game and Fish Department. The first reintroduction of bighorn sheep occurred in the Seminoe mountain range in 1958, followed by multiple supplementation events until 1985 (Donovan et al. 2020). Numbers dropped to near zero in the late 1990s (Donovan et al. 2020), attributed to the June lambing of translocated sheep from higher elevation source herds that caused mothers to miss the high-quality forage that occurs in April–May. In winter 2009, reintroduction events began again to boost population numbers with nonmigratory, low-elevation, early lambing sheep. Eight translocations, totaling 166 bighorn sheep, were conducted since 2009, the first two from eastern Oregon and the remainder from the Devil's Canyon herd in northern Wyoming. The last reintroduction during our analysis occurred in February 2018. Predators of bighorn sheep in the area included black bears (*Ursus americanus*), coyotes (*Canis latrans*), and mountain lions (*Puma concolor*). Hunting on the population began in 2013 with one ram harvested each year until 2016. Two rams were harvested in 2016 and 2017, and four rams were harvested in 2018.

Telemetry data.—We used GPS collar data collected from 92 translocated bighorn sheep between 2011 and 2018 in the Ferris and Seminoe mountain ranges. Collar data were collected for 18 males and 74 females by the Wyoming Game and Fish Department. Animals were equipped with store-on-board (released between 2009 and 2015) and satellite upload (released between 2016 and 2018) GPS collars from Telonics Inc. (Mesa, Arizona) and Advanced Telemetry Systems (Isanti, Minnesota). Helicopter net-gunning was used to capture all animals. Captured animals were processed following state agency (Oregon Department of Fish and Wildlife, Wyoming Game and Fish Department [WGFD] Chapter 10–1535 and Chapter 33–750 permits) and institutional (University of Wyoming Institutional Animal Care and Use Committee approved protocol 12012011) approved protocols and complied with the American Society of Mammologists guidelines (Sikes et al. 2016).

The duration of monitoring for each animal varied depending on collar failure and mortality (ranging from 1 to 31 months). GPS collar fix rates also varied by individual, ranging from 1- to 13-h intervals. Collar failure, particularly associated with ATS collars in 2016, led to gaps in time series of location data for certain individuals. A study of postrelease acclimation of translocated bighorn sheep in the Ferris–Seminoe herd found that animals had a mean acclimation period of ~30 days (Clapp et al. 2014). Thus, we removed the first 30 days of recorded locations following each individual's release date from our data sets, so bighorn sheep acclimation following translocation was not included in our assessment of habitat selection.

Habitat selection assessments often focus on evaluating whether a designated wildlife species occurs in areas more often than would be expected at random (Manly et al. 2002). We used 103,844 bighorn sheep GPS locations and generated an equal number of random points distributed across the population's range (third-order selection) for our analysis (Johnson 1980). Because our population represented a recently reintroduced group of bighorn sheep, we created a separate 100% minimum convex polygon (MCP) of population range for each year of our analysis to account for the potential range expansion of sheep.

Because wildlife response can vary by sex and season, we first created four different data groupings: female summer data, female winter data, male summer data, and male winter data. We derived summer and winter seasons using the mean dates of initiation and completion of migration in spring and autumn. We determined migration dates by visualizing net-squared displacement of animals that displayed migratory behaviors (Aikens et al. 2017). Seven sheep in particular exhibited strong migratory behaviors across eight autumn migration events and nine spring migration events. We used the average dates of these migration events to calculate summer and winter seasons. Spring migration start dates ranged from 10 April to 31 May, and autumn migration start dates ranged from 27 August to 11 December depending on individual and year. Our final summer season ranged from 23 May to 24 October. Winter occurred from 25 October to 22 May.

Resource variables.—We measured land cover of annual forbs and grasses, perennial forbs and grasses, shrubs, trees, litter, and bare ground using a land cover classification sourced from the Rangeland Analysis Platform (Jones et al. 2018). This data set contained Landsat-derived estimates of yearly percent cover at 30-m resolution for each land cover class from 1984 to 2018. We measured the percent cover of each land cover class at each recorded and random location, along with percent cover within 50-, 150-, 300-, and 600-m radius buffers surrounding each location to account for the potential of habitat selection varying across spatial scales (Kie et al. 2002; Lesmerises et al. 2013; McGarigal et al. 2016). We calculated percent cover within each buffered area by converting percent cover within each cell into an area value, summing these values across all cells in the buffered area, and then calculating percent cover across the area of the buffer. We conducted land cover extractions and calculations within buffers in R statistical software version 3.5.2 (R Core Team 2018) using the raster package (Hijmans 2019).

We measured the cumulative normalized difference vegetation index (cNDVI) at each recorded and random location using Landsat-derived 30-m resolution NDVI for the conterminous United States (Robinson et al. 2017). NDVI is one of the most commonly used vegetation indices derived from satellite imagery that is used to indicate vegetation productivity (Pettorelli et al. 2011; Garroutte et al. 2016). Within buffers surrounding each location point, we summed NDVI to gauge the overall level of productivity within the surrounding landscape. We conducted NDVI extractions and calculations in R statistical software (raster package—Hijmans 2019).

We measured low-, moderate-, and high-severity fire within fire perimeters using Monitoring Trends in Burn Severity Project (MTBS) thematic fire severity classifications (MTBS Project 2019). Fire severity is classified by MTBS using thresholds in Normalized Burn Ratios (NBR), a metric used to classify changes in aboveground biomass following fire (Eidenshink et al. 2007). Four fire perimeters were present in our study area, including a 1,032-ha prescribed burn conducted in 2011, and three wildfires: Ferris Mountain (2011; 610 ha), Seminoe (2012; 1,472 ha), and Bear Mountain Complex (2012; 3,366 ha). We recorded whether each random and recorded location fell within unburned and low-, moderate-, or high-severity regions. We measured the percent cover of each fire severity class within each buffer size surrounding each location. We calculated percent cover within each buffer by dividing the number of cells classified for each severity type by the total number of cells within the buffer. Fire severity extractions and calculations were conducted in Google Earth Engine (Gorelick et al. 2017).

Slope, aspect, elevation, and terrain ruggedness influence habitat selection of bighorn sheep and indicate characteristics of escape terrain—an important attribute of bighorn sheep habitat (Dunn 1996; DeCesare and Pletscher 2006; Clapp and Beck 2016). Previous assessments have measured escape terrain as > 30° slopes (Dunn 1996; DeCesare and Pletscher 2006). Using a 10-m resolution digital elevation model (DEM) from the U.S. Geological Survey, we classified pixels with > 30° slope as escape terrain using a binary classification system. We measured whether a recorded or random location occurred in a pixel classified as escape terrain, the distance to escape terrain from each recorded and random location, and the percentage of escape terrain within each buffer radius for each location. In addition, we measured elevation, terrain ruggedness index (TRI—Riley et al. 1999), mean slope, and Topographic Radiation Aspect Index (TRASP) at each location. TRI represents the mean difference in elevation between a focal pixel and its surrounding cells (eight-cell neighborhood—Riley et al. 1999). TRASP represents a linear transformation of circular aspect, with a value of zero representing land in the north to northeast directions and one representing south to southwest directions. TRASP, mean slope, and TRI were calculated using the Surface Gradient and Geomorphometric modeling toolbox (Evans et al. 2014) in ArcGIS version 10.3.

Spatial scale selection.—The spatial scale at which an animal interacts with habitat can differ across habitat features, sex, regions, and time scales (McGarigal et al. 2016). We used model selection to assess the spatial scale (i.e., 30-m pixel, or 50-, 150-, 300-, and 600-m buffer radius) that best described bighorn sheep response to specific habitat features across our four data groupings (i.e., female winter data, male summer data, etc.). We chose an exploratory range of buffer radii, as to our knowledge, no previous multiscale assessments for bighorn sheep habitat selection have been conducted. Using used and random GPS locations, we created a generalized linear mixed-effects model with a binomial family (Bates et al. 2015) for each measured spatial scale and data grouping for vegetation variables, fire severity variables, and escape terrain. For instance, for summer female data, we created five models representing the five different spatial scales of measure for low-severity fire. These models included one model that evaluated the probability that a bighorn sheep would occur in a given location with low-severity fire (30-m pixel spatial scale) and four models that evaluated the probability that a bighorn sheep would occur in a given location relative to the percentage cover of low-severity fire within each of our buffer radii (e.g., Supplementary Data SD2). To account for dependencies caused by the hierarchical structure of our data, we used individual bighorn sheep as a random intercept within our assessment (Zuur et al. 2009; Donovan et al. 2017).

To determine the spatial scale that was best for modeling bighorn sheep response to each variable, we used Akaike's Information Criterion (Akaike 1973; Burnham and Anderson 2002; McGarigal et al. 2016). The model with the highest probability of being the top model (highest AIC weight [*W*]) was selected as the best spatial scale to measure bighorn sheep response to that habitat variable (Supplementary Data SD2–SD12).

Sex and seasonal differences in response to heterogeneity.—Within each data grouping (female summer, male summer, etc.), we tested for collinearity among predictor variables using pairwise correlations among explanatory variables. When two variables were highly correlated ($r > 0.60$), we removed one variable from the model. Across all data groupings, moderate-severity fire and mean slope were highly correlated with at least one other variable and were thus removed from all analyses (Supplementary Data SD1). We also removed TRI from our analysis because it was highly correlated with other variables in almost every data grouping (Supplementary Data SD1). We standardized the remaining variables to improve model convergence (Zuur et al. 2009) by subtracting the mean of the variable from each observed value and then dividing by the standard deviation of the variable.

We generated 15 models in our candidate model set (Table 1). We generated models based on two themes that are consistent with bighorn sheep habitat selection found in the literature: (1) forage availability (Peek et al. 1979; Festa-Bianchet 1988) and (2) predator avoidance and visibility (DeCesare and Pletscher 2006; Sappington et al. 2007; Poole et al. 2016). A number of models also combined these two themes (Table 1). Some models would not converge with all interaction terms. We sequentially removed these terms from models to assist with model convergence.

Results

Spatial scale of selection.—Broad spatial patterns in fire, vegetation, and topography predicted bighorn sheep habitat selection better than spatial patterns occurring within a sheep's immediate vicinity (Supplementary Data SD2–SD12). Sheep were more likely to select habitat based on patterns in fire severity at the largest spatial scales of analysis (Supplementary Data SD2–SD4). Across vegetation types, the percentage cover of vegetation in the surrounding landscape was continuously a better predictor of bighorn sheep selection than the finest spatial grain (i.e., 30-m pixel), with the exception of litter cover (Supplementary Data SD5–SD11). Sheep were more likely to select habitat based on NDVI and perennial forb and grass cover at the largest spatial scale of analysis (Supplementary Data SD5 and SD6). However, there was variation in the spatial scale of bighorn sheep response relative to annual forbs and grass cover, shrub cover, tree cover, bare ground cover, and litter cover depending on sex and season (Supplementary Data SD7–SD11). Regardless of sex, distance to escape terrain predicted bighorn sheep selection best during winter (Supplementary Data SD12). During summer, bighorn sheep were more likely to make habitat decisions based on the percentage of escape terrain within the surrounding landscape (radius distance between 150 and 300 m; Supplementary Data SD12).

Table 1.—Candidate model sets used to assess female and male bighorn sheep habitat selection during the summer and winter, Ferris and Seminoe Mountains, Wyoming, United States, 2011–2018. Spatial scales of each variable varied by data grouping based on spatial scale selection analysis. EscpT = escape terrain (distance to or % within a given radius); HighSev = high-severity fire (% within a given radius); LowSev = low-severity fire (% within a given radius); NDVI = summed NDVI within a given radius; PFGC = perennial grass and forb cover (% within a given radius); AFGC = annual grass and forb cover (% within a given radius); BG = bare ground cover (% within a given radius); Tree = tree cover (% within a given radius); Litter = litter cover (% within a given radius); Shrub = shrub cover (% within a given radius).

Model #	Candidate model
1	~EscpT + Year
2	~EscpT + HighSev * Year
3	~EscpT * Elevation + Year
4	~EscpT * Elevation + HighSev * Year
5	~EscpT * Elevation + HighSev * Year + Tree
6	~EscpT * Elevation + (HighSev + LowSev) * Year
7	~EscpT * Elevation + HighSev * Year + PFGC + AFGC + BG
8	~EscpT * Elevation + (HighSev + LowSev) * Year + PFGC + AFGC
9	~EscpT * Elevation + (HighSev + LowSev) * Year + PFGC + AFGC + Shrub
10	~EscpT * Elevation + PFGC + AFGC + Shrub + Year
11	~NDVI + PFGC + AFGC + Shrub + BG + Litter + Year
12	~NDVI + PFGC + AFGC + Shrub + TRASP +Year
13	~PFGC + AFGC + Shrub + LowSev * Year
14	~PFGC + LowSev * Year
15	~PFGC + Year
16	~1

Sex and seasonal differences in response to heterogeneity.—Across seasons and sexes, habitat selection of bighorn sheep was most influenced by fire severity, topography, and vegetation (Table 2). The model including escape terrain, elevation, high and low fire severity, year, annual and perennial forb and grass cover, and shrub cover (Model 9; Table 1) was consistently the most parsimonious model to describe habitat selection of bighorn sheep (Table 2). This model consistently held 100% of model weight in the candidate model set.

Habitat selection differed between summer and winter seasons for female bighorn sheep in response to topography and fire severity. During summer, female sheep selected for areas with higher elevation, while in winter they avoided higher elevations (Table 3; Fig. 2). During summer, females were more likely to select an area based on the cumulative amount of escape terrain within a 300-m radius of their location, but in winter, distance to escape terrain was better at predicting the probability of habitat selection (Supplementary Data SD12). Regardless of season, female bighorn sheep selected for escape terrain (Table 3; Fig. 2); however, escape terrain had a greater impact on the probability of bighorn sheep habitat selection during winter compared with summer (Table 3).

Female sheep selected for high- and low-severity burned areas dependent on time since fire. Regardless of season, female sheep increased their use of areas that had a greater amount of low-severity burned area as time since fire increased (Table 3; Fig. 3). This interaction varied based on season when considering high-severity fire. Female sheep were more likely to use

Table 2.—Relative support for the top 5 candidate models used for female and male bighorn sheep resource selection for annual and seasonal time scales, Ferris and Seminoe mountain ranges, Wyoming, United States, 2011–2018. *Indicates models that had interaction terms removed to assist with convergence.

Model #	*K*	LL	AIC	ΔAIC	*W*
Summer, female					
9*	12	−20,333.33	40,690.67	0.00	1
8	12	−20,405.42	40,834.84	144.17	0
6	10	−20,584.97	41,189.93	499.26	0
5	9	−23,166.88	46,351.76	5,661.09	0
10	9	−23,355.41	46,728.82	6,038.15	0
Summer, male					
9	13	−9,710.51	19,447.03	0.00	1
8	12	−9,815.85	19,655.71	208.68	0
6	10	−9,854.54	19,729.09	282.06	0
10	9	−9,916.23	19,850.47	403.44	0
7	11	−9,917.23	19,856.47	409.44	0
Winter, female					
9*	12	−25,961.83	51,947.65	0.00	1
8	11	−26,434.44	52,890.88	943.22	0
6	10	−26,697.20	53,414.41	1,466.76	0
7*	10	−28,953.62	57,927.24	5,979.59	0
10*	8	−30,075.46	60,166.92	8,219.26	0
Winter, male					
9	13	−8,995.07	18,016.15	0.00	1
8*	11	−9,120.78	18,263.57	247.42	0
6	10	−9,142.07	18,304.16	288.01	0
7	11	−9,619.54	19,261.09	1,244.94	0
4	8	−9,804.00	19,624.00	1,607.85	0

Table 3.—Standardized model coefficients, including the log odds (Estimate), standard error (*SE*), upper (Upper CI) and lower (Lower CI) confidence intervals, and *P*-value (*P*), for the top candidate model for female and male bighorn sheep during summer and winter, Ferris and Seminoe mountain ranges, Wyoming, United States, 2011–2018.

Variable	Estimate	*SE*	Lower CI	Upper CI	*P*
Summer, female					
EscpT_300m	2.20	0.02	2.17	2.24	<0.01
Elevation	0.15	0.02	0.11	0.19	<0.01
HighSev_50m	0.18	0.02	0.13	0.22	<0.01
LowSev_600m	1.06	0.02	1.02	1.10	<0.01
Year	0.48	0.07	0.36	0.61	<0.01
HighSev_50m:Year	0.05	0.03	<0.01	0.10	0.05
LowSev_600m:Year	0.70	0.03	0.65	0.76	<0.01
PFGC_600m	0.29	0.02	0.26	0.33	<0.01
AFGC_600m	−0.02	0.02	−0.05	0.01	0.04
Shrub_300m	0.42	0.02	0.38	0.45	<0.01
Summer, male					
EscpT_150m	1.98	0.03	1.92	2.04	<0.01
Elevation	−0.53	0.03	−0.59	−0.48	<0.01
EscpT_150m:Elevation	−0.38	0.03	−0.43	−0.33	<0.01
HighSev_600m	0.19	0.04	0.11	0.27	<0.01
LowSev_600m	0.40	0.03	0.35	0.46	<0.01
Year	0.34	0.08	0.17	0.49	<0.01
HighSev_600m:Year	−0.09	0.06	−0.22	0.03	0.14
LowSev_600m:Year	−0.21	0.04	−0.29	−0.12	<0.01
PFGC_600m	0.05	0.03	<0.01	0.10	0.05
AFGC_300m	0.04	0.02	<0.01	0.08	0.07
Shrub_600m	0.38	0.02	0.33	0.44	<0.01
Winter, female					
EscpT_Dist	−7.85	0.10	−8.04	−7.66	<0.01
Elevation	−0.34	0.02	−0.37	−0.30	<0.01
HighSev_600m	0.55	0.03	0.49	0.60	<0.01
LowSev_600m	1.06	0.02	1.02	1.09	<0.01
Year	0.58	0.04	0.49	0.67	<0.01
HighSev_600m:Year	−0.10	0.04	−0.18	−0.03	<0.01
LowSev_600m:Year	0.38	0.02	0.34	0.42	<0.01
PFGC_600m	0.21	0.02	0.18	0.24	<0.01
AFGC_600m	−0.05	0.01	−0.08	−0.02	<0.01
Shrub_300m	0.46	0.02	0.43	0.49	<0.01
Winter, male					
EscpT_Dist	−7.96	0.18	−8.30	−7.61	<0.01
Elevation	−0.01	0.09	−0.19	0.17	0.91
EscpT_Dist:Elevation	0.80	0.20	0.40	1.20	<0.01
HighSev_600m	0.55	0.06	0.44	0.66	<0.01
LowSev_600m	0.62	0.03	0.57	0.68	<0.01
Year	0.61	0.09	0.44	0.79	<0.01
HighSev_600m:Year	−0.23	0.08	−0.38	−0.07	<0.01
LowSev_600m:Year	0.54	0.03	0.48	0.60	<0.01
PFGC_600m	−0.02	0.03	−0.07	0.03	0.44
AFGC_600m	−0.12	0.02	−0.17	−0.08	<0.01
Shrub_600m	0.37	0.03	0.33	0.43	<0.01

locations with greater amounts of high-severity burned area with lower time since fire in winter (Table 3; Fig. 3). In contrast, in summer, they increased their use of areas that burned at high severity with greater time since fire (Table 3; Fig. 3).

In summer and winter, female sheep selected for perennial forbs and grasses and shrub cover within the surrounding landscape (Table 3; Fig. 2). Shrub cover had a greater influence on bighorn sheep habitat selection than perennial forb and grass cover (Table 3; Fig. 2). Female sheep avoided annual forb and grass cover on the landscape during both seasons. Annual forb and grass cover had the lowest relative impact on bighorn sheep habitat selection of all variables in our top model (Table 3; Fig. 2).

Like female sheep, male habitat selection differed among seasons. In summer, male bighorn sheep were more likely to select for greater levels of escape terrain within a 150-m radius of their location as elevation decreased (Table 3; Fig. 4). In winter, male bighorn sheep were more likely to select areas closer to escape terrain at lower elevations (Table 3; Fig. 4).

In winter and summer, male bighorn sheep had a higher probability of using a location with greater amounts of high-severity burned area when those areas had a lower time since fire (Table 3; Fig. 5). Similarly, during summer, male bighorn sheep were more likely to use locations with greater amounts of low-severity burned area when those areas had lower time since fire (Table 3; Fig. 5). In contrast, in winter, male bighorn sheep had a higher probability of using areas with greater amounts of low-severity burned areas as time since fire increased (Table 3; Fig. 5).

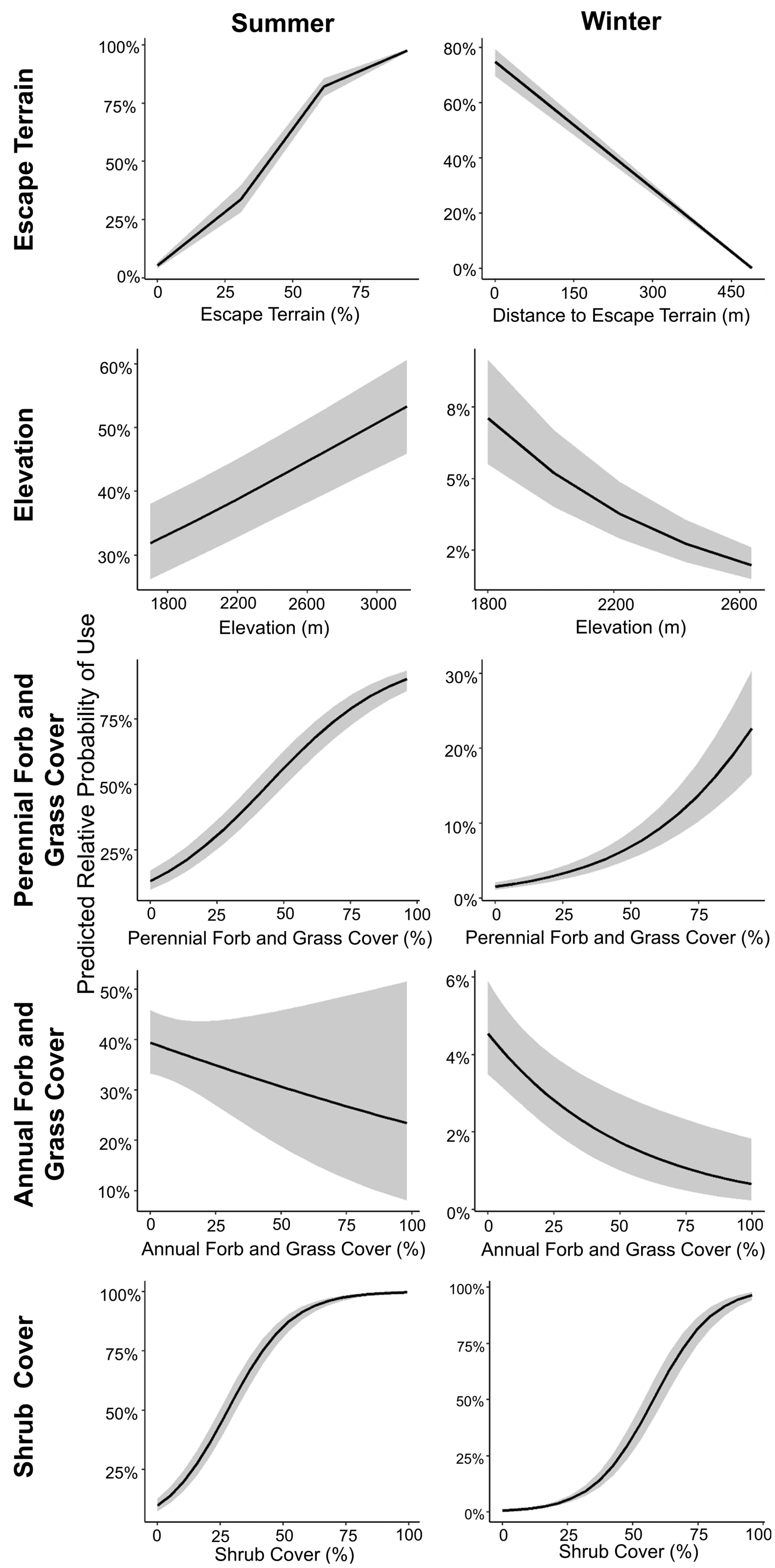

Fig. 2.—Predicted relative probabilities of habitat selection by female Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) in response to escape terrain, elevation, perennial forb and grass cover, annual forb and grass cover, and shrub cover during summer and winter in the Ferris and Seminoe mountain ranges, south-central, Wyoming, United States. Shaded areas represent 95% confidence intervals.

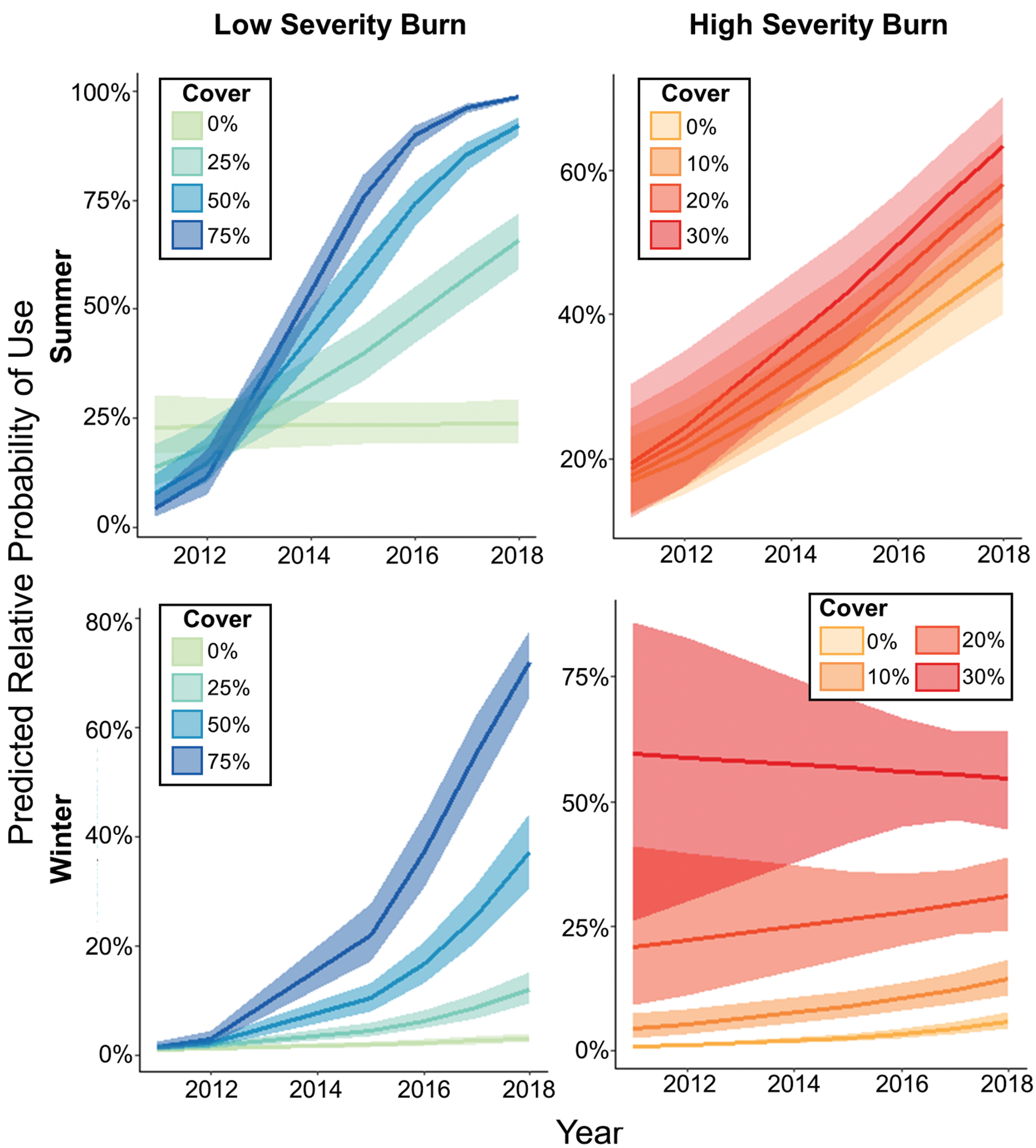

Fig. 3.—Predicted relative probabilities of habitat selection by female Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) in response to fire severity and year during summer and winter in the Ferris and Seminoe mountain ranges, south-central, Wyoming, United States. Fires burned in 2011 and 2012. Shaded areas represent 95% confidence intervals.

Male sheep selected for perennial forbs and grasses, annual forbs and grasses, and shrubs during summer, although shrub cover had by far the greatest impact on habitat selection (Table 3). During winter, male sheep avoided perennial and annual forbs and grasses (Table 3; Fig. 4). However, male sheep selected for shrub cover in winter, with the probability of their habitat use increasing with an increase in shrub cover (Table 3; Fig. 4).

Discussion

Bighorn sheep demonstrated complex responses to heterogeneity created by fire severity and time since fire at broad spatial scales. Areas that burned at low and high severity influenced bighorn sheep selection across sexes and seasons. The interactions and magnitude of response to fire severity and time since fire varied by season and sex, adding additional complexity to

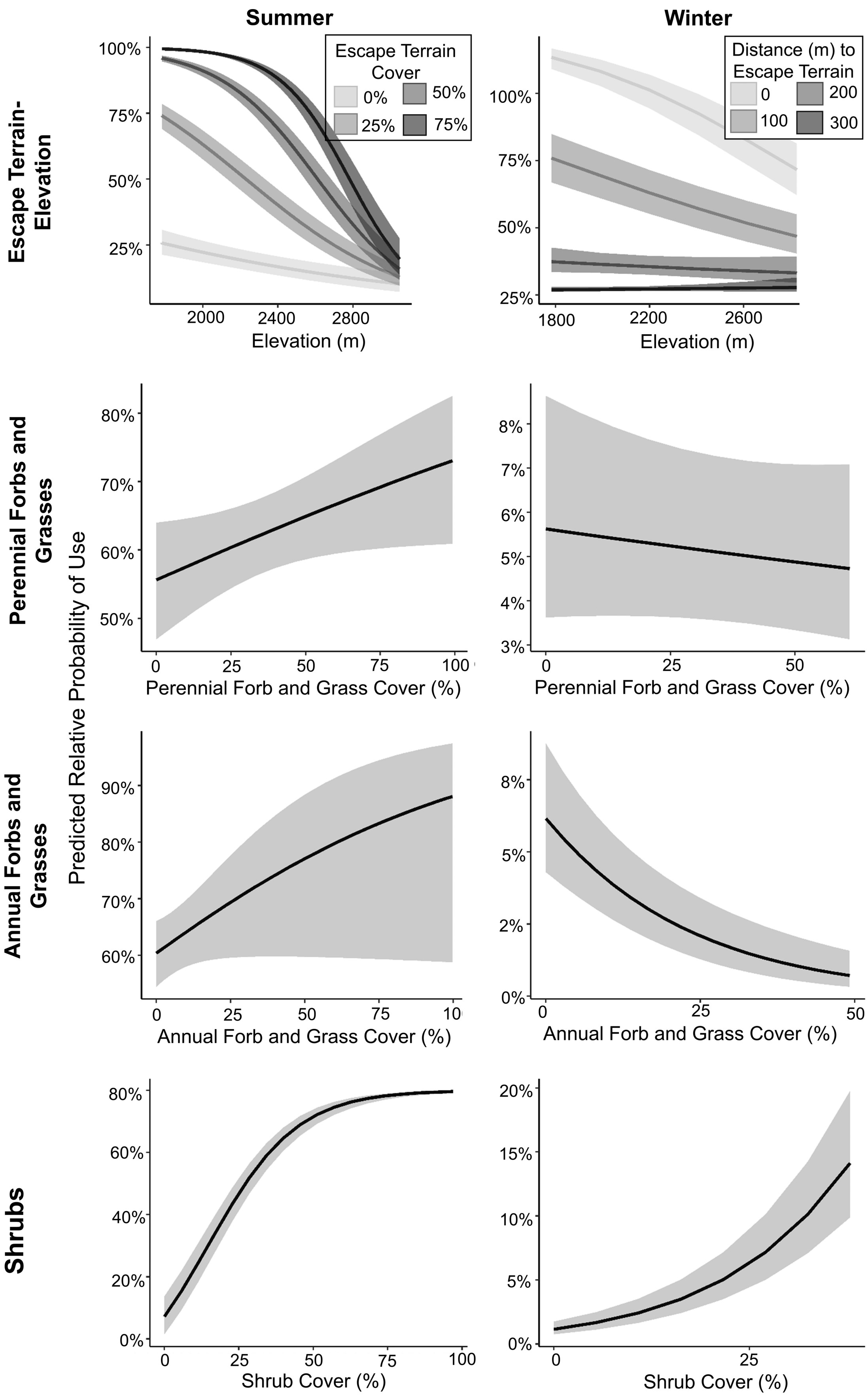

Fig. 4.—Predicted relative probabilities of habitat selection by male Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) in response to escape terrain, elevation, perennial forb and grass cover, annual forb and grass cover, and shrub cover during summer and winter in the Ferris and Seminoe mountain ranges, south-central, Wyoming, United States. Shaded areas represent 95% confidence intervals.

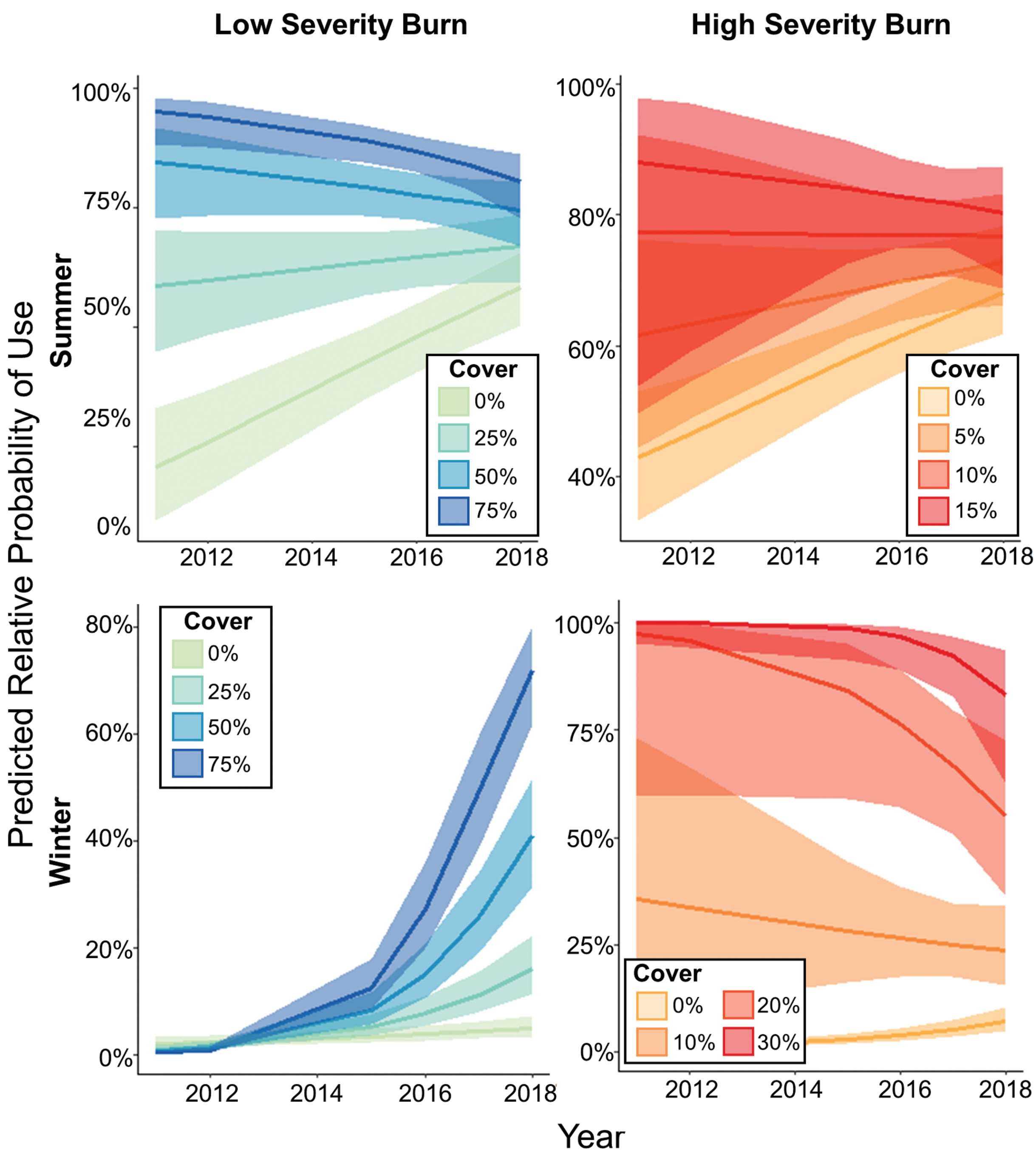

Fig. 5.—Predicted relative probabilities of habitat selection by male Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) in response to fire severity and year during summer and winter in the Ferris and Seminoe mountain ranges, south-central, Wyoming, United States. Fires burned in 2011 and 2012. Shaded areas represent 95% confidence intervals.

wildlife–fire interactions. For instance, male sheep used recently burned areas during summer, while females used burned areas with greater time since fire. Past studies show that bighorn sheep select for burned areas (Peek et al. 1979; Holl and Bleich 2010; Holl et al. 2012). Bighorn sheep populations can increase in burned areas, likely because of increasing nutrient availability and visual openness of habitat (Holl et al. 2004; Bleich et al. 2008). Fire severity and time since fire impacted bighorn seasonal resource use beyond the fire versus no fire viewpoint. Our findings support other studies that suggest incorporating fire-driven heterogeneity into our understanding of ecosystem function, which will improve conservation and restoration efforts (Hutto 2008; Johnstone et al. 2016; Donovan et al. 2019).

Oversimplifying variability can result in inconsistent or undesirable outcomes of management (Twidwell et al. 2013), including decreases in diversity and system complexity (Holling and Meffe 1996; Noss et al. 2006; Donovan et al. 2019). Bighorn sheep were consistently positively associated with areas that burned at high severity, suggesting habitat benefits that may be distinctive to these areas. However, many prescribed burn treatments currently emphasize low-severity fire regimes. Mixed responses of bighorn sheep to prescribed fire

(Bentz and Woodard 1988; Smith et al. 1999; Holl and Bleich 2010; Clapp and Beck 2016) might be tied to differences in fire severity patterns across prescribed fires. Future applications of prescribed fire could target greater heterogeneity in time since fire and fire intensity across the landscape. Our findings are counter to DeCesare and Pletscher (2006), who found that female bighorn sheep avoided high-severity burned areas. This difference could be due partly to differences in study location, as well as tied to differences in the time scales over which our studies were conducted. We found that female sheep were more likely to select high-severity burned areas with greater time since fire. DeCesare's and Pletscher's (2006) models included female bighorn sheep response 1–2 years post fire while our assessments ranged from 0 to 8 years. The heterogeneity created by mixed-severity fire can persist on landscapes for decades (Johnstone et al. 2016; Roberts et al. 2019). Our findings highlight the importance of considering both fire severity and time since fire in assessments of bighorn sheep response to fire and integration of fire into bighorn sheep management.

Spatial and temporal variation in disturbance creates heterogeneity across landscapes. A number of wildlife species use habitats in various stages of succession to fulfill different life requirements (Kaufman et al. 1988; Smucker et al. 2005; Long et al. 2008; Hutto and Patterson 2016). Our findings indicate that disturbance-driven heterogeneity is important for bighorn sheep. The magnitude of influence of high-severity fire on habitat selection varied greatly based on season and sex, suggesting that high-severity fire likely plays a more predominant role in the habitat selection of bighorn sheep during certain times of the year. Time since fire also played an important role in influencing bighorn sheep distribution. For instance, females were more likely to use older burned areas during summer, while males were more likely to use more recently burned areas. Past research has shown inverse relationships between time since fire and forage quality (highest at early time since fire) and quantity (highest at later time since fire—Peek et al. 1979; Allred et al. 2011). Differences in response between sexes and seasons could suggest differential response to foraging opportunities or could be tied to trade-offs between predator aversion and forage at different times of the year (Festa-Bianchet 1988). For instance, recently burned areas are likely to have higher visibility that could assist sheep with predator aversion (Holl et al. 2004, 2012; Bleich et al. 2008). However, we found that male bighorn sheep were more likely to select recently burned areas, while female bighorn sheep selected burned areas with greater time since fire, even though female sheep are more likely to prioritize predator aversion (Schroeder et al. 2010). This suggests that the primary reason for selecting recently burned areas is unlikely tied solely to visibility. Integrating predator movement and predation data into future studies could help reconcile the trade-offs between foraging opportunity and predation risk tied to fire severity and time since fire.

Most assessments of habitat selection focus on a single spatial scale to assess wildlife response to an environmental variable (e.g., a 30-m pixel), rather than incorporating multiscale perspectives to determine the spatial scale that best represents how an animal perceives its habitat. In a review of habitat selection studies in 32 journals between 2009 and 2014, McGarigal et al. (2016) found that only 4% of habitat selection studies included multiscale assessments of habitat variables tied to habitat selection. It is becoming increasingly clear that focusing solely on small scales in resource selection studies can lead to inefficient and ineffective species management (Smith et al. 2020). We demonstrate the importance of assessing animal response to habitat variables across multiple spatial scales for assessments of Rocky Mountain bighorn sheep. For instance, although "distance to escape terrain" is one of the most commonly used variables in bighorn sheep habitat selection (Shannon et al. 1975; Clapp and Beck 2016; Poole et al. 2016), we found that distance to escape terrain was the best measure to describe bighorn sheep response to escape terrain only during winter. In summer, bighorn sheep were more likely to make decisions based on the cumulative amount of escape terrain surrounding their location, regardless of sex. Similarly, response to fire severity and functional group cover were tied to the abundance of cover over broad areas in the surrounding landscape. Bighorn sheep might select for fire severity and functional group cover at large scales in response to predator aversion and foraging opportunities. For instance, horizontal visibility is an important variable in determining habitat selection of bighorn sheep (Smith et al. 1991; Johnson and Swift 2000; Zeigenfuss et al. 2000). Higher concentrations of perennial forb and grass cover along with high- and low-severity fire across the broader landscape are likely to increase visibility and represent more open habitats necessary for bighorn sheep survival. Higher concentrations of low-severity fire, shrubs, and perennial forb and grass cover in the surrounding landscape also likely present greater foraging opportunities with lower energy expenditure (Peek et al. 1979; Risenhoover et al. 1988; Wagner and Peek 2006; Allred et al. 2011). These findings stress the importance of evaluating the scales at which animals respond to resources to more fully understand resource use and significance of landscape heterogeneity to wildlife.

Acknowledgments

Funding for this project was provided by the University of Nebraska's Institute of Agriculture and Natural Resources, the University of Wyoming, the National Science Foundation (OIA-1920938), the Wyoming Game and Fish Department, the Wyoming Governor's Big Game License Coalition, and the Wyoming Wild Sheep Foundation. We acknowledge support of the Haub School of Environment and Natural Resources at the University of Wyoming. We thank Mathew O. Jones, Brady W. Allred, and David E. Naugle from the University of Montana and Daniel R. Uden from the University of Nebraska for providing and assisting us with yearly percent vegetation cover data. We thank Andrew J. Tyre from the University of Nebraska and Carissa L. Wonkka from the USDA Agricultural Research Service for assisting with statistical interpretation.

Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Pairwise Pearson correlations coefficients (*r*) of variables with a Pearson's *r* that was greater than or equal to 0.60 for bighorn sheep resource selection modeling in the Ferris and Seminoe Mountains, Wyoming, United States, 2011–2018.

Supplementary Data SD2.—Relative support for candidate models used for spatial scale selection of female and male bighorn sheep response to low-severity fire (LowSev) across seasons, Ferris and Seminoe Mountains, Wyoming, United States, 2011–2018.

Supplementary Data SD3.—Relative support for candidate models used for spatial scale selection of female and male bighorn sheep response to moderate–severity fire (ModSev) across seasons, Ferris and Seminoe Mountains, Wyoming, United States, 2011–2018.

Supplementary Data SD4.—Relative support for candidate models used for spatial scale selection of female and male bighorn sheep response to high-severity fire (HighSev) across seasons, Ferris and Seminoe Mountains, Wyoming, United States, 2011–2018. Quasi-perfect separation was indicated in models with missing values.

Supplementary Data SD5.—Relative support for candidate models used for spatial scale selection of female and male bighorn sheep response to Normalized Differences Vegetation Index (NDVI) across seasons, Ferris and Seminoe Mountains, Wyoming, United States, 2011–2018.

Supplementary Data SD6.—Relative support for candidate models used for spatial scale selection of female and male bighorn sheep response to perennial forb and grass cover (PFGC) across seasons, Ferris and Seminoe Mountains, Wyoming, United States, 2011–2018.

Supplementary Data SD7.—Relative support for candidate models used for spatial scale selection of female and male bighorn sheep response to annual forb and grass cover (AFGC) across seasons, Ferris and Seminoe Mountains, Wyoming, United States, 2011–2018.

Supplementary Data SD8.—Relative support for candidate models used for spatial scale selection of female and male bighorn sheep response to tree cover across seasons, Ferris and Seminoe Mountains, Wyoming, United States, 2011–2018.

Supplementary Data SD9.—Relative support for candidate models used for spatial scale selection of female and male bighorn sheep response to shrub cover across seasons, Ferris and Seminoe Mountains, Wyoming, United States, 2011–2018.

Supplementary Data SD10.—Relative support for candidate models used for spatial scale selection of female and male bighorn sheep response to bare ground cover (BG) across seasons, Ferris and Seminoe Mountains, Wyoming, United States, 2011–2018.

Supplementary Data SD11.—Relative support for candidate models used for spatial scale selection of female and male bighorn sheep response to litter across seasons, Ferris and Seminoe Mountains, Wyoming, United States, 2011–2018.

Supplementary Data SD12.—Relative support for candidate models used for spatial scale selection of female and male bighorn sheep response to > 30° slope (EscpT) across seasons, Ferris and Seminoe Mountains, Wyoming, United States, 2011–2018.

Supplementary Data SD13.—Frequency of female bighorn sheep locations during summer relative to variables included in the top habitat selection model in the Ferris and Seminoe Mountains, Wyoming, United States, between 2011 and 2018.

Supplementary Data SD14.—Frequency of female bighorn sheep locations during winter relative to variables included in the top habitat selection model in the Ferris and Seminoe Mountains, Wyoming, United States, between 2011 and 2018.

Supplementary Data SD15.—Frequency of male bighorn sheep locations during summer relative to variables included in the top habitat selection model in the Ferris and Seminoe Mountains, Wyoming, United States, between 2011 and 2018.

Supplementary Data SD16.—The frequency of male bighorn sheep locations during winter relative to variables included in the top habitat selection model in the Ferris and Seminoe Mountains, Wyoming, United States, between 2011 and 2018.

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Submitted 29 April 2020. Accepted 3 March 2021.

Associate Editor was Chris Pavey.