

HABITAT SELECTION AND SPATIAL RESPONSES OF BIGHORN SHEEP TO FOREST
CANOPY IN NORTH-CENTRAL WASHINGTON

By

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Abstract

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Fire suppression has allowed conifers to encroach into historically open grasslands and shrublands across western North America. Woody encroachment may reduce habitat quantity and quality for bighorn sheep (*Ovis canadensis*), which rely on open escape terrain. We examined the influence of conifer canopy cover, along with topography and forage resources, on habitat selection by bighorns in north-central Washington, where thinning and prescribed fire treatments have been applied to encroaching forest to restore historic landscape conditions within and adjacent to existing bighorn habitat. To model habitat selection of bighorn sheep using Resource Selection Functions (RSFs), we estimated Utilization Distributions (UDs) from GPS (Global Positioning System) locations of 21 collared bighorns (14 females and 7 males) using the Brownian bridge movement model. After creating annual, lambing, summer, and winter 99% home ranges from UD, we generated random points within each 99% home range to represent available habitat. We then used logistic regression to compare bighorn GPS locations (i.e., “use”) to random points (i.e., “available”) after linking them to habitat variables which we created in a geographic information system. As we predicted, bighorn sheep selected areas with lower tree canopy cover, even when controlling for topography and potential foraging habitat, and canopy cover was the only habitat variable that significantly predicted habitat selection by bighorn sheep

in population-level models across all demographic groups and seasons. Bighorns also selected for steeper slopes; however, other topographic variables (i.e., distance to escape terrain, aspect, ruggedness, and slope \times ruggedness), as well as our forage variables (i.e., distance to forage and categories of Tasseled Cap greenness) varied in their ability to predict habitat selection by bighorn sheep. Our results show that bighorn sheep select areas with lower canopy cover, thus restoring or maintaining open habitat in areas with woody encroachment may influence movements and increase the value of habitat for bighorn sheep. The RSF models we created can be used by state and federal agencies to plan forest restoration at a landscape scale to manage for bighorn sheep and other species that have adapted to similar habitat types.

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Manuscript Attribution

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INTRODUCTION

Fire suppression has promoted encroachment by woody shrubs and trees into historically open grasslands and shrublands across western North America (Arno et al. 1995, Arno and Fiedler 2005, Hessburg et al. 2005, Heyerdahl et al. 2006). These changes can reduce the quantity and quality of habitat for many plant and wildlife species (Ratajczak et al. 2012). For example, woody encroachment can fragment landscapes, reducing dispersal and gene flow (Brisson et al. 2003, Roland and Matter 2007) and isolating populations of organisms requiring open habitats (U.S. Fish and Wildlife Service 2000, 2003). Changes in habitat caused by woody encroachment can also reduce vital rates and fitness in species such as eastern collared lizards (*Crotaphytus collaris collaris*, Brisson et al. 2003, Sexton et al. 1992). In fact, woody encroachment caused by fire suppression was identified as the primary threat to species such as the northern Idaho ground squirrel (*Spermophilus brunneus brunneus*, U.S. Fish and Wildlife Service 2000, 2003) and Mardon skipper (*Polites mardon*, Miller and Hammond 2007), and woody encroachment caused by decreased fire frequency was identified as an extinction risk for the greater sage-grouse (*Centrocercus urophasianus*, Connelly et al. 2004, U.S. Fish and Wildlife Service 2005, 2014). Habitats may cease to support sage-grouse when the density and height of conifers increases (Connelly et al. 2004). Fire suppression and forest succession were reported to have severely reduced grasslands and consequently carrying capacity for wild ungulates in Canadian national parks (Stelfox 1976).

Bighorn sheep (i.e., *Ovis canadensis canadensis* and *O. c. californiana*) are of conservation concern in many parts of their native range (Risenhoover et al. 1988, Toweill and Geist 1999, Festa-Bianchet 2008, Wehausen et al. 2011, Brewer et al. 2014, Washington Department of Fish and Wildlife [WDFW] 2014), and seem to be especially sensitive to woody

encroachment into their native habitat (Wakelyn 1987, Toweill and Geist 1999, Utah Division of Wildlife Resources 2013). Because bighorns are habitat specialists, requiring open areas that provide forage adjacent to steep, rough terrain for security cover, suitable habitat is naturally patchy and limited compared to that of other ungulates (Bailey 1980, Toweill and Geist 1999). Bighorns rely on open habitat (Toweill and Geist 1999) for predator detection and visual communication (Risenhoover and Bailey 1985) and have been found to forage more efficiently in open areas because they spend less time being vigilant, surveying their surroundings for predators or visual cues of other bighorns alerting them to predators (Bailey 1980, Risenhoover and Bailey 1980, Risenhoover and Bailey 1985). Furthermore, bighorns are especially sensitive to several respiratory diseases (Buechner 1960, Monello et al. 2001, Cassirer and Sinclair 2007, Wehausen et al. 2011, WDFW 2014; see Frey 2006 for a good summary) that can increase when fragmented habitat impedes movements (Risenhoover et al. 1988, Singer et al. 2001). Therefore, woody encroachment through forest succession reduces and fragments high-visibility habitat, encourages bighorns to be sedentary, and likely increases their vulnerability to nutritional deficiency, predation, harassment by humans, and disease (Wakelyn 1987, Risenhoover et al. 1988, Holl et al. 2004, Utah Division of Wildlife Resources 2013). The lack of open habitat has been suggested as the most serious threat to Rocky Mountain bighorn sheep in Colorado (Wakelyn 1987) and a major impediment to recovery of the Sierra Nevada bighorn sheep (*O. c. sierrae*, U.S. Fish and Wildlife Service 2007).

To improve habitat for bighorns, some studies have examined the value of setting back succession and preventing further woody encroachment, using clear-cut logging, selective thinning, and prescribed burning (Peek et al. 1979, Hobbs and Spowart 1984, Smith et al. 1999, Dibb and Quinn 2006, 2008, Arno and Fiedler 2005). These treatments, along with naturally-

occurring fires, have improved forage quality (Holl et al. 2004) and quantity (Hobbs and Spowart 1984), and greatly increased the use of treated areas by bighorns (Smith et al. 1999, Arno and Fiedler 2005, Dibb and Quinn 2006, 2008). These tools might be particularly valuable in areas such as the Sinlahekin Valley in north-central Washington, USA, where populations of bighorns were extirpated in the early 1900s, reintroduced in 1957, and have been monitored and managed since (Trefethen 1975, WDFW 2006, Toweill and Geist 1999). Despite augmentation in 2003, this population has remained small (~ 30-95 individuals over the last 10 years) and seems to be limited by habitat quality (WDFW 2014). Fires have been suppressed in the Sinlakeekin Valley since the 1920s (Demyan et al. 2006, WDFW 2006), and 100-yr old photo points document conifer (*Pinus ponderosa* and *Pseudotsuga menziesii*) encroachment over that period (Fig. 1, WDFW 2006). Using forest measurements, Haeuser (2014) found relatively homogeneous and rapid encroachment of conifers into historically open or shrub-steppe areas in the Sinlahekin as a function of fire suppression, Pacific Decadal Oscillation phase (climate/rainfall), and topographic factors. Where trees occurred historically, she demonstrated increased tree density via in-filling.



Figure 1. Historic photo point comparison showing conifer encroachment at the same location in the Sinlahekin Valley on a) 10 December 1910 (photo by Frank Matsura, courtesy of Okanogan County Historical Society), and b) 30 September 2006 (photo by Dale Swedberg).

Therefore, in this study, we examined the influence of canopy cover of conifers, along with topography and forage resources, on habitat selection by bighorns in the Sinlahekin Valley, where thinning and prescribed fire treatments have been applied to encroaching and in-filling ponderosa pine forest to restore historic landscape conditions within and adjacent to existing bighorn habitat. Because of its effect on visual obstruction (Dawkins 1963) and forage abundance (Mueggler 1985, Peek et al. 2001, Stam et al. 2008), we expected bighorns to select for lower canopy cover. We also expected that bighorns would select for steeper and more rugged topography and select areas closer to escape terrain for security (Geist 1971, Van Dyke 1983, Taylor et al. 1998, Shackleton 1999, Shackleton et al. 1999, Toweill and Geist 1999). In addition, we expected bighorns to select areas that provided abundant, nutritious grasses and forbs (Stelfox 1976, Risenhoover and Bailey 1985, Shackleton 1999, Partridge 1978). For example, grasses and forbs arranged in a dense, continuous arrangement at a low height to allow bighorns to maximize nutrient intake without compromising predator detection by obstructing visibility (Bailey 1980, Risenhoover and Bailey 1985). Moreover, we expected bighorns to select areas where forage was near escape terrain (Geist 1971, Shannon et al. 1975, Risenhoover 1981, Berkley 2005). During the winter and lambing seasons, we expected bighorns to select south and west aspects to take advantage of these areas of high solar heat loads that may provide softer snow for better foraging, early vegetation, and warmth (Geist 1971, Stelfox 1976, Shannon et al. 1975, Shackleton 1999, Valdez and Krausman 1999, Singer et al. 2000).

To test our hypotheses, we modeled habitat selection of 21 bighorns (14 females and 7 males) within the annual home range of each bighorn and for 3 biologically meaningful seasons (i.e., lambing, summer, and winter) using Resource Selection Functions (RSFs) with GPS (Global Positioning System) locations obtained from radiocollared bighorns and values of habitat

variables from layers we created in a GIS (Geographic Information System). In addition, we expected habitat selection to vary by sex during lambing season because of the differing biological demands on females and males. Previous observations show that females are more solitary during lambing and prioritize safety over foraging (Geist 1971, Festa-Bianchet 1988, Toweill and Geist 1999), whereas males may exploit habitats with superior forage (Bleich et al. 1997). Therefore, we expected females to select for areas closer to escape terrain before, during, and directly after parturition (Geist 1971, Festa-Bianchet 1988, Bleich et al. 1997, Rachlow and Bowyer 1998, Toweill and Geist 1999) and for males to select areas closer to forage, but show no selection for escape terrain (Festa-Bianchet 1986, Bleich et al. 1997).

STUDY AREA

The Sinlahekin Valley is located in Okanogan County, north-central Washington near the town of Loomis (pop. 159, U.S. Census Bureau; Fig. 2). This U-shaped valley runs north to south and was glacially-carved during the Pleistocene, with wall to wall widths ranging from 0.6 to 2 km. Our study area, which we delineated by creating a minimum bounding geometry around the merged 99% Utilization Distributions (home ranges) of our collared bighorns, encompassed the entire Sinlahekin Valley, covering an area of $>500 \text{ km}^2$. At approximately 46 km long, our study area reached within 8.5 km of British Columbia on the north, extending south to the southern tip of the Sinlahekin Valley, and 7 km east and 9 km west of the town of Loomis, Washington. Slopes ranged from 0 to 73°, and elevation ranged from 348 m to 2304 m. The study area included several lakes, the largest of these being Palmer (8.26 km²), Blue (0.83 km²), and Spectacle (1.26 km²), and various other sources of water including streams, springs, and irrigation water.

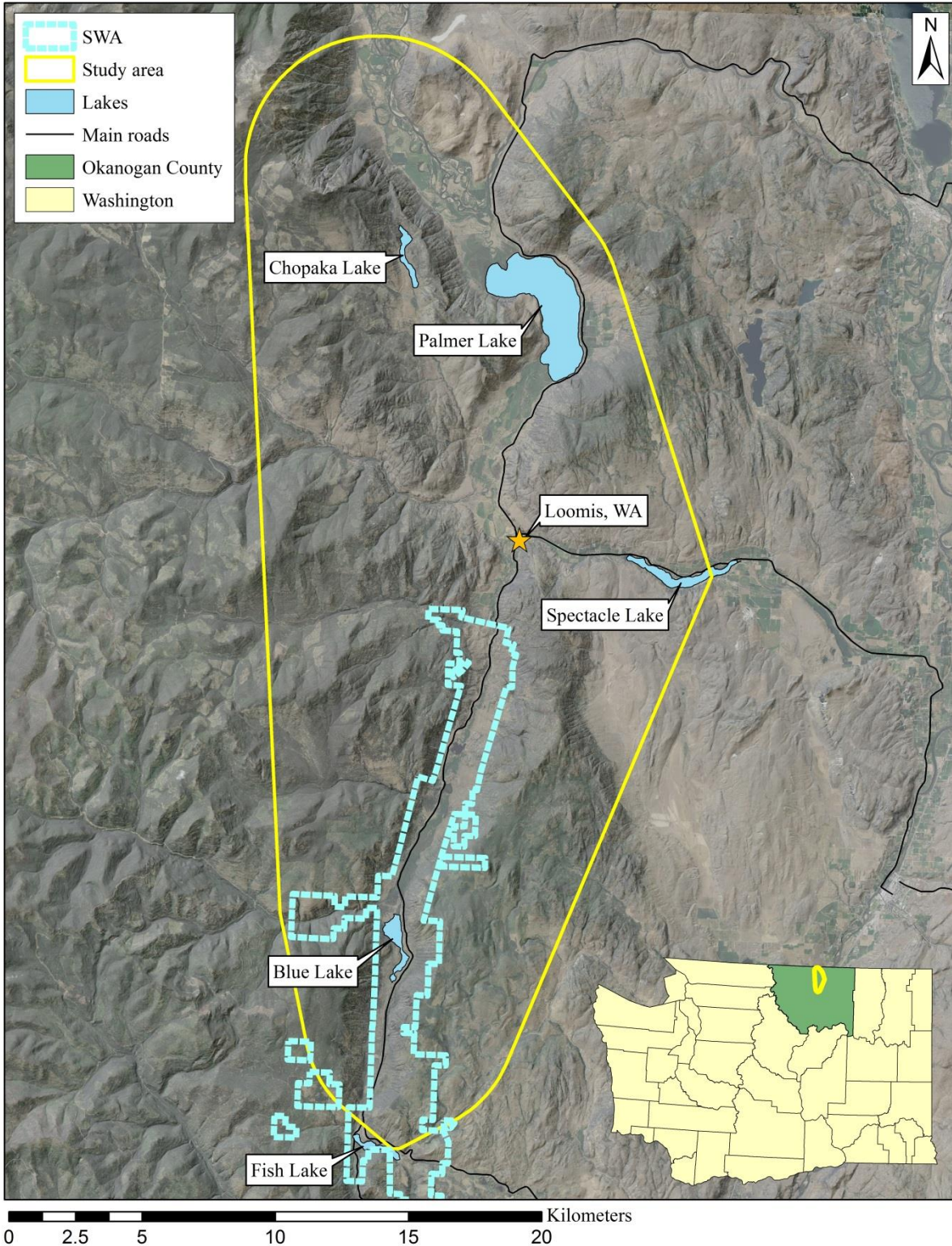


Figure 2. Location of Sinlahekin Wildlife Area within Sinlahekin Valley study area in Okanogan County, Washington. Source: Orthophoto, lakes, and roads - Washington Department of Natural Resources, Washington Counties - Washington State Office of Financial Management, Sinlahekin Wildlife Area boundary - Washington Department of Fish and Wildlife.

The climate was relatively continental, with mean July temperatures at 19.8° C, and mean January temperatures at -5.6° C (Western Regional Climate Center 2015). Mean annual precipitation was 37.6 cm, with most falling as snow in the winter (\bar{x} = 96.8 cm of snow annually). The most common soils were the Leiko and Kartar series ashy-sandy loams, with interspersed granodioritic rock outcrops (Rubble complex) and xerofluventic soils in perennial drainages (Natural Resource Conservation Service 2010). The underlying bedrock is primarily granodiorite associated with the Loomis Pluton (Rinehart and Fox 1972). Geologic processes during the Pleistocene resulted in glacial and colluvial deposits in valley bottoms, which have also experienced fluvial reworking in meandering stream channels.

Plant communities included sagebrush shrub-steppe (*Artemisia tridentata*/*Festuca idahoensis*), bitterbrush/sagebrush shrub-steppe (*Purshia tridentata*/*Artemisia tridentata* association), open grassland (*Festuca* spp., *Poa* spp., and other grasses), ponderosa pine savanna and closed forest (usually *Ponderosa pine*/*Purshia tridentata* association), and riparian broadleaf forest (*Salix* spp. and *Populus* spp.). Isolated stands of aspen (*Populus tremuloides*) occur in the valley bottom and in concavities on the valley walls, usually in locations free from encroaching conifers and with abundant early-season soil moisture. Mixed-conifer forest (including *Pseudotsuga menziesii* and *Larix occidentalis*) was present but uncommon due to the xeric climate and the shallow rocky soils, and possibly also historic selective influences associated with a frequent fire regime. The Sinlahekin Wildlife Area (SWA), administered by the Washington Department of Fish and Wildlife (WDFW), was centrally located within the Sinlahekin Valley study area and covered approximately 58 km². Other ownership within the study area included private non-industrial owners, the United States Forest Service, the Bureau of Land Management, and the Washington Department of Natural Resources. Before its

purchase by WDFW, the SWA experienced logging and grazing (WDFW 2006), and other portions of the valley were used for agriculture (predominantly orchards and pasture for domestic livestock) during our study. Management priorities for the SWA included maintaining wildlife habitat, especially bighorn sheep (*Ovis canadensis*) and mule deer (*Odocoileus hemionus*), and providing recreational opportunities (e.g., fishing, hunting, hiking, and wildlife observation) (WDFW 2006). Besides bighorn sheep and mule deer, the SWA supported white-tailed deer (*Odocoileus virginianus*), black bears (*Ursus americanus*), and cougars (*Puma concolor*) (WDFW 2006).

A large portion of the Sinlahekin Valley was open to public access with 28 access sites within the SWA and a network of roads including the partially-paved Loomis-Oroville Road / Sinlahekin Road, which ran the length of the valley, with gravel roads branching off (Toats Coulee, Funk Mountain, “Rattlesnake Grade” (to Chopaka Lake), and Sinlahekin Creek). The Sinlahekin Valley, especially the SWA, received considerably heavy use during several mule deer and white-tailed deer hunting seasons between September and December, and during the summer camping and fishing seasons, as did the road to and access site at Chopaka Lake, which was a popular fly-fishing destination (personal observation and personal communication with WDFW staff). Traditionally, bighorn sheep hunting was available by lottery permit, but was discontinued in the mid-1990s (WDFW 2006). Hunting reopened in 2010 allowing the harvest of 1 male bighorn sheep each year, but was closed after the 2012 hunting season when herd numbers fell below WDFW management guidelines for harvest (WDFW 2014).

METHODS

Capturing bighorns and acquiring locations

To determine seasonal locations of bighorn sheep remotely, 21 bighorn sheep were captured using net-gunning in March 2010 (10 females, 2 males) and February 2011 (4 females, 5 males) in the northern end of the Sinlahekin Valley near Palmer Lake and the town of Loomis, and on the southern end of the valley near Blue Lake. After capture, bighorns were hobbled, blindfolded, placed in transport bags, and then slung via helicopter to processing sites. At processing sites, WDFW crews fitted them with GPS/VHF (Very High Frequency) radio collars (GPS7000SA or GPS4400M; Lotek Wireless Inc., Newmarket, Ontario, Canada) and marked them with ear tags. Only males that were $\leq 1/2$ curl were collared to reduce risk of hunting mortality while they were being monitored. Animal capture and handling procedures used by WDFW followed the Wild Sheep Capture Guidelines sponsored by the Northern Wild Sheep and Goat Council and the Desert Bighorn Council (Foster 2005).

All collars were programmed to acquire GPS locations at 5-hr intervals and transmit a VHF radio signal for 7 hr/day (to extend battery life to approximately 2 yr) from 0800 to 1500 hr (0900-1600 hr during Daylight Savings Time). Data were stored on each collar and retrieved remotely using 2 methods. Nineteen collars (GPS7000SA) were programmed to upload stored location data to an Argos data collection system (CLS America, Inc. Lanham, MD) on a 14-day interval with a 90-second upload window. Collars were equipped with a drop-off mechanism set to release after 2 years. We accessed Argos-uploaded location data through a secure login on the ArgosWeb (www.argos-system.org) website. We extracted GPS positions and time stamps from all Argos-uploaded data using Lotek Argos-GPS Data Processor software (V3.5, Lotek Wireless Inc., Newmarket, Ontario, Canada) for Lotek Argos-GPS Collars. This software also removed

duplicate locations and performed an error check on GPS locations via a cyclic redundancy check. Two males during the 2010 capture were fitted with download-on-demand (GPS4400M) GPS collars and were fitted with a cotton spacer instead of a drop-off mechanism. We remotely downloaded location data from these collars to a Handheld Command Unit (HCU) using an ultra-high frequency (UHF) antenna and then downloaded the data from the HCU to a computer using GPS Total Host software (Version 3.7.0.18, Lotek Wireless, Inc., Newmarket, Ontario, Canada).

Radiotransmitters were programmed to emit a mortality signal after 24 hours of inactivity. To ensure proper collar function and detect mortalities, we monitored bighorns every month via VHF radio signal and every 14 days through Argos uploads. For monitoring via VHF radio signal, we used a R-1000 telemetry receiver (Communications Specialists, Inc., Orange, CA), a handheld directional antenna (“H” RA-2AK antenna; Telonics, Inc., Mesa, AZ and 3-element Yagi antenna), and/or an omni-directional whip antenna with a magnetic mount. We determined each collar’s beacon mode (live vs. mortality) and attempted to triangulate the collar if we detected a mortality signal. We used the Argos-uploaded GPS data both to initially detect mortalities and to obtain an approximate location once a mortality signal was detected through the VHF radio signal. We accomplished this by displaying the GPS data in a GIS (ArcMap 9.2-10.2.2; Environmental Systems Research Institute, Inc., Redlands, CA) and looking for consecutive bighorn locations that were in the same spot and/or forming a grid pattern which indicated the collar was not moving. We retrieved the collar as expediently as possible to assess evidence to determine cause of death.

Delineating seasons

We modeled habitat selection for an annual period and for 3 biologically meaningful seasons: lambing, summer, and winter. The annual period began on the date the bighorns were captured in February – March and continued for 365 days. Lambing, summer, and winter seasons were defined after reviewing literature and visually identifying seasonal patterns of movement of collared bighorns in a GIS. The timing and duration of lambing seasons vary by climate and species of bighorn (Hass 1997), where lambing in colder climates occurs during a short period of time and later in the year, and lambing in warmer climates is less synchronous and occurs earlier in the year (Sugden 1961). The climate and elevation in the Sinlahekin Valley were similar to that of DeCesare and Pletscher's (2006) study area in western Montana where lambing generally occurred from early May through late July, and Risenhoover and Bailey's (1988) study area in the lower-elevations of Colorado where the peak of lambing was reported to occur during the first week of May, but spanned from mid-April to mid-July. Festa-Bianchet (1988) reported that pregnant females in British Columbia migrated to lambing areas in May and Geist (1971) found that females began to withdraw 2-3 weeks before parturition and rejoined the group about 5-7 days after parturition. Therefore, we defined lambing season from 1 May to 15 June to encompass the estimated peak and range of days surrounding parturition, after estimating timing of lambing in the Sinlahekin Valley through field observations of our study bighorns and personal communication with local WDFW staff (J. C. Heinlen, D. A. Swedberg, and J. B. Haug). The summer season spanned from 16 June to 15 September, including the period of warmer weather and longer days, but excluding lambing and rutting activity (Sugden 1961) and the winter season spanned from 1 December to 29 February, including the period of colder weather, shorter days and snow accumulation (Western Regional Climate Center 2015).

Creating habitat variables

To model habitat selection within the home range of each bighorn for each season we created 9 habitat variable layers in ArcGIS, including slope, surface ruggedness, distance to escape terrain, aspect, percent canopy cover, distance to forage areas (1 for lambing and 1 for other seasons) and forage greenness (3 levels; 1 for lambing and 1 for other seasons). Pixel resolution for all layers was 30 m unless otherwise specified.

We derived a continuous slope layer (in degrees, 10-m pixels) from a 2011, 10 m × 10 m digital elevation model (DEM) from the U.S. Geological Survey National Elevation Dataset (DEM, <http://nationalmap.gov/>, accessed 21 Jan 2013) and also calculated a continuous vector ruggedness measure (ruggedness) layer in ArcMap (Terrain Ruggedness (VRM), <http://arcscrips.esri.com/details.asp?dbid=15423>, accessed 31 Dec 2012) with a moving window of 90 m (Sappington et al. 2007). Sappington et al. (2007) found that VRM quantified local variation in terrain more independently (i.e., was less correlated with slope) than a land surface ruggedness index or a terrain ruggedness index. We defined escape terrain as slopes $\geq 27^\circ$ ($\geq 50.95\%$) (Van Dyke et al. 1983, Gionfriddo and Krausman 1986, Smith et al. 1991, Taylor et al. 1998, Singer et al. 2000) within a minimum patch size of 2 ha (Van Dyke et al. 1983, Smith et al. 1991, Turner et al. 2004). We then used the Euclidean Distance tool to create a continuous distance to polygons of escape terrain. We transformed an aspect layer (also derived from the DEM) according to the algorithm proposed by Stage (1976) to create a continuous layer scaled from 1 to -1 (with NE as 1 and SW as -1) and smoothed it (30 m × 30 m moving window averaging convolution) to reduce interference from tree crowns. We used 10% classes of canopy cover from a LANDFIRE Forest Canopy Cover layer (U.S. Geological Survey, <http://www.landfire.gov/>, accessed 2 Feb 2012) for our percent canopy cover layer.

We created two categorical variables representing forage greenness by calculating Tasseled Cap greenness from a Landsat image from May 2011 for lambing season and July 2011 for summer season. Tasseled Cap greenness has been used in ungulate studies (Carroll et al. 2001). Tasseled Cap greenness was calculated with the coefficients published for Landsat 5 Thematic Mapper (TM) (Crist and Cicone 1984). We made a greenness (forage) "cookie cutter" using the May and July Tasseled Cap layers by first choosing a value for each layer (-20 for May, -12 for July) that was the best exclusion of non-forage areas (i.e., water bodies and talus slopes) and creating 2 new layers that represented and contained values in only forage areas. We also chose an elevation cutoff that best represented available forage for both May and July, excluding forage areas that we considered to be unavailable during certain time periods (e.g., some May Tasseled Cap forage areas were covered with snow in the spring, whereas July Tasseled Cap forage areas were decadent by late summer). We created 2 new layers: 1) May Tasseled Cap for all pixels with an elevation of < 1230 m and 2) July Tasseled Cap for all pixels ≥ 1230 m elevation, and then merged these 2 layers. The resulting layer contained May Tasseled Cap values for areas below 1230 m in elevation and July Tasseled Cap values for areas ≥ 1230 m.

Next, we masked out areas of canopy cover greater than 30% (United Nations Food and Agriculture Organization 2002) and water features (obtained by B. Maletzke from Washington Department of Natural Resources) that weren't automatically excluded. We manually digitized orchards using imagery from the 2009 National Agriculture Imagery Program (obtained by J. Haug from Washington Department of Natural Resources) and a Cropland Data Layer (CropScape - Cropland Data Layer, <http://nassgeodata.gmu.edu/CropScape/>, accessed 26 Mar 2013) and then masked these areas of orchard out as well. Because bighorns were observed

using hay fields as a forage resource, we used the Cropland Data Layer to identify hay fields that had been excluded and then reincorporated them into the forage layer. The result was a binary layer of forage areas and non-forage areas that we combined via pixel-to-pixel raster multiplication separately with first May Tasseled Cap (for lambing season) and then July Tasseled Cap (for summer season). From these 2 layers, forage areas with May Tasseled Cap values and forage areas with July Tasseled Cap values, we were able to build 2 categorical greenness layers (one for lambing and one for summer) and 2 distance-to-forage layers (continuous Euclidean distance; one for lambing and one for summer).

To create 3 categories of greenness for the lambing season, we used the “Raster to ASCII” tool to generate a text file of May Tasseled Cap greenness values (non-forage areas excluded), which were divided into 30% quantiles of low, medium, and high greenness, resulting in 4 forage categories – non-forage and 3 levels of greenness. We performed these same steps using the July Tasseled Cap raster to create a categorical greenness forage layer for the summer season. For the distance-to-forage layer, we divided the greenness values into 2 quantiles, defining forage as greenness values $\geq 50\%$ and converted this to a polygon layer. We specified a minimum patch size (area) of 2 ha and then calculated Euclidean distance to the forage polygon layer to produce a continuous raster distance-to-forage layer.

Modeling habitat selection

We modeled habitat selection within sheep home ranges (3rd order selection, Johnson 1980) from used and available locations using Resource Selection Function models (Manly et al. 2002). Our measures of habitat features used were determined from three-dimensional (4 satellites - locational error of 5-10 m) and two-dimensional (3 satellites - locational error variable, but >10 m) bighorn GPS locations. To estimate the GPS location error of our

radiocollars we calculated the root mean square error of post-mortality locations, and of a pre-deployment test location on a roof to represent location error without interference from topography. Data were fit to a 95% Weibull distribution and error averaged 18.4 m (SD = 13.7 m, 95% CI, $8.8 \leq 18.4 \leq 27.8$). We also removed obvious erroneous locations (e.g., clearly many kilometers away from either previous or subsequent locations).

To measure availability of habitat features within each animal's home range, we created 99% Utilization Distributions (UD) for each sheep for each season (annual, lambing, summer, and winter) for each year (137 UD's total) using the Brownian bridge movement model package (BBMM) (Horne *et al.* 2007) in R: A language and environment for statistical computing (R Core Team 2013, Version 1.5, www.r-project.org, accessed 06 Apr 2013) and Geospatial Modeling Environment (GME Version 0.7.2.1, <http://www.spatalecolgy.com>, accessed 6 Apr 2013). In the BBMM command, we specified a cell size of 30 m, a location error of 20 m, left the 'time.step' argument at the default of 0.1, allowed the 'time.lag' argument to be calculated from input location data according to the default algorithm, and did not specify a value for the 'max.lag' argument. To keep all cells of bighorn UD's geospatially aligned, we created code that found the bounding coordinates of all bighorn location data (for a specific batch), buffered this bounding rectangle by a manual input, and then rounded to the nearest multiple of 30 m. We then sourced the result of this code to the 'area.grid' argument. To represent the area of available habitat within the home range, we used full (100%) UD's estimated in the BBMM to create 99% contours in GME and then trimmed each 100% UD to a 99% home range. In ArcMap, we generated random points equal to the number of sheep locations used for each season to represent available habitat within the 99% home range of each individual sheep. However, for the 14 of the 121 instances where sheep locations occurred at densities of <10

locations/km², the number of random points generated was equal to the home range area (km²) multiplied by 10 to meet a minimum of 10 random points/km² to better represent available habitat. When the number of random points was greater than the number of sheep locations, we created a weighting function to give random points and sheep locations equal importance (within each season and year).

To ensure that multicollinearity of predictor variables was not an issue in the calculation of the RSFs, we used a correlation matrix to determine that the 9 habitat variables that we used for our RSF models were not highly correlated ($R < 0.52$), with most variables having an R value < 0.30 . We extracted all habitat layer values to sheep locations and random points in ArcMap. The same 9 habitat variables were included for summer, winter, and annual RSF models. However, we used May Tasseled Cap greenness instead of July, to represent forage availability in our lambing RSF models. For our categorical forage greenness variable, the non-forage category was used as the reference category and all greenness categories of low, medium, and high were compared to non-forage.

Because each habitat variable included in the model was based on *a priori* hypotheses, we ran all possible model combinations (512 per sheep/season, with years combined), which included a null (intercept-only) model, and calculated an Akaike Information Criterion (AIC) value. We ranked models by lowest AIC value and calculated Akaike weights of only “top” models (i.e., only models within 2 AIC of the lowest AIC value, Burnham and Anderson 2002). We then used these top model weights to average across top models (Burnham and Anderson 2002) for each individual sheep/season combination home range. Habitat variables that did not appear in a specific model were averaged as zero. We then used the average model coefficients and standard errors of each individual bighorn sheep (for each season) to average across 3

demographic groups: all males, all females, and both sexes combined, to create population-level habitat selection models for the bighorn sheep in the Sinlahekin Valley for each season (using eq. 3 minus eq. 2 in Marzluff et al. 2004) and calculated 95% confidence intervals. We considered habitat variables to have a significant effect on habitat selection when the 95% confidence interval did not overlap zero. We did not average top RSF models for females and males for the lambing season because of differing biological demands during this time period.

RESULTS

Of the 12 bighorns (2 M, 10 F) captured in 2010, 3 females died within the year, and 3 more died in 2011. Of the 9 bighorns (5 M, 4 F) captured in 2011, 1 male died in 2011. Mortalities occurred 23 to 502 days after capture (mean = 259 days). Causes of death were unknown because conclusive evidence was not obtained. However, we suspected that 1 female died in a landslide after heavy rainfall, the male died from capture myopathy, and one female was predated or scavenged. From March 2010 to February 2013, we obtained an average of 2716 (1760-3482) useable GPS locations from each of 17 sheep collars for the annual time period (2 years combined). We obtained an average of 18 months of data for each sheep and 22 months of data for each sheep that survived for at least 2 years.

The average number of top models (models within 2 AIC of the top model) for each sheep was 3.5 with a range of 1 to 13 for the annual period, 7.5 with a range of 2 to 17 for the lambing season, 5.2 with a range of 1 to 12 for the summer season, and 5.8 with a range of 2 to 21 for the winter season. The null (intercept-only) model was never within 2 AIC of our top RSF models and usually ranked last, having the highest AIC value.

As we predicted, bighorn sheep selected areas with lower canopy cover. Canopy cover was included in the top RSF models for almost all bighorns in all seasons (Table 1). In addition, it was the only variable we included in our full model that significantly predicted habitat selection by bighorns in population-level models for all demographic groups and seasons (i.e., 95% confidence intervals did not overlap 0, Tables 2-6).

Topographic variables varied in their ability to predict habitat selection by bighorns. Slope, distance to escape terrain, and aspect were included in the top models of at least half of the individuals in all seasons, whereas ruggedness and slope \times ruggedness was included in less than half of the individual models for most demographic groups and seasons (Table 1). During annual, lambing, and summer seasons, both males and females selected for steeper slopes (Tables 2-6).

Distance to escape terrain did not significantly predict habitat selection by females, but males selected for areas closer to escape terrain during annual and winter seasons (Tables 2-6). Females selected southwest aspects in summer only, but aspect did not significantly predict habitat selection in males (Tables 2-6). Neither ruggedness, nor slope \times ruggedness, predicted habitat selection by sheep, except during lambing season when ewes selected for more ruggedness.

Contrary to our expectations, sheep did not select habitats that had higher greenness indices or those that were closer to areas we designated as forage using remote sensing. Although greenness was included in all the individual models for the annual time period (Table 1), in all seasons, males selected areas with lower Tasseled Cap greenness values or avoided areas with higher values (Tables 2-6). Greenness was less predictive of habitat selection by females, but females selected for lower greenness values (“low” and “medium” categories) in

winter (Tables 2-6). The number of individuals with distance to forage and the interaction between distance to forage and escape terrain in their top RSF models varied with season and sex (Table 1), and these variables were inconsistent in their ability to significantly predict habitat selection (Tables 2- 6). Males selected areas closer to forage only during the lambing season. In summer, males selected areas where forage and escape terrain were closer together, whereas females selected areas where forage and escape terrain were closer together for the annual time period only, but not for any individual seasons (Tables 2-6).

Table 1. Habitat variables present in the top Resource Selection Function model (lowest Akiake Information Criterion value) for each bighorn sheep (*Ovis canadensis*) for each season (years combined) in Okanogan County, Washington, March 2010 to February 2013. Annual time period was one full year, starting on the date sheep were captured (e.g. Mar 5 2010 to Mar 5 2011). Lambing season spanned May 1 to Jun 15, summer season Jun 16 to Sep 15, and winter Dec 1 to Feb 29.

Model variables	Annual		Lambing		Summer		Winter	
	M (n=6)	F (n=11)	M (n=6)	F (n=13)	M (n=6)	F (n=12)	M (n=6)	F (n=11)
Canopy cover ^a (%)	6	11	4	9	6	9	3	10
Slope (°)	6	10	6	13	6	11	5	9
Dist. to escape terrain (m) ^b	6	11	3	8	5	7	4	8
Aspect ^c	4	11	3	10	5	9	4	10
Ruggedness ^d	1	6	3	9	2	9	3	5
Slope × ruggedness	2	9	1	6	3	4	3	6
Low greenness ^e	6	11	2	6	6	9	6	8
Med. greenness ^e	6	11	2	6	6	9	6	8
High greenness ^e	6	11	2	6	6	9	6	8
Dist. to forage areas (m) ^f	3	11	3	8	4	8	4	9
Dist. to escape terrain × dist. to forage areas	6	11	2	3	5	11	5	7

^aContinuum of 10% classes.

^bContinuous habitat variable defined as areas ≥ 2.0 ha with slopes $\geq 27^\circ$ and calculated using Euclidean distance.

^cScaled from 1 (NE) to -1 (SW).

^dContinuous vector ruggedness measure (ruggedness) calculated using the Terrain Ruggedness (VRM) tool in ArcMap with a moving window of 90 m (Sappington et al. 2007).

^eGreenness categories represent 30% quantiles of Tasseled Cap greenness indexes with low being the lowest 30% of values, after excluding 30% canopy cover, orchards (digitized manually in a GIS), and water.

^fContinuous habitat variable defined as $\geq 50\%$ Tasseled Cap values after excluding canopy cover $\geq 30\%$, orchards (digitized manually in a GIS), and water and calculated using Euclidean distance.

Table 2. Averaged top Resource Selection Function models of 17 bighorn sheep (*Ovis canadensis*) in Okanogan County, Washington, from March 2010 to February 2013 for the annual time period. Asterisks denote coefficients with confidence intervals that do not overlap 0.

Model variables	Males (n=6)				Females (n=11)				Population (n=17)			
	coeff.	SE	95% CI		coeff.	SE	95% CI		coeff.	SE	95% CI	
			Lower	Upper			Lower	Upper			Lower	Upper
Intercept	-0.712	0.790	-2.261	0.837	-1.902*	0.765	-3.402	-0.402	-1.482*	0.571	-2.601	-0.362
Canopy cover ^a (%)	-0.044*	0.010	-0.063	-0.025	-0.036*	0.008	-0.052	-0.021	-0.039*	0.006	-0.051	-0.027
Slope (°)	0.041*	0.017	0.007	0.075	0.048*	0.016	0.017	0.079	0.045*	0.012	0.022	0.068
Dist. to escape terrain (m) ^b	-3.885*	1.195	-6.227	-1.542	0.004	1.106	-2.164	2.172	-1.369	0.933	-3.197	0.460
Aspect ^c	-0.257	0.261	-0.768	0.254	-0.258	0.333	-0.910	0.395	-0.258	0.229	-0.706	0.191
Ruggedness ^d	3.131	2.136	-1.056	7.317	8.453	8.842	-8.878	25.784	6.575	5.709	-4.615	17.764
Slope × ruggedness	-0.024	0.128	-0.275	0.227	0.239	0.297	-0.344	0.822	0.146	0.197	-0.239	0.531
Low greenness ^e	0.093*	0.043	0.009	0.178	0.103	0.152	-0.194	0.400	0.099	0.098	-0.092	0.291
Med. greenness ^e	-0.160	0.125	-0.405	0.086	-0.288	0.174	-0.628	0.053	-0.242*	0.119	-0.476	-0.009
High greenness ^e	-0.627*	0.260	-1.136	-0.118	-0.439	0.291	-1.010	0.131	-0.506*	0.206	-0.909	-0.102
Dist. to forage areas (m) ^f	-0.400	0.607	-1.589	0.789	0.512	1.094	-1.631	2.656	0.190	0.732	-1.245	1.626
Dist. to escape terrain × dist. to forage areas	-18.227	13.634	-44.950	8.496	-24.631*	10.006	-44.243	-5.019	-22.371*	7.857	-37.770	-6.971

^aContinuum of 10% classes.

^bContinuous habitat variable defined as areas ≥ 2.0 ha with slopes $\geq 27^\circ$ and calculated using Euclidean distance.

^cScaled from 1 (NE) to -1 (SW).

^dContinuous vector ruggedness measure (ruggedness) calculated using the Terrain Ruggedness (VRM) tool in ArcMap with a moving window of 90 m (Sappington et al. 2007).

^eGreenness categories represent 30% quantiles of Tasseled Cap greenness indexes with low being the lowest 30% of values, after excluding 30% canopy cover, orchards (digitized manually in a GIS), and water.

^fContinuous habitat variable defined as $\geq 50\%$ Tasseled Cap values after excluding canopy cover $\geq 30\%$, orchards (digitized manually in a GIS), and water and calculated using Euclidean distance.

Table 3. Averaged top Resource Selection Function models of 19 bighorn sheep (*Ovis canadensis*) in Okanogan County, Washington, from March 2010 to February 2013 for the lambing season. Asterisks denote coefficients with confidence intervals that do not overlap 0.

Model variables	Males (n=6)				Females (n=13)			
	coeff.	SE	95% CI		coeff.	SE	95% CI	
			Lower	Upper			Lower	Upper
Intercept	-1.731*	0.525	-2.760	-0.702	-4.050*	0.499	-5.028	-3.073
Canopy cover ^a (%)	-0.033*	0.010	-0.053	-0.012	-0.017*	0.007	-0.030	-0.003
Slope (°)	0.064*	0.011	0.042	0.086	0.097*	0.011	0.076	0.118
Dist. to escape terrain (m) ^b	-2.027	1.051	-4.086	0.032	-0.924	1.712	-4.280	2.432
Aspect ^c	-0.015	0.154	-0.317	0.288	0.056	0.299	-0.529	0.642
Ruggedness ^d	18.786	9.961	-0.737	38.309	30.521*	6.038	18.687	42.355
Slope × ruggedness	-0.241	0.199	-0.630	0.148	-0.225	0.154	-0.527	0.078
Low greenness ^e	0.258*	0.119	0.025	0.490	0.273	0.183	-0.084	0.631
Med. greenness ^e	0.180	0.112	-0.038	0.399	-0.279	0.153	-0.579	0.021
High greenness ^e	0.002	0.048	-0.092	0.096	-1.543	1.631	-4.739	1.653
Dist. to forage areas (m) ^f	-0.649*	0.249	-1.137	-0.161	-0.312	0.837	-1.952	1.328
Dist. to escape terrain × dist. to forage areas	-3.058	3.700	-10.309	4.194	-16.772	9.051	-34.513	0.968

^aContinuum of 10% classes.

^bContinuous habitat variable defined as areas ≥ 2.0 ha with slopes $\geq 27^\circ$ and calculated using Euclidean distance.

^cScaled from 1 (NE) to -1 (SW).

^dContinuous vector ruggedness measure (ruggedness) calculated using the Terrain Ruggedness (VRM) tool in ArcMap with a moving window of 90 m (Sappington et al. 2007).

^eGreenness categories represent 30% quantiles of Tasseled Cap greenness indexes with low being the lowest 30% of values, after excluding 30% canopy cover, orchards (digitized manually in a GIS), and water.

^fContinuous habitat variable defined as $\geq 50\%$ Tasseled Cap values after excluding canopy cover $\geq 30\%$, orchards (digitized manually in a GIS), and water and calculated using Euclidean distance.

Table 4. Averaged top Resource Selection Function models of 18 bighorn sheep (*Ovis canadensis*) in Okanogan County, Washington, from March 2010 to February 2013 for the summer season. Asterisks denote coefficients with confidence intervals that do not overlap 0.

Model variables	Males (n=6)				Females (n=12)				Population (n=18)			
	coeff.	SE	95% CI		coeff.	SE	95% CI		coeff.	SE	95% CI	
			Lower	Upper			Lower	Upper			Lower	Upper
Intercept	-1.558*	0.343	-2.231	-0.884	-0.920	0.542	-1.981	0.142	-1.132*	0.379	-1.875	-0.389
Canopy cover ^a (%)	-0.033*	0.008	-0.048	-0.017	-0.029*	0.006	-0.040	-0.018	-0.030*	0.005	-0.039	-0.022
Slope (°)	0.048*	0.007	0.035	0.061	0.027*	0.012	0.004	0.051	0.034*	0.008	0.018	0.051
Dist. to escape terrain (m) ^b	-1.880	1.340	-4.506	0.746	-7.371	5.336	-17.830	3.088	-5.541	3.602	-12.601	1.519
Aspect ^c	-0.208	0.152	-0.506	0.090	-0.47*	0.196	-0.854	-0.086	-0.383*	0.141	-0.658	-0.107
Ruggedness ^d	13.048	9.702	-5.967	32.063	3.611	5.128	-6.439	13.661	6.757	4.548	-2.157	15.670
Slope × ruggedness	-0.487	0.321	-1.116	0.143	0.553	0.353	-0.139	1.244	0.206	0.280	-0.342	0.754
Low greenness ^e	0.795*	0.149	0.504	1.087	-0.251	0.141	-0.528	0.025	0.097	0.159	-0.214	0.409
Med. greenness ^e	0.532*	0.207	0.127	0.938	-0.425*	0.154	-0.726	-0.123	-0.106	0.163	-0.425	0.214
High greenness ^e	-0.175	0.231	-0.627	0.278	-0.133	0.216	-0.556	0.291	-0.147	0.160	-0.461	0.167
Dist. to forage areas (m) ^f	0.440	0.990	-1.501	2.380	-0.323	1.018	-2.317	1.672	-0.069	0.743	-1.525	1.387
Dist. to escape terrain × dist. to forage areas	-17.889*	4.012	-25.752	-10.025	-16.716	8.886	-34.133	0.700	-17.107*	6.024	-28.914	-5.300

^aContinuum of 10% classes.

^bContinuous habitat variable defined as areas ≥ 2.0 ha with slopes $\geq 27^\circ$ and calculated using Euclidean distance.

^cScaled from 1 (NE) to -1 (SW).

^dContinuous vector ruggedness measure (ruggedness) calculated using the Terrain Ruggedness (VRM) tool in ArcMap with a moving window of 90 m (Sappington et al. 2007).

^eGreenness categories represent 30% quantiles of Tasseled Cap greenness indexes with low being the lowest 30% of values, after excluding 30% canopy cover, orchards (digitized manually in a GIS), and water.

^fContinuous habitat variable defined as $\geq 50\%$ Tasseled Cap values after excluding canopy cover $\geq 30\%$, orchards (digitized manually in a GIS), and water and calculated using Euclidean distance.

Table 5. Averaged top Resource Selection Function models of 17 bighorn sheep (*Ovis canadensis*) in Okanogan County, Washington, from March 2010 to February 2013 for the winter season. Asterisks denote coefficients with confidence intervals that do not overlap 0.

Model variables	Males (n=6)				Females (n=11)				Population (n=17)			
	coeff.	SE	95% CI		coeff.	SE	95% CI		coeff.	SE	95% CI	
			Lower	Upper			Lower	Upper			Lower	Upper
Intercept	-1.069*	0.407	-1.866	-0.272	-2.479*	0.854	-4.153	-0.805	-1.981*	0.585	-3.129	-0.834
Canopy cover ^a (%)	-0.035*	0.015	-0.065	-0.006	-0.037*	0.010	-0.056	-0.017	-0.036*	0.008	-0.052	-0.020
Slope (°)	0.023	0.014	-0.004	0.051	0.048*	0.021	0.007	0.090	0.039*	0.015	0.011	0.068
Dist. to escape terrain (m) ^b	-5.623*	1.900	-9.347	-1.898	-2.852	2.244	-7.251	1.547	-3.830*	1.601	-6.969	-0.691
Aspect ^c	0.030	0.263	-0.485	0.545	-0.075	0.485	-1.026	0.875	-0.038	0.321	-0.667	0.590
Ruggedness ^d	1.520	9.315	-16.737	19.777	0.579	8.273	-15.635	16.793	0.911	6.132	-11.107	12.929
Slope × ruggedness	0.113	0.336	-0.547	0.772	0.209	0.253	-0.287	0.705	0.175	0.197	-0.211	0.561
Low greenness ^e	1.183*	0.328	0.541	1.825	0.554*	0.148	0.265	0.844	0.776*	0.163	0.457	1.096
Med. greenness ^e	0.630*	0.293	0.055	1.204	0.253*	0.105	0.046	0.459	0.386*	0.128	0.136	0.636
High greenness ^e	-0.435	0.554	-1.520	0.650	-1.307	1.365	-3.983	1.369	-1.000	0.888	-2.740	0.741
Dist. to forage areas (m) ^f	-1.288	1.320	-3.875	1.299	-0.324	1.145	-2.567	1.920	-0.664	0.859	-2.347	1.019
Dist. to escape terrain × dist. to forage areas	-34.417	21.394	-76.350	7.516	-12.793	12.851	-37.981	12.394	-20.425	11.158	-42.294	1.444

^aContinuum of 10% classes.

^bContinuous habitat variable defined as areas ≥ 2.0 ha with slopes $\geq 27^\circ$ and calculated using Euclidean distance.

^cScaled from 1 (NE) to -1 (SW).

^dContinuous vector ruggedness measure (ruggedness) calculated using the Terrain Ruggedness (VRM) tool in ArcMap with a moving window of 90 m (Sappington et al. 2007).

^eGreenness categories represent 30% quantiles of Tasseled Cap greenness indexes with low being the lowest 30% of values, after excluding 30% canopy cover, orchards (digitized manually in a GIS), and water.

^fContinuous habitat variable defined as $\geq 50\%$ Tasseled Cap values after excluding canopy cover $\geq 30\%$, orchards (digitized manually in a GIS), and water and calculated using Euclidean distance.

Table 6. Averaged top Resource Selection Function models of bighorn sheep (*Ovis canadensis*) in Okanogan County, Washington, March 2010 to February 2013. Annual time period was one full year, starting on the date sheep were captured (e.g. Mar 5 2010 to Mar 5 2011). Lambing season spanned May 1 to Jun 15, summer season Jun 16 to Sep 15, and winter Dec 1 to Feb 29. Plus (+) and minus (-) signs indicate the variable was a significant predictor of habitat selection. Plus (+) signs indicate a positive relationship with the habitat variable and minus (-) signs indicate a negative relationship with the habitat variable.

Model variables	Annual			Lambing		Summer			Winter		
	M (n=6)	F (n=11)	All (n=17)	M (n=6)	F (n=13)	M (n=6)	F (n=12)	All (n=18)	M (n=6)	F (n=11)	All (n=17)
Canopy cover ^a (%)	-	-	-	-	-	-	-	-	-	-	-
Slope (°)	+	+	+	+	+	+	+	+		+	+
Dist. to escape terrain (m) ^b	-								-		-
Aspect ^c							-	-			
Ruggedness ^d					+						
Slope × ruggedness											
Low greenness ^e	+			+		+			+	+	+
Med. greenness ^e			-			+	-		+	+	+
High greenness ^e	-		-								
Dist. to forage areas (m) ^f				-							
Dist. to escape terrain × dist. to forage areas		-	-			-		-			

^aContinuum of 10% classes.

^bContinuous habitat variable defined as areas ≥ 2.0 ha with slopes $\geq 27^\circ$ and calculated using Euclidean distance.

^cScaled from 1 (NE) to -1 (SW).

^dContinuous vector ruggedness measure (ruggedness) calculated using the Terrain Ruggedness (VRM) tool in ArcMap with a moving window of 90 m (Sappington et al. 2007).

^eGreenness categories represent 30% quantiles of Tasseled Cap greenness indexes with low being the lowest 30% of values, after excluding 30% canopy cover, orchards (digitized manually in a GIS), and water.

^fContinuous habitat variable defined as $\geq 50\%$ Tasseled Cap values after excluding canopy cover $\geq 30\%$, orchards (digitized manually in a GIS), and water and calculated using Euclidean distance.

DISCUSSION

Bighorn sheep in north-central Washington selected areas with lower tree canopy cover, even when controlling for topography and potential foraging habitat. In fact, canopy cover was the only habitat variable that significantly predicted habitat selection by bighorn sheep in population-level models across all demographic groups and seasons. Bighorn sheep may have selected areas with lower canopy cover because they provided a lower perceived predation risk or because they may provide more abundant, nutritious forage.

One reason bighorns might have selected areas with lower tree canopy is that they have lower stem density and basal area (Dawkins 1963), which may afford bighorn sheep higher visibility to detect predators and easier access to rugged escape terrain (Myserud and Østbye 1999), and provide less hiding cover for ambush predators (e.g., cougars). High stem density and basal area can obstruct a bighorn's vision below the canopy, and the tree canopy itself can contribute to visual obstruction when the topography varies sharply, changing the sight plane from straight to angled (Thomas et al. 1979). Like in our study, Risenhoover (1981) and Risenhoover and Bailey (1985), found that bighorns avoid or minimize use of areas with poor visibility. Some large ungulates, such as deer and elk (*Cervus elaphus*) (Thomas et al. 1979, Shackleton 1999), often seek areas with high concealment cover and visual obstruction to avoid being detected by predators. Other ungulates, such as bighorns, use a different predator-evasion strategy that relies on detecting predators early and escaping to rugged terrain, thus areas of low visibility are often disadvantageous. Bighorn sheep have excellent vision enabling them to detect predators from great distances (≥ 914 m, Geist 1971:12) and a gregarious social structure (Geist 1971, Bailey 1980) which they use to visually communicate alarm postures to each other when a predator is detected (Geist 1971). They are not equipped with long legs and slender

bodies for outrunning predators, but instead have short, blocky bodies (Geist 1971, Toweill and Geist 1999) with sure footing and considerable jumping ability (Geist 1971) that enables them to outmaneuver their predators when they reach steep, broken terrain. In addition, bighorns also have small ears relative to their head size compared to other ungulates such as white-tailed deer, mule deer, elk, and moose (*Alces alces*), which suggests that they rely on vision more than hearing to detect predators. Therefore, they rely on open areas of high visibility and low visual obstruction, such as grasslands containing low-growing plants and rocky outcrops, to avoid predation (Bailey 1980, Risenhoover and Bailey 1985, Toweill and Geist 1999).

Not only might high stem density of trees obstruct vision and decrease predator detection, it could also impede movement to escape terrain if a predator was detected (Geist 1982, Mysterud and Østbye 1999). Kittle et al. (2008) found that elk selected for partially cut and sparse forest instead of dense coniferous forest, suggesting that these areas provided both better visibility and more accessible escape routes that may offset the increased risk of an encounter with a predator. Dense woody vegetation may obstruct the path or slow the retreat of bighorn sheep to the safety of escape terrain and, therefore, decrease the chance of survival if a predator is encountered.

Using habitats they perceive as unsafe, such as areas with high visual obstruction, may elicit undesirable physiological or behavioral responses in wild ungulates. For example, Stemp (1983) observed an increase in heart rates as free-ranging wild sheep approached forested areas, and heart rate was negatively correlated with visibility in a study by Hayes et al. (1994). Increased heart rate can increase energy expenditure and could indicate stress, which can cause physiological damage if frequent or chronic (see Stemp 1983: Appendix A for a detailed description of stress responses and detrimental consequences). Stress decreases the resistance of

bighorns to disease organisms such as *Pasteurella* spp. bacteria, rendering them vulnerable to infection and subsequent pneumonia and potential die-offs (Shackleton et al. 1999). Many studies have observed that ungulates increase the time they spend vigilant (e.g., alert with head up) and increase group size in risky habitat (McNamara and Houston 1992). For example, Goldsmith (1990) reported that pronghorns (*Antilocapra americana*) significantly increased vigilance (both scan duration and frequency) in shrub habitats when compared with meadows. In 5 species of African antelopes, reedbuck (*Redunca arundinum*), impala (*Aepyceros melampus*), tsessebe (*Damaliscus lunatus*), blue wildebeeste (*Connochaetes taurinus*), and buffalo (*Syncerus caffer*), animals in dense vegetation spent more time looking compared to animals in open habitats, and for 4 out of the 5 species studied, vigilance decreased as group size increased (Underwood 1982). In addition, the time animals spent vigilant was also affected by location within the group, whereby animals more centrally located within the group scanned less and fed more. Similar behavior has also been documented in elk (Robinson and Merrill 2013). Bighorn sheep seem to respond to habitats with poor visibility similarly. Risenhoover and Bailey (1985) found that bighorn sheep were more vigilant and foraged more closely together in habitats where visibility was poor, possibly to remain in contact with one another to assist in detecting predators.

Although these behavioral responses allow bighorn sheep or other ungulates to use more risky areas (Risenhoover and Bailey 1985), they may come at a cost (Bertram 1978, Robinson and Merrill 2013,), even if animals are able to handle food (i.e., chew) while being vigilant (i.e., scanning or looking) (Fortin et al. 2004). For many ungulates, including bighorn sheep (Berger 1978, Risenhoover and Bailey 1985), foraging efficiency declines with increasing time spent vigilant (Fortin et al. 2004, Robinson and Merrill 2013). In addition, intraspecific competition

caused by bighorns foraging closer together (Bertram 1978), may also decrease foraging efficiency (Clark and Mangel 1984, 1986). Reductions in foraging efficiency can have direct effects on survival and reproduction (Geist 1971, Krebs and Davies 1978, Kie 1999), thus risky, low-visibility habitats force trade-offs between maximizing foraging (energetic gain) and avoiding predation (Houston et al. 1993).

Although we did not directly measure activity patterns and physiological responses, or actual predation risk of bighorn in relation to canopy cover, previous studies have documented predation of bighorn sheep by cougars (Hornocker 1970, Krausman et al. 1989, Rominger et al. 2004, Wehausen 1996, Realé et al. 2003, Holl et al. 2004, Mooring et al. 2004). It has also been suggested that bighorn sheep have shifted their use of habitat in response to cougars (Dibb and Quinn 2008), and experienced dramatic declines due to predation by cougars (Wehausen 1996, Holl et al. 2004). Kertson et al. (2011) found that cougars were positively associated with conifer forest cover. As described in a study by Realé et al. (2003), all 4 documented cougar attacks on bighorn sheep occurred while bighorns were close to the forest edge. Cougars are ambush predators and seek vegetation (e.g., shrubs or trees) or terrain (e.g., canyons or draws) suitable for hiding cover that enables them to approach within attacking distance of prey (Hornocker 1970, Logan and Irwin 1985), and it has been suggested that reducing woody vegetation may reduce ambush opportunities for cougars (Rominger et al. 2004). Therefore, areas of higher canopy cover may increase the vulnerability of bighorn sheep to ambush predators, and bighorn sheep may select areas of lower canopy cover as a predator-evasion strategy.

Not only might high canopy cover reduce perceived or actual security of bighorns, it might also provide less nutritious forage. Because tree canopy, especially of conifers, restricts

the amount of light that can penetrate to the forest floor (Jennings et al. 1999), understory biomass is usually inversely related to canopy cover (Mueggler 1985, Peek et al. 2001, Stam et al. 2008, Abella 2009). In addition, dense conifer canopies can decrease available water, both through evapotranspiration (Baker 1986, Moore 1991) and interception (Moore 1991), and the root systems of conifers can outcompete grasses for surface water after rainfall via lateral, fine root-filaments (Foxx and Tierney 1987) and during drought via deep taproots (Tennesen 2008). Dense conifer canopies may also cause a deep buildup of litter (especially when fire is suppressed), which may inhibit growth of grasses and forbs by restricting water access into the soil (Moore 1991) and covering soil needed for seed germination. As a grazing ruminant, bighorn sheep forage primarily on grasses and low-growing forbs (Shackleton 1999). Because these plants are generally low and variable in nutritional quality, bighorns must spend much of their day searching for and consuming sufficient amounts of nutritious vegetation (Shackleton 1999). To meet these foraging demands, bighorn sheep have adaptations such as specialized teeth for grinding and chewing vegetation, an elongated jaw to feed more selectively, and a combination of micro-organisms and a fermentation process for breaking down and digesting plant cellulose (Shackleton 1999). To survive and reproduce, bighorns must select landscapes, patches, and plants that provide both adequate biomass and nutritional quality of plants that allows them to maximize nutrient intake, while avoiding predation (Krebs and Davies 1978, Kie 1999). Some studies have found that herbivores select forage with higher crude protein content within a given area when compared to available (Berger 1991, Festa-Bianchet 1988, Ulappa et al. 2014) and selection may change depending on spatial and temporal scale (Kittle et al. 2008, van Beest et al. 2010). Therefore, areas with lower canopy may simultaneously provide both maximization of nutrient intake and predator avoidance.

Despite the clear value of areas with abundant, nutritious forage to bighorn sheep, the variables we used to reflect the availability of nutritious forage (i.e., forage greenness in 30% classes and forage patches $\geq 50\%$ greenness and ≥ 2 ha) were relatively poor predictors of habitat selection in our study. For example, distance to forage was only important in models predicting habitat selection of males during the lambing season. Furthermore, in models in which greenness was a significant variable, bighorns selected areas with lower, rather than of higher, greenness. Forage variables were derived from remotely-sensed data that may have had classification and location errors. We attempted to minimize classification error by removing greenness values reflected from water and talus; however some misclassification may have persisted, and together with location errors may have reduced the accuracy of forage areas or greenness levels. In addition, we excluded all areas of $\geq 30\%$ tree canopy cover (also a remotely-sensed data layer with potential inaccuracies in classification and location) because the spectral reflectance from the overstory (i.e., trees) would not represent understory forage (Borowik et al. 2013). We assumed these areas underneath canopy cover exceeding 30% would not provide sufficient forage and excluded them when creating our forage habitat variables; however there may have been adequate forage in these areas.

Another reason our forage variables may have been poor predictors of habitat selected by bighorn sheep is that Tasseled Cap greenness may have been inadequately correlated with the abundance and nutritional quality of forages preferred by bighorns. Bighorn sheep generally prefer grasses and forbs, including perennial grasses such as bluebunch wheatgrass (*Pseudoroegneria spicata*), Idaho fescue (*Festuca idahoensis*), bluegrass (*Poa* spp.), Indian ricegrass (*Achnatherum hymenoides*), and some annual grasses (e.g. cheatgrass (*Bromus tectorum*)) during spring and also winter after prescribed burning (Hobbs and Spowart 1984),

and asters (*Aster* spp.) and arrowleaf balsamroot (*Balsamorhiza sagittata*; Smith 1954, Stelfox 1976, Van Dyke 1983, Hobbs and Spowart 1984, Tilley et al. 2012). Bighorn sheep may also opportunistically include some browse in their diet, such as willows (*Salix* spp.), Douglas maple (*Acer glabrum*), Saskatoon (*Amelanchier alnifolia*), antelope-bush (*Purshia tridentata*), and mock orange (*Philadelphus lewisii*; Shackleton 1999). Smith (1954) observed substantial use of arrowleaf balsamroot shoots and roots by bighorn sheep in Idaho. Tasseled Cap greenness may not have predicted habitat selection by bighorns because some of these palatable plants may not have spectral signatures that correspond with high values of the greenness index. Potential reasons include coloration which is not naturally a vibrant green (e.g., arrowleaf balsamroot has leaves that are silvery white to green and flowers that are yellow) or in the absence of fire, there may be a buildup of decadent grass which would also not reflect a “high” greenness value. Coloration of plants is determined by a number of factors, including chlorophyll content, cuticle thickness, presence of pubescence or hairs on leaf surfaces, and the ratio of photosynthetic surface to structural or decadent plant components (Lillesand and Kiefer 2015). A given pixel in a landscape may be dominated by an undesirable or non-green species, but have high quality forage intermixed or vertically beneath the dominant species. Greenness indices may only be useful for comparing a given vegetation type (especially grass or forb vegetation) between years or different times of year. In addition, even if the “greenness” of a plant is appropriately reflected, the plant may not be preferred by bighorns or could actually be toxic and unpalatable.

Greenness values also may not have represented forage that was preferred by or available to bighorn sheep based on our selection of quantiles (i.e., the range of values to include in each greenness category). To correct for this, sensitivity analysis could be performed to determine which greenness values appear to be most attractive to bighorn sheep before designating forage

area polygons. This could be done, for example, by dividing greenness values into more quantiles. After preference for greenness values was determined, forage polygons could be defined based on these findings. Additional complication may have resulted from our selection of forage areas ≥ 2 ha. Again, sensitivity analysis to different patch sizes (e.g., 0.5 ha, 1.0 ha, 1.5 ha, and 2.0 ha) could be used to determine what patch sizes bighorn sheep are willing to use.

Biological reasons may also explain why our forage variables were poor predictors of habitat selection by bighorn sheep. Sheep are specialized grazers. Their teeth are adapted to grazing and they have a larger rumen compared to deer of equal size (Geist 1971), so they have the ability to live on hard, abrasive, dry plants. Therefore, they may be able to exploit areas of poor forage that other herbivores cannot (Geist 1971). Although bighorns may select more abundant, succulent forage in the absence of predation risk, they may be trading off this higher quality forage for more security (Festa-Bianchet 1988, Berger 1991, Rachlow and Bowyer 1998, Berkley 2005).

For these reasons, directly measuring the biomass and nutritional quality of available forage across the landscape would likely allow our model to better predict the importance of forage in habitat selection by bighorns (Shannon et al. 1975). Forage biomass is commonly measured by clipping, drying and weighing plants on plots (Shannon et al. 1975, Stelfox 1976, Wagoner 2011), and wet chemistry techniques are used for determining nutritional value of available plants directly related to survival and reproduction (i.e., digestible energy and protein) (Krausman et al. 1989, Willis et al. 2009). Further, plant biomass and nutritional quality could be combined to estimate nutritional carrying capacity using methods of Hobbs and Swift (1985) and Hanley et al. (2012). However these measures are time-consuming and difficult to apply across a large landscape. Using a combination of ground-based measurements and remote-

sensing, as demonstrated by Hebblewhite and Merrill (2011), to model forage availability, or using a model based on topographic variables to predict potential vegetation might be more useful (Franklin 1995). However, extensive sampling would still be required for estimation, as well as use as a training set for the model.

In addition to selecting for lower canopy cover, bighorns of all demographic groups and seasons selected steeper slopes, with the exception of males during the winter. As part of their predator-evasion strategy, bighorn sheep are generally associated with steep slopes, so this finding was consistent with other studies (Dicus 2002, DeCesare and Pletscher 2006, Bleich et al. 2009). We also expected distance to escape terrain would be a significant predictor of habitat selection because our variable for escape terrain was defined, in part, by slope (slopes $\geq 27^\circ$). However escape terrain and other topographic variables (i.e. aspect, ruggedness, and slope \times ruggedness) did not consistently predict habitat selection even though many of these variables are common in habitat selection models (Bailey 1980, Berger 1991, Rubin et al. 2002, 2009, DeCesare and Pletscher 2006) and habitat evaluations (Geist 1971, Stelfox 1976, Van Dyke et al. 1983, Taylor et al. 1998) for bighorns throughout their range.

Multiple studies have found escape terrain to be an important habitat feature (Stemp 1983, Risenhoover and Bailey 1985, McKinney et al. 2003, Bleich et al. 2009), but results can be difficult to interpret or compare because studies vary in how escape terrain is defined, whether qualitatively (Stemp 1983, Gionfriddo and Krausman 1986, Wakelyn 1987, Rachlow and Bowyer 1998) or quantitatively (Smith et al. 1991, Dicus 2002, McKinney et al. 2003, Bleich et al. 2009). When escape terrain is defined quantitatively, it is often delineated using slope and/or ruggedness and sometimes a minimum patch size or buffer (e.g. 150-m buffer zone with 40-60% slopes – McKinney et al. 2003). Similar to our results, Bleich et al. (2009) found that bighorns

selected for steeper slopes and lower terrain roughness and did not indicate selection for aspect. However, although our definition of escape terrain was similar to that of Bleich et al. (2009), we observed different results. Bleich et al. (2009) found that sheep were more likely to be near escape terrain, but we found that distance to escape terrain rarely predicted habitat selection by bighorns when slope was also included in the model candidate sets.

Because escape terrain was defined, in part, by slope, escape terrain and slope were the most highly correlated of variables in our models ($R = 0.52$). Although slope was a better predictor of habitat selection than escape terrain, they may be functionally interchangeable (i.e. they may substitute for each other). For example, in the only population-level model where slope did not significantly predict habitat selection (males during winter, Tables 5 and 6), escape terrain did significantly predict habitat selection. Overall, steep slopes were more important than escape terrain as we defined it, and redefining escape terrain with a higher minimum slope (e.g. $\geq 30^\circ$) could potentially make it a better predictor of habitat selection by bighorns.

Besides its correlation with slope, our definition of escape terrain may have influenced its usefulness in predicting habitat selection of bighorns. We excluded patches of escape terrain ≤ 2 ha, but sheep in our study may use smaller patches as seen by DeCesare and Pletscher (2006), who observed sheep using patches of escape terrain as small as 0.7 ha. Sensitivity analysis, as previously suggested for determining patch size for forage areas, may also be beneficial for assessing the lower limit of escape terrain patch sizes used by bighorn sheep. For example, escape terrain patch sizes to compare in a sensitivity analysis may include 0.7 ha (DeCesare and Pletscher 2006), 1.6 ha (Idaho Bureau of Land Management 1997), and 2.0 ha (Smith et al. 1991). In addition, sheep use escape terrain for different activities or time periods (Geist 1971, Stemp 1983) and the area of escape terrain needed may vary by the purpose for which it will be

used. For example, Van Dyke et al. (1983) indicated that cliffs < 0.16 ha can be used for bedding and thermal areas, but to provide escape terrain, cliffs need to be ≥ 0.16 ha and to suffice as a lambing area, cliffs need to be ≥ 2 ha. We did not measure activity in our study, so were unable to assess use of terrain based on activity. Bighorns are primarily diurnal, thus may use habitat during the day very differently than at night. At night, for example, bighorns may limit their habitat use to more secure areas such as cliffs, which are common bedding areas (Stemp 1983). However, during the day, they may move further from secure areas to forage, and bouts of foraging may also vary by time of day (Geist 1971). Therefore, our analysis, which included data from all time periods, may have reduced our ability to detect the value of escape terrain.

Another limitation of our analysis is that we did not take into account that sheep may be willing to range further from escape terrain if multiple “routes” of escape are available as suggested by Van Dyke et al. (1983) and implied by others evaluating habitat (Singer et al. 2000). For example, if escape terrain is spatially arranged in a manner that allows bighorns to flee from predators in either of 2 different directions, bighorns may feel more secure with this extra avenue of escape. In addition, some of the bighorns in our study resided near the town of Loomis and may not have used escape terrain as frequently because they were more habituated to human activity and human presence reduced the threat of predation (Kittle et al. 2008:172, Kertson et al. 2011).

Similar to escape terrain, ruggedness was a poor predictor of habitat selection by bighorns, predicting selection in only one season for one demographic group. However, as we expected and is well-documented (Geist 1971, Bleich et al. 1997, Rachlow and Bowyer 1998), female bighorns selected for more rugged areas during the lambing season, when they are most

sensitive to predation (Festa-Bianchet 1988, Berger 1991). Ruggedness may not have been a strong predictor of habitat selection in other models because sheep may select for ruggedness at larger spatial scales than we measured (e.g., when selecting home ranges within the landscape, Johnson 1980). This is likely because the entire Sinlahekin Valley has a high degree of ruggedness compared to other valleys within the landscape.

Although aspect, unlike ruggedness, was present in a high percentage of top models (annual-88%, lambing-68%, summer-78%, winter-82%), it also proved to be a poor predictor of habitat selection by bighorns. We expected bighorns to select for south and west aspects during the winter and lambing seasons to take advantage of high solar heat loads that may provide softer snow for better foraging, early vegetation, and warmth (Geist 1971, Stelfox 1976, Shannon et al. 1975, Shackleton 1999, Valdez and Krausman 1999, Singer et al. 2000). However, aspect was only a significant predictor of habitat selection by female bighorns in summer, when they selected for more south and west-facing slopes. Perhaps a solar radiation index would be a better predictor of winter habitat selection by bighorns, as reported by DeCesare and Pletscher (2006), because it combines latitude, slope and aspect to more directly measure the accumulation of radiant energy.

Our relatively small sample size (21 sheep, and 19 with useable data) may have influenced our ability to detect subtle patterns of habitat selection. However, our sample size was approximately 21% of the estimated population size (90-95 individuals, WDFW 2014) in our study area during the second year of our study. Therefore, our sample size, as a percent of the upper population estimate, is comparable to that (~11%) of DeCesare and Pletscher (2006), and thus likely adequately represents the population. However, the number of locations varied greatly among individuals and seasons (i.e., 28 to 436) because some GPS collars performed

poorly or were programmed incorrectly (Appendix A) and the topography sometimes restricted high fix rates. To ensure we used the highest quality data possible, we removed sheep that did not have locations for at least half the season, ensured habitat was represented by ≥ 10 random points/km², and removed erroneous locations.

Although our study created models predicting habitat choices made by bighorn sheep in the SWA, future research should be directed at establishing the fitness value of habitat features, especially the actual predation risk and nutritional value of areas with lower canopy cover (Toweill and Geist 1999, DeCesare and Pletscher 2006). Since 2005, extensive forest thinning (303.5 ha) and prescribed fire (768.9 ha) has been employed in the SWA (WDFW 2014) to reduce tree encroachment and increase forage. Determining whether bighorns not only select treated areas, but also whether these treatments increase adult and juvenile survival and reproductive rates, would benefit land managers in the region and across the range of bighorn sheep.

In addition, habitat loss and sedentariness is detrimental to bighorn sheep populations (Wakelyn 1987, Risenhoover et al. 1988) and after visually examining locations to detect seasonal movement patterns of bighorns in a GIS, we determined bighorns in the Sinlahekin Valley were fairly sedentary (non-migratory). Risenhoover et al. (1988) emphasized the importance of not only protecting and expanding remaining bighorn habitats, but also prioritizing migration corridors through identification of factors limiting movement of bighorns and then intensively managing these corridors to encourage movement. Further research should examine how canopy cover and other habitat features influence dispersal between the Sinlahekin herd and nearby (~14 km away) Mount Hull herd (Appendix B). Movement between these 2 herds has not been documented, however individual sheep have been known to travel between the Mount

Hull herd and a herd approximately 58 km south near Omak Lake (J. C. Heinlen, personal communication). Finally, we examined only selection of habitat features within the bighorn's home range (3rd order selection, Johnson 1980), but because animals may select for different habitat features at different spatial and temporal scales (Kittle et al. 2008, van Beest et al. 2010), further insight into habitat choices made by bighorns may be gained by examining additional scales.

MANAGEMENT IMPLICATIONS

Active restoration for bighorn sheep habitat

Our results, similar to those of other investigations (Risenhoover 1981, Smith et al. 1999), suggest that bighorn sheep select areas with lower canopy cover; thus restoring or maintaining open habitat in areas with conifer encroachment may influence movements and increase the value of the habitat for bighorn sheep. Because of extensive changes to interior forest communities over the last century (Hessburg and Agee 2003), the effects of natural or prescribed fires alone will likely be insufficient for restoring to pre-fire suppression landscapes (Arno and Fiedler 2005). Instead, forest thinning and prescribed burning should be applied at stand to landscape scales to maintain and expand suitable habitat for bighorn sheep. However, care should be taken when planning and implementing (e.g. Harrod et al. 1999, Demyan et al. 2006) habitat improvements to minimize negative effects (e.g., loss of forage through inappropriate burn timing or too much area burned at once, or introduction/germination of exotic or invasive species via soil disturbance and tree removal methods) and maximize positive outcomes (e.g., protecting desired vegetation and promoting reseeding of preferred grasses and forbs; Agee 1996). Prescribed burning should be applied before the growing season, especially before

inflorescence, but can also be done in the fall (Peek et al. 1979, Agee and Lolley 2006).

Prescribed burns should be low to medium intensity, and selective thinning should occur prior to burning to potentially decrease intensity (Agee 1996) and salvage marketable trees, providing revenue to fund management activities. Because fire suppression can cause fuel-loading (build-up of duff, litter and woody debris, Cooper 1960), care should be taken to prevent mortality of old growth trees (Agee 1996) in areas of high fuel loads (and protect other remaining trees if necessary). Mechanical reductions of woody fuels may be necessary prior to reintroduction of fire as a process (Arno and Fiedler 2005). Conifers that have encroached into aspen (*Populus tremuloides*) stands (or areas nearby) should be removed to yield higher forage biomass and potentially encourage greater proportions of herbs rather than shrubs (Mueggler 1985).

Specifics of active management

Opening of the landscape through complete removal of trees might be intuitively appealing, but is not realistic or appropriate for a number of reasons. There were old, large-diameter trees present in the Sinlahekin historically, and many of these persist today (Haeuser 2014), suggesting that historic forest structure did not impede bighorn use of the Sinlahekin. Grass production, important for bighorn sheep, may actually decline on drier slope expositions due to loss of facilitative shading effects (Naumburg and DeWald 1999, Scholes and Archer 1997). A number of wood-dependent species could be negatively impacted, such as woodpeckers (e.g., pileated woodpecker, *Dryocopus pileatus*) and the northern goshawk (*Accipiter gentilis*). Bighorns themselves have been observed in the Sinlahekin bedding just inside the edge of small clumps of trees during summer, and use of forested areas by bighorns has been observed elsewhere (Smith 1954). Finally, there would likely be substantial public

opposition to such dramatic landscape alterations in the Sinlahekin, due to its popularity as a recreational area.

Treatments designed to create a patchy low-density structure are most likely to meet both the needs of bighorns and co-occurring species. Although bighorns might simply require long sight-lines and lack of forest canopy suppression of forage, the needs of other organisms can be accounted for by further considering the creation of spatial complexity, snags and down woody debris, and residual areas of high density trees (Larson and Churchill 2012, Graham and Jain 2005). Franklin et al. (2013) provide comprehensive guidance for restoration actions in dry forest types of Oregon's east Cascades; the principles and techniques described therein are relevant for the forests of the Sinlahekin. Management guidelines should take historic fire intervals (e.g. Demyan et al. 2006) into consideration and attempt to mimic natural fire sequences once the habitat has been restored to pre-fire suppression status to maintain suitable habitat for bighorn sheep and other wildlife adapted to these habitat types.

Spatial aspects of prioritizing treatment areas

The results of this work suggest that areas of the Sinlahekin in proximity to escape terrain that have experienced increases in forest density should be prioritized for restoration thinning and burning, and habitat quality augmentation such as seeding of native grasses and forbs. Management goals should not only include improvement of existing habitat, but also focus on adjacent habitat and potential migration / movement corridors between suitable habitat to encourage herd movement and habitat expansion (Risenhoover et al. 1988, Taylor et al. 1998). At landscape scales, areas that include steep slopes should be prioritized to expand well-connected bighorn habitat. Locally, slopes around Fish Lake, north-facing slopes (because of greater increases in forest density as a result of more mesic site conditions) in the Loomis-

Tonasket corridor, and other areas adjacent to existing bighorn sheep habitat should be considered for restoration actions. In addition, restoration efforts focused on areas low in understory species richness may return maximum benefits (Dodson et al. 2008).

Ideally, habitat improvement would occur on adjacent lands outside the SWA and the surrounding area could be used as a model for integrated restoration of landscapes incorporating open grassland, shrublands, and open-forest landscapes across the range of local bighorn sheep populations. However, management coordination would have to occur across ownerships, increasing the complexity of achieving this objective (Lindenmayer and Franklin 2002).

Treatment impacts

Restoration actions such as thinning and use of prescribed fire could promote growth of shrubs, some of which may be valuable forage. However, high densities of shrubs could be detrimental. A study in the Blue Mountains of Oregon showed that browsing by deer and elk prevented shrub establishment and favored development of grasses and forbs (Edgerton 1987). The SWA does not support an elk population, but does support a large deer population (WDFW 2006), including an increasing population of white-tailed deer, which may help prevent shrub encroachment. In addition, seed conservation programs are beneficial because soil disturbances can also introduce or encourage the spread of invasive plant species (Taylor et al. 1998). Reseeding disturbed areas with a mix of desired grasses and forbs (i.e. native vegetation palatable by bighorn sheep and possibly mule deer) should promote growth of these desirable species, thus increasing forage for bighorn sheep and avoiding costly weed control.

A number of wildlife species, including some with endangered or conservation status, require or facultatively use open habitats (Swanson et al. 2014). Management for bighorn sheep

could function as an “umbrella species” strategy, where smaller or more obscure organisms benefit from restoration activities focused on bighorns. Although the umbrella species concept may not ensure conservation of all species in a landscape or region (Roberge and Angelstam 2004), it may still have value for the conservation of groups of organisms associated with a given habitat type (Fleishman et al. 2000, Suter et al. 2002). The bighorn in the Sinlahekin Valley meets the criteria for an effective umbrella species due to its relative lack of use of the landscape within the SWA and its sensitivity to the loss of open conditions. Restoring relatively open forest stands in the Sinlahekin may benefit a number of species common in historic ponderosa pine forests, including flammulated owls (*Psiloscops flammeolus*; Lehmkuhl et al. 2007), white-headed woodpeckers (*Picoides albolarveatus*), pygmy nuthatches (*Sitta pygmaea*), mule deer (*Odocoileus hemionus*, Arno et al. 1995), and a number of butterflies (order Lepidoptera; Waltz and Covington 2004).

Conclusion

An important step to seeing this and other habitat improvement / restoration projects succeed is the active recruitment of public support and partnering. Educational information should be disseminated through a variety of avenues (e.g. internet, pamphlets, seminars, meetings) to reach, and gain support from, the maximum number of individuals and organizations. Emphasis should be placed on how these restoration treatments will not only benefit a plethora of wildlife species, but will also improve overall forest health. Improvements such as reducing the risk of insect and disease outbreaks and reducing hazardous fuel loads, thereby protecting humans and the areas in which we live and recreate, may have greater influence on obtaining public support, especially in light of recent, catastrophic fires (e.g. Okanogan Complex Fire, Appendix C).

RSF models can be used by state and federal agencies to plan forest restoration at a landscape scale to manage for bighorn sheep and other species that have adapted to similar habitat types. Our data represent a baseline of use before and during habitat restoration treatments, and collaring additional sheep (with the intent of monitoring habitat use) now could help assess whether restoration efforts were successful and may guide future restoration efforts (assist in determining suitable locations for treatments, as well as type and intensity of treatments).

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Associate Editor:

APPENDIX A. DATA ACQUISITION LIMITATIONS

Data acquisition was limited by the frequency of ARGOS uploads (which was a programming choice/option) and could not be corrected via the ARGOS system after the collars were deployed on bighorns. Our 14-day interval for uploading to ARGOS only obtained approximately 60-67% of location data. Because of the short time interval between attempted fixes (i.e., every 5 hours), the number of fixes that accumulated on GPS collars between ARGOS uploads was too large to be completely transferred during 1 upload of 90 seconds. Future studies attempting to use this GPS/ARGOS location system need to evaluate how much data will be on the collar and how frequent ARGOS uploads need to be to obtain all location data. Ninety seconds is currently the maximum time length of an ARGOS upload and more frequent (e.g., every 7 days) uploads would be needed for sufficient data transfer when collars are programmed to obtain fixes at short time intervals.

APPENDIX B. WASHINGTON BIGHORN SHEEP HERDS

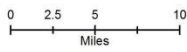


Source: WDFW. 2015. Conservation, Wildlife Health, Bighorn Sheep and Pneumonia, Washington bighorn sheep herds.
<http://wdfw.wa.gov/conservation/health/pneumonia/graphics/bighorn_sheep_herds.gif>.
Accessed 25 Aug 2015.

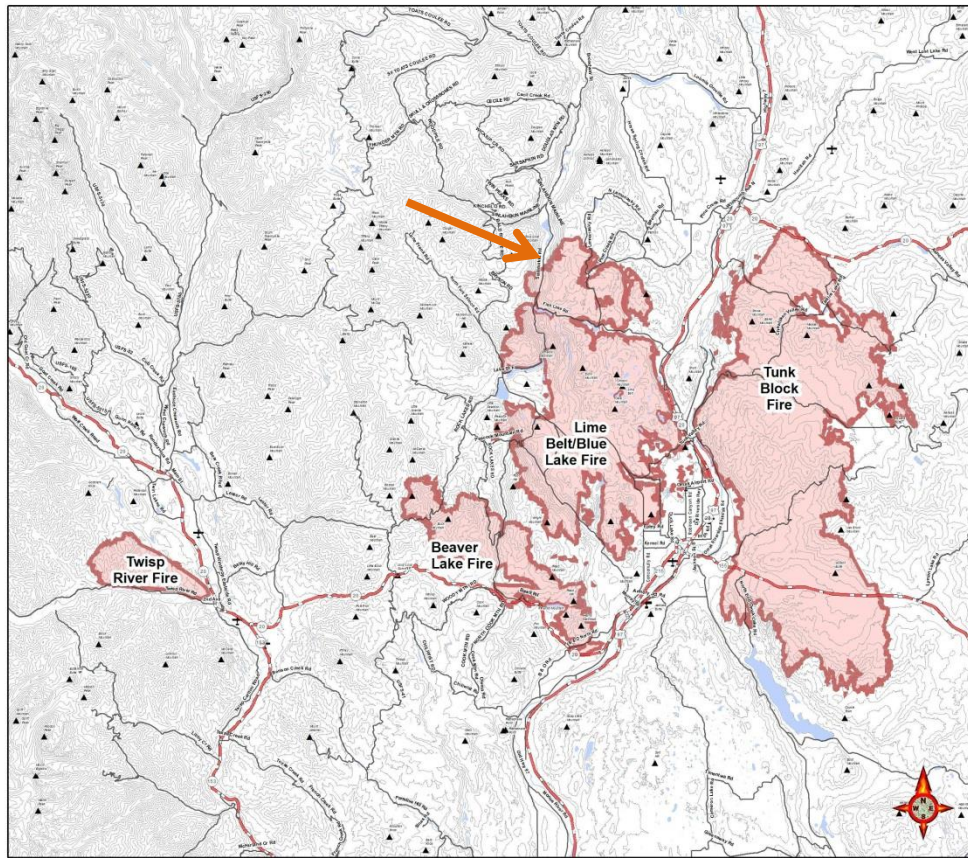
APPENDIX C. OKANOGAN COMPLEX FIRE

**OKANOGAN
COMPLEX FIRE**
Public Information Map
08/22/2015
Approx: 222,484 ac

- ▲ Summits
- Fire Area
- Roads
- ~ 200-ft Contours



More Information:
<http://inciweb.nwcg.gov>



Note: The orange arrow shows the Lime Belt / Blue Lake Fire burning north and west into the southern part of the Sinlahekin Valley study area near Blue Lake.