California Fish and Game 105(4):205-224; 2019

Habitat selection by bighorn sheep in a mesic ecosystem: the San Rafael Mountains, California, USA

VERNON C. BLEICH[1]*, MARCUS E. BLUM[2], KEVIN T. SHOEMAKER[2], DIEGO SUSTAITA[3], AND STEPHEN A. HOLL[4†]

[1] *Sierra Nevada Bighorn Sheep Recovery Program, California Department of Fish and Game, 407 West Line Street, Bishop, CA 93514, USA*

[2] *Department of Natural Resources and Environmental Science, University of Nevada Reno, Mail Stop 186, 1664 North Virginia Street, Reno, NV 89557, USA*

[3] *Department of Biology, California State University Northridge, 18111 Nordhoff Street, Northridge, CA 91330, USA*

[4] *Steve Holl Consulting, 7049 Pine View Drive, Folsom, CA 95630, USA*

Present address: Department of Natural Resources and Environmental Science, University of Nevada Reno, Mail Stop 186, 1664 North Virginia Street, Reno, NV 89557 USA (VCB)

Present address: Department of Biological Sciences, California State University San Marcos, 333 South Twin Oaks Valley Road, San Marcos, CA 92096 USA (DS)

**Corresponding Author:* vcbleich@gmail.com

[†]*Deceased*

Bighorn sheep (*Ovis canadensis*) were extirpated from the San Rafael Mountains, Ventura County, California, about 1915, and remained so for 70 years. They were reintroduced to that range, which is near the western extreme of their historical distribution, in 1985 and 1987. We used aerial telemetry to investigate habitat selection by 18 bighorn sheep from 1985 to 1989. Resource selection showed some support for both sex and seasonal differences, but only seasonal variations appeared in the top model. Relative to availability, bighorn sheep selected locations closer to water and farther from roads, with higher elevations, steeper slopes and increased terrain ruggedness, and areas that had burned recently, and had lower concentrations of xeric, mesic, and conifer habitat types during the summer. These results generally are consistent with observations of habitat use by bighorn sheep comprising the source population in the San Gabriel Mountains. Our results also support previous reports that burned areas, whether the result of natural or prescribed fire, are an important component of bighorn sheep habitat dominated by chaparral vegetation. Further, these results justify the use of prescribed fire to maintain high-quality habitat for bighorn sheep in the study area and elsewhere in the transverse range of California. The finding of seasonal differences in resource selection probabilities will facilitate development of an efficacious aerial survey strategy, and provide investigators with an objective method of assessing habitat for future reintroductions.

Key words: bighorn sheep, California, chaparral, fire history, habitat selection, *Ovis canadensis*, reintroduction, San Rafael Mountains, translocation

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Bighorn sheep (*Ovis canadensis*) are among the most recognizable large mammals inhabiting North America. The geographic range of these iconic ungulates extends southward ~3,500 km from the northern Rocky Mountains in British Columbia, Canada (approximate latitude 54° N) to the Sierra de la Giganta, Baja California Sur, Mexico (approximate latitude 24° N). Historically, the distribution of bighorn sheep extended eastward from approximate longitude 127° W in British Columbia (Cowan 1940; Demarchi et al. 2000) to the badlands of North Dakota and South Dakota (approximate longitude 100° W), a distance of ~1,600 km. Thus, the distribution of bighorn sheep included parts of two provinces in Canada, portions of 15 American states, and ≥6 states in Mexico (Baker and Greer 1962; Monson 1980; Garcia-Mendoza and Lopez-Gonzalez 2013). The number of bighorn sheep that once inhabited the United States is open to question (Welles 1962; Valdez 1988), but there are far fewer individuals with a more restricted distribution than historically was the case (Buechner 1960). Bighorn sheep were extirpated from the San Rafael Mountains, Ventura County, California, near the westernmost extreme of their distribution in the continental United States (Buechner 1960), by about 1915 (Freel 1984). Factors contributing to this extirpation are unconfirmed, but likely include illegal hunting, diseases contracted from domestic sheep, and competition with domestic livestock (Buechner 1960; Freel 1984).

In 1971 and 1972, Richard A. Weaver of the California Department of Fish and Game (CDFG) conducted several overflights and on-the-ground evaluations of potential areas suitable for the reintroduction (*sensu* Hale and Koprowski 2018) of bighorn sheep to the San Rafael Mountains, near the western terminus of California's transverse range (Figure 1). Subsequent investigations by DeYoung (1975) and Fox (1983) led to the conclusion that San Rafael Peak and Cobblestone Mountain were suitable locations at which animals could be reestablished in that range (Freel 1984). As a result, bighorn sheep were reintroduced to the San Rafael Mountains in 1985 and 1987 (Peterson and Peterson 1987; Bleich et al. 1990). Our objectives are to explore habitat selection by bighorn sheep immediately following the reintroduction, develop models to provide an objective method of assessing

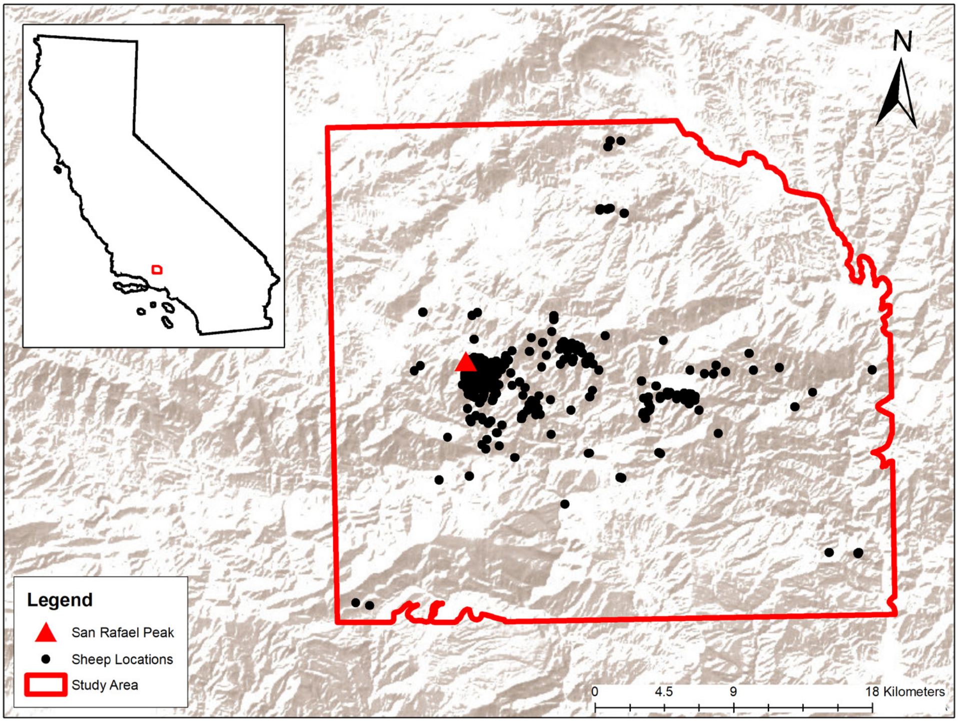

Figure 1. The study area, delineated by the red line in the San Rafael Mountains, Ventura County, is near the western terminus of California's transverse range, which extends nearly 400 km from west to east in Santa Barbara, Ventura, Los Angeles, and San Bernardino counties, California, USA. The release site at San Rafael Peak, Ventura County, is shown for reference within the study area.

habitat suitability for future reintroductions, and to assist in development of an efficacious aerial survey strategy based on seasonal selection of habitat. We then use the results of those models to suggest habitat management options that likely will be of benefit to bighorn sheep conservation and are appropriate in that mesic environment.

METHODS

Study area

The transverse range in southern California extends nearly 400 km eastward from the Santa Ynez Mountains in Santa Barbara County to the Little San Bernardino Mountains, San Bernardino County. In the San Gabriel Mountains, the source of animals translocated to the San Rafael Mountains, the distribution of bighorn sheep ranges in elevation from approximately 300 m at the base of the cismontane side of the mountains to 3,350 m at Mt. San Antonio (Holl and Bleich 1983). Chaparral and coastal sage habitats are used heavily by mountain sheep and are widespread throughout the transverse range and are the dominant vegetation types on cismontane slopes in the San Gabriel Mountains below 1,800 m (Kuchler 1977; Holl and Bleich 1983).

Bighorn sheep occupy eight winter-spring seasonal ranges in the San Gabriel Mountains (Weaver et al. 1972; Holl and Bleich 1983), but habitat use is influenced strongly by periodic fire (Bleich et al. 2008; Holl and Bleich 2010; Holl et al. 2012). Habitat occupied by bighorn sheep in the San Gabriel Mountains has been described in detail elsewhere (Weaver et al. 1972; DeForge 1980; Holl and Bleich 1983, 2009, 2010; Bleich et al. 2008; Holl et al. 2012) and is similar to that in historically occupied areas of the San Rafael Mountains (DeYoung 1975; Fox 1983; Freel 1984). Further, the decision to use source stock from the San Gabriel Mountains was consistent with current recommendations for reintroductions, whereby ecological similarities between source and reintroduction locations should be a primary consideration (Wehausen 1989, Whiting et al. 2012; Brewer et al. 2014; Bleich et al. 2018; Coggins and Coggins 2018).

The San Rafael Mountains vary in elevation from about 75 m to 2,080 m. Vegetation consists predominately of chaparral and coastal sage scrub, with coniferous forests at upper elevations, riparian forests in canyon bottoms, and some grassy potreros scattered across the area (DeYoung 1975; Fox 1983; Freel 1984). Elsewhere, vegetation in the transverse range has been characterized in general terms as predominantly chaparral and coastal scrub with occasional woodlands, riparian communities, and grasslands (Soza et al. 2013).

Climate in the San Rafael and San Gabriel mountains is typical of Mediterranean ecosystems, with hot, dry summers and moist, mild winters (Bailey 1966). During winter, precipitation in both areas frequently occurs as snow at elevations above 1,500 m (Holl and Bleich 1983; Freel 1984). Except for grizzly bear (*Ursus arctos*; Storer and Tevis 1955), both mountain ranges support a full complement of native carnivores capable of preying on large ungulates, including bobcat (*Lynx rufus*), mountain lion (*Puma concolor*), and coyote (*Canis latrans*; Freel 1984). Black bear (*Ursus americanus*) likely colonized the western part of the transverse range following extirpation of the grizzly bear (Grinnell et al. 1937), but were introduced (*sensu* Hale and Koprowski 2018) to the San Gabriel Mountains in 1933 (Burghduff 1935).

In the early 1980s, >700 bighorn sheep inhabited the San Gabriel Mountains (Holl and Bleich 1983, 2009, 2010). That population has varied substantially in size over many decades (Holl et al. 2004), but evidence indicates it is isolated from other populations of bighorn sheep (Bleich et al. 1996; Buchalski et al. 2016). Mule deer (*Odocoileus hemionus*) are the only other native ungulate occupying the transverse range.

Reintroduction

In the early 1980s approximately 130 bighorn sheep occurred on the Cattle Canyon winter range in the San Gabriel Mountains (Holl and Bleich (1983). We used a drop-net to capture adult (≥1 year-of-age) bighorn sheep in Cattle Canyon (34.2555 N, 117.6842 W) in December 1985 and again in January 1987 (Kock et al. 1987; Bleich et al. 1990; Jessup et al. 2014). The drop-net was baited each morning with fermented apple pulp (Schmidt et al. 1978) and high-quality alfalfa hay, and after >1 month several dozen bighorn sheep were conditioned to the presence of a human and reliably coming to the trap site each day (Figure 2). A single drop of the net was sufficient to capture an adequate number of animals in 1985 and, again, in 1987.

Upon capture, animals were restrained physically, blindfolded, sedated with xylazine, and airlifted by helicopter to a nearby processing area (Jessup et al. 2014) where each was examined, biological samples were collected, ages were determined, and animals were fitted

Figure 2. Bighorn sheep were provided with high-quality alfalfa hay and fermented apple mash daily to ensure they would be 'under the net' when personnel arrived to implement the capture operation. Bill McIntyre, a volunteer representing the Society for the Conservation of Bighorn Sheep, carried out this critically important task in Cattle Canyon, San Gabriel Mountains, Los Angeles County, California, USA in 1985 and 1987 (photo © B. Moose Peterson).

with VHF telemetry collars incorporating a mortality sensor with a 6-hour delay (Mod 500, Telonics, Inc., Mesa, AZ, USA), or with individually identifiable marking collars. Animals then were placed in specially modified horse trailers and transported westward about 120 km to the San Rafael Mountains where they were held overnight in the trailers; alfalfa hay and water were provided *ad libitum* during confinement. During both years, we constructed a temporary corral at the release site proximate to San Rafael Peak in which animals would be held temporarily following aerial transport and, thereby, ensure all animals could be released simultaneously (Figure 3; Thompson et al. 2001).

Early in the morning following the 1985 capture event we used physical restraint to transfer each animal from the trailers to shipping crates (0.5 × 1.0 × 1.5 m) for aerial transport. Upon delivery to the release site, we transferred bighorn sheep to the corral where each was held for a short time ($\bar{x}$ = 4 h; range 2–6 h) before all animals were released simultaneously (Figure 3). To minimize disturbance, the 8-person handling crew was not extracted for several hours following release of the animals, and the corral was not retrieved until several weeks later.

Bighorn sheep captured in 1987 again were held overnight, but high winds precluded early morning transport to the release site. Thus, we held animals in the trailers for an additional 6 hours, after which they were placed in crates and transported by truck to an alternative release site at MacDonald Peak, ~6 km east of San Rafael Peak. Weather conditions improved substantially during vehicular transport and, upon arrival at MacDonald Peak, the animals were flown to San Rafael Peak and transferred from the crates to the corral as in

Figure 3. Bighorn sheep were held in a special enclosure for up to 6 hours to ensure that animals would be released as a single group at San Rafael Peak, San Rafael Mountains, Ventura County, California, USA in 1985 and 1987 (photo © B. Moose Peterson).

1985. Animals were held in the corral ($\overline{x}$ = 1.5 h; range 0.5–2.5 h) until the final individual was delivered, and then for an additional hour before being released simultaneously. Total time from capture to release in 1987 was ~7 h greater than in 1985.

Monitoring

We conducted telemetry flights from December 1985 to December 1989 at approximately 2-week intervals, weather permitting ($\overline{x}$ = 14.7 days between flights). We used a fixed-wing aircraft with an H-type antenna on each wing strut and located animals in a manner adapted from that described by Krausman et al. (1984). We plotted the location of each telemetered individual on a 7.5' United States Geological Survey (USGS) topographic map and converted those locations to digital format. Safety concerns precluded visual confirmation of locations determined by aerial telemetry (Bleich et al. 2001), but telemetry error polygons in similar terrain elsewhere in the transverse range were small ($\overline{x}$ = 0.098 km^2; Nicholson et al. 1997) relative to home ranges of bighorn sheep in the San Rafael Mountains ($\overline{x}$ = 25.24 ± 6.84 [SE] km^2).

Habitat modeling

We incorporated all locational data into a master file for further analysis. We used ArcGIS 10.4 (Environmental Systems Research Institute, Redlands, CA, USA) and multiple sources of digital data to project bighorn sheep locations and derive habitat features associated with each of those locations. We used Los Padres National Forest (LPNF) coverages of vegetation and fire history to derive habitat type and years since the most recent fire. Areas that had burned ≥30 years prior were treated as a single category given the uncertainty of what may represent a typical fire regime in the chaparral ecosystems of southern California (Keeley 2006). There is general agreement that fires historically were smaller than those that occur today and that most ignitions occurred during summer. Conflagrations occurring in the present, however, account for the bulk of the landscape affected by fire, and occur primarily during fall (Keeley and Fotheringham 2003). The historic fire regime likely involved several major fires per century that occurred at intervals of 30 to 40 years, and small fires have burned on winter-spring ranges used by bighorn sheep at fire return intervals of ≥ 20 years (Holl et al. 2012).

We removed habitat variables that did not appear in locations used by sheep, or that appeared very infrequently (inhibiting convergence of resource selection models). Habitat types removed were barren (0 used locations), lake (0 used locations), and urban land (0 used locations). Habitat types retained for analysis included conifer forest, xeric chaparral, mesic chaparral, coastal sage scrub, and oak woodland. We derived elevation, percent slope rise, and sine (-1 = due west and 1 = due east) and cosine of aspect (-1 = due south and 1 = due north) from a 10-m resolution USGS digital elevation model (http://nationalmap.gov/viewer.html). We used those data to calculate an index of terrain ruggedness (VRM; Sappington et al. 2007) and developed 3 such layers (neighborhood sizes of 3, 11, and 21) to account for multiple scales of ruggedness. We also created Euclidian distances from dirt roads or trails and from perennial streams using the LPNF coverages and the USGS National Hydrography Dataset (https://nhd.usgs.gov/).

Locations obtained with aerial telemetry were associated with larger errors than would have been the case with satellite collars incorporating GPS technology that have since become available, and complicated our ability to determine habitat type at each animal location. Therefore, we created a buffer of 0.098 km^2 around each location and calculated the percentage of each habitat type within those polygons (Bleich et al 2009). Additionally, we used those percentages to compute Shannon's diversity index for each location (Shannon 1948). Similarly, to address potential error with the topographic and distance layers (e.g., distance to water), we used the Zonal Statistics Tool in ArcGIS to compute average values across each buffered sheep location.

To represent resource units available to this translocated population, we generated 2 random locations for each animal location and used the same procedures to extract habitat attributes for each. These locations were drawn randomly from a defined study area that was delineated by creating a minimum convex hull around the used bighorn sheep locations and buffered by 1,000 m to account for potential movement by individuals (Bleich et al. 1997). The random and used locations were compiled into a single dataset for further analysis. No predictor variable was highly correlated ($r > |0.6|$) with any other, and we retained all of them for fitting resource selection models. We standardized all continuous predictor variables prior to calculating resource selection functions to facilitate comparison among variables.

We constructed resource selection models using mixed-effects logistic regression from the "glmmTMB" package in R 3.02 (Brooks et al. 2017). We first specified a full model that included all measured environmental covariates along with corresponding interactions with sex and season (Fall [September–November], Winter [December–February], Spring [March–May], and Summer [June–August]). Individual ID and year were included in the model as random intercept terms. Since the full model (all measured covariates along with corresponding interactions with sex and season) would not converge, and because the habitat-class covariates (percent cover of oak, coastal sage scrub, xeric chaparral, mesic chaparral, and conifer) were subject to a unit-sum constraint, we selected one habitat-class covariate (coastal sage scrub) for exclusion from the full model; this model (full model without coastal sage scrub) converged, and we therefore considered it to be our 'global' model for further model selection (see below). We tested the adequacy of the model fit for the global model by visualizing scaled (quantile) residuals and performing diagnostic tests (uniformity across the range of predictions, presence of excessive outliers, and overdispersion) based on these residuals (Hartig 2019).

To determine which of the 3 different terrain ruggedness scales was most informative, we fitted the global model with each of the 3 ruggedness indices in turn and compared model fit using Akaike's Information Criterion (AIC). The largest-scale terrain ruggedness measure (Ruggedness21) strongly outperformed the other variables (ΔAIC = 6.4), so this metric was used to represent ruggedness in the final model selection procedure. We then used a backward stepwise elimination procedure (implemented in the buildmer package in R, using AIC as the selection criterion; Voeten 2019) to select the best-fit model from all covariates and interaction terms included in the global model. This final model was used to generate partial-dependence plots and prediction maps, using the 'Raster Calculator' tool in ArcGIS 10.4, to aid in visualization of resource selection patterns across seasons.

To assess the predictive strength of our model, we used a modified form of leave-one-out cross-validation in which all telemetry locations from unique individual sheep were left out of model fitting in turn and subsequently were used for model validation (Shoemaker et al. 2018). In this cross-validation scheme, model performance was assessed using the area under the curve (AUC) metric from a Receiver Operating Characteristic analysis (Boyce et al. 2002).

RESULTS

We captured 21 bighorn sheep (16♀, 5 ♂) in December 1985 in Cattle Canyon, Los Angeles County, and released them at San Rafael Peak (34.6236 N, 119.0017 W) in the San Rafael Mountains, Ventura County (Figure 1). In January 1987 we again captured bighorn sheep in Cattle Canyon and released 15 (11 ♀, 4 ♂) at the same location. We used aerial telemetry locations (n = 757) from 4 ♂ and 14 ♀ individual bighorn sheep in our analyses ($\bar{x}$ = 42 locations*,* SD = 15.8*,* Range = 11–63).

Best performing model

We found little support for sex-based resource selection in that interactions between sex and environmental gradients were not present in the final model. We did, however, find variation in selection coefficients across seasons (Table 1; Figures 4 and 5). Bighorn sheep (males and females combined) selected higher elevations, steeper slopes (not significant during summer months), and more rugged terrain than were available across the landscape (Figure 4). Additionally, individuals selected areas closer to water (indicated by a negative regression coefficient) and areas further from roads across the landscape (Figure 4). Bighorn sheep also selected habitat patches that were burned more recently across all seasons (albeit

Table 1. Results from the top mixed-effects logistic regression model for bighorn sheep reintroduced to the San Rafael Mountains, Ventura County, California, 1985–1989. Beta estimates, standard errors, and *P*-values are reported to highlight population-level selection by bighorn sheep. Positive values denote selection and negative values indicate avoidance of continuous variables across the landscape. This relationship is reversed, however, for "distance to" variables (i.e., "Distance to Road" and "Distance to Water"). In addition, negative values for "Years Since Fire" indicate selection for areas that have burned more recently.

Habitat Variable	β	Standard Error	*P*-Value
Intercept	-1.54057	0.43137	< 0.001
Elevation	2.03356	0.14899	< 0.001
Slope	0.24706	0.17033	> 0.05
Ruggedness	0.45620	0.11609	< 0.001
Cos Aspect	-0.51838	0.11050	< 0.001
Sin Aspect	0.41345	0.08044	< 0.001
Distance to Road	0.34120	0.09090	< 0.001
Distance to Water	-0.59932	0.10983	< 0.001
Years Since Fire	-0.74212	0.13916	< 0.001
Conifer Forest	-1.15560	0.24510	< 0.001
Mesic Chaparral	-0.86246	0.21021	< 0.001
Xeric Chaparral	-0.60986	0.24576	< 0.05
Oak Woodland	-0.46081	0.10859	< 0.001
Slope:Winter	1.06979	0.27220	< 0.001
Slope:Spring	1.41257	0.30904	< 0.001
Slope:Fall	1.39987	0.33289	< 0.001
Fire:Winter	-0.40370	0.26175	> 0.05
Fire:Spring	-0.42629	0.27578	< 0.05
Fire:Fall	-1.05857	0.36822	< 0.01
Cos Aspect:Winter	0.24510	0.20415	> 0.05
Cos Aspect:Spring	0.71919	0.244410	< 0.01
Cos Aspect:Fall	0.20676	0.27810	> 0.05
Conifer:Winter	-0.08958	0.39389	> 0.05
Conifer:Spring	-0.06702	0.37636	> 0.05
Conifer:Fall	1.40517	0.52815	< 0.01
Xeric:Winter	-0.03937	0.39734	> 0.05
Xeric:Spring	-0.50633	0.40006	> 0.05
Xeric:Fall	1.14301	0.55355	< 0.05
Mesic:Winter	-0.13534	0.34901	> 0.05
Mesic:Spring	-0.27615	0.35380	> 0.05
Mesic:Fall	1.05927	0.46650	< 0.05

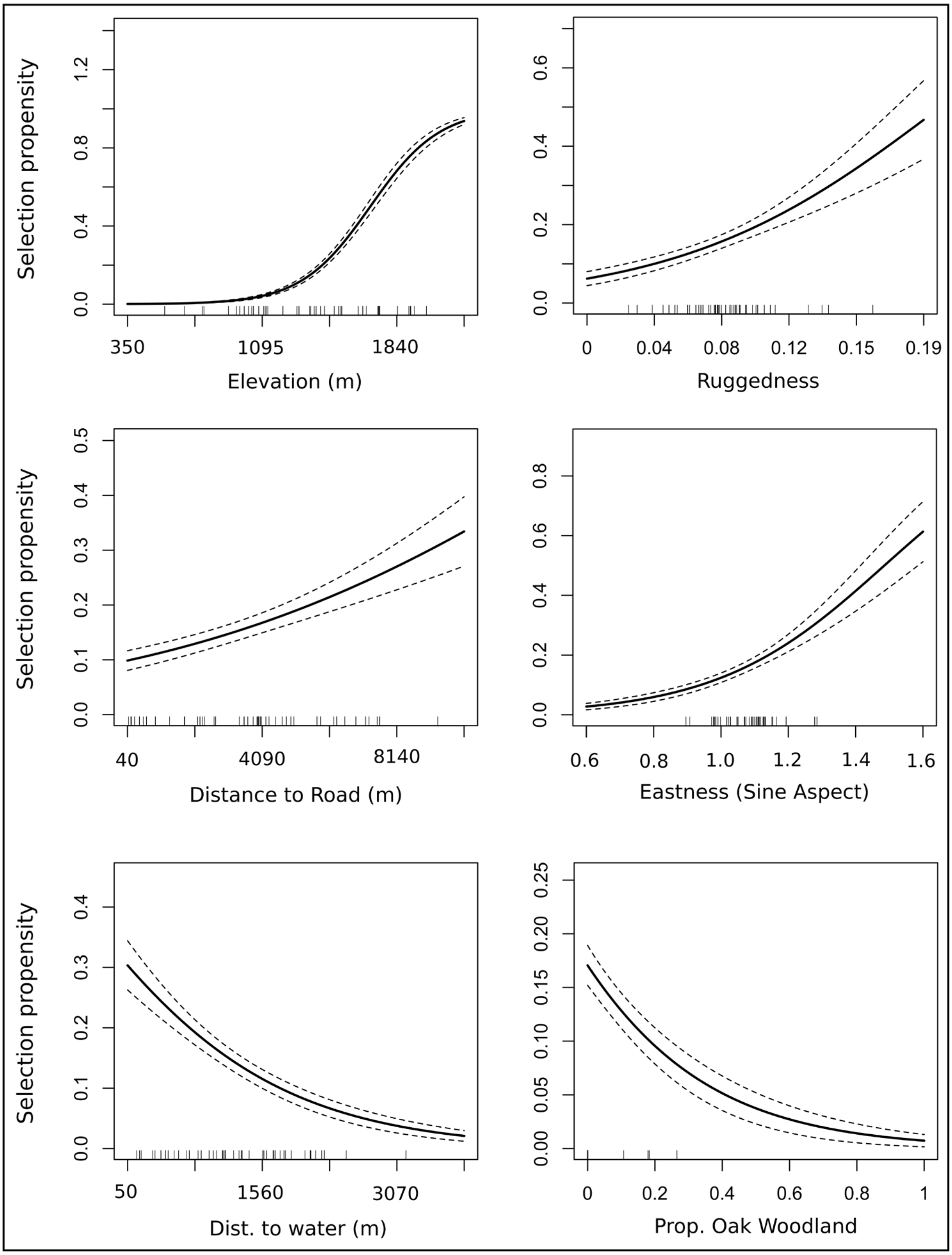

Figure 4. Partial dependence plots illustrating seasonally independent responses of bighorn sheep to environmental gradients in the San Rafael Mountains, California. Each panel represents a different environmental gradient, and each curve represents predictions from our best-performing resource selection model across each environmental gradient, with all other covariates held at mean values. Our best-performing resource selection model indicated little or no evidence for seasonal variation in selection propensity for all environmental gradients depicted in this figure. Dashed lines denote 95% confidence intervals.

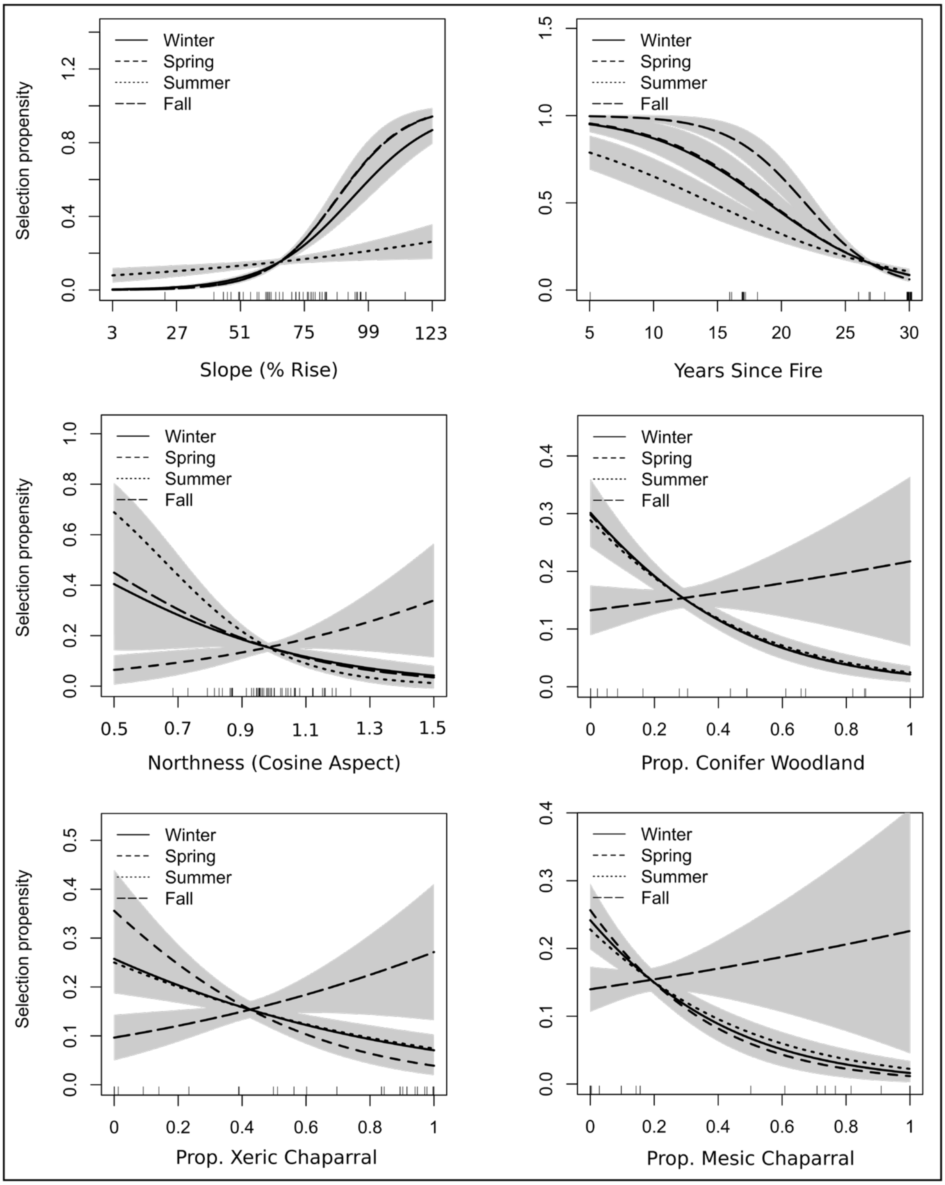

Figure 5. Partial dependence plots illustrating seasonally dependent responses of bighorn sheep to environmental gradients in the San Rafael Mountains, California. Each panel represents a different environmental gradient, and each curve represents season-specific predictions from our best-performing resource selection model across each environmental gradient, with all other covariates held at mean values. Our best-performing resource selection model included a seasonal interaction term for all environmental gradients depicted in this figure. Shaded areas denote 95% confidence intervals.

not significant during winter months; Figure 5). Magnitude of selection or avoidance varied by season in addition to some variables shifting between negative and positive effects on selection. Bighorn sheep selected southeastern slopes during summer and more northeastern slopes during spring, while fall and winter interaction terms were not significant (Table 1).

Although selection for topographic variables generally was consistent across seasons, selection for specific habitat types was less pronounced (Table 1). Seasonal variation in selection for habitat-classes was most pronounced in fall and summer. During fall, bighorn sheep selected areas with greater percentages of conifer cover, xeric chaparral, and mesic chaparral compared to summer, but selected for areas with lower concentrations of oak woodland, conifer cover, mesic chaparral, and xeric chaparral during summer. Additionally, the habitat diversity variable did not appear in any seasonal model, indicating that individuals did not select areas having a higher diversity of habitat types over areas with high percentages of specific habitats. Our cross validation returned an AUC value of 0.85, indicating strong predictive ability for our top resource selection model. Finally, we used the regression coefficients from the top model to predict bighorn sheep habitat use during each season (Figure 6).

DISCUSSION

Reintroductions have played an important role in the restoration of bighorn sheep to historically occupied areas (Brewer et al. 2014). Although post-translocation assessments are expensive and labor-intensive, such information is important for informing future management decisions (Thompson et al. 2001; Brewer et al. 2014; Tetzlaff et al. 2019). Nonetheless, increasing responsibilities among wildlife biologists working in state or federal agencies (Meine et al. 2006), declining operating budgets (Hutchins et al. 2009), and shifting priorities within management agencies (Capen 1989) often have precluded the timely assessment, analysis, or publication of results despite what appear to have been successful management actions, and such has been the case with bighorn sheep reintroduced to the San Rafael Mountains.

In our study, habitat selection was similar to that described by Holl and Bleich (1983) for bighorn sheep comprising the source population in the San Gabriel Mountains. The absence of sex as an interaction term, however, was surprising given that males generally range more widely than do females, but with females characteristically using areas most likely to enhance safety for themselves and offspring, and males seeking areas in which to maximize nutrient intake to be competitive during the mating season (Bleich et al. 1997).

The absence of a sex-interaction in the top model may be explained by several factors, among which are a lack of familiarity with the reintroduction site in that monitoring occurred for a period of time inadequate to allow segregation by habitat (Bowyer 2004) to develop into a regular pattern, an extended period of exploratory movements by bighorn sheep as they adapted to the new location (Thompson et al. 2001), small sample size of males, or the level of precision associated with telemetry data. If additional research on habitat selection in the San Rafael Mountains occurs, we anticipate that the long-term presence of this population in that range, combined with telemetry collars employing geographic positioning system technology will yield intersexual differences in habitat selection, a behavioral trait of polygynous ungulates that characteristically segregate by sex during their annual cycle (Bowyer 2004).

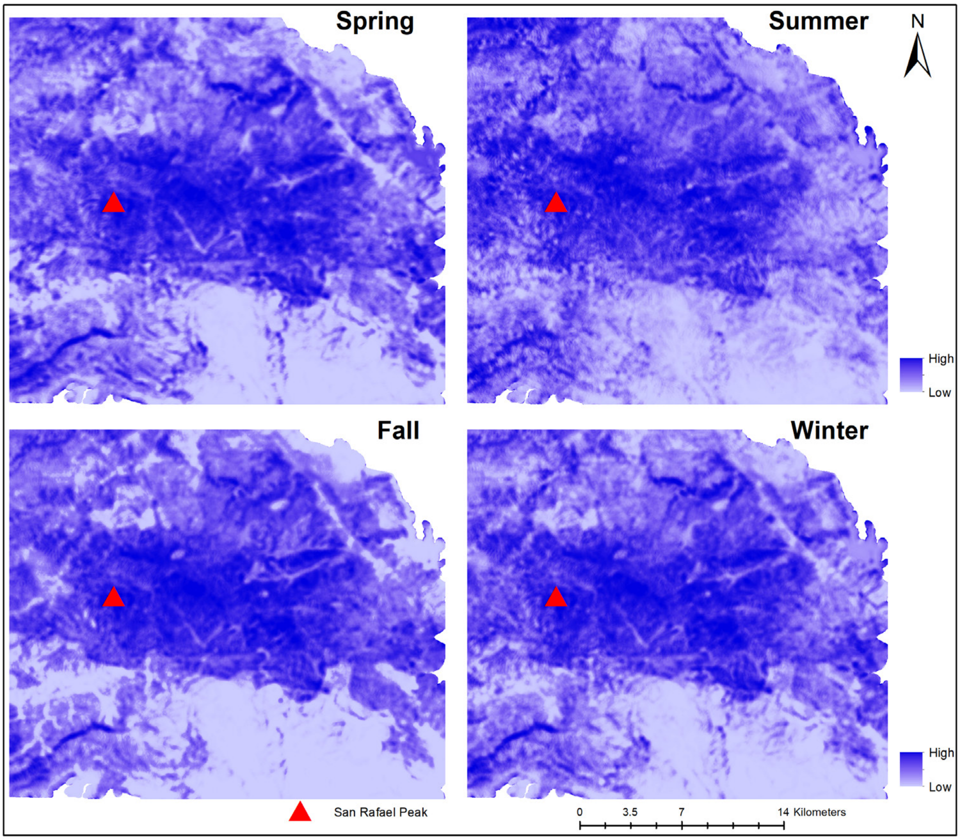

Figure 6. Prediction maps of resource selection during spring, summer, fall and winter seasons for a translocated population of bighorn sheep in the San Rafael Mountains, Ventura County, California, USA. Darker areas represent locations with higher selection probability, while lighter areas represent locations with lower selection probability based on seasonal resource selection functions, 1985–1989. For reference, the release site at San Rafael Peak is indicated on the maps.

Bighorn sheep demonstrated differential selection of habitat types on a seasonal basis, and prediction maps indicated areas of highest prediction probabilities were smaller in size during fall and summer when compared to winter or spring (Figure 6), results that may have occurred because we subdivided chaparral into subcategories rather than treating it as a single vegetation type. Nevertheless, bighorn sheep did select areas that had burned more recently than were available across the landscape, consistent with results from the San Gabriel Mountains (Bleich et al. 2008), and there was a strong seasonal effect during winter, spring and fall consistent with habitat use by herbivores dependent on open terrain and the best available forage (Risenhoover and Bailey 1980, 1985; Holl 1982; Bleich and Holl 1982; Etchberger et al. 1989). Chaparral is a fire-adapted plant community and bighorn sheep rely on recently burned areas both for nutritious forage and for openness, the latter being a key factor in detecting and evading predators (Bleich and Holl 1982; Holl and Bleich 1983, 2010; Bleich et al. 1997, 2008; Holl et al. 2012).

Terrain characteristics, such as slope, aspect, or ruggedness, are important attributes of bighorn sheep habitat (McCarty and Bailey 1994). Bighorn sheep selected higher elevations and more rugged terrain, but steepness of slope was important only during winter, spring, and summer (Table 1). Steepness of slope alone does not necessarily imply ruggedness, but still may enhance the ability of bighorn sheep to evade predation (Bleich et al. 1997). These results are consistent with those for bighorn sheep elsewhere in the transverse range (Bleich et al. 2009; Anderson et al. 2017; Anderson 2018) as well as bighorn sheep in general (McCarty and Bailey 1994; Bleich et al. 1997).

Bighorn sheep selected east-facing aspects during spring and fall, and south-facing slopes were selected during summer, but aspect did not appear in the winter model. Bleich et al. (1997), who also used aerial telemetry in their investigation of habitat selection by bighorn sheep in the Mojave Desert, did not include aspect in their analyses because of its sensitivity to resolution associated with the small size of aspect polygons relative to potential location error. Further, there was no selection for aspect by bighorn sheep in the Sonoran Desert when hot and cool seasons were compared, but females did avoid 'level' terrain (Andrew et al. 1999). Similarly, bighorn sheep in the San Bernardino Mountains demonstrated no significant selection for aspect (Bleich et al. 2009). Given the confounding nature of locational error and the absence of selection for aspect reported by others, we suggest investigators view selection of aspect reported here with some level of caution.

Overall, bighorn sheep in the San Rafael Mountains selected for areas closer to water and further from roads during all seasons, consistent with bighorn sheep inhabiting the Sonoran and Mojave deserts elsewhere in California (Bleich et al. 1997; Andrew et al. 1999). Our index to habitat diversity, however, failed to enter our models. This was somewhat surprising because an increase in precipitation occurs with elevation in the Mediterranean climate (Aschmann 1973) typical of the San Rafael Mountains and diversity of vegetation can enhance forage quality in some systems (Wehausen and Jaeger 2016). The absence of a diversity effect reported here may be explained by the short duration over which monitoring was carried out, extensive exploratory movements by reintroduced bighorn sheep, or other factors that are yet unrecognized.

Management Implications

Collectively, bighorn sheep selected areas closer to water when compared to random points and selected recently burned areas during all seasons, and the importance of topographic attributes is clear. These results are consistent with reports from elsewhere in the transverse range and provide useful information with which to evaluate the suitability of additional areas for reintroductions therein (Holl 1982). Moreover, seasonal effects on habitat selection and resulting selection probabilities (Figure 6) have important implications for the design or timing of aerial surveys, or interpretation of aerial survey data (Schaller and Junrang 1988; Bleich et al. 1997; Rubin and Bleich 2005; Wehausen and Bleich 2007).

Our results clearly demonstrate the importance of the role of fire to bighorn sheep in the San Rafael Mountains, and provide a platform upon which future investigators can base more complex models. Managing for habitat burned at intervals of ≤15 years and that is selected by bighorn sheep elsewhere in the transverse ranges (Bleich et al. 2008) is inconsistent, however, with the natural variation in fire-return intervals in coastal chaparral systems. Moreover, fires occurring at <15-year intervals increase the spread of exotic herbaceous plants (Keeley and Fotheringham 2003). The careful application of prescribed fire to simulate a more natural fire regime will, however, enhance habitat for bighorn sheep

(Holl et al. 2012) and must receive serious consideration for the population to remain viable.

Legislation (U.S. Congress 1994) enacted since the reintroduction currently presents serious obstacles to the application of prescribed fire in wilderness (Bleich 2016). As a result, administrators now must consider actions necessary to maintain a tangible resource and a near-intact ecosystem relative to the sociological (Spurr 1966), intangible (Larsen 1997; Fredrickson and Anderson 1999; Tin 2012), or sociopolitical (Corliss 2019) aspects of wilderness. Current fire management strategies and the constraints imposed by Congress may jeopardize the ability to manage habitat for the benefit of bighorn sheep and other species dependent upon early successional stages of chaparral vegetation.

This population also may provide a refugium for bighorn sheep adapted specifically to the relatively mesic habitats typical of the western transverse range, and could be a source of reintroduction stock should an outbreak of respiratory disease among bighorn sheep inhabiting the San Gabriel or San Bernardino mountains result in a catastrophic loss (Schommer and Woolever 2008; Clifford et al. 2009). In the absence of a strategy to restore a natural fire regime, however, the utility of the San Rafael Mountains as a refugium for a unique ecotype of bighorn sheep is in question.

ACKNOWLEDGMENTS

This paper is dedicated to the memory of CDFG Wildlife Biologist Richard A. Weaver—known throughout the American West as Mr. Bighorn—whose efforts on behalf of the conservation of bighorn sheep are legendary and long will be remembered. Funding was provided by the Society for the Conservation of Bighorn Sheep (SCBS), Los Angeles County Fish and Game Commission, USFS, California Chapter of the Wild Sheep Foundation, Eastern Sierra Center for Applied Population Ecology, CDFG Federal Aid in Wildlife Restoration Project W-26-D (Wildlife Habitat Development), and we thank R. Barboza (CDFG) for arranging financial support for some of our initial analyses. B. McIntyre (SCBS) spent several months living alone in a remote location while baiting the drop net to ensure timely and successful capture events. Helicopter pilots, the late D. Landells, B. Novak, as well as S. deJesus (Landells Aviation), and others from the Los Angeles County Sheriff's Department, ensured safe ingress and egress to capture and release sites, and helicopter pilots from the Ventura County Sheriff's Department provided additional aerial support following the reintroduction. R. Anthes (CDFG) conducted most of the fixed-wing telemetry flights. M. Freel and B. Brown (USFS) played pivotal roles in facilitating the translocations, D. Bedford and M. Borchert (USFS) provided access to digital vegetation maps and fire histories, and B. McIntyre, B. Woods, S. Kimple (CDFG), and T. Nichols (USFS) provided essential field support following the reintroduction. Additionally, we thank staff from the CDFG Wildlife Investigations Lab and Region 5, staff from the San Bernardino, Angeles, and Los Padres national forests, and volunteers representing SCBS for assistance with the capture, transport, and release of bighorn sheep. B. Peterson (Wildlife Research Photography) kindly provided the photographs included in the paper. We thank the Associate Editor and two anonymous reviewers for their critical comments and numerous suggestions that resulted in substantial improvements to the manuscript. Stephen A. Holl passed away before the manuscript was finalized; thus, his coauthors assume responsibility for the final content. This is Professional Paper 120 from the Eastern Sierra Center for Applied Population Ecology.

Author Contributions

Conceived and designed the study: VCB, SAH
Collected the data: VCB, DS, SAH
Performed analyses of the data: MEB, KTS, VCB, DS
Authored the manuscript: VCB, MEB, KTS
Provided revisions of the manuscript: VCB, MEB, KTS, DS

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Submitted 31 July 2018
Accepted 17 April 2019
Associate Editor was J. Villepique