HAUB SCHOOL OF ENVIRONMENT AND NATURAL RESOURCES

Trends in Dispersal and Resource Use of Ferris-Seminoe Bighorn Sheep 2019 Research Brief

MONTEITH SHOP

UW UNIVERSITY OF WYOMING

TABLE OF CONTENTS

This research brief was prepared by Samantha Dwinnell[1], Victoria Donovan[2], and Kevin Monteith[1,3]

[1]Haub School of Environment and Natural Resources, University of Wyoming, Laramie, WY
[2]Department of Agronomy and Horticulture, University of Nebraska, Lincoln, NE
[3]Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, WY

Project Background

In recent decades, substantial efforts have been made to recover bighorn sheep (*Ovis canadensis*) populations of North America to historic numbers (Hurley et al. 2015). Such efforts in recovering sheep populations have nearly tripled overall sheep abundance in the lower 48 (Valdez and Krausman 1999). For example, bighorn sheep populations in Wyoming had increased from an estimated 2,000 animals in 1960 to nearly 7,000 in 2014 (WGFD, 2017 Wyoming State Wildlife Action Plan). Modifications to hunting regulations, targeted habitat enhancements, and translocations of bighorn sheep to recolonize areas within their historic distribution have undoubtedly contributed to increases in abundance of bighorn sheep throughout Wyoming. Yet, certain populations remain well below desired objectives. This is a concern for managers and conservation groups, and bighorn sheep in Wyoming are considered a Species of Greatest Conservation Need. Indeed, targeted wildlife action plans in some areas are aimed at further promoting population performance and abundance.

The bighorn sheep that occur in the Ferris and Seminoe mountains of southcentral Wyoming are a population that has been targeted for restoration by Wyoming Game and Fish Department. A combination of habitat enhancements, such as prescribed burning and translocation of sheep from robust source populations, have been implemented to bolster sheep abundance of the Ferris-Seminoe herd unit (Clapp et al. 2014). Between the late-1950s and mid-1980s, a total of 236 sheep had been transplanted to reestablish the Ferris-Seminoe sheep population, but these efforts

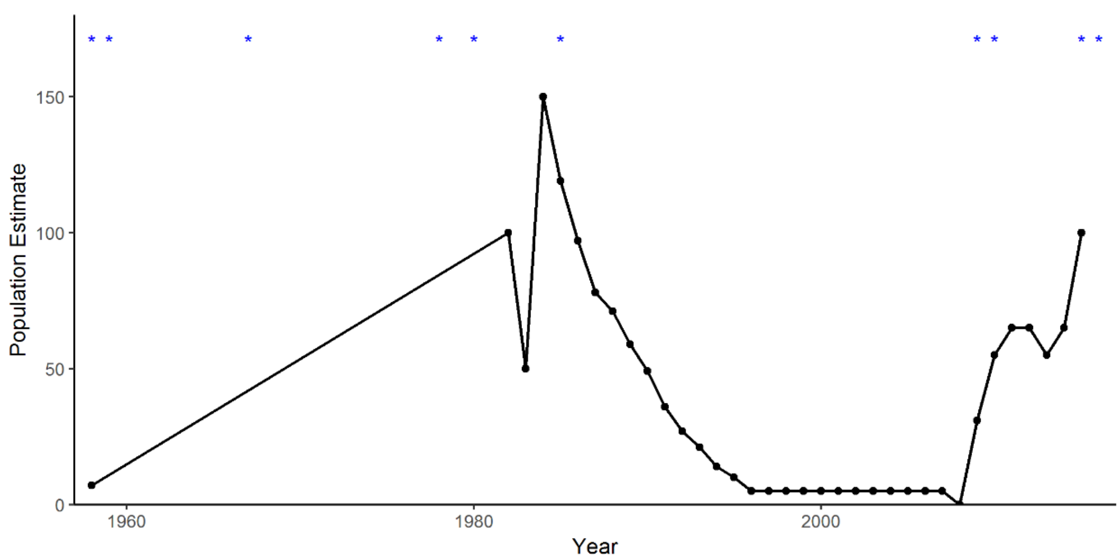


Figure 1. Population trends of Ferris-Seminoe bighorn sheep in Wyoming. Blue stars at the top indicate translocation events.

were mostly unsuccessful. By 2009, there were fewer than 10 surviving animals (Fig. 1). To prevent extirpation, several additional translocations have subsequently occurred. Starting in winter 2009/2010, 52 animals were released in the Seminoe mountains, and an additional 114 sheep were released in the Ferris and Seminoe mountains between 2015 and 2018. A combination of fire treatments and the more recent translocations appear to have been largely successful in recovering the Ferris-Seminoe population.

Rocky Mountain bighorn sheep are generally regarded as a habitat specialist, requiring open, rugged terrain intermixed with foraging opportunities in proximity to escape terrain that is often spatially isolated (Geist 1971, Risenhoover and Bailey 1985, Schroeder et al. 2010). Further, sheep are behaviorally adapted to the habitat conditions and phenology of resources of their environment (Jesmer et al. 2018). Thus, the success of translocation efforts is often dependent on the similarity of the environment of the transplant location with the source location. Sheep released into the Ferris-Seminoe starting in 2015 were translocated from the similar, high-desert habitats of Devil's Canyon and Diablo Mountain in Oregon. Although translocations of sheep from similar environments of their source population have bolstered sheep abundance in the Ferris-Seminoe population, dispersal into unoccupied, suitable habitats is rare. Thus, bringing into question why sheep do not seem to be dispersing into other suitable habitats.

Herein, we evaluated patterns in resource and space use of bighorn sheep of the Ferris-Seminoe population with the underlying objective of characterizing suitable habitat and factors affecting its use to help inform recovery and capacity for the range to support bighorn sheep. The following highlights our preliminary analyses associated with these research efforts.

Dispersal and Seasonal Ranges

Since translocations that began in 2009, 149 GPS-collars have been deployed on bighorn sheep that were translocated to the Ferris-Seminoe population. Using available data from 111 of those animals (Table 1; Fig. 2), we evaluated general patterns in dispersal and use of seasonal ranges. We plotted net-squared displacement and visualized movements of male and female bighorn sheep to identify patterns in dispersal and migration.

Table 1**.** The number of male and female bighorn sheep of the Ferris-Seminoe population from which we collected GPS-data.

Year	Male	Female	Total
2009	2	9	11
2010	6	20	26
2015	2	6	8
2016	3	19	22
2017	6	15	21
2018	3	20	23
Total	22	89	111


Mark Gocke

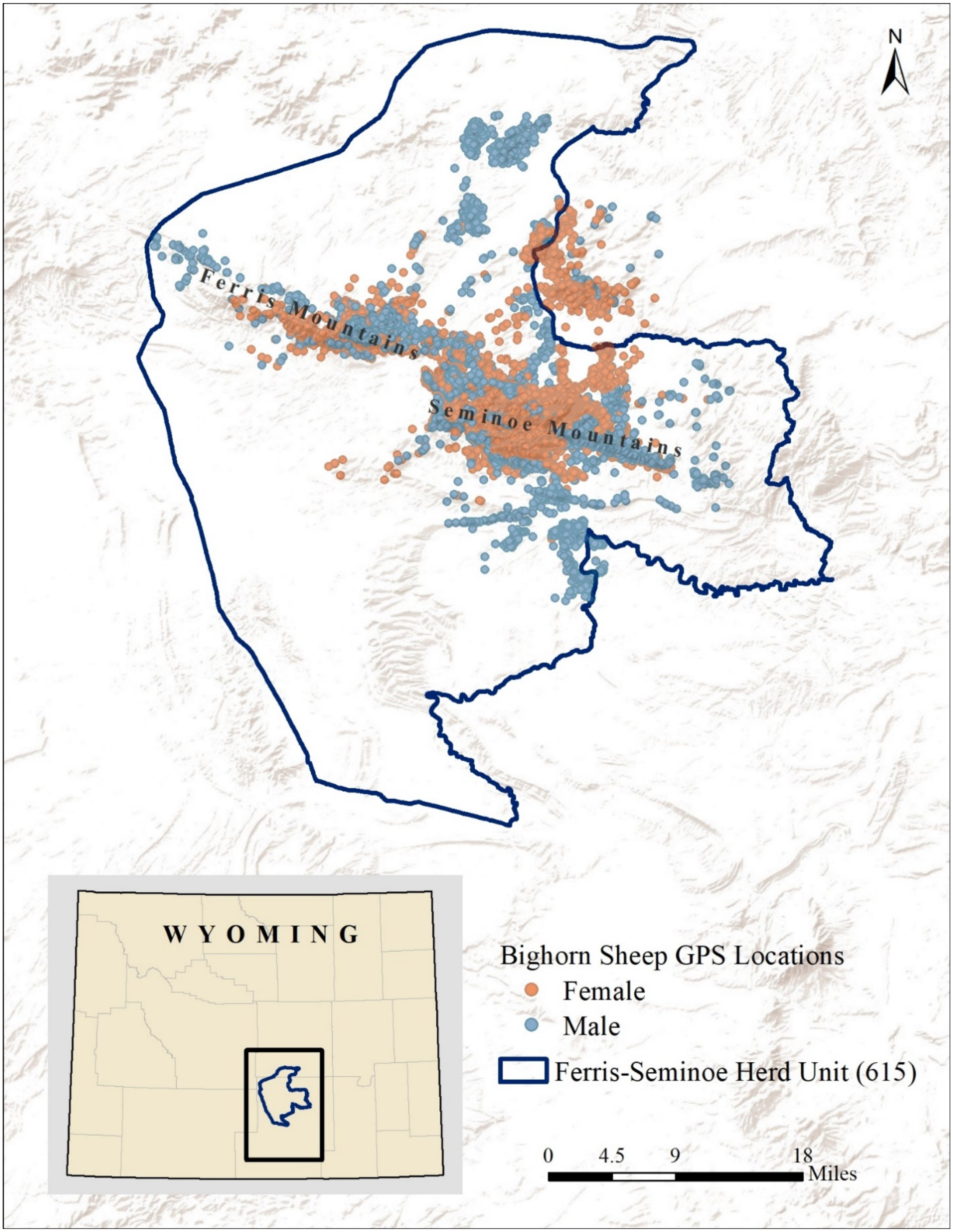


Figure 2. GPS locations of male (blue) and female (orange) bighorn sheep that were translocated into the Ferris-Seminoe herd unit (HU615) of southcentral Wyoming, 2009-2018.

Dispersal

Bighorn sheep often have high fidelity to seasonal home ranges, but males tend to have a higher propensity for dispersal when compared to females (Geist 1971). High densities of animals may prompt dispersal (Mysterud et al. 2011), unless cultural knowledge and fidelity restrict dispersal behavior (Jesmer et al. 2018, Sawyer et al. 2019). Within 3 years post-release, the majority of translocated animals to the Ferris-Seminoe did not disperse far from the release location, and only 25% of collared sheep exhibited movements of dispersal (e.g., Figures 3 and 4). Most other animals remained within 10km of the released location. A greater proportion of male sheep (55%) dispersed compared with the proportion of female sheep that dispersed (18%). The maximum distance animals dispersed was comparable between the sexes (29km for females and 31km for males; Figure 5).

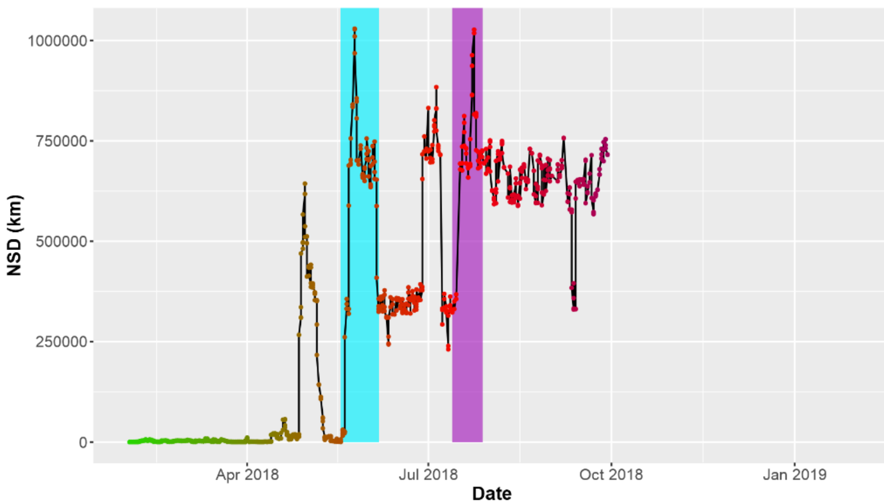


Figure 3. Dispersal movements as indicated by net-squared displacement (NSD) plot of a male bighorn sheep (AID150) translocated into the Ferris Mountains in 2017. The initial dispersal movement (blue stripe) occurred 166 days after translocation with a second dispersal (purple stripe) that occurred an additional 56 days later.

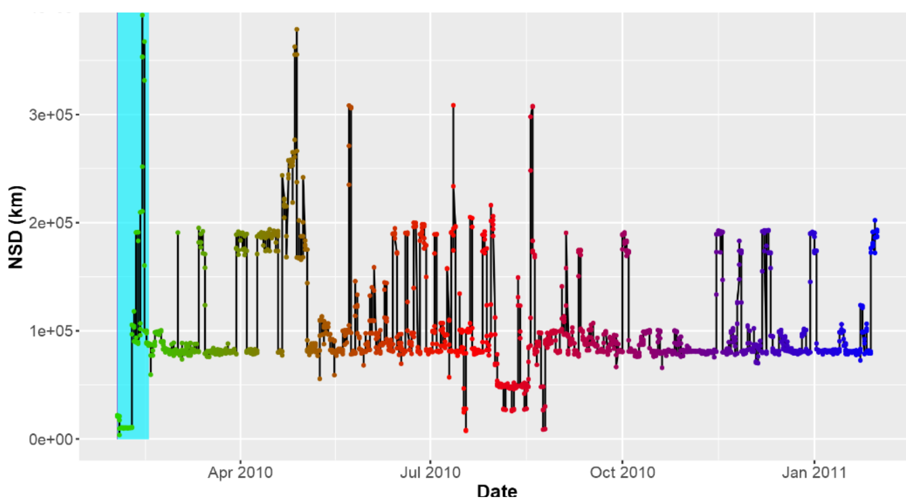


Figure 4. Dispersal movement as indicated by net-squared displacement (NSD) plot of a female bighorn sheep (AID 021) translocated into the Seminoe Mountains in 2010. The initial dispersal movement (blue stripe) occurred 9 days following translocation.

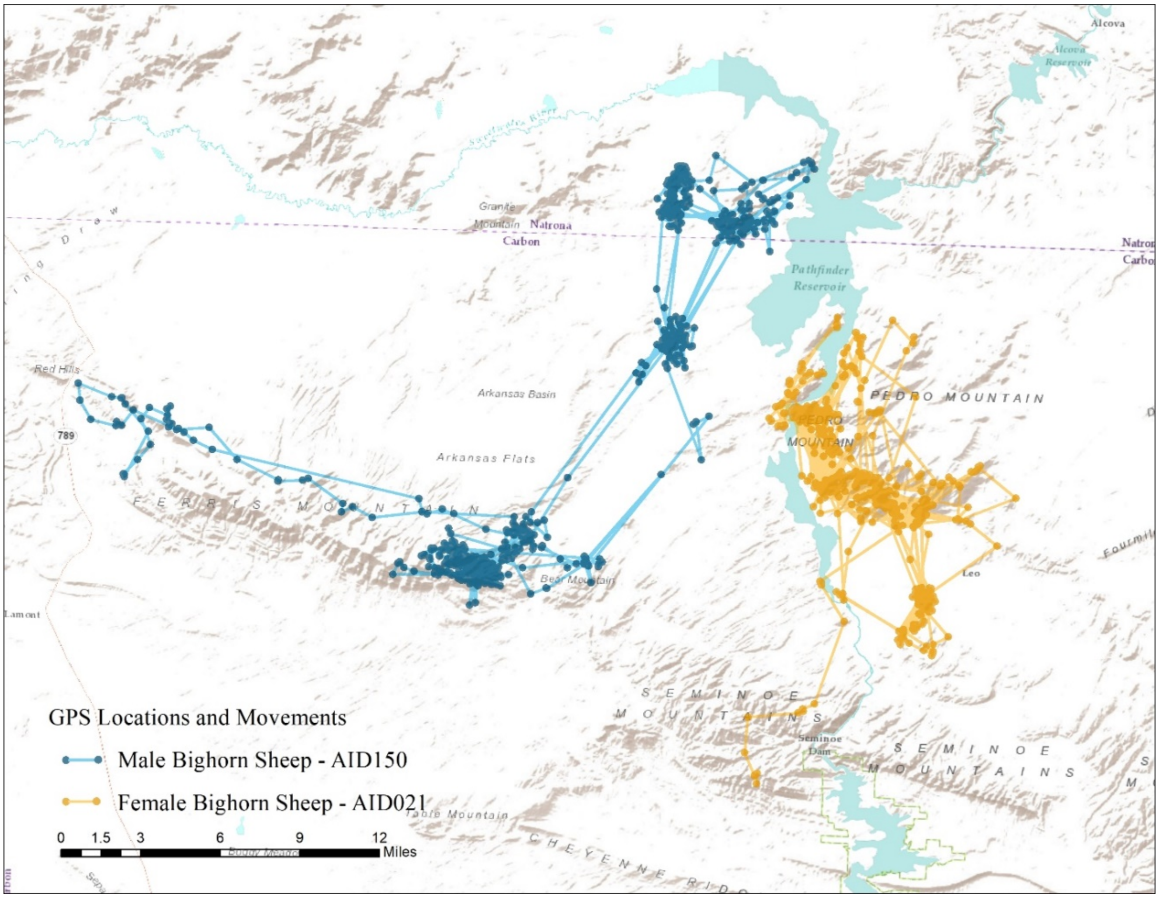


Figure 5. Dispersal movements of a male bighorn sheep (AID150; blue) translocated into the Ferris Mountains in 2017 and a female bighorn sheep (AID 021; orange) translocated into the Seminoe Mountains in 2010.

Seasonal Ranges

Most animals did not occupy discrete summer and winter ranges, and thus were largely non-migratory. Areas of summer and winter home ranges, calculated by 95% Kernel utilization distributions (KUD), did not differ (mean winter and summer home ranges were 1.2km^2 and 1.1km^2, respectively). Only 7 of the 111 (6%) sheep appeared to exhibit migration behaviors (e.g., Figure 6 and 7). Similar to dispersal patterns, a greater proportion of male sheep exhibited migratory behavior (18%) compared with females (3%). The source population of these sheep are generally regarded as non-migratory, whether these few migratory sheep are carrying on the legacy of migration from their source population, are quickly learning how to exploit their new environment, or are learning it from other animals in the relocation area is unknown.

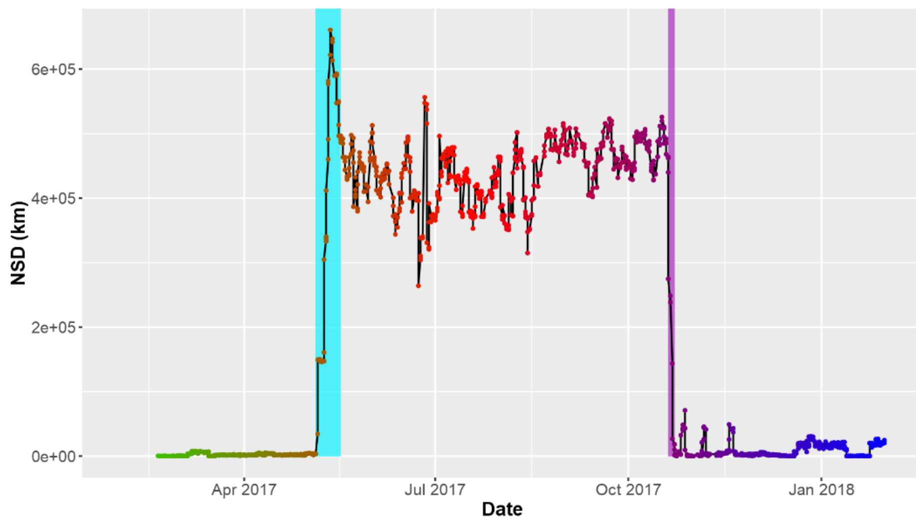


Figure 6. Migration movements as indicated by net-squared displacement (NSD) plot of a male bighorn sheep (AID 138) that was translocated to the Ferris Mountains in 2017. Spring migration (blue stripe) occurred May 5 – May 17 and autumn migration (purple stripe) occurred October 20 – October 23 in 2017.

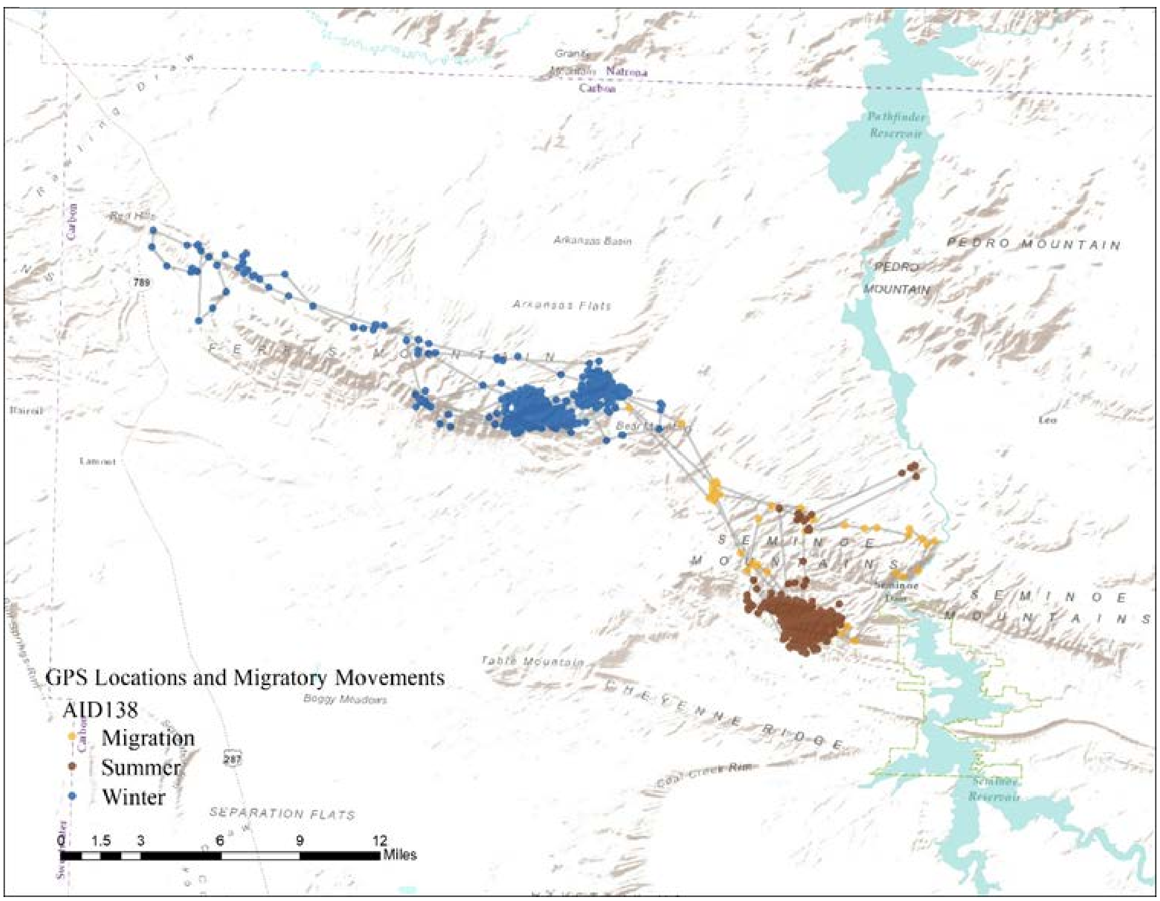


Figure 7. Migratory movements of a male bighorn sheep (AID 138) that was translocated in 2017. Blue dots represent winter locations in the Ferris Mountains, red represent summer locations in the Seminoe Mountains, and orange dots represent locations during migration. Gray lines connect the movements between each location.

Predicting Resource Use of Translocated Bighorn Sheep

We used Random Forest (RF) models to predict areas that sheep would use relative to the available resources of known importance to bighorn sheep, including topographic ruggedness, distance to escape terrain, land cover, fire severity, and vegetation (see Table 2 for further details on variables used for modeling). Random Forest models are a form of machine learning that conveniently copes with multicollinearity across covariates and typically leads to greater predictive power and accuracy than traditional modeling approaches (Shoemaker et al. 2018). Nevertheless, they are of greater value for prediction than they are for drawing inference. We created separate models for male and female bighorn sheep in "summer" and "winter" seasons. We defined summer and winter seasons by the mean date of migration derived from the few animals that migrated (summer=May 23–October 24; winter=October 25–May 22). Additionally, we constructed two separate RF models for male and female sheep combined across all seasons. We used a RF model improvement ratio to select the most parsimonious set of variables for each RF model. We used 501 trees for each model because error convergence of models occurred at <200 trees. We calculated variable importance for each model to identify landscape features that were best at predicting sheep use. Finally, we used independent cross-validation with a 30% data withhold to assess model accuracy.

Table 2. List of variables used in predicting occurrence of bighorn sheep using Random Forest modeling.

Variable	Code	Type	Source/Reference
Distance to terrain with >30 degree slopes (m)	Dist_Escp30	Topography	Extracted from DEM using Raster package in R; DeCesare et al. 2006
Distance to terrain with >60 degree slopes (m)	Dist_Escp60	Topography	Extracted from DEM; using Raster package in R
Distance to terrain ruggedness index >498 (m)	Dist_TRI498	Topography	Extracted from DEM using Geomorphometry and Gradient Toolbox version 2.0 in ArcGIS; Riley et al. 1999; Evans et. al. 2014
Elevation (m)	Elevation	Topography	DEM; National Elevation Data; U.S. Geological Survey 2009
Mean slope (10m2)	MeanSlope	Topography	Extracted from DEM using Geomorphometry and Gradient Toolbox version 2.0 in ArcGIS; Evans et. al. 2014
Slope > 30 degrees	Slope30	Topography	Extracted from DEM; using Raster package in R; DeCesare et al. 2006
Topographic radiation aspect index	TRASP	Topography	Extracted from DEM using Geomorphometry and Gradient Toolbox version 2.0 in ArcGIS; Roberts and Cooper 1989; Evans et. al.2014
Topographic ruggedness index	TRI	Topography	Extracted from DEM using Geomorphometry and Gradient Toolbox version 2.0 in ArcGIS; Riley et al. 1999; Evans et. al. 2014
Fire Severity (1-6)	Fire_Severity	Fire	Monitoring Trends in Burn Severity Project; USGS, USFS, USDOI, USDA
Time since fire in days	TSF_days	Fire	Monitoring Trends in Burn Severity Project; USGS, USFS, USDOI, USDA
Percent cover of annual forb-grass	AnnForbGrass	Land Cover	Rangeland Analysis Platform; Jones et al. 2018
Percent cover of bare ground	BarGround	Land Cover	Rangeland Analysis Platform; Jones et al. 2018

Percent cover of litter	Litter	Land Cover	Rangeland Analysis Platform; Jones et al. 2018
Percent cover of perennial forb-grass	PerForbGrass	Land Cover	Rangeland Analysis Platform; Jones et al. 2018
Percent cover of shrub	Shrub	Land Cover	Rangeland Analysis Platform; Jones et al. 2018
Percent cover of tree	Tree	Land Cover	Rangeland Analysis Platform; Jones et al. 2018
Cumulative normalized difference vegetation index	cNDVI	Vegetation	Landsat NDVI; Robinson et al. 2017
Distance to location of release (m)	Dist_ReleaseLoc	Other	Wyoming Game and Fish Department

Variables that Best Predict Occurrence of Sheep

Among all models, the most important variable in predicting use by sheep was distance to the area from which translocated sheep were released (Figures 8-13). Considering the low frequency of dispersal observed in sheep (25%) and the relatively short distance animals moved when they did disperse (<31km), distance to release location held strong underpinnings for where sheep were likely to occur. Other variables of importance among models were distance to escape terrain, mean slope, and elevation. Fire severity was more important for female and male sheep in the summer, but of less importance in the winter.

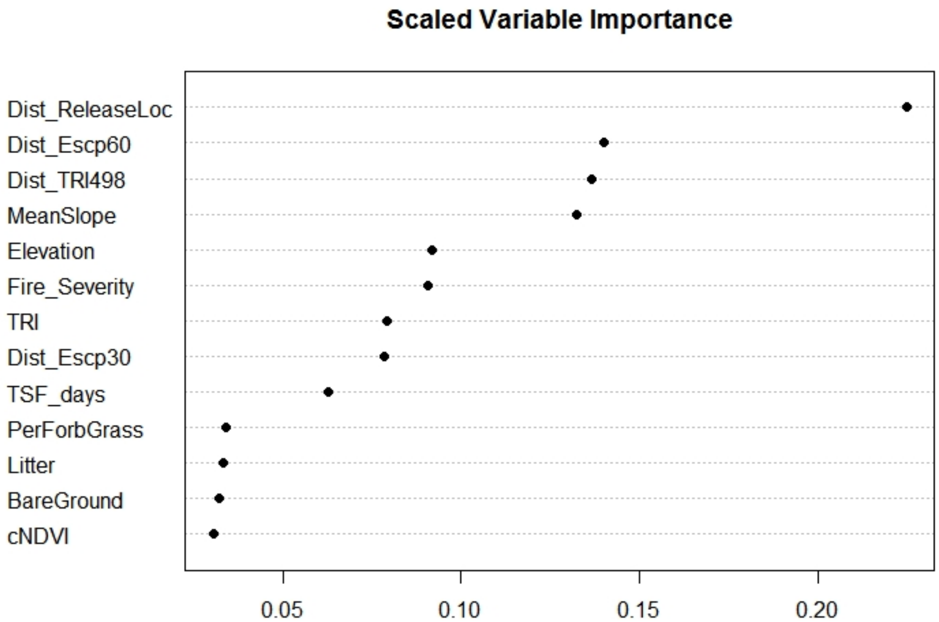


Figure 8. Importance of variables in predicting use by FEMALE bighorn sheep. Estimated out-of-bag error was 4.67% and model accuracy was 95.27%.

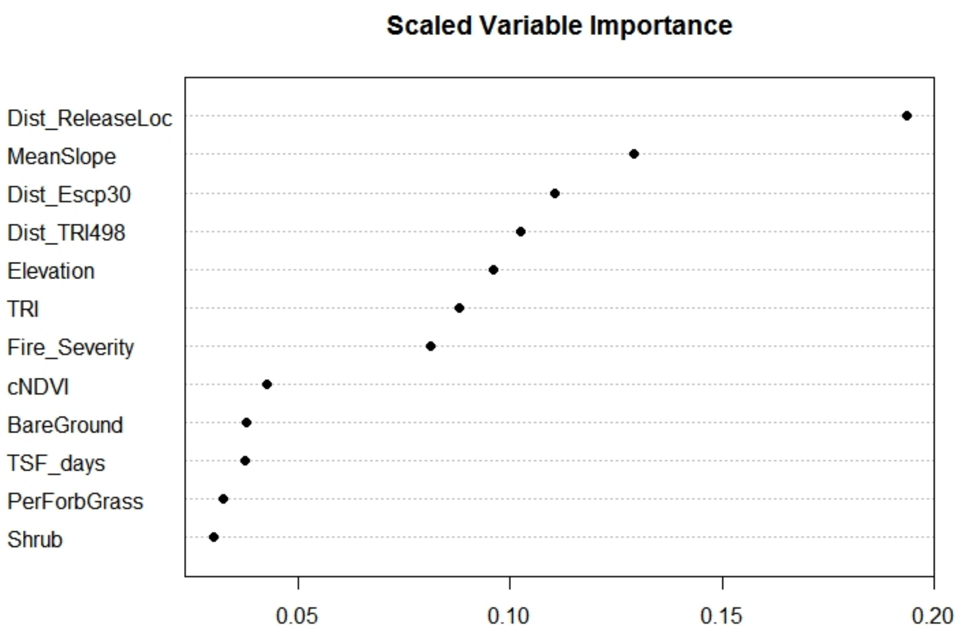


Figure 9. Importance of variables in predicting use by MALE bighorn sheep. Estimated out-of-bag error was 6.53% and model accuracy was 92.92%.

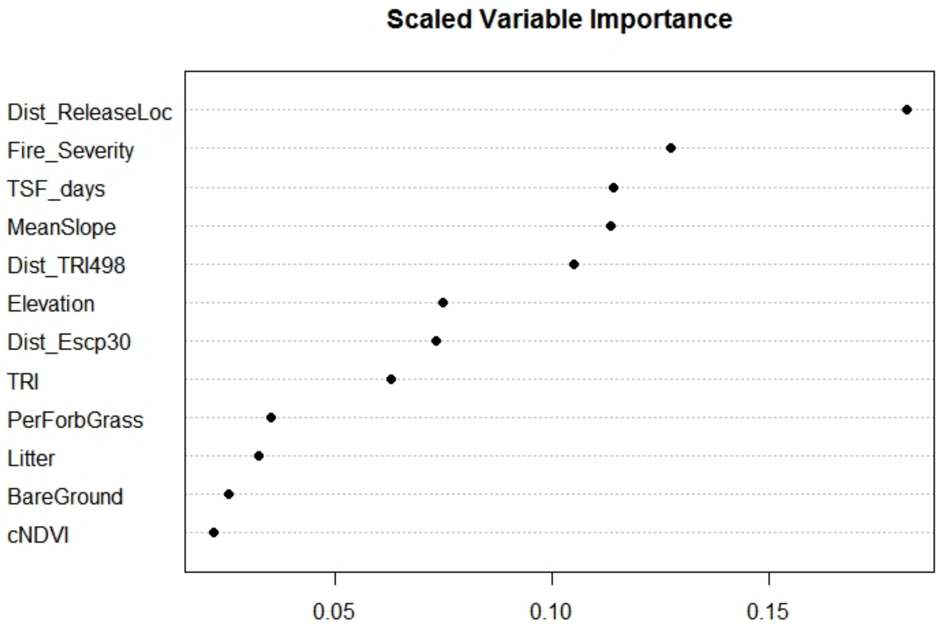


Figure 10. Importance of variables in predicting use by FEMALE bighorn sheep in SUMMER. Estimated out-of-bag error was 4.00% and model accuracy was 95.75%.

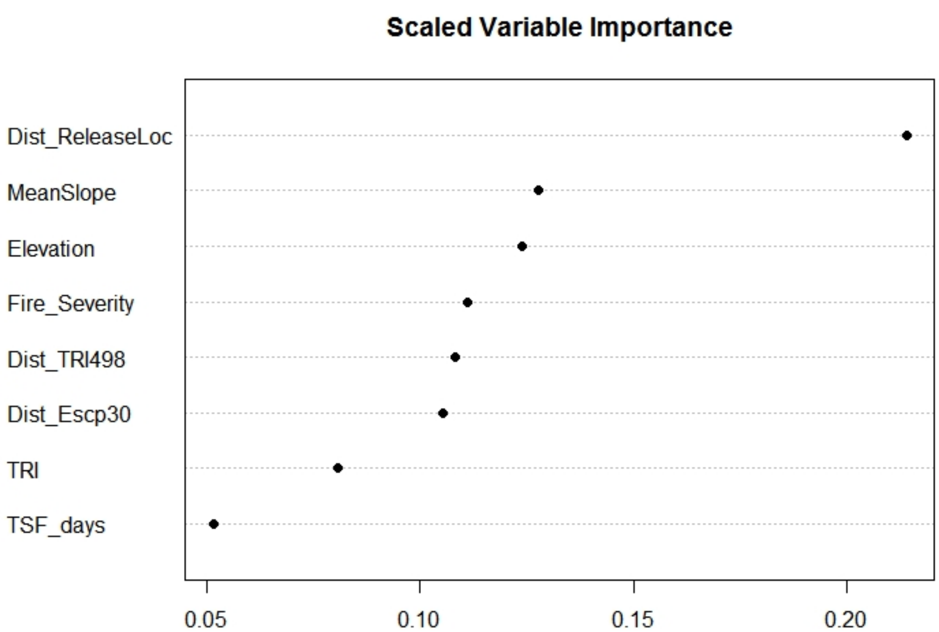


Figure 11. Importance of variables in predicting use by MALE bighorn sheep in SUMMER. Estimated out-of-bag error was 6.71% and model accuracy was 92.84%.

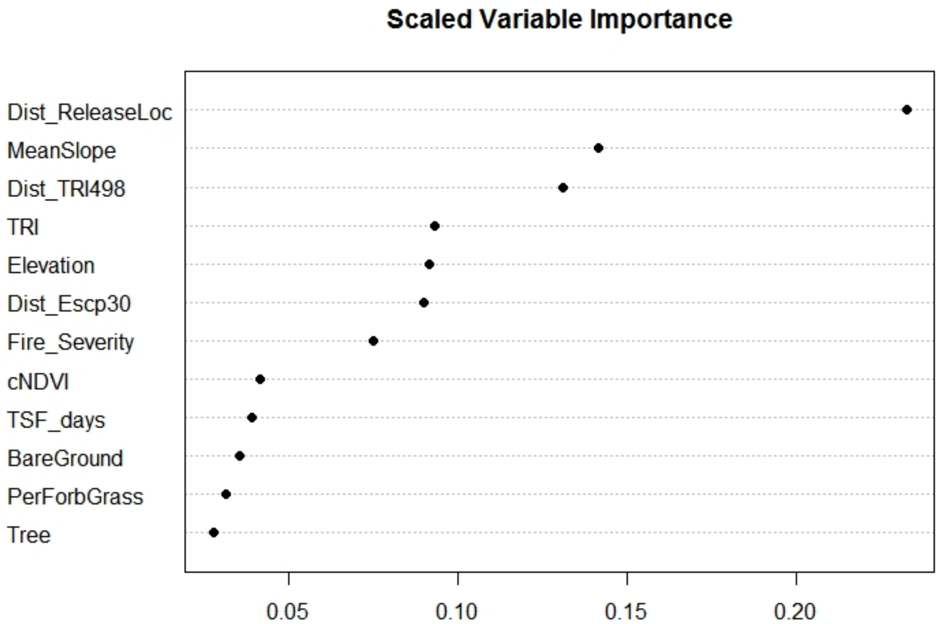


Figure 12. Importance of variables in predicting use by FEMALE bighorn sheep in WINTER. Estimated out-of-bag error was 4.74% and model accuracy was 94.82%.

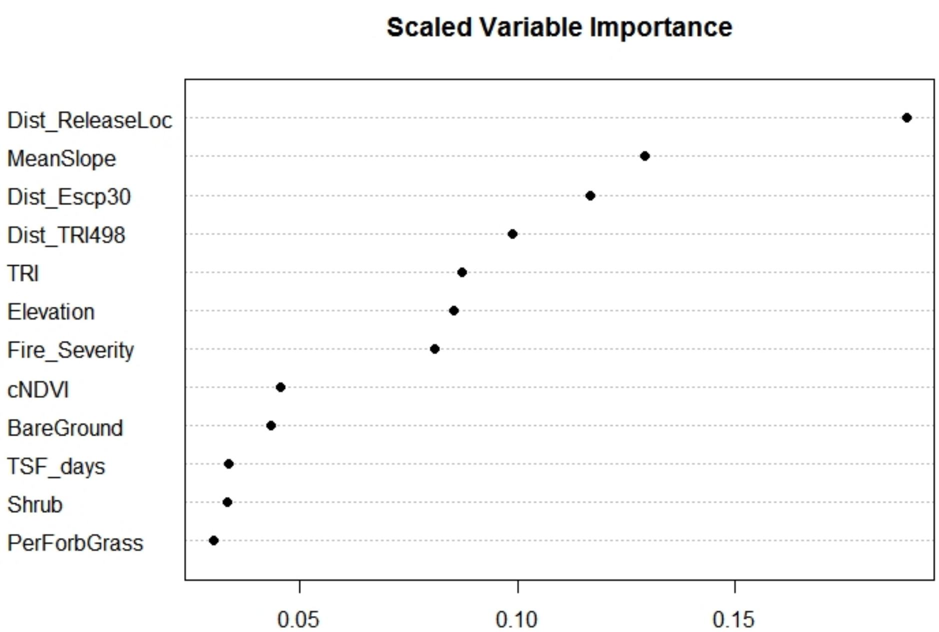


Figure 13. Importance of variables in predicting use by MALE bighorn sheep in WINTER. Estimated out-of-bag error was 6.07% and model accuracy was 93.53%.

Resource and Space Use by Bighorn Sheep

Based on predicted resource use of the Ferris-Seminoe Mountains by translocated bighorn sheep, it appeared that sheep were using the suitable habitats near where they had been translocated (Figures 14-15 and 18-19). Consequently, release locations and general lack of dispersal, or other wide-ranging movements, limit the exploitation of other suitable habitats that could be available to the population. Nevertheless, we did not have longitudinal data on sheep movements and behavior beyond three years following translocations, which could reveal that animals are indeed increasing their exposure to other suitable habitat through exploratory movements and learning (Jesmer et al. 2018).

To aid in identification of the potential for other suitable habitat, we implemented two additional steps in our modeling effort, but with the same general procedures. First, we modeled seasonal habitat use without the restrictive and overwhelming effect of release location to allow the identification of habitat and landscape variables most consistent with use (Figures 16 and 20). Second, we overlaid probability of use based on our original layers that included release location to identify areas of potential suitable habitat that are currently unoccupied (Figures 17 and 21). Doing so facilitated identification of potential suitable habitat if additional relocations sites nearby may help promote occupancy by sheep.

Predicted Use by Females

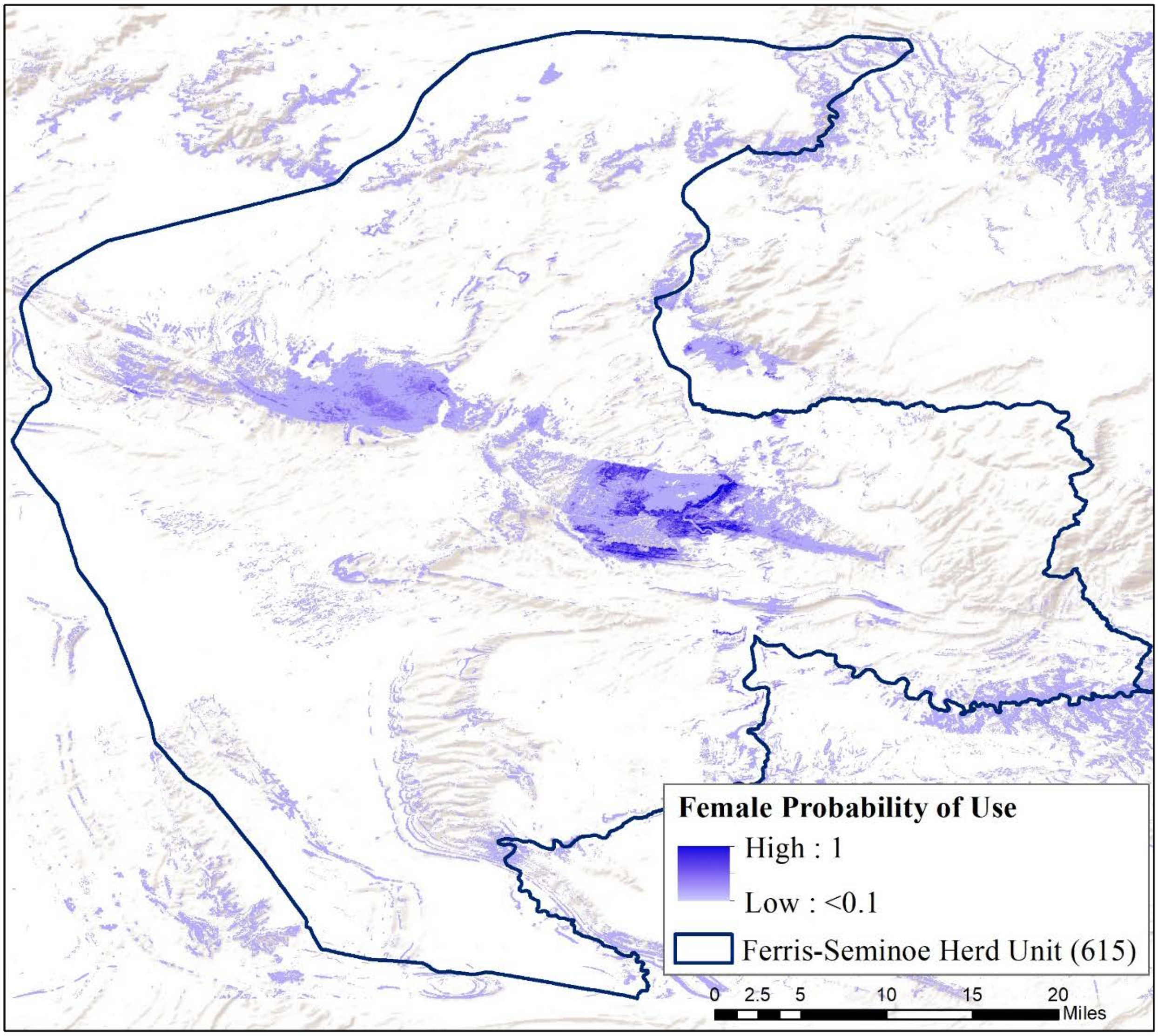


Figure 14. Probability of use by FEMALE bighorn sheep of the Ferris-Seminoe herd unit using GPS-collar data from 2009-2018. The variables most influential in predicting use by females were distance to release location, distance to escape terrain, and topography. Model accuracy was 95.27%.

Female GPS-Locations 2009-2018

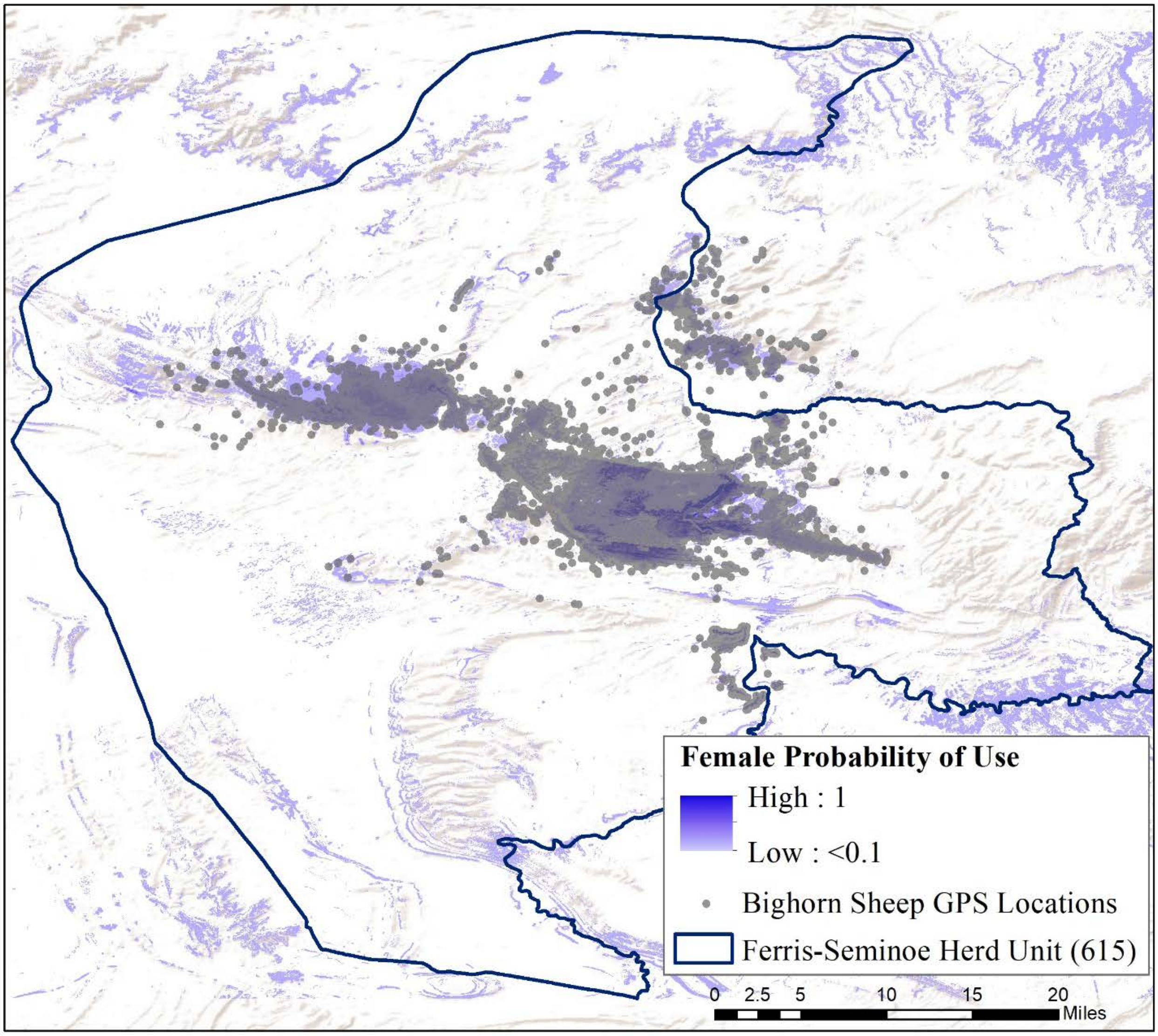


Figure 15. GPS-collar data from FEMALE bighorn sheep of the Ferris-Seminoe herd unit in 2009-2018 overlaid on predicted probability of use by female sheep. Female sheep tended to remain near areas from which they were released.

Potential Habitat Use by Females

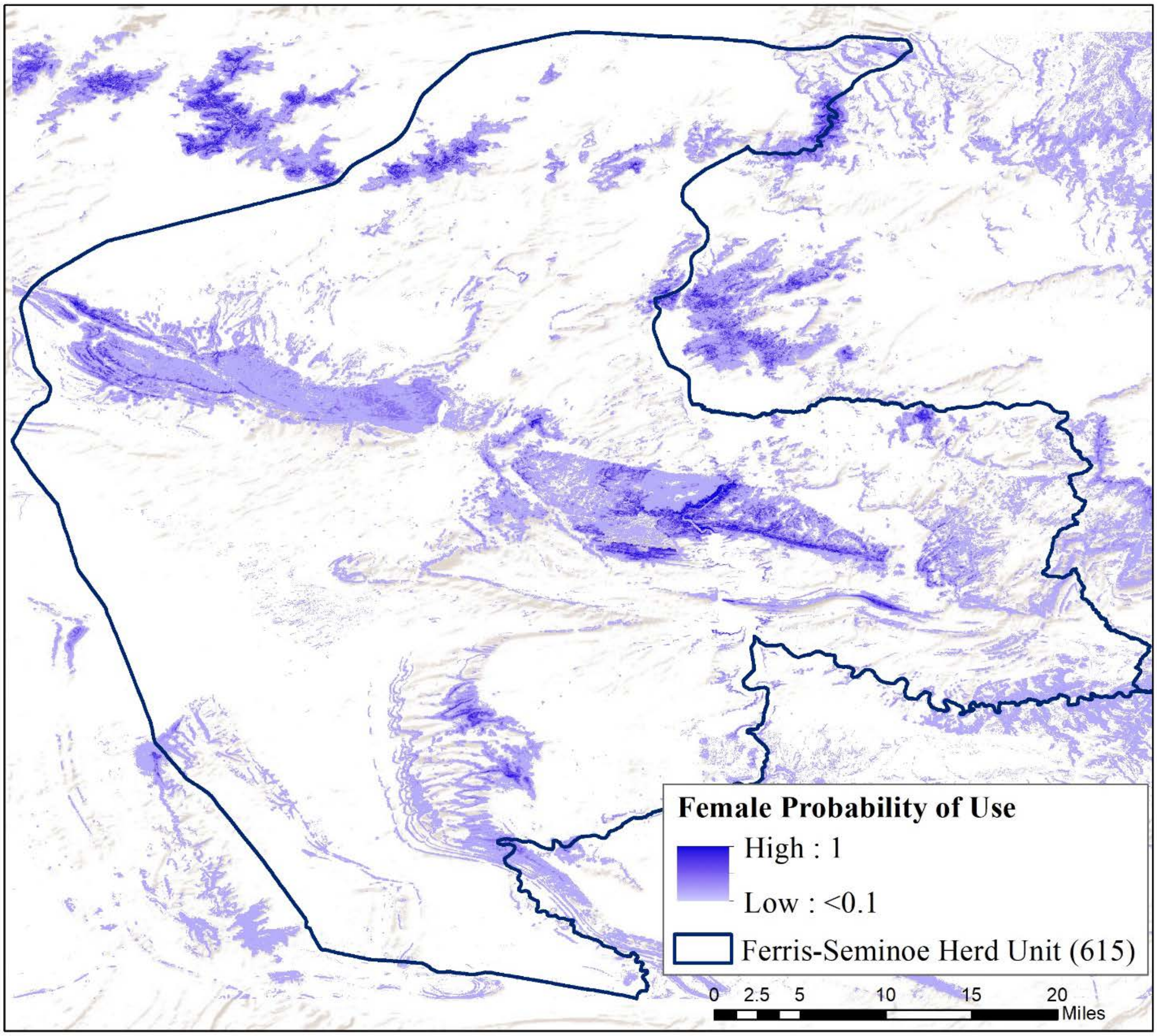


Figure 16. Probability of use by FEMALE bighorn sheep of the Ferris-Seminoe herd unit using GPS-collar data from 2009-2018 after release location was removed from the predictive model. Removing the strong effects of release location from the RF model allowed for evaluation of potential habitat that female bighorn sheep would be predicted to use, when no longer restricted to relocation sites. Out-of-bag error of this RF model was 6.54% and accuracy was 93.37%.

Predicted Use by Females with Additional Relocation Sites

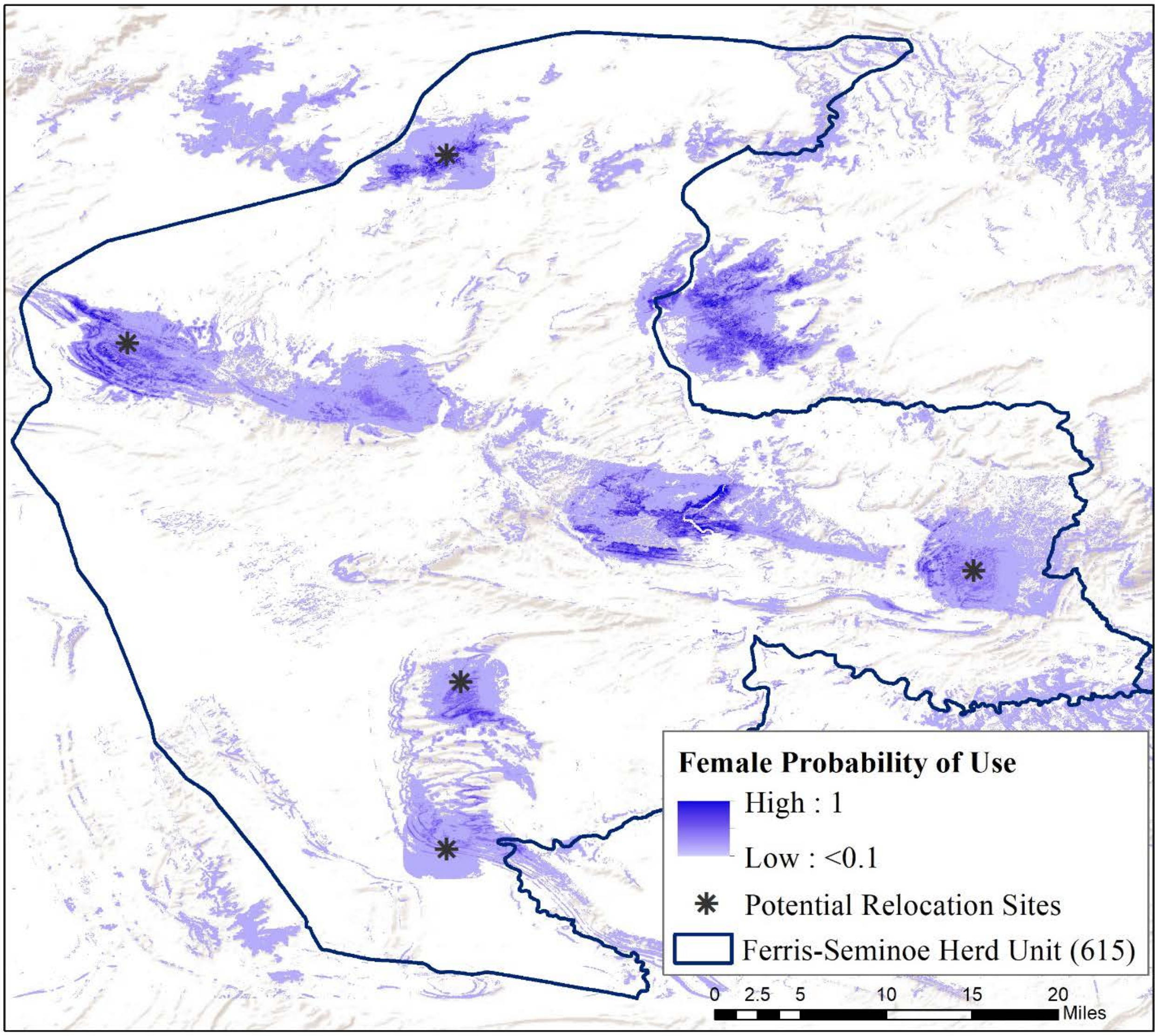


Figure 17. Probability of use by FEMALE bighorn sheep of the Ferris-Seminoe herd unit using GPS-collar data from 2009-2018 if additional female sheep were released at new relocation sites in potentially suitable habitat.

Predicted Use by Males

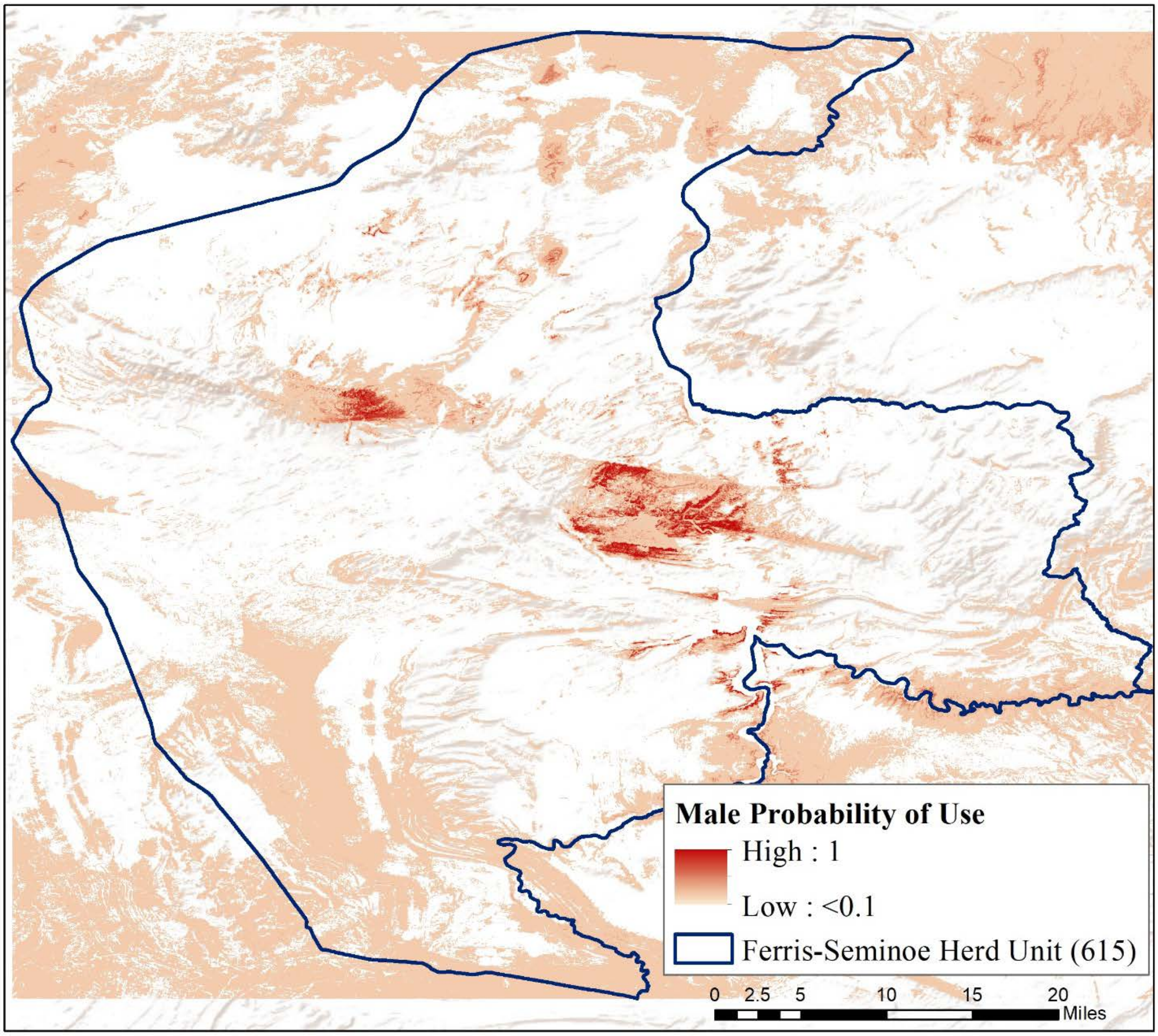


Figure 18. Probability of use by MALE bighorn sheep of the Ferris-Seminoe herd unit using GPS-collar data from 2009-2018. The variables most influential in predicting use by males were distance to release location, distance to escape terrain, and topography. Model accuracy was 92.92%.

Male GPS Locations 2009-2018

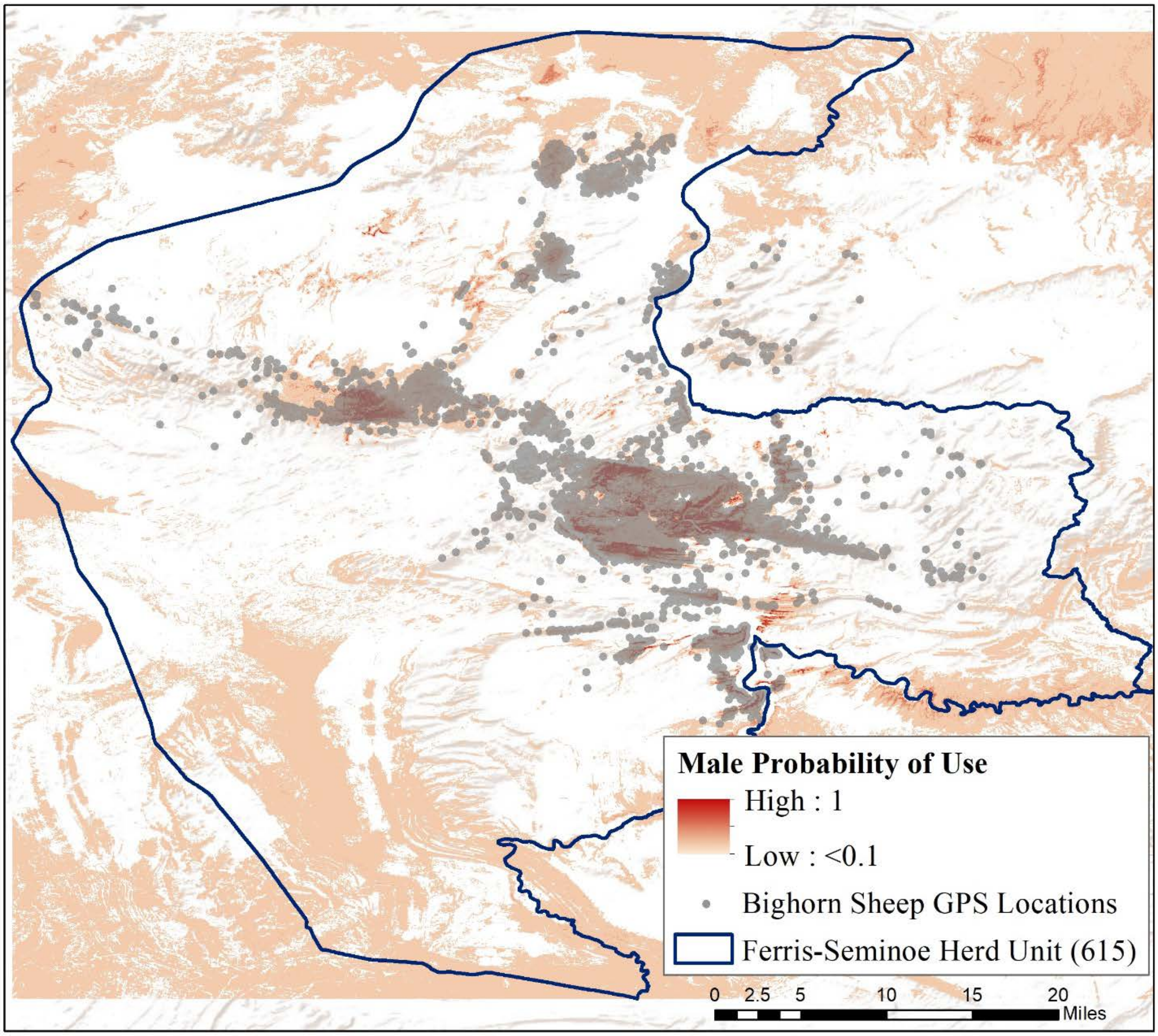


Figure 19. GPS-collar data from MALE bighorn sheep of the Ferris-Seminoe herd unit in 2009-2018 overlaid on predicted probability of use by male sheep. Male sheep were more likely to disperse from areas from which they were released relative to female sheep.

Potential Habitat Use by Males

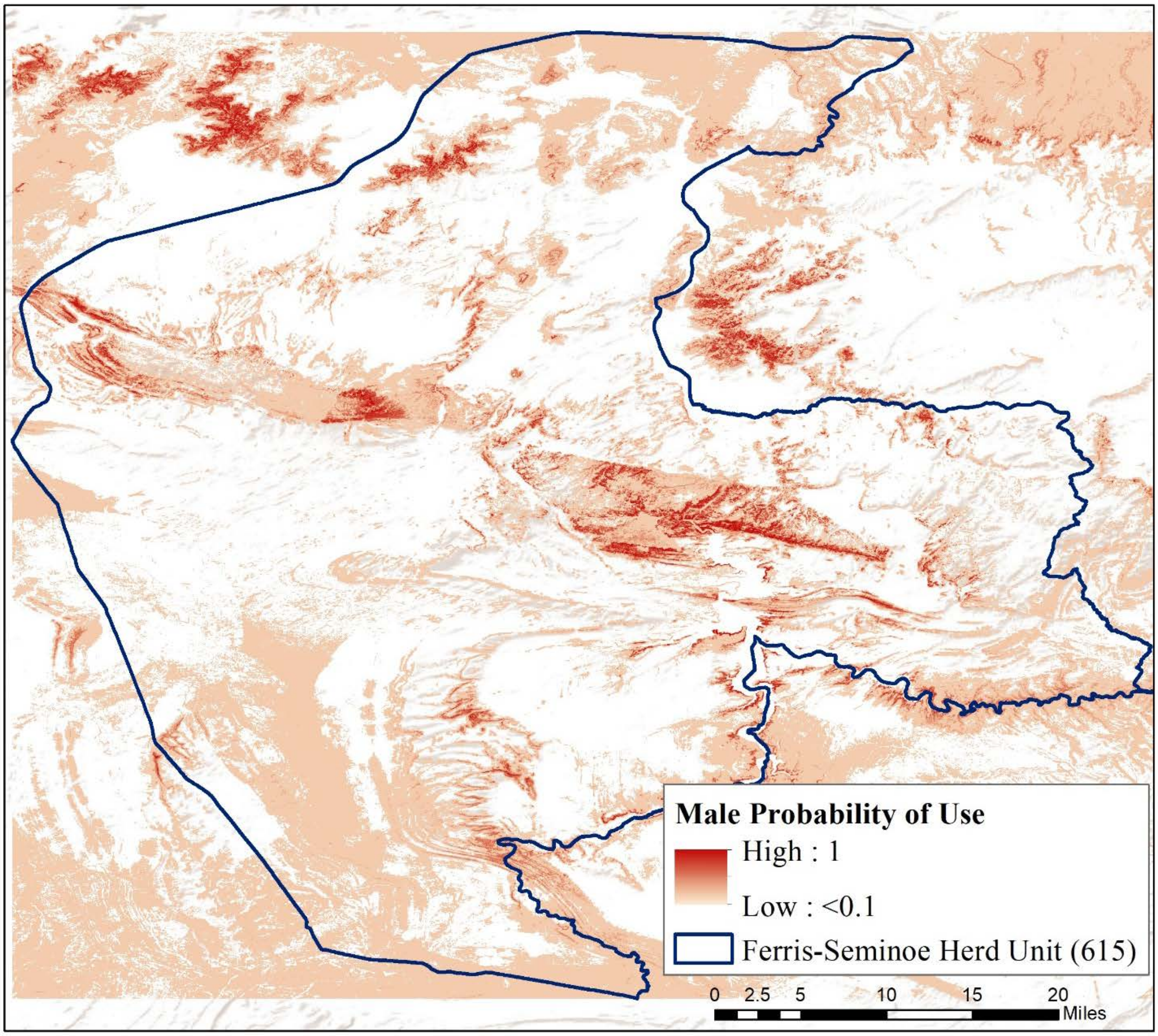


Figure 20. Probability of use by MALE bighorn sheep of the Ferris-Seminoe herd unit using GPS-collar data from 2009-2018 after release location was removed from the predictive model. Removing the strong effects of release location from the RF model allowed for evaluation of potential habitat that male bighorn sheep would be predicted to use, when no longer restricted to relocation sites. Out-of-bag error of this RF model was 9.28% and accuracy was 90.84%.

Predicted Use by Males with Additional Relocations Sites

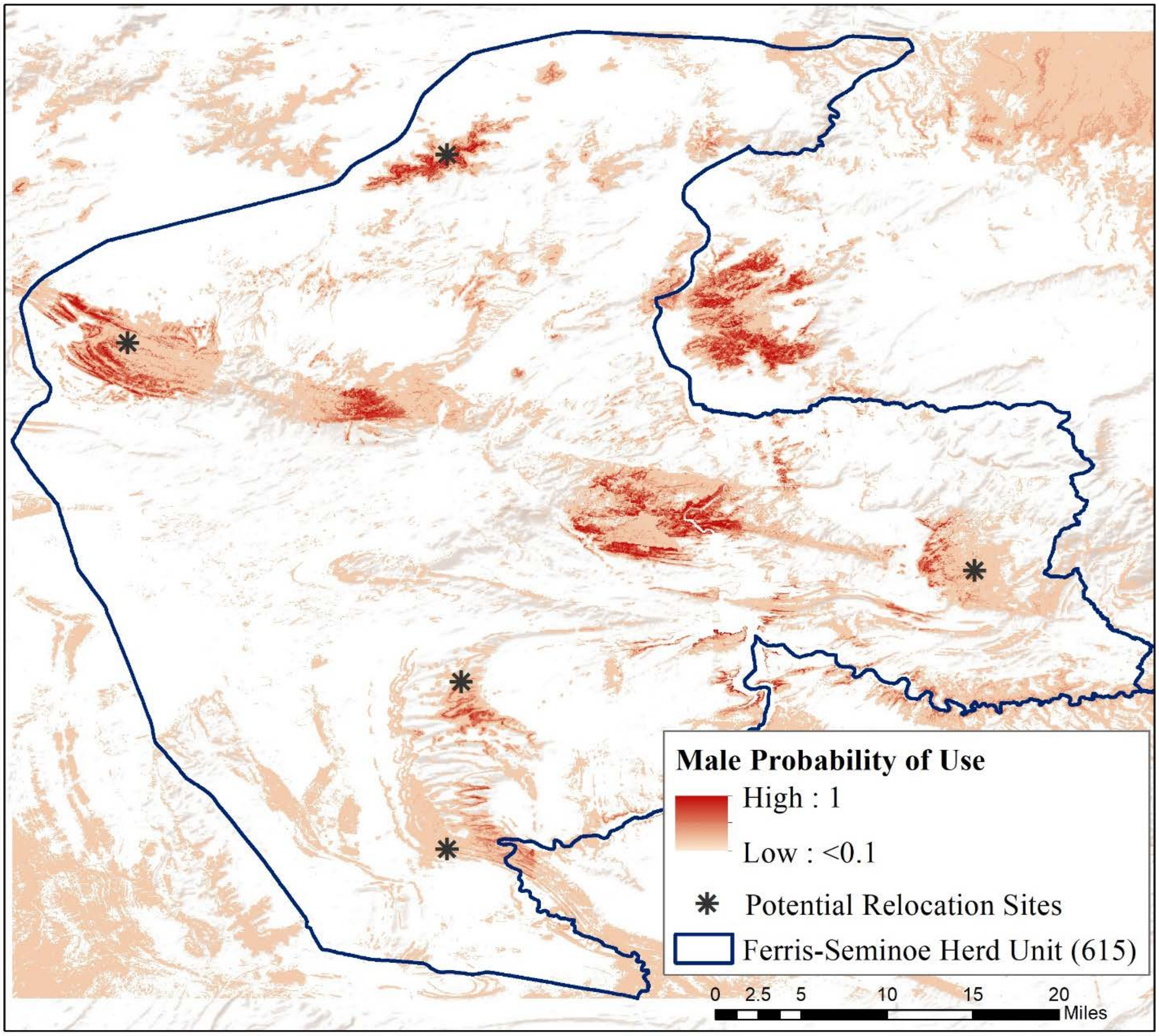


Figure 21. Probability of use by MALE bighorn sheep of the Ferris-Seminoe herd unit using GPS-collar data from 2009-2018 if additional male sheep were released at new relocation sites in potentially suitable habitat.

Intensity of Use by Translocated Bighorn Sheep

We calculated intensity of use by bighorn sheep by summing the number of summer and winter home ranges that overlapped in each year 2009-2018. We delineated seasonal home range using the 95% KUD for males and females in summer (May 23–Oct. 24) and winter (Oct. 25–May 22).

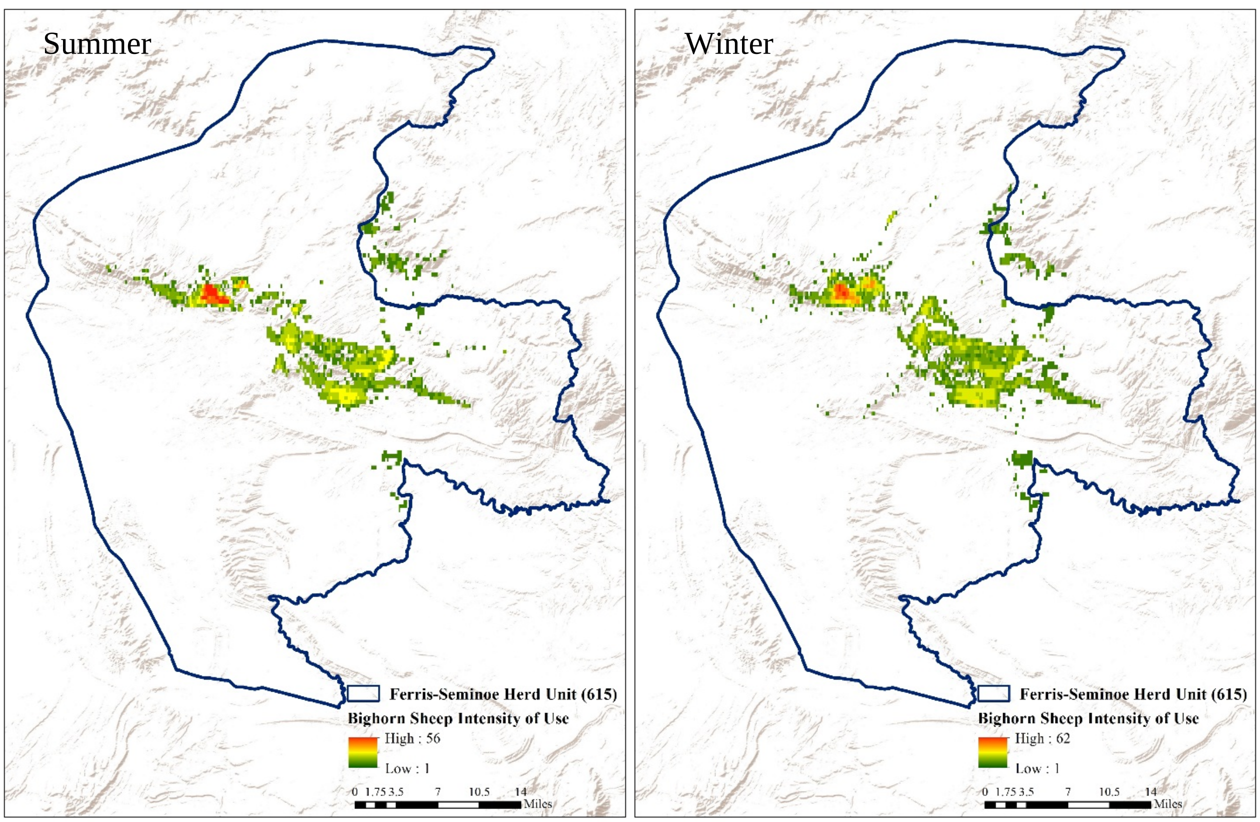


Figure 22. Total intensity of use by FEMALE bighorn sheep as measured by the number of overlapping home ranges (95% KUD) in summer (left) and winter (right) 2009-2018.

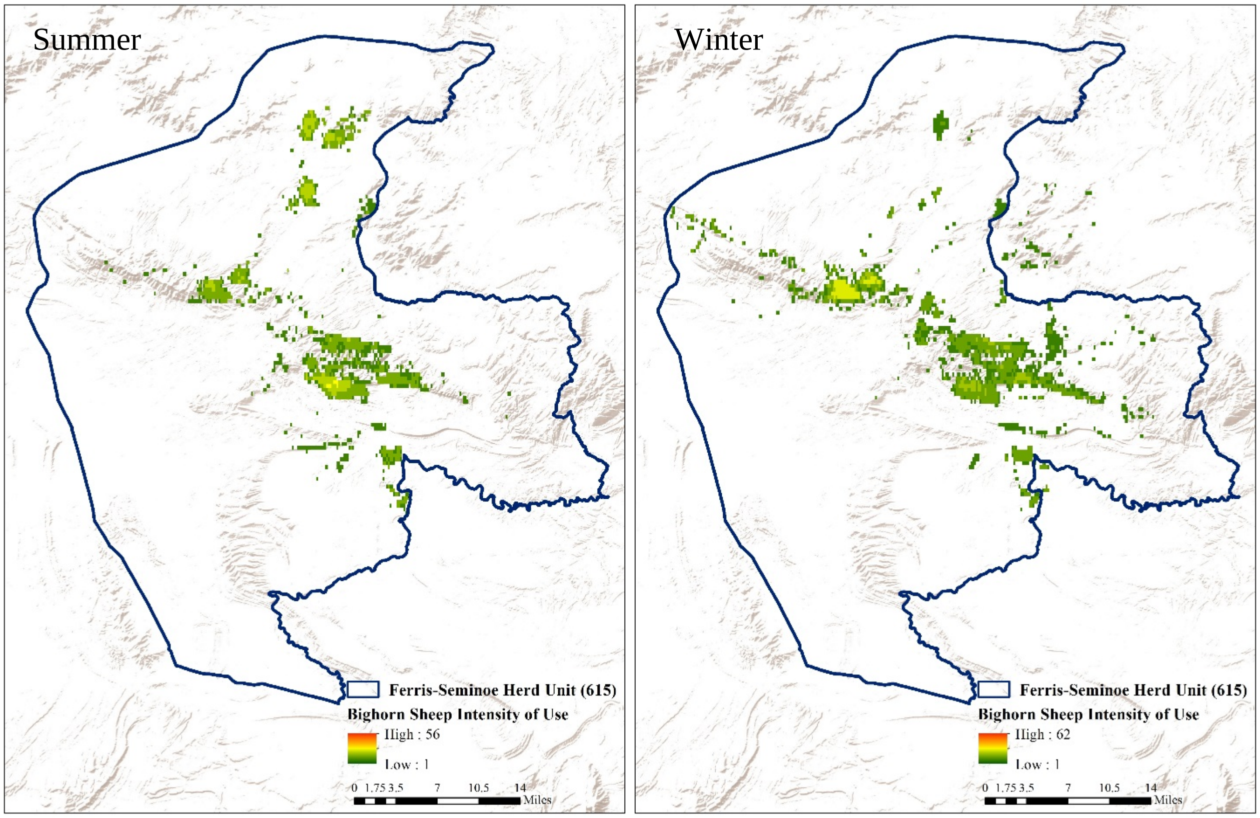
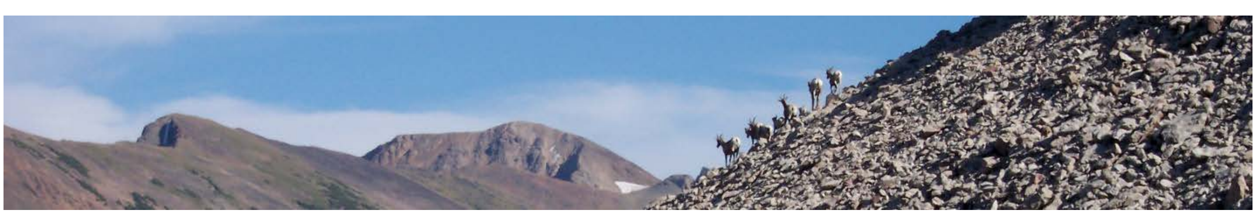


Figure 23. Total intensity of use by MALE bighorn sheep as measured by the number of overlapping home ranges (95% KUD) in summer (left) and winter (right) 2009-2018.

Use of Available Biomass

The quality and quantity of forage on a landscape is the primary determinate of the nutritional carrying capacity (*NCC*;(Hobbs et al. 1982). Yet, the relationship between forage and animal density is complex. The interactive characteristics of quality and quantity often drive the way large herbivores, such as bighorn sheep, use available forage (Festa-Bianchet 1988), but quantity, or biomass, of key forage often is considered the greatest limiting factor in foraging opportunities for animals. Like other ungulates, bighorn sheep, in general, select for habitats with greater foraging opportunities (Charnov 1976). As animal densities increase, exploitation of available food can be depleted to an extent of which measurable biomass is decreased (Stewart et al. 2006, Hamel et al. 2009); therefore, understanding the relationship between sheep density and biomass may glean insight into the proximity of a population to *NCC*.

To aid in understanding the potential proximity of Ferris-Seminoe bighorn sheep to *NCC* of the population, we evaluated the effects of intensity of use on biomass using vegetation data collected by WGFD and BLM in summer 2018 (Fig. 24). Here, we evaluated the prediction that



if biomass was negatively affected by intensity of use, sheep may be exhausting their available food resources in a way suggestive of a population near *NCC*.

We used linear regression models to evaluate the influence of intensity of use by female bighorn sheep in summer 2018 on biomass (g) of grasses and forbs that was available to them. Biomass was unrelated to intensity of use (all *p*-values > 0.30). There was, however, a weak relationship between total biomass of grasses and forbs and areas used by sheep, in that areas used by sheep had greater biomass (mean weight = 117.2g±23.8) compared with areas not used by bighorn sheep (mean weight = 76.7g±7.7), albeit not significant (*p*-value = 0.12; Fig. 25). We considered areas to be "used" if at least one summer home range (95% KUD) overlapped the sampling location. The lack of a negative relationship between intensity of use and biomass may appear that sheep are not exploiting available forage to an extent to deplete summer range. Nevertheless, we did not have the data needed to understand the proportion of available biomass being consumed. For example, and in accordance with optimal foraging theory, sheep can consume more biomass from patches with greater initial biomass, but the biomass that is remaining after consumption may be similar to a patch of lower initial biomass that was minimally used by sheep. Essentially, to have a comprehensive understanding of the relationship between biomass and intensity of use, longitudinal data that tracks changes in available

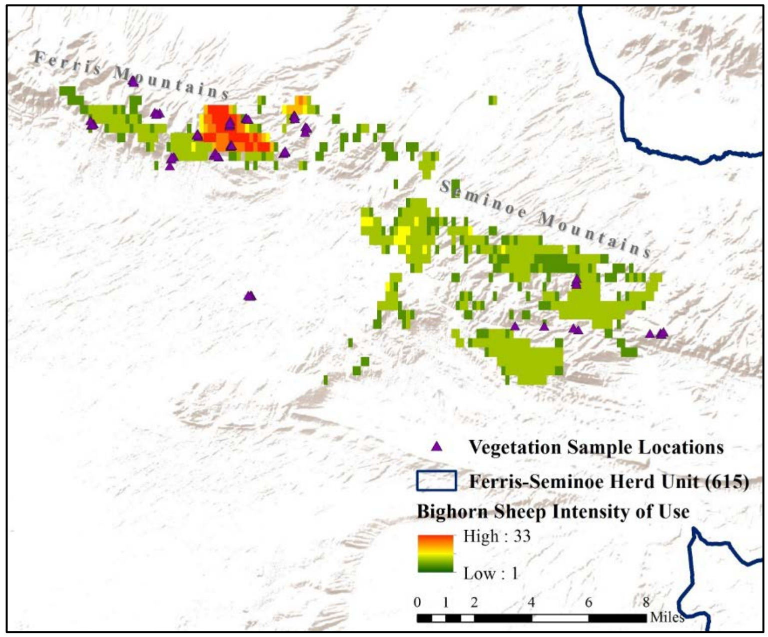


Figure 24. Locations of vegetation sample locations, where data on biomass (g) of grasses and forbs were measured, as it relates to intensity of use by female bighorn sheep as measured by the number of overlapping home ranges (95% KUD) in summer 2018.

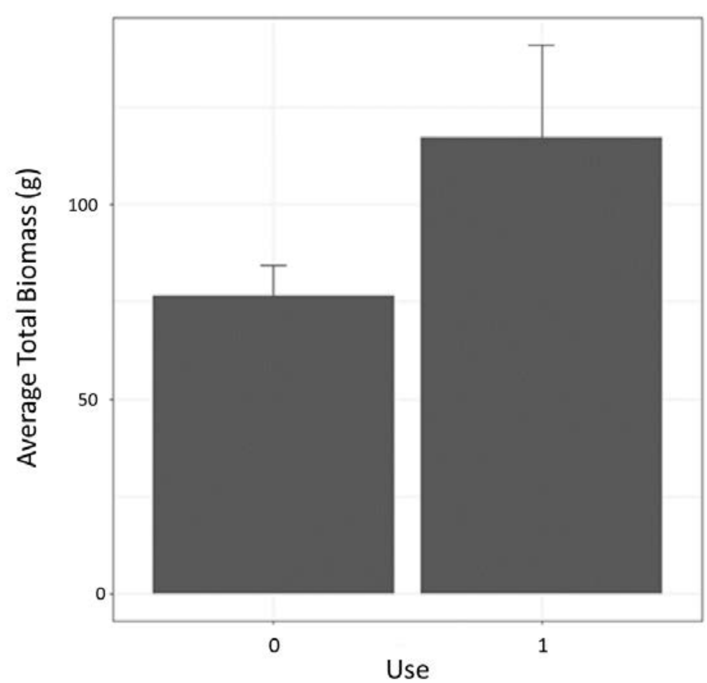


Figure 25. Average total biomass (g) of grasses and forbs between areas used by female bighorn sheep in summer 2018.

biomass and used biomass are needed. Further, data on biomass were only available for summer of 2018 and the relationship between biomass and intensity of use by sheep in winter remains unknown. Indeed, to understand the *NCC* of a predominately non-migratory population, such as Ferris-Seminoe bighorn sheep, evaluations of the habitat limitations in winter and summer are needed.

Predicting Intensity of Use

Similar to our approach in predicting resource use by bighorn sheep during 2009–2018, we used Random Forest (RF) models to predict intensity of use relative to the available resources of known importance to bighorn sheep, including topographic ruggedness, distance to escape terrain, land cover, fire severity, and vegetation (Table 2). We focused our predictions of intensity of use on female bighorn sheep in summer and winter because abundance of the female sector of a population has a greater influence on population performance than males. Variables that had the greatest importance in predicting intensity of use included topographical features in winter and summer, but fire severity also had increased importance in predicting intensity of use in summer (Fig. 26-27).

Potential Intensity of Use by Female Bighorn Sheep in Winter

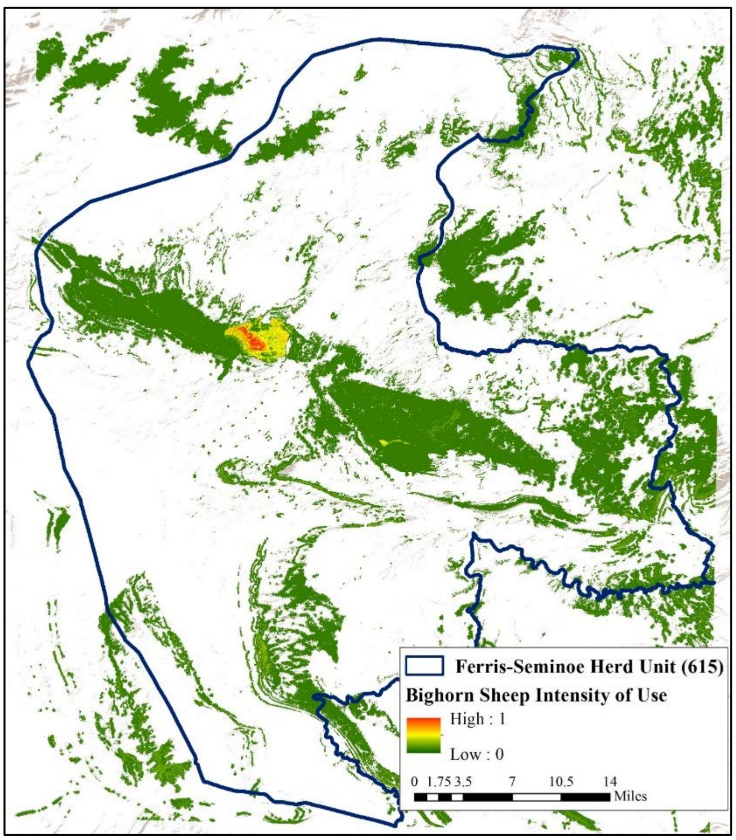


Figure 26. Intensity of use by female bighorn sheep of the Ferris-Seminoe herd unit in winter using GPS-collar data from 2009-2018. Using independent validation, R^2 for the model was 48.05%.

Potential Intensity of Use by Female Bighorn Sheep in Summer

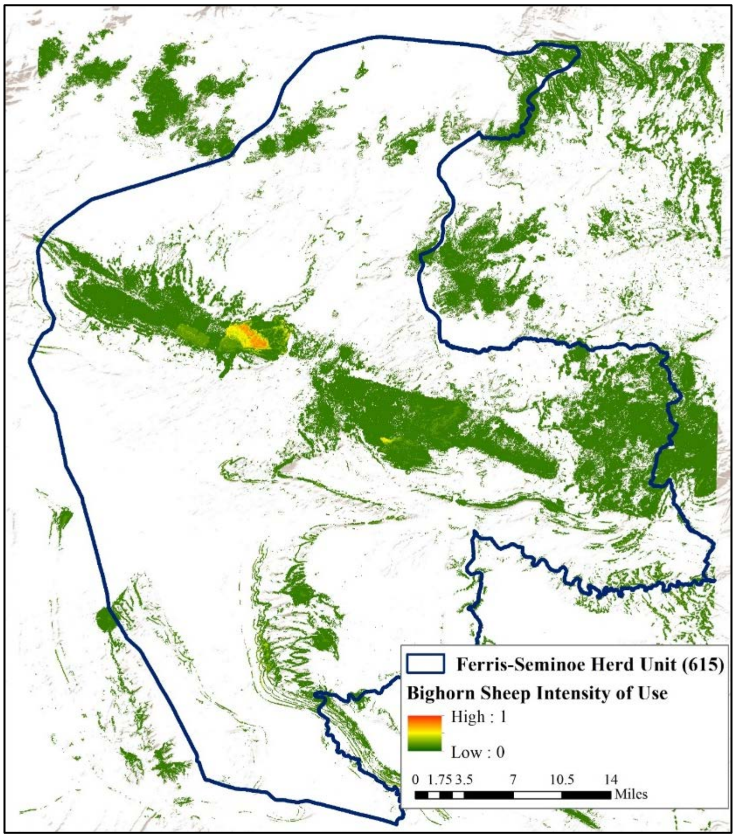


Figure 27. Intensity of use by female bighorn sheep of the Ferris-Seminoe herd unit in summer using GPS-collar data from 2009-2018. Using independent validation, R^2 for the model was 63.61%.

Observed Relative to Potential Intensity of Use by Bighorn Sheep

Spatial predictions of intensity of use, resulting from our RF model, provided us with an index to the potential intensity of use by bighorn sheep throughout the Ferris-Seminoe herd unit based on habitat and landscape features. Using results from our predicted models, we compared the observed intensity of use relative to the predicted intensity of use. Our aim was to evaluate the proportion of the potential intensity of use that is currently used by female bighorn sheep in summer and winter based on the following equation:

mean observed intensity of use / mean predicted intensity of use

Note, the proportion of the observed intensity of use relative to the potential of the landscape is reliant on the premise that observed intensity of use is a proportional representation of use for the current population during 2016–2018. These data represent the most current distribution of sheep (n = 39).

Our results revealed that within the entire area of the Ferris-Seminoe herd unit, intensity of use was 22.5% in winter and 19.6% in summer of its potential in 2018. Although there appears to be substantial habitat that could be occupied by bighorn sheep throughout the entire area of the herd unit (~2million acres; Fig. 26 and 27), current intensity of use is concentrated near where translocated sheep were released (Fig. 28 and 30). Within the area of concentrated use by GPS-collar data in 2018 (10% of the entire area), intensity of use was 76.02% in winter and 62.94% in summer of its potential in 2018 (Fig. 28-31).

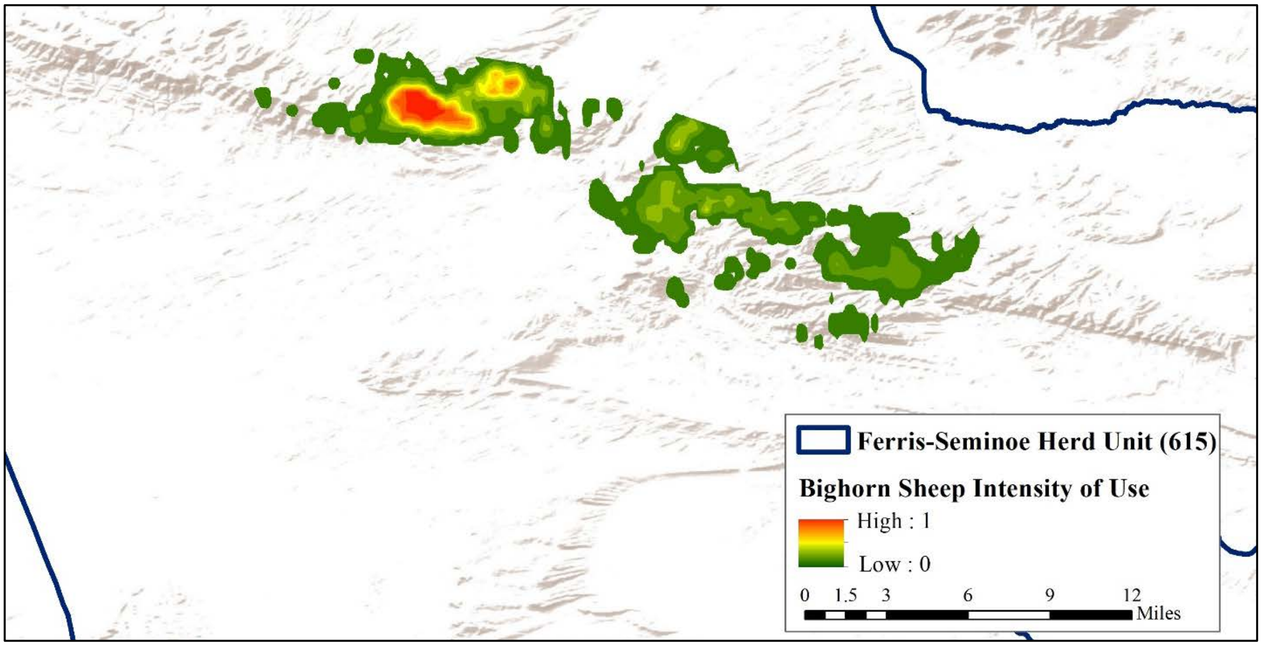


Figure 28. Intensity of use as observed in winter in 2018 in the area of current concentrated use by female bighorn sheep.

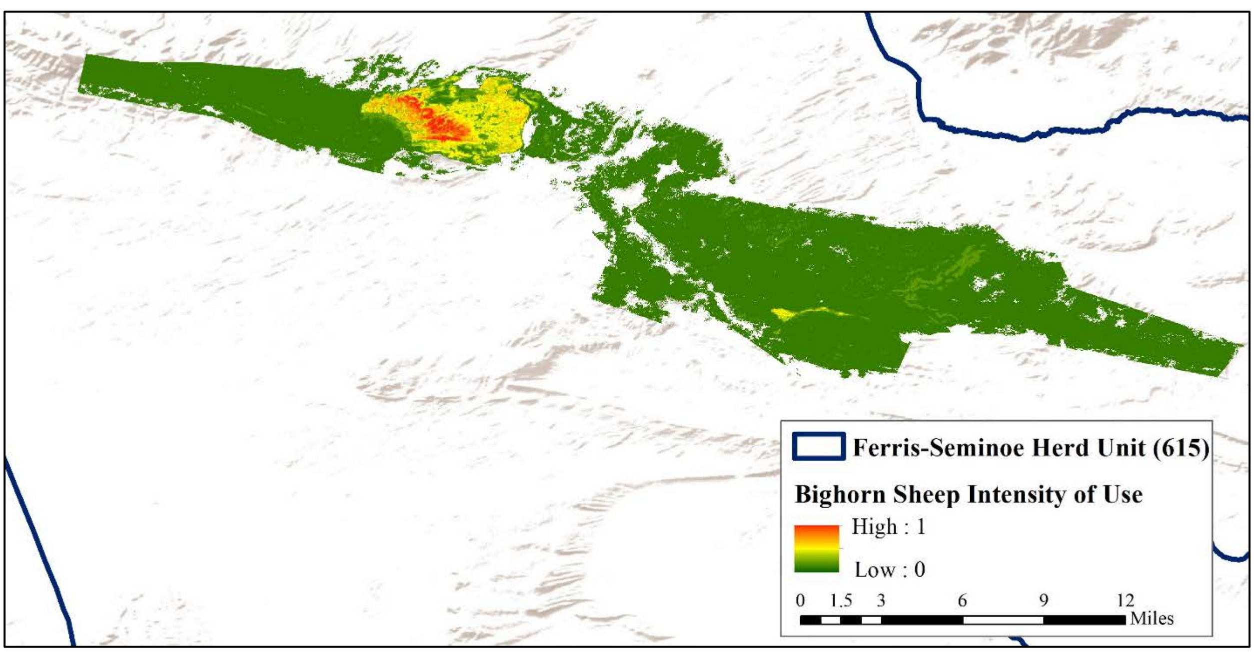


Figure 29. Potential intensity of use as predicted by our RF model in winter 2018 in the area of current concentrated use by female bighorn sheep.

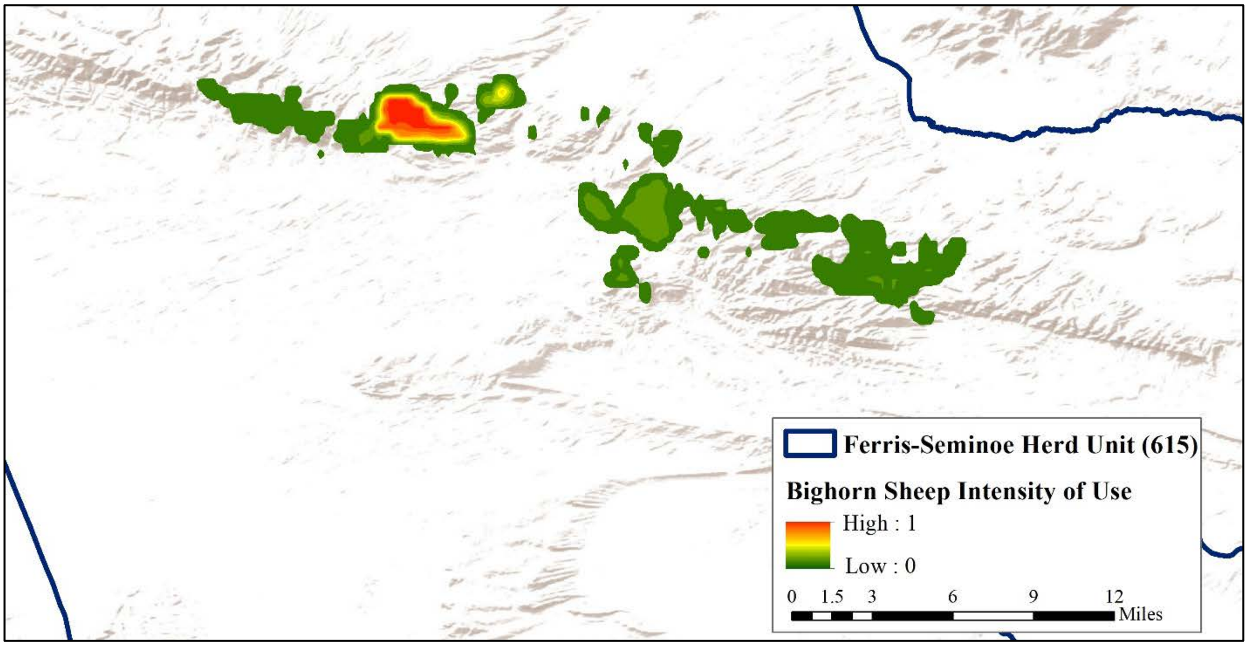


Figure 30. Intensity of use as observed in summer in 2018 in the area of current concentrated use by female bighorn sheep.

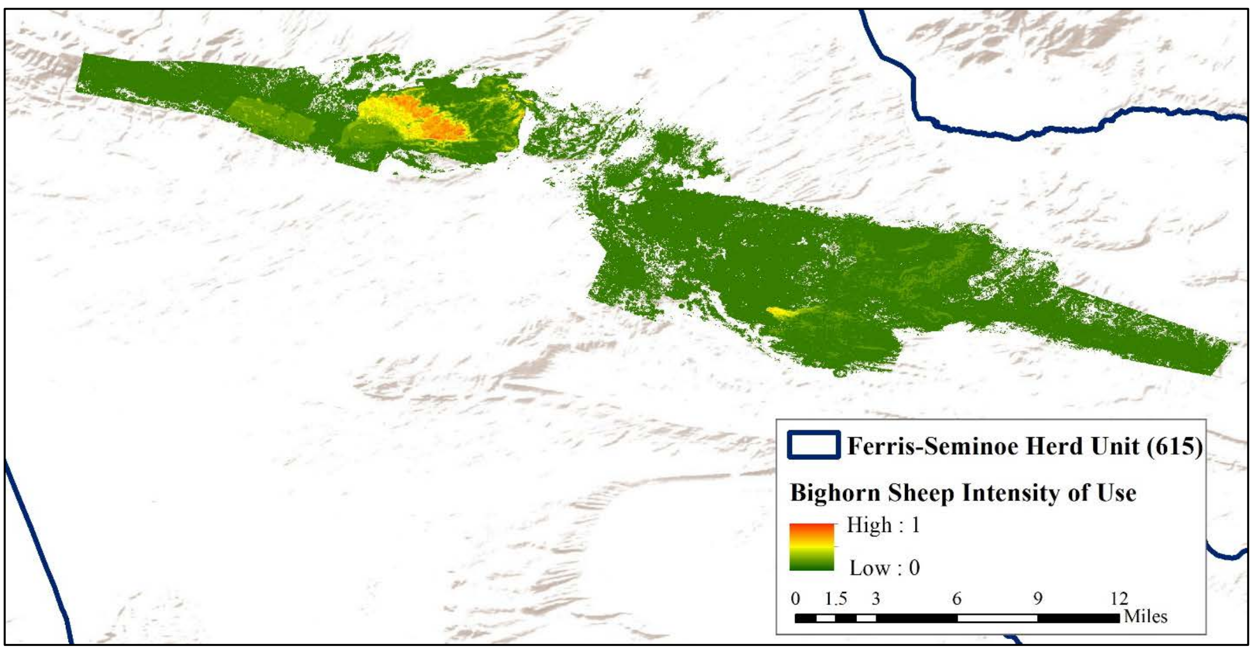


Figure 31. Potential intensity of use as predicted by our RF model in summer 2018 in the area of current concentrated use by female bighorn sheep.

Management Implications

Current distribution of and intensity of use by bighorn sheep in the Ferris-Seminoe reflects areas consistent with habitat (i.e., previous fire) and landscape (i.e., rugged terrain) characteristics important for the species. Indeed, topographically rich country offering high visibility with quality forage near escape terrain are generally accepted as optimal habitat for this mountain ungulate (Bleich et al. 1997, Holl et al. 2012). Nevertheless, the general lack of propensity to migrate or disperse, especially among females, calls to question whether other suitable habitat may exist that would help promote population growth and sustainability. Our iterative assessment of this potential indicates that other areas within the mountain range may well contain suitable habitat, but also that adjacent release locations would be necessary to promote occupancy in those areas. Further, additional release locations would be needed if increased abundance of sheep in the Ferris-Seminoe mountains is the desired outcome because intensity of use in the areas near where sheep were relocated is currently estimated at over 75% of the potential use that area can support. Notably however, additional areas for releasing sheep would have to satisfy year-round requirements, and may require further analysis of seasonal suitability to evaluate their year-round potential.

Fire is recognized as a tool to benefit bighorn sheep by not only opening up habitat and setting back succession, but also bolstering forage abundance and quality (Hobbs and Spowart 1984, Etchberger et al. 1989, Holl and Bleich 2010). Indeed, fire influenced probability and intensity of use by sheep in the Ferris-Seminoe, especially in summer, but directionality of the influence of fire is still unclear with our modeling approach. Although fire likely still serves as a management tool used for expanding viable habitat for sheep in the region, further evaluation is needed on how burn severity influences habitat use by bighorn sheep.

When food resources are abundant and accessible, ungulate populations have the potential to grow rapidly in abundance through nutritional links between female survival, reproduction, and survival of young (Forsyth and Caley 2006, Monteith et al. 2018). With rises in population density, however, comes density-dependent feedback through heightened competition for resources that leads to reductions in per capita resources and nutritional condition with cascading effects of life history (Bowyer et al. 2014, Monteith et al. 2014). Like other ungulates, bighorn sheep exhibit strong evidence of density dependence affecting a suite of life-history characteristics and population dynamics (Jorgenson et al. 1993a, Jorgenson et al. 1993b, Festa-Bianchet et al. 1995, Bérubé et al. 1996, Jorgenson et al. 1998, Monteith et al. 2018). Moreover, cyclical dynamics associated with repeat epizootic die-offs in chronically infected populations (Monello et al. 2001) has spawned the hypothesized link between animal density, nutrition, and disease (Monteith et al. 2018). Underlying any conversation associated with management of a large ungulate population is the fundamental question of whether a population should be conservatively managed at carrying capacity (the question of whether or not carrying capacity is or can be known notwithstanding; Monteith et al. 2014), or if it should be managed below carrying capacity at a level wherein density-dependent effects on habitat and the population are dampened (Monteith et al. 2015, Monteith et al. 2018). In the following, we discuss some of the biological nuances associated with considerations of the herd unit objective in light of our efforts herein, and the ecology of the species in question.

Increase herd unit objective.—Our analyses indicate that there currently exist areas within the Ferris-Seminoe range that are either unoccupied or perhaps, sheep exist at a level below what predicted use could be possible. Based on the current distribution of most sheep, intensity of use reflects >76% of predicted use (Fig. 28-31), indicating that sheep likely are near capacity of use based on current concentration. Nevertheless, with the consideration of expansion of sheep range, current intensity of use reflects a smaller proportion of the predicted potential (23%). Therefore, based on our analyses and current conditions, it would appear that the greater Ferris-Seminoe range holds the capacity for a higher abundance of sheep. Notably however, the gain in abundance would be most effectively achieved by expanding current sheep range to outlying or adjacent areas, and the only way of doing so, given the general lack of dispersal and expansion of range, would be to consider additional translocation points to help promote occupancy of adjacent habitat (Fig. 17 and 21). The capacity of habitat to support a certain abundance is only realized if the habitat is actually used and thus, integrated in to the dynamics of a population (Sawyer et al. 2016). Translocation site had a strong influence on where sheep were likely to occur, and thus, our analyses indicate that considerations of new translocation sites should be an effective tool to foster occupancy of new habitat.

Maintain current herd unit objective.—There often exists a long-standing desire to increase abundance of wildlife populations wherever it may be possible. Although it often seems as though more is better, and that more should allow for a more stable population or hunting opportunities, the evidence in support of these seemingly logical conclusions is tenuous. Indeed, with increases in density, per capita availability of forage is incrementally reduced resulting in nutritional limitation with subsequent cascading effects on survival and productivity (Bowyer et al. 2014, Monteith et al. 2014). Therefore, there may be more animals in the population, but the yield from the population may change little. Indeed, because of density dependent feedbacks within populations, increases in abundance rarely yield a greater abundance of males for harvest but may actually reduce available males for harvest through nutritional limitations that prompt negative feedbacks on growth and productivity (Jorgenson et al. 1993b, Clutton-Brock et al. 2002).

Although rarely considered as an effective tool in sheep management, female harvest remains the most effective way to regulate abundance of populations at a level below their carrying capacity to enhance nutritional dynamics and reduce herbivory on forage (Monteith et al. 2018). For example, in a relatively small (38 to 52 females) and isolated population of bighorn sheep in Alberta, Canada, an annual harvest of 12–24% of the female segment of the population occurred for 9 years, followed by a cessation of female harvest. Following cessation of harvest, the population nearly tripled in size (Jorgenson et al. 1993b). In contrast to expected increases in production of harvestable males, there were no more legal (4/5 curl) males available for harvest after the population nearly tripled. Instead, the proportion of 6–7yr old males that attained legal status decreased from 66% to 34%, because of the rise in nutritional limitation within the population following the rapid rise in density (Jorgenson et al. 1993b). As per capita resources declined with rises in abundance, females allocated fewer resources to support their growing offspring (Festa-Bianchet and Jorgenson 1998), males had fewer resources to allocate to horn growth (Festa-Bianchet et al. 2004), with males growing shorter and thinner horns as a consequence (Jorgenson et al. 1998). Indeed, although maximal size of populations may commonly be viewed as being best and yielding the greatest opportunities for harvest, with density-dependent feedbacks associated with forage limitation, maintaining a moderate density that is below the capacity of the current habitat can yield a more productive and more stable population with greater yield of large males (Monteith et al. 2018).

One of the challenges in striving to manage within some range of the capacity of the habitat is that nutritional carrying capacity (*NCC*; ability of the habitat in any one year to promote

population growth given current population size) is not stable, but is an interactive and dynamic component that is subject to habitat and environmental conditions (Monteith et al. 2014). Consequently, the population may be well below carrying capacity in one year, and despite being at a similar abundance the next year, be right at carrying capacity because of the variable environment (McCullough 1999). Therefore, providing a population with a buffer against a stochastic environment can be achieved by maintaining a population below its *NCC* and thereby, not only providing a nutritional buffer against environmental variation to individuals but also giving some wiggle room for the years where forage production is low. Indeed, populations maintained below carrying capacity and thus, at a lower population size may be more stable and productive in the face of a stochastic environment (Herfindal et al. 2006, Monteith et al. 2015, Hansen et al. 2019).

Currently, one of the greatest risks to bighorn sheep populations is that of epizootic pneumonia—a dynamic that appears to be not independent of animal density. Occurrence of epizootic die-offs associated with pneumonia are more likely to occur near peak population density (Monello et al. 2001), suggestive of density-dependent interactions among social dynamics and forage limitation being linked to disease tolerance or immunocompetence (Monteith et al. 2018). Therefore, maintaining moderate density instead of allowing a population to grow to its maximum capacity given the habitat, may well have some potential advantage associated with frequency or intensity of epizootic die-offs that have become so commonplace for bighorn sheep populations.

Decrease herd unit objective.—Based on current abundance of sheep, and our efforts to predict potential intensity of use based on habitat and landscape characteristics, the Ferris-Seminoe appear to be able to support the current abundance of sheep. Changing environmental conditions or abundance of other herbivores on the landscape could affect the ability of the current landscape to support current abundance, however, notwithstanding those changes, current evidence indicates that habitat capacity can support current abundance.

Future Considerations

With the discussion focused on reconsiderations of the herd unit objective, there are key bits of information in going forward that might be considered to better understand where the population is with respect to *NCC*. Evaluating nutritional condition of females is perhaps the most integrative and powerful lens to understand the degree of nutritional limitation within a population and thus, the proximity to *NCC* (Monteith et al. 2014, Monteith et al. 2018). In lieu of the opportunity to monitor condition of females directly, closely monitoring recruitment rates (i.e., young at heel in autumn) in conjunction with adult survival can yield meaningful indices to the degree of nutritional limitation as density potentially changes over time or in conjunction with environmental variation (Monteith et al. 2014). Should the decision be to increase the current objective and allow for population growth, monitoring of nutritional condition or recruitment in conjunction with population growth will be important to understand at what point density begins to affect nutrition and productivity. Finally, should the decision be to implement a female harvest to maintain abundance at a particular level, we encourage using such a hunt as a data collection and outreach tool. Working with hunters to garner information through kidney collections, lactation status, and age, can not only yield meaningful data on female condition over time but also can be a powerful outreach and education tool (Monteith et al. 2014). Therefore, a female harvest could serve dual purpose through regulating abundance and yielding important data.

Literature cited

Bérubé, C. H., M. Festa-Bianchet, and J. T. Jorgenson. 1996. Reproductive costs of sons and daughters in Rocky Mountain bighorn sheep. Behavioral Ecology 7:60-68.

Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: Resources or predation? Wildlife Monographs 134:1-50.

Bowyer, R. T., V. C. Bleich, K. M. Stewart, J. C. Whiting, and K. L. Monteith. 2014. Density dependence in ungulates: A review of causes, and concepts with some clarifications. California Fish and Game 100:550-572.

Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology 9:129-136.

Clapp, J. G., J. L. Beck, and K. G. Gerow. 2014. Post-release acclimation of translocated low-elevation, non-migratory bighorn sheep. Wildlife Society Bulletin 38:657-663.

Clutton-Brock, T. H., T. N. Coulson, E. J. Milner-Gulland, D. Thomson, and H. M. Armstrong. 2002. Sex differences in emigration and mortality affect optimal management of deer populations. Nature 415:633-637.

DeCesare, N. J. and D. H. Pletscher. 2006. Movements, connectivity, and resource selection of Rocky Mountain bighorn sheep. Journal of Mammalogy 87: 531-538.

Etchberger, R. C., P. R. Krausman, and R. Mazaika. 1989. Mountain sheep habitat characteristics in the pusch ridge wilderness, arizona. The Journal of Wildlife Management 53:902-907.

Evans J.S., J. Oakleaf, S.A. Cushman, and D. Theobald. 2014. An ArcGIS Toolbox for Surface Gradient and Geomorphometric Modeling, version 2.0-0.

Festa-Bianchet, M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia 75:580-586

Festa-Bianchet, M., D. W. Coltman, L. Turelli, and J. T. Jorgenson. 2004. Relative allocation to horn and body growth in bighorn rams varies with resource availability. Behavioral Ecology 15:305-312.

Festa-Bianchet, M., and J. T. Jorgenson. 1998. Selfish mothers: Reproductive expenditure and resource availability in bighorn ewes. Behavioral Ecology 9:144-150.

Festa-Bianchet, M., J. T. Jorgenson, M. Lucherini, and W. D. Wishart. 1995. Life-history consequences of variation in age of primiparity in bighorn ewes. Ecology 76:871-881.

Forsyth, D. M., and P. Caley. 2006. Testing the irruptive paradigm of large-herbivore dynamics. Ecology 87:297-303.

Geist, V. 1971. Mountain sheep. University of Chicago Press, Chicago, Illinois, USA.

Hansen, B. B., M. Gamelon, S. D. Albon, A. M. Lee, A. Stien, R. J. Irvine, B.-E. Sæther, L. E. Loe, E. Ropstad, V. Veiberg, and V. Grøtan. 2019. More frequent extreme climate events stabilize reindeer population dynamics. Nature Communications 10:1616.

Hamel, S., S. D. Cote, J. M. Gaillard, and M. Festa-Bianchet. 2009. Individual variation in reproductive costs of reproduction: high-quality females always do better. Journal of Animal Ecology 78:143-151.

Herfindal, I., B. E. Saether, E. J. Solberg, R. Andersen, and K. A. Hogda. 2006. Population characteristics predict responses in moose body mass to temporal variation in the environment. Journal of Animal Ecology 75:1110-1118.

Hobbs, N. T., and R. A. Spowart. 1984. Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. Journal of Wildlife Management 48:551-560.

Hobbs, N. T., and D. M. Swift. 1985. Estimates of habitat carrying-capacity incorporating explicit nutritional constraints. Journal of Wildlife Management, 49:814-822.

Holl, S. A., and V. C. Bleich. 2010. Responses of large mammals to fire and rain in the San Gabriel Mountains, California. Proceedings of the Northern Wild Sheep and Goat Council 17:139-156.

Holl, S. A., V. C. Bleich, B. W. Callenberger, and B. Bahro. 2012. Simulated effects of two fire regimes on bighorn sheep: The San Gabriel Mountains, California, USA. Fire Ecology 8:88-103.

Hurley, K., C. Brewer, and G. N. Thornton. 2015. The role of hunters in conservation, restoration, and management of North American wild sheep. International Journal of Environmental Studies 72:784-796.

Jesmer, B. R., J. A. Merkle, J. R. Goheen, E. O. Aikens, J. L. Beck, A. B. Courtemanch, M. A. Hurley, D. E. McWhirter, H. M. Miyasaki, K. L. Monteith, and M. J. Kauffman. 2018. Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. Science 361:1023-1025.

Johnson, C.J., Parker, K.L. & Heard, D.C. 2001. Foraging across a variable landscape: behavioural decisions made by woodland caribou at multiple spatial scales. Oecologia, 71:590– 602.

Bérubé, C. H., M. Festa-Bianchet, and J. T. Jorgenson. 1996. Reproductive costs of sons and daughters in Rocky Mountain bighorn sheep. Behavioral Ecology 7:60-68.

Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: Resources or predation? Wildlife Monographs 134:1-50.

Bowyer, R. T., V. C. Bleich, K. M. Stewart, J. C. Whiting, and K. L. Monteith. 2014. Density dependence in ungulates: A review of causes, and concepts with some clarifications. California Fish and Game 100:550-572.

Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology 9:129-136.

Clapp, J. G., J. L. Beck, and K. G. Gerow. 2014. Post-release acclimation of translocated low-elevation, non-migratory bighorn sheep. Wildlife Society Bulletin 38:657-663.

Clutton-Brock, T. H., T. N. Coulson, E. J. Milner-Gulland, D. Thomson, and H. M. Armstrong. 2002. Sex differences in emigration and mortality affect optimal management of deer populations. Nature 415:633-637.

Etchberger, R. C., P. R. Krausman, and R. Mazaika. 1989. Mountain sheep habitat characteristics in the Pusch Ridge Wilderness, Arizona. The Journal of Wildlife Management 53:902-907.

Festa-Bianchet, M. 1988. Seasonal range selection in bighorn sheep: Conflicts between forage quality, forage quantity, and predator avoidance. Oecologia 75:580-586.

Festa-Bianchet, M., D. W. Coltman, L. Turelli, and J. T. Jorgenson. 2004. Relative allocation to horn and body growth in bighorn rams varies with resource availability. Behavioral Ecology 15:305-312.

Festa-Bianchet, M., and J. T. Jorgenson. 1998. Selfish mothers: Reproductive expenditure and resource availability in bighorn ewes. Behavioral Ecology 9:144-150.

Festa-Bianchet, M., J. T. Jorgenson, M. Lucherini, and W. D. Wishart. 1995. Life-history consequences of variation in age of primiparity in bighorn ewes. Ecology 76:871-881.

Forsyth, D. M., and P. Caley. 2006. Testing the irruptive paradigm of large-herbivore dynamics. Ecology 87:297-303.

Geist, V. 1971. Mountain sheep. University of Chicago Press, Chicago, Illinois, USA.

Hamel, S., J. M. Gaillard, M. Festa-Bianchet, and S. D. Cote. 2009. Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. Ecology 90:1981-1995.

Hansen, B. B., M. Gamelon, S. D. Albon, A. M. Lee, A. Stien, R. J. Irvine, B.-E. Sæther, L. E. Loe, E. Ropstad, V. Veiberg, and V. Grøtan. 2019. More frequent extreme climate events stabilize reindeer population dynamics. Nature Communications 10:1616.

Herfindal, I., B. E. Saether, E. J. Solberg, R. Andersen, and K. A. Hogda. 2006. Population characteristics predict responses in moose body mass to temporal variation in the environment. Journal of Animal Ecology 75:1110-1118.

Hobbs, N. T., D. L. Baker, J. E. Ellis, D. M. Swift, and R. A. Green. 1982. Energy-based and nitrogen-based estimates of elk winter-range carrying-capacity. Journal of Wildlife Management 46:12-21.

Hobbs, N. T., and R. A. Spowart. 1984. Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. Journal of Wildlife Management 48:551-560.

Holl, S. A., and V. C. Bleich. 2010. Responses of large mammals to fire and rain in the san gabriel mountains, California. Proceedings of the Northern Wild Sheep and Goat Council 17:139-156.

Holl, S. A., V. C. Bleich, B. W. Callenberger, and B. Bahro. 2012. Simulated effects of two fire regimes on bighorn sheep: The san gabriel mountains, California, USA. Fire Ecology 8:88-103.

Hurley, K., C. Brewer, and G. N. Thornton. 2015. The role of hunters in conservation, restoration, and management of North American wild sheep. International Journal of Environmental Studies 72:784-796.

Jesmer, B. R., J. A. Merkle, J. R. Goheen, E. O. Aikens, J. L. Beck, A. B. Courtemanch, M. A. Hurley, D. E. McWhirter, H. M. Miyasaki, K. L. Monteith, and M. J. Kauffman. 2018. Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. Science 361:1023-1025.

Jorgenson, J. T., M. Festa-Bianchet, M. Lucherini, and W. D. Wishart. 1993a. Effects of body size, population density, and maternal characteristics on age at first reproduction in bighorn ewes. Canadian Journal of Zoology 71:2509-2517.

Jorgenson, J. T., M. Festa-Bianchet, and W. D. Wishart. 1993b. Harvesting bighorn ewes: Consequences for population size and trophy ram production. Journal of Wildlife Management 57:429-435.

Jorgenson, J. T., M. Festa-Bianchet, and W. D. Wishart. 1998. Effects of population density on horn development in bighorn rams. Journal of Wildlife Management 62:1011-1020.

McCullough, D. R. 1999. Density dependence and life-history strategies of ungulates. Journal of Mammalogy 80:1130-1146.

Monello, R. J., D. L. Murray, and E. F. Cassirer. 2001. Ecological correlates of pneumonia epizootics in bighorn sheep herds. Canadian Journal of Zoology 79:1423-1432.

Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, J. G. Kie, and R. T. Bowyer. 2014. Life-history characteristics of mule deer: Effects of nutrition in a variable environment. Wildlife Monographs 186:1-62.

Monteith, K. L., R. W. Klaver, K. R. Hersey, A. A. Holland, T. P. Thomas, and M. J. Kauffman. 2015. Effects of climate and plant phenology on recruitment of moose at the southern extent of their range. Oecologia 178:1137-1148.

Monteith, K. L., R. A. Long, T. R. Stephenson, V. C. Bleich, R. T. Bowyer, and T. N. Lasharr. 2018. Horn size and nutrition in mountain sheep: Can ewe handle the truth? The Journal of Wildlife Management 82:67-84.

Mysterud, A., L. Loe, B. Zimmermann, R. Bischof, V. Veiberg, and E. Meisingset. 2011. Partial migration in expanding red deer populations at northern latitudes - a role for density dependence? Oikos 120:1817 - 1825.

Risenhoover, K. L., and J. A. Bailey. 1985. Foraging ecology of mountain sheep - implications for habitat management. Journal of Wildlife Management 49:797-804.

Sawyer, H., J. A. Merkle, A. D. Middleton, S. P. H. Dwinnell, and K. L. Monteith. 2019. Migratory plasticity is not ubiquitous among large herbivores. Journal of Animal Ecology 88:450-460.

Sawyer, H., A. D. Middleton, M. M. Hayes, M. J. Kauffman, and K. L. Monteith. 2016. The extra mile: Ungulate migration distance alters the use of seasonal range and exposure to anthropogenic risk. Ecosphere 7:e01534.

Schroeder, C. A., R. T. Bowyer, V. C. Bleich, and T. R. Stephenson. 2010. Sexual segregation in Sierra Nevada bighorn sheep, *Ovis canadensis sierrae*: Ramifications for conservation. Arctic, Antarctic, and Alpine Research 42:476-489.

Shoemaker, K., L. Heffelfinger, N. J. Jackson, M. Blum, T. Wasley, and K. Stewart. 2018. A machine-learning approach for extending classical wildlife resource selection analyses. Volume 8.

Stewart, K. M., R. T. Bowyer, R. W. Ruess, B. L. Dick, and J. G. Kie. 2006. Herbivore optimization by North American elk: Consequences for theory and management. Wildlife Monographs:1-24.

Acknowledgments

We thank Mathew O. Jones, Brady W. Allred, and David E. Naugle from the University of Montana and Daniel Uden from the University of Nebraska in Lincoln for providing us with annual percent vegetation cover data. Also, we thank Dirac Twidwell and Jeffrey Beck for their assistance facilitating collaborations.

Project Partners

MONTEITH SHOP
HAUB SCHOOL OF ENVIRONMENT & NATURAL RESOURCES
WYOMING COOPERATIVE FISH & WILDLIFE RESEARCH UNIT

WYOMING GAME & FISH DEPARTMENT

UNIVERSITY OF Nebraska Lincoln®

For More Information, Contact Us:

University of Wyoming

Samantha Dwinnell
sdwinnel@uwyo.edu

Kevin Monteith
kevin.monteith@uwyo.edu

University of Nebraska-Lincoln

Victoria Donovan
victoria.donovan@huskers.unl.edu

Wyoming Game and Fish Department

Greg Hiatt
greg.hiatt@wyo.gov

Amy Anderson
amy.anderson@wyo.gov

Daryl Lutz
daryl.lutz@wyo.gov

Haub School of Environment and Natural Resources

Academic Programs | Biodiversity Institute | Ruckelshaus Institute

Bim Kendall House
804 E Fremont St
Laramie, WY 82072