A Robust Approach for Modeling Bighorn Sheep Habitat

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ABSTRACT Bighorn sheep (*Ovis canadensis*) are endemic to dry, mountainous regions of North America, but many populations were extirpated shortly after European colonization. Consequently, reintroducing bighorn sheep has been a major undertaking throughout the western United States. GIS has been used to evaluate bighorn sheep habitat since the 1990's. In this study, we developed habitat-use models for female bighorn sheep using GIS and logistic regression. We created habitat models for two study areas in north-central Utah, which classified 85.2 to 95.9% of bighorn locations correctly. When the habitat models were extrapolated to areas with bighorn sheep and validated with known bighorn locations, they correctly classified 94.0 to 95.4% of locations. We found slope and tree cover to be robust variables that accurately predicted habitat-use of bighorns. Our results provide managers with a tool to predict habitat-use of bighorn sheep at a landscape scale.

INTRODUCTION

Bighorn sheep (*Ovis canadensis*) are medium-sized ungulates endemic to dry, mountainous regions of North America (Shackleton et al. 1999). Many populations were reduced severely or extirpated shortly after European colonization (Krausman 2000), in large part due to disease and unregulated harvest (Buechner 1960, Goodson 1982). Consequently, reintroducing bighorn sheep to previously occupied areas has been a major undertaking throughout the western United States. Bighorn sheep reintroductions, however, have varied in their levels of success (Smith et al. 1988). From 1923 to 1997, only 41% of bighorn reintroductions were successful in 6 western states (Singer et al. 2000). Additionally in Utah, where virtually all Rocky Mountain bighorns (*O. c. canadensis*) were extirpated, only 23% of reintroduced populations have been successful (Shannon et al. in review).

Although bighorns inhabited nearly every mountain range in Utah prior to European settlement in the mid 1800s (Dalton and Spillett 1971), it is not possible to restore bighorns to all their former habitats. One reason for this limitation is the distribution of domestic sheep throughout the state (Smith et al. 1990, Shannon et al. in review). Bighorn sheep are highly susceptible to pathogens carried by domestic livestock (Foreyt et al. 1994, Monello et al. 2001), and domestic sheep, in particular, carry a respiratory disease that commonly kills bighorn sheep (Foreyt and Jessup 1982). Some bighorns may survive a die-off, but recruitment can be suppressed for several years following an epidemic (Cassirer and Sinclair 2007). Vaccines are being developed, but currently, spatial separation is the only viable solution to prevent bighorns from experiencing large scale die-offs due to foreign diseases. Spatial separation is difficult, however, because both species are social and may actively seek each other's company.

Another difficulty associated with bighorn sheep restoration is the change to landscapes caused by fire suppression, resulting in increased shrub and tree cover (Wakelyn 1987). Bighorn sheep are considered habitat specialists (Shackleton et al. 1999). They prefer open areas with low-growing vegetation and high visibility, because it allows them to detect potential predators (Risenhoover and Bailey 1985). Mountain lions (*Puma concolor*), however, are stalking predators that use cover to approach prey species and have severely reduced some populations of bighorn sheep (Wehausen 1996, Hayes et al. 2000). It follows that tree and shrub encroachment may diminish habitat quality for bighorns by increasing predation risk. Indeed, shrub and tree encroachment may have been ultimately responsible for increased mountain lion predation rates in New Mexico (Rominger et al. 2004).

Although vegetation structure is important; steep, rugged terrain is the defining characteristic of bighorn sheep habitat, especially for females (Bleich et al. 1997). Bighorns use precipitous topography, termed escape terrain (slopes 27°-85°), to evade predators and reduce predation of their neonates (Geist 1971, Bleich et al. 1997). Escape terrain is so vital that female bighorns typically stay within 300 m of escape terrain at all times (Fairbanks et al. 1987, Smith et al. 1990). Population size is also correlated with the amount and configuration of escape terrain, and it has been recommended that desert bighorn sheep be reintroduced to areas with at least 15 km^2 of escape terrain (McKinney et al. 2003).

Habitat variables that are biologically important to bighorn sheep, such as escape terrain, can be quantified at a landscape scale using Geographic Information Systems (GIS). This technology has been used to assess habitat quality and evaluate habitat use of bighorn sheep for nearly 2 decades (Smith et al. 1990, Johnson and Swift 2000, Whiting et al. 2004). Habitat-use variables used in early studies included escape terrain, aspect, elevation, distance to water, and visibility (Smith et al. 1990, Smith and Flinders 1992, Sweanor et al. 1998). Recent studies have incorporated measures of landscape ruggedness (Divine et al. 1996, Sappington et al. 2007) and a GIS-based measure of visibility called viewshed (Bangs et al. 2005).

Modeling bighorn sheep habitat accurately is becoming increasingly important because (1) land-use decisions regarding grazing and appropriate spatial separation from domestic sheep may be based on model results (USFS 2006), (2) models may improve the success rate of costly reintroductions, (3) management of endangered subspecies may be improved (Turner et al. 2004), and (4) habitat treatments such as water developments and prescribed burning may be applied more judiciously. In this study, we developed a habitat model for female bighorn sheep that was robust enough to predict use over a wide geographic area. We used variables that quantified the physical structure of habitats, such as topography and tall vegetation. We then extrapolated models developed in this paper to other areas with bighorn sheep, and validated them with observed locations of bighorns.

STUDY AREAS

Our first study area was Antelope Island State Park (40°95´N, 112°21´W) located in the Great Salt Lake in northern Utah (Fig. 1). Bighorn Sheep were established in this area in 1997 with animals from British Columbia, Canada and Nevada. The extent of this area was 113 km^2, and elevation ranged from 1,278 m to 2,134 m. Precipitation averaged 39 cm a year, and natural water sources were abundant and used extensively by bighorns (Whiting et al. in review). During the study, vegetation on the island was dominated by grasses that included annual bromes (*Bromus* spp.) and wheat grasses (*Elymus* spp.) and low-growing brush such as sagebrush (*Artemisia* spp.). Tree cover was sparse. Escape terrain for bighorn sheep comprised only 8 km^2 of the available area (Olson et al. in review). Potential predators were bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and golden eagles (*Aquila chrysaetos*). Wild ungulates that occupied

Antelope Island included bison (*Bison bison*), mule deer (*Odocoileus hemionus*), and pronghorn (*Antilocapra americana*).

Our second study area was the Stansbury Mountains (40°71´N, 112°63´W) located near the southwest shores of the Great Salt Lake, 45 km from Antelope Island (Fig. 1). Bighorn sheep were reintroduced to this mountain range from Antelope Island in 2005. The study area encompassed 650 km^2, and elevation ranged between 1,280 m and 3,362 m. Precipitation at valley elevations (35 cm) was similar to Antelope Island, but higher elevations received >140 cm (Taye 1981). Vegetation below 2200 m was similar to Antelope Island, but with more extensive juniper (*Juniperus* spp.) cover. Above 2200 m, there was substantial tree cover that included aspen (*Populus tremuloides*), Douglas fir (*Psuedotsuga menziesii*), and Englemann spruce (*Picea englemannii*), as well as alpine habitat. The Stansbury Mountains are a rugged mountain range, and 29% of the area was considered escape terrain for bighorn sheep (Olson et al. in review). Potential predators of bighorn sheep were bobcats, coyotes, golden eagles, and mountain lions. Sympatric wild ungulates included elk (*Cervus elaphus*) in limited numbers and mule deer. Domestic cattle were permitted to graze on public and private lands in this area.

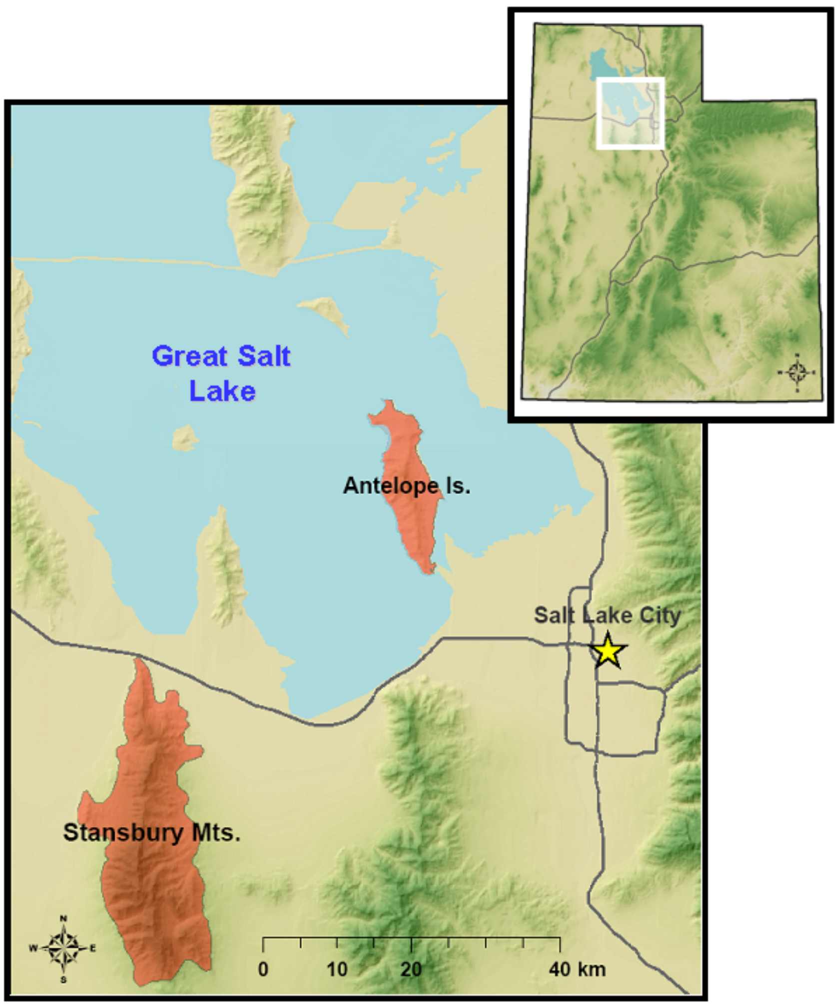

Figure 1. Antelope Island State Park and the Stansbury Mountains are located in north-central, Utah.

METHODS

Data Collection

We gathered habitat-use information for bighorn sheep on Antelope Island from 2005 to 2006. We located animals throughout the year using binoculars and spotting scopes. Few bighorns were radio marked in this study area, therefore we located bighorns by following established transects. When bighorns were sighted, we recorded group demographics (number of females, males, yearlings, and lambs) and the location of animals was marked on a topographic map. In an effort to reduce temporal autocorrelation, observed groups were not sampled more than once a day (Smith et al. 1999). Because male and female bighorn sheep have different habitat requirements based on alternative reproductive strategies (Bleich et al. 1997), we focused on female habitat use. We defined female groups as sightings with at least 1 adult female.

On the Stansbury Mountains, we collected habitat-use information from 2005 to 2008. Greater than 90% (n = 57) of the animals initially released were fitted with radio tracking collars manufactured by Lotek wireless (Newmarket, Ontario, Canada). We used systematic sampling to locate radio-collared individuals. Opportunistic sightings of unmarked animals were also used in our analyses. Observed groups were not sampled more than once a day.

Habitat-use Variables

For each bighorn sheep location, we used GIS to estimate values for slope, percent ruggedness, percent tree cover, and solar radiation. Slope, ruggedness, and solar radiation calculations all required a Digital Elevation Model (DEM) as an input layer. We acquired a 5 m resolution DEM from the Utah GIS portal (2008). We used the Slope tool in Spatial Analyst within ArcGIS 9.2 (ESRI, Redlands, CA) to create a slope layer from the DEM. The Focal Statistics tool is a neighborhood function available in Spatial Analyst. The user defines the size and shape of the neighborhood (i.e. a 20 m x 20 m area) from which the Focal Statistics tool generates a new raster layer with a mean value for the defined neighborhood. We used the Focal Statistics tool to calculate the mean slope value for a 1 ha square. A 1 ha buffer was used to account for inherent errors in mapping locations and in the habitat-use layers that were used in this analysis.

To measure landscape ruggedness, we used the Vector Ruggedness Measure (VRM) model developed and tested by Sappington et al. (2007). VRM estimates the degree of terrain ruggedness by calculating the dispersion of vectors orthogonal to the landscape surface. Unlike other measures of landscape ruggedness, VRM is less correlated with slope, because slope is only 1 of several variables used to calculate VRM (Sappington et al. 2007). We created a ruggedness layer for both study areas from a 5 m DEM using the VRM tool (Fig. 2). We also used the Focal Statistics tool to calculate the mean ruggedness value for a 1 ha area.

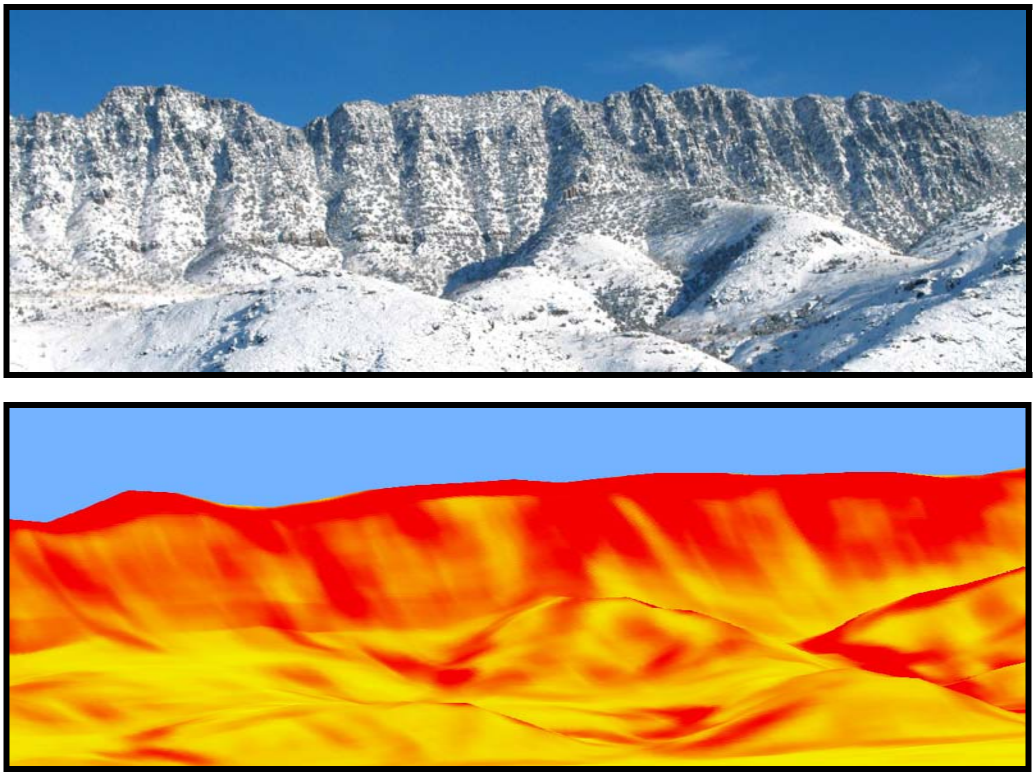

Figure 2. Rugged terrain used by bighorn sheep for lambing habitat on the Stansbury Mountains, Utah and the associated Vector Ruggedness Measure (VRM) model displayed in ArcScene. Red indicates rugged terrain and yellow indicates less rugged terrain.

For each study area, we generated a layer with percent tree cover. As a base layer for our tree cover calculations, we used a 1-m resolution color National Agriculture Imagery Program (NAIP) image obtained from the Utah GIS portal (2008). We performed an unsupervised classification on this image using the Classifier function in Erdas Imagine (Erdas Inc., Norcross, GA). We visually inspected the 30 classes that were created to determine which classes defined tree cover. We then reclassified the output into 2 groups: tree cover and non-tree cover (Fig. 3). Finally, we used the Focal Statistics tool to calculate percent tree cover for a 1 ha area.

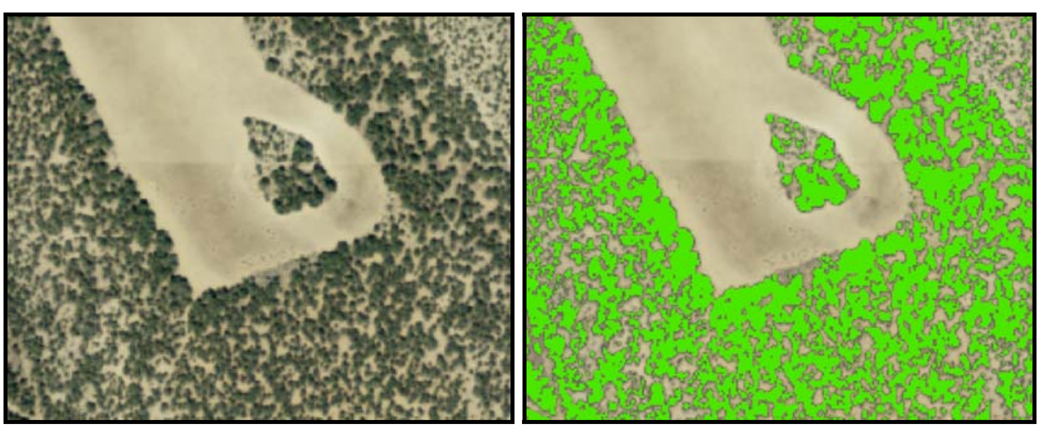

Figure 3. One-meter resolution NAIP color image of juniper cover on the Stansbury Mountains, Utah (left photo). Juniper cover (right photo) delineated using an unsupervised classification of the NAIP image.

The last variable we measured was incident solar radiation. We created this layer using the Area Solar Radiation tool in Spatial Analyst. This tool generated a raster layer in which each pixel was assigned a value of watt hours per square meter (WH/m^2) for a one year period. It calculated this value by modeling the path of the sun in relationship to the slope, aspect, and surrounding topography of a pixel. We then calculated the mean daily solar radiation for each pixel. As for all other variables, we also used the Focal Statistics tool to scale the variable to 1 ha.

To account for seasonal variation, we defined three seasons for our study areas that were biologically important for female bighorns: winter (Oct 1-Mar 14), lambing (Mar 15-May 14), and summer (May 15-Sep 30). We created these seasons based on annual variation in reproductive behavior and climate. Lambing season was defined from known birth dates of bighorn lambs in both study areas (Olson et al. in review). The summer season encompassed the hottest, driest months of the year (Fig. 4).

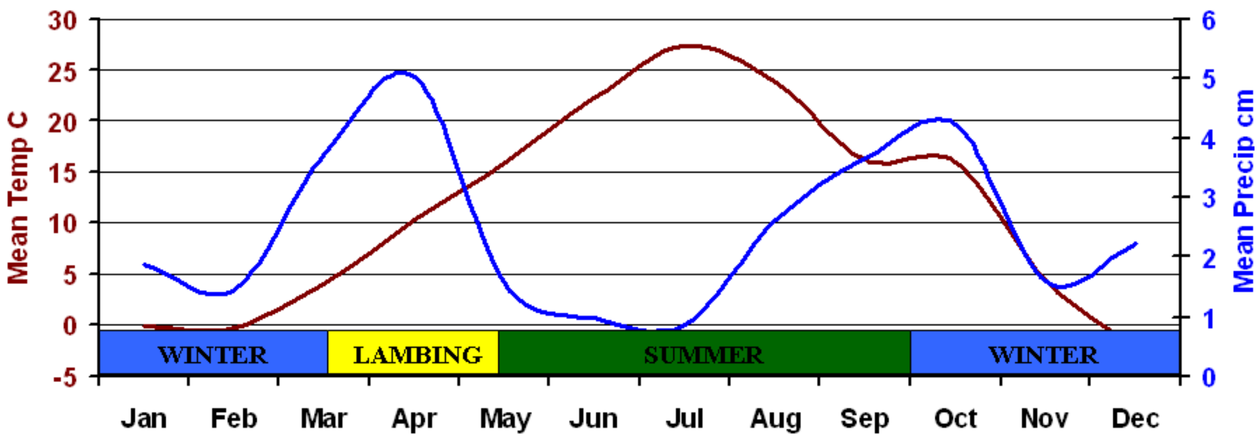

Figure 4. Mean monthly temperature (°C) and mean monthly precipitation (cm) were plotted for the Stansbury Mountains, Utah. Three seasons (winter, lambing, and summer) for bighorn sheep were delineated based on reproductive behavior of bighorns and climatic variation.

<u>Model Selection</u>

To model habitat use of bighorns on Antelope Island and the Stansbury Mountains, we used logistic regression. Logistic regression is a robust Generalized Linear Model (GLM) that has been applied to habitat studies of wildlife (Mladenoff et al. 1999, Manly et al. 2002, D'Eon and Serrouya 2005). Ideally, logistic regression requires data from used and un-used sites to generate a Resource Selection Probability Function (RSPF). The use of logistic regression, however, has been expanded to analyze use-availability data (Manly et al. 2002). In this study design, habitat attributes at known use sites are compared with random points, which may or may not be used by a species. The output of this model is termed a Resource Selection Function (RSF), which approximates the RSPF (Johnson et al. 2006). In this study, we used the use-availability design to create an RSF. We generated random points in our study areas using the Create Random Points tool in Spatial Analyst. The number of random points equaled the number of bighorn locations for each area. From a list of a priori models (Table 1), we used Akaike's Information Criterion (AIC) to select the most parsimonious models that best fit the data (Akaike 1973). All statistical analyses were performed in R 2.7 (R Development Core Team 2007). To assess the fit of selected models, we evaluated the significance values of variables included in the models and the percent of bighorn locations classified correctly. After fit was assessed, the RSFs were extrapolated to test their predictive power. For example, we extrapolated the RSF created for Antelope Island to the Stansbury Mountains, and then used bighorn locations on the Stansbury Mountains to validate the model**.**

Table 1. This set of A priori models relates the influence of slope, ruggedness, tree cover, and solar radiation to habitat-use by female bighorn sheep.

Model No.	Model Type[a]	Hypothesis Description	Model Structure
1	Year/Season	Female habitat use varied by slope	Slope
2	Year/Season	Female habitat use varied by ruggedness	Ruggedness
3	Year/Season	Female habitat use varied by tree cover	Tree Cover
4	Season	Female habitat use varied by solar radiation	Solar radiation
5	Year/Season	Female habitat use varied by slope and ruggedness in an additive manner	Slope+ruggedness
6	Year/Season	Female habitat use varied by slope and tree cover in an additive manner	Slope+tree cover
7	Season	Female habitat use varied by slope and solar radiation in an additive manner	Slope+solar radiation
8	Year/Season	Female habitat use varied by slope, ruggedness, and tree cover in an additive manner	Slope+ruggedness+tree cover
9	Season	Female habitat use varied by slope, ruggedness, solar radiation in an additive manner	Slope+ruggedness+solar radiation
10	Season	Female habitat use varied by slope, tree cover, and solar radiation in an additive manner	Slope+tree cover+solar radiation
11	Season	Female habitat use varied by slope, ruggedness, tree cover, and solar radiation in an additive manner	Slope+ruggedness+tree cover+solar radiation
12	Year/Season	Female habitat use varied by ruggedness and tree cover in an additive manner	Ruggedness+tree cover
13	Season	Female habitat use varied by ruggedness and solar radiation in an additive manner	Ruggedness+solar radiation
14	Season	Female habitat use varied by ruggedness, tree cover and solar radiation in an additive manner	Ruggedness+tree cover+solar radiation
15	Season	Female habitat use varied by tree cover and solar radiation in an additive manner	Tree cover+solar radiation

[a] Model type describes which models were used in yearlong (Year) and seasonal (Season) analyses.

RESULTS

Model Selection

A total of 183 locations for female groups were collected on Antelope Island. On Antelope Island, we evaluated 7, yearlong models for habitat-use of female bighorn sheep (Table 1). Based on AIC, the model that included only the effect of slope best fit the data for yearlong use (Table 2). Slope was highly significant in this model ($P < 0.001$). The coefficient value for slope was positive, and it was estimated that a 2 fold increase in slope increased the odds of bighorn use by 37%. The yearlong model classified correctly 94.5% of bighorn locations on Antelope Island (Table 3., Fig. 5).

Table 2. Yearlong models for habitat use by female bighorn sheep on Antelope Island were ranked using AIC.

Model No.	Model Structure	K[a]	AIC[b]	ΔAIC
1	Slope	2	87.1	0.0
5	Slope+ruggedness	3	88.9	1.8
6	Slope+tree cover	3	88.9	1.8
8	Slope+ruggedness+tree cover	4	90.5	3.4
12	ruggedness+tree cover	3	190.9	103.8
2	Ruggedness	2	198.1	111.0
3	Tree cover	2	506.9	419.8

[a] Number of parameters
[b] Akaike's Information Criterion

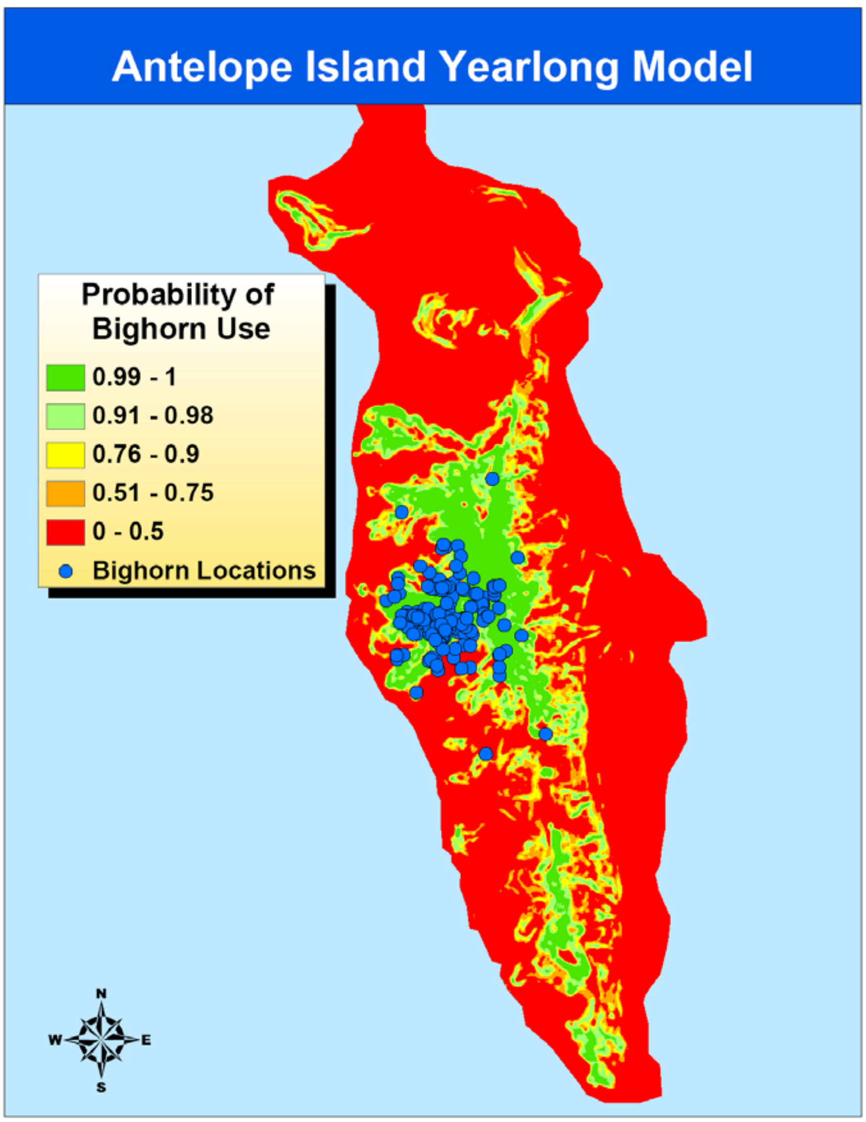

Figure 5. Yearlong habitat-use model for female bighorn sheep on Antelope Island, Utah depicting estimated probabilities of use.

Table 3. Listed here are coefficients and significance values of yearlong and seasonal logistic regression models of habitat use by female bighorn sheep on Antelope Island, Utah.

Model	Model No.	% Classified Correctly	Parameter	Estimate	*SE*	*P*
Yearlong	1	94.5	Intercept	-5.9924	0.748	< 0.001
			Slope	0.4309	0.058	< 0.001
Winter	1	94.0	Intercept	-5.7291	0.750	< 0.001
			Slope	0.3905	0.059	< 0.001
Lambing	1	85.2	Intercept	-10.8609	3.221	0.001
			Slope	0.5586	0.170	0.001
Summer	1	86.9	Intercept	-9.1581	1.956	< 0.001
			Slope	0.4947	0.104	< 0.001

For seasonal use on Antelope Island, we evaluated 15 a priori habitat models (Table 1). Some seasonal models failed to converge (Table 4), and these models were excluded from the analysis. For all seasons (winter, lambing, summer), the slope model was again the top model (Table 4). Slope was also highly significant in these models ($P \leq 0.001$), and all slope coefficients were positive. The top models for winter, lambing, summer accurately predicted bighorn locations for those seasons, and the percent of locations classified correctly varied between 85.2 and 94.0 (Table 3).

Table 4. Seasonal models for habitat use by female bighorn sheep on Antelope Island, Utah were ranked using AIC.

Season	Model No.	Model Structure	K[a]	AIC[b]	ΔAIC
Winter	1	Slope	2	81.1	0.0
	5	Slope+ruggedness	3	82.8	1.7
	6	Slope+tree cover	3	82.9	1.8
	8	Slope+ruggedness+tree cover	4	84.4	3.3
	12	Ruggedness+tree cover	3	148.0	66.9
	14	Ruggedness+tree cover+solar radiation	4	148.3	67.2
	13	Ruggedness+solar radiation	3	150.5	69.4
	2	Ruggedness	2	151.0	69.9
	15	Tree cover+solar radiation	3	230.3	149.2
	4	Solar	2	231.1	150.0
	3	Tree cover	2	243.6	162.5
	7	Slope+solar radiation	3	NA[C]	NA[C]
	9	Slope+ruggedness+solar radiation	4	NA[C]	NA[C]
	10	Slope+tree cover+solar radiation	4	NA[C]	NA[C]
	11	Slope+ruggedness+tree cover+solar radiation	5	NA[C]	NA[C]
Season	Model No.	Model Structure	K[a]	AIC[b]	ΔAIC
Lambing	1	Slope	2	19.7	0.0
	6	Slope+tree cover	3	21.1	1.4
	12	Ruggedness+tree cover	3	72.6	52.9
	2	Ruggedness	2	73.0	53.3
	4	Solar	2	285.6	265.9
	15	Tree cover+solar	3	287.23	267.5
	3	Tree cover	2	308.8	289.1
	5	Slope+ruggedness	3	NA[C]	NA[C]
	7	Slope+solar radiation	3	NA[C]	NA[C]
	8	Slope+ruggedness+tree cover	4	NA[C]	NA[C]
	9	Slope+ruggedness+solar radiation	4	NA[C]	NA[C]
	10	Slope+tree cover+solar	4	NA[C]	NA[C]
	11	Slope+ruggedness+tree cover+solar radiation	5	NA[C]	NA[C]
	13	Ruggedness+solar radiation	3	NA[C]	NA[C]
	14	Ruggedness+tree cover+solar radiation	4	NA[C]	NA[C]
Season	Model No.	Model Structure	K[a]	AIC[b]	ΔAIC
Summer	1	Slope	2	28.2	0.0
	5	Slope+ruggedness	3	29.2	1.0
	6	Slope+tree cover	3	30.1	1.9
	8	Slope+ruggedness+tree cover	4	31.1	2.9
	12	Ruggedness+tree cover	3	91.3	63.1
	14	Ruggedness+tree cover+solar radiation	4	93.1	64.9
	2	Ruggedness	2	93.5	65.3
	13	Ruggedness+solar radiation	3	95.5	67.3
	3	Tree cover	2	273.7	245.5
	15	Tree cover+solar radiation	3	274.2	246.0
	4	Solar radiation	2	274.5	246.3
	7	Slope+solar	3	NA[C]	NA[C]
	9	Slope+ruggedness+solar radiation	4	NA[C]	NA[C]
	10	Slope+tree cover+solar radiation	4	NA[C]	NA[C]
	11	Slope+ruggedness+tree cover+solar radiation	5	NA[C]	NA[C]

[a] Number of parameters
[b] Aikaike's Information Criterion
[c] Model did not converge and no AIC value was reported

On the Stansbury Mountains, we evaluated the same number of yearlong and seasonal models as we did for Antelope Island. For yearlong use, the model with the effects of slope and tree cover was the top model (Table 5). Slope and tree cover were both highly significant ($P \leq 0.001$). Similar to Antelope Island, the slope coefficient was positive (Table 6). The coefficient for tree cover, however, was negative, which indicated that bighorns were avoiding dense tree cover. Given these data, it was estimated that a 2-fold increase in slope increased the odds of use by 30%. Alternatively, a 2-fold increase in tree cover decreased the odds of use by 10%. The yearlong model was accurate, and classified correctly 95.4% of bighorn locations on the Stansbury Mountains (Table 6, Fig. 6).

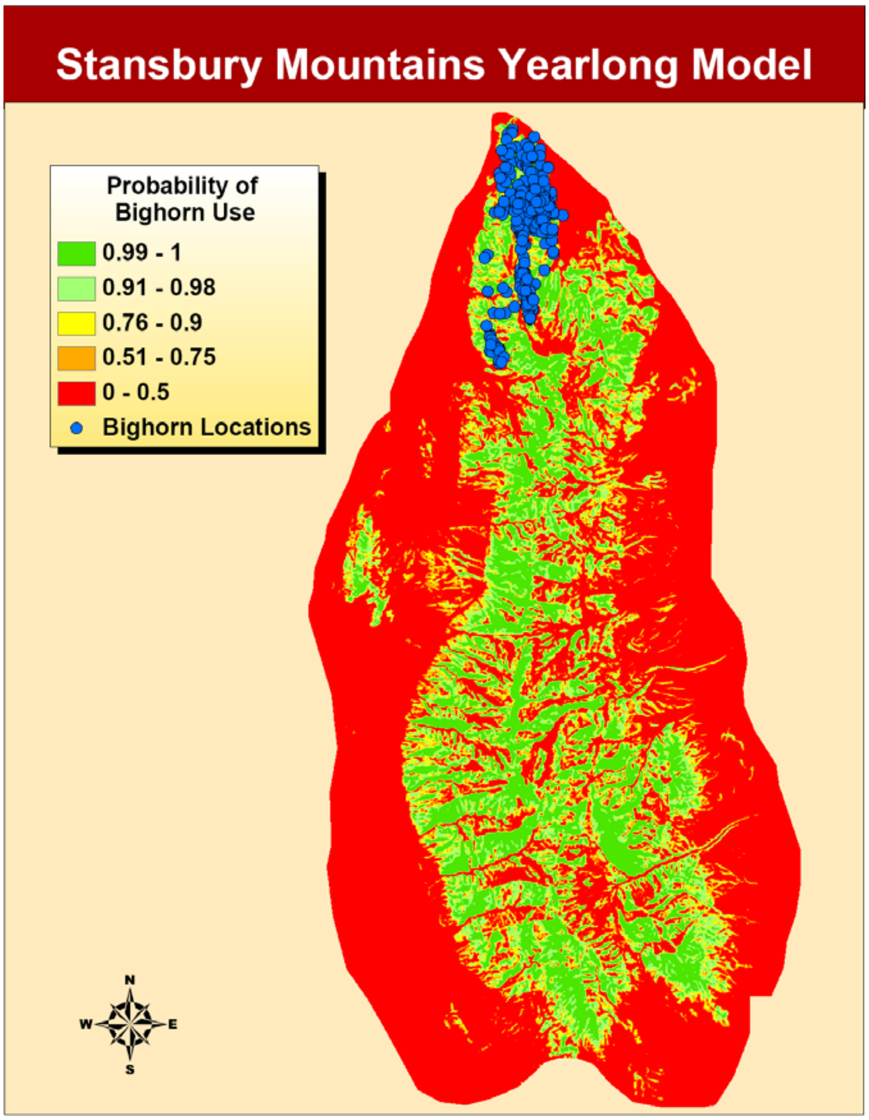

Figure 6. Yearlong habitat-use model for bighorn sheep on the Stansbury Mountains depicting estimated probabilities of use.

Table 5. Yearlong models for habitat use by female bighorn sheep on the Stansbury Mountains, Utah were ranked using AIC.

Model No.	Model Structure	K[a]	AIC[b]	ΔAIC
6	Slope+tree cover	3	235.9	0.0
8	Slope+ruggedness+tree cover	4	237.0	1.1
1	Slope	2	359.3	123.4
5	Slope+ruggedness	3	360.9	125.0
12	Ruggedness+tree cover	3	744.8	508.9
2	Ruggedness	2	805.6	569.7
3	Tree cover	2	1156.6	920.7

[a] Number of parameters
[b] Aikaike's Information Criterion

Table 6. Listed here are coefficients and significance values of yearlong and seasonal logistic regression models of habitat use by female bighorn sheep on the Stansbury Mountains, Utah.

Model	Model No.	% Classified Correctly	Parameter	Estimate	*SE*	*P*
Yearlong	6	95.4	Intercept	-5.4805	0.454	< 0.001
			Slope	0.3794	0.028	< 0.001
			Tree Cover	-0.0863	0.010	< 0.001
Winter	11	95.0	Intercept	30.4865	6.651	< 0.001
			Slope	0.3503	0.053	< 0.001
			Ruggedness	0.3865	0.212	0.068
			Tree Cover	-0.2082	0.002	< 0.001
			Solar Radiation	-0.0088	0.035	< 0.001
Lambing	11	89.9	Intercept	19.2404	8.803	0.029
			Slope	0.4233	0.092	< 0.001
			Ruggedness	0.5542	0.256	0.030
			Tree Cover	-0.1791	0.002	0.001
			Solar Radiation	-0.0070	0.053	< 0.001
Summer	11	95.9	Intercept	22.9919	4.812	< 0.001
			Slope	0.3257	0.043	< 0.001
			Ruggedness	0.3560	0.172	0.038
			Tree Cover	-0.1722	0.001	< 0.001
			Solar Radiation	-0.0068	0.026	< 0.001

For seasonal habitat use during winter, lambing, and summer on the Stansbury Mountains, the model that best fit the data included slope, ruggedness, tree cover, and solar radiation (Table 7). All variables were significant, except for ruggedness in winter ($P = 0.068$). All slope and ruggedness coefficients were positive, while all tree cover and solar radiation coefficients were negative. Seasonal habitat-use models in this study area also predicted bighorn locations well; the percent of locations classified correctly varied from 89.9% during lambing to 95.9% during summer (Table 6).

Table 7. Seasonal models for habitat-use by female bighorn sheep on the Stansbury Mountains, Utah were ranked using AIC

Season	Model No.	Model Structure	K[a]	AIC[b]	ΔAIC
Winter	11	Slope+ruggedness+tree cover+solar radiation	5	79.1	0.0
	10	Slope+tree cover+solar radiation	4	81.2	2.1
	6	Slope+tree cover	3	149.8	70.7
	8	Slope+ruggedness+tree cover	4	151.0	71.9
	7	Slope+solar radiation	3	215.8	136.7
	9	Slope+ruggedness+solar	4	217.7	138.6
	1	Slope	2	226.0	146.9
	5	Slope+ruggedness	3	227.9	148.8
	14	Ruggedness+tree cover+solar radiation	4	230.0	150.9
	15	Tree cover+solar radiation	3	354.1	275.0
	13	Ruggedness+solar radiation	3	400.3	321.2
	12	Ruggedness+tree cover	3	436.8	357.7
	4	Solar radiation	2	473.9	394.8
	2	Ruggedness	2	510.8	431.7
	3	Tree cover	2	662.4	583.3
Season	Model No.	Model Structure	K[a]	AIC[b]	ΔAIC
Lambing	11	Slope+ruggedness+tree cover+solar radiation	5	46.9	0.0
	10	Slope+tree cover+solar radiation	4	51.9	5.0
	8	Slope+ruggedness+tree cover	4	63.6	16.7
	6	Slope+tree cover	3	69.7	22.8
	5	Slope+ruggedness	3	76.5	29.6
	9	Slope+ruggedness+solar radiation	4	78.1	31.2
	1	Slope	2	87.0	40.1
	7	Slope+solar radiation	3	88.8	41.9
	14	Ruggedness+tree cover+solar radiation	4	121.8	74.9
	13	Ruggedness+solar radiation	3	165.1	118.2
	12	Ruggedness+tree cover	3	235.2	188.3
	2	Ruggedness	2	237.1	190.2
	15	Tree cover+solar radiation	2	262.4	215.5
	4	Solar radiation	2	290.7	243.8
	3	Tree cover	2	536.8	489.9
Season	Model No.	Model Structure	K[a]	AIC[b]	ΔAIC
Summer	11	Slope+ruggedness+tree cover+solar radiation	5	115.8	0.0
	10	Slope+tree cover+solar radiation	4	119.1	3.3
	6	Slope+tree cover	3	177.7	61.9
	8	Slope+ruggedness+tree cover	4	179.0	63.2
	7	Slope+solar radiation	3	240.0	124.2
	9	Slope+ruggedness+solar radiation	4	241.9	126.1
	1	Slope	2	248.7	132.9
	5	Slope+ruggedness	3	250.6	134.8
	14	Ruggedness+tree cover+solar radiation	4	259.8	144.0
	15	Tree cover+solar radiation	3	368.1	252.3
	13	Ruggedness+solar radiation	3	400.2	284.4
	4	Solar radiation	2	443.5	327.7
	12	Ruggedness+tree cover	3	494.9	379.1
	2	Ruggedness	2	525.5	409.7
	3	Tree cover	2	644.7	528.9

[a] Number of parameters
[b] Aikaike's Information Criterion

Model Validation

When we validated the yearlong Antelope Island model on the Stansbury Mountains, we found that it predicted bighorn locations with a high degree of accuracy. The model classified correctly 95.4% (*n* = 416) of female bighorn locations on the Stansbury Mountains (Fig. 7). When we validated the yearlong Stansbury Model to Antelope Island, it also predicted accurately female use. The model classified correctly 94% (*n* = 183) of bighorn locations on Antelope Island (Fig. 8).

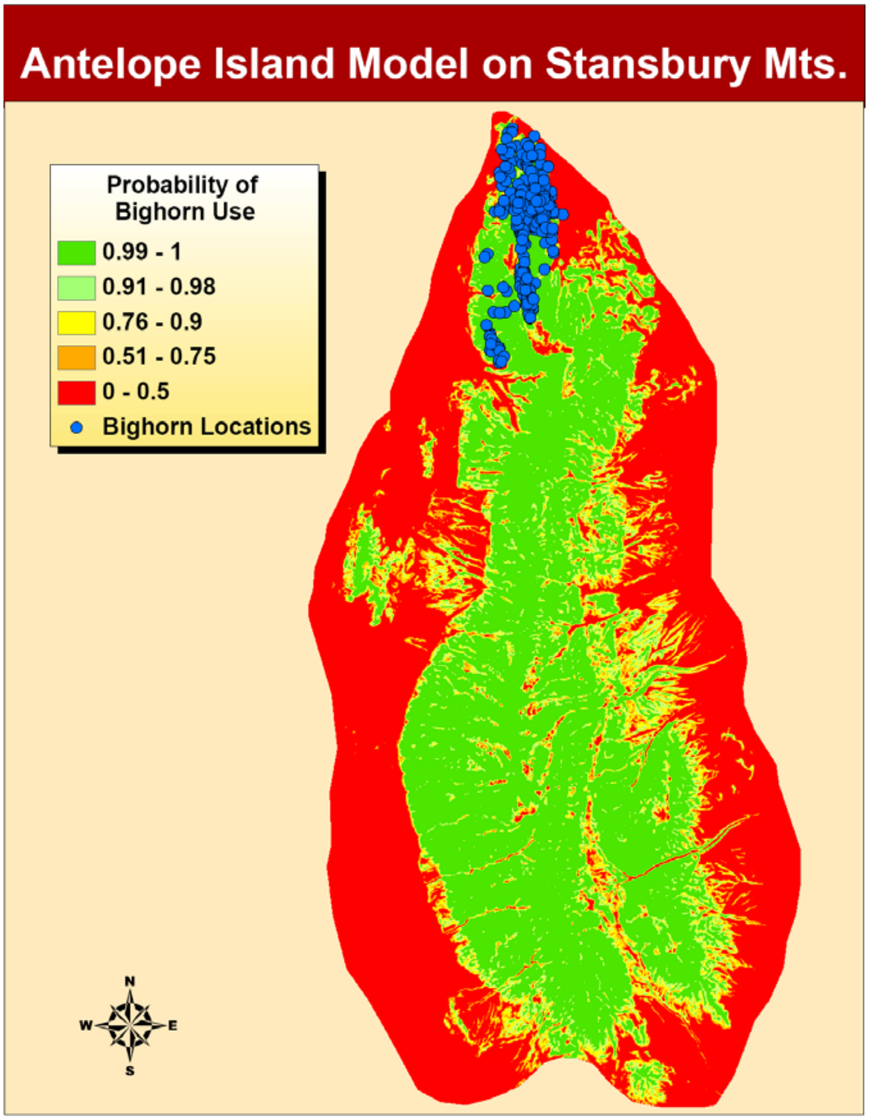

Figure 7. Yearlong Antelope Island habitat-use model extrapolated to the Stansbury Mountains depicting estimated probabilities of use.

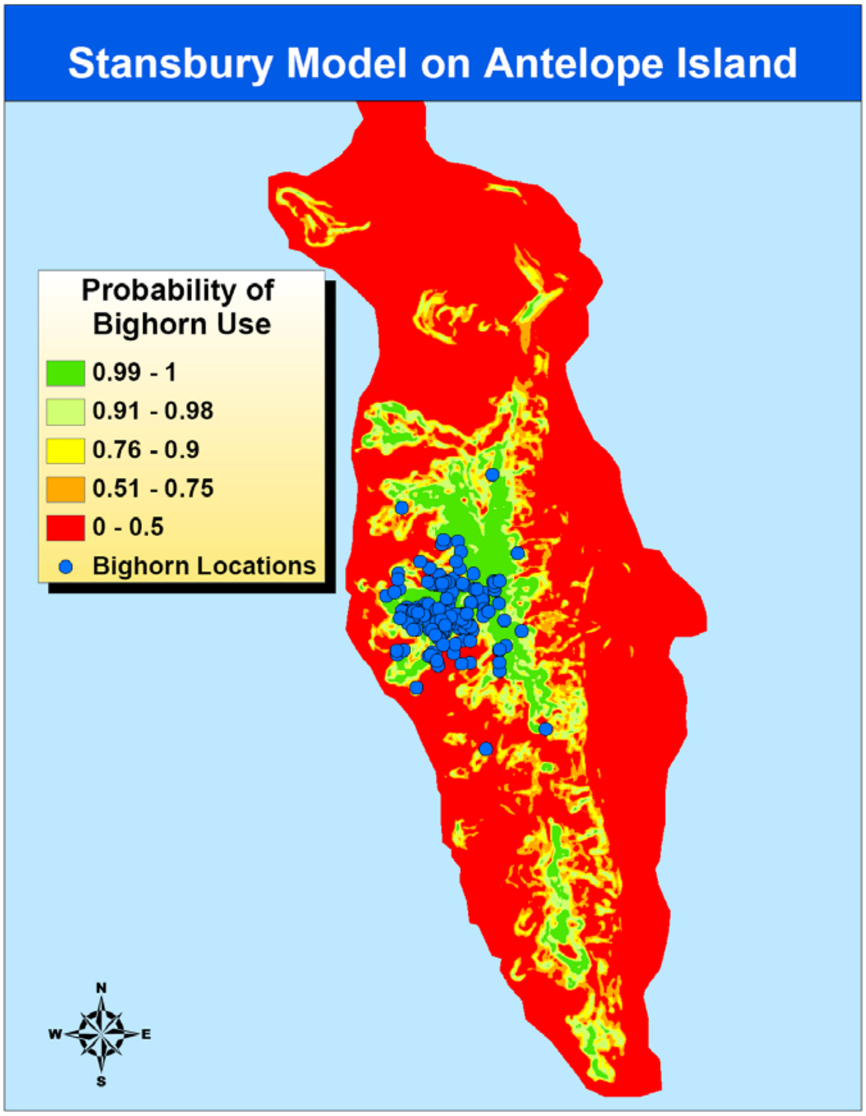

Figure 8. Yearlong habitat-use model for the Stansbury Mountains extrapolated to Antelope Island depicting estimated probabilities of use.

DISCUSSION

When we modeled habitat use of female bighorn sheep on Antelope Island and the Stansbury Mountains, we found that slope was the most important variable for describing use. Slope was included in all seasonal and yearlong models for both study areas, and the coefficient values indicated strong selection for steep slopes. This finding coincides with the large body of research that has documented the importance of escape terrain for bighorn sheep (Fairbanks et al. 1987, Smith et al. 1990, Bleich et al. 1997, McKinney et al. 2003). This variable clearly has broad applicability in describing habitat use across the geographic range of bighorn sheep.

Ruggedness has been thought to be an important component of escape terrain for bighorn sheep, and indeed, it has been documented that bighorns use rugged terrain (Bleich et al. 1997, Bangs et al. 2005, Sappington et al. 2007). We predicted that ruggedness would be included in the top models for yearlong use on Antelope Island and the Stansbury Mountains. Although this result did not occur, ruggedness is still an important variable in describing bighorn use in our study areas. We found the model with ruggedness ranked within 2 AIC units of the top models for yearlong use, and was included in the top models for seasonal use on the Stansbury Mountains. One reason ruggedness failed to occur in all top models may be attributed to bighorns selecting rugged terrain at a scale larger than 1 ha. For example, Bangs et al. (2005) found female bighorns selected ruggedness at a 6.25 ha scale during spring.

Tree cover was included in all models on the Stansbury Mountains, but was not included in models for Antelope Island. These conflicting results may be explained by the availability of tree cover in each study area. Antelope Island has little tree cover; therefore, we were unable to demonstrate selection for or against it. Conversely, the Stansbury Mountains has dense tree cover, and our models revealed bighorns avoided these areas. Furthermore, we likely underestimated the adverse impact of tree cover because the Classifier function in Erdas Image we used had difficulty distinguishing tree cover from shadows. Consequently, the tree cover layer we used for this analysis may have confounded the results by showing bighorns were using tree cover when they were only in a shadow. As methods to classify tree cover improve and the resolution of remotely sensed data increases, this bias will be reduced.

Distance to water may influence the distribution of bighorn sheep in some areas. For instance in California, Turner et al. (2004) found that 97% of observations of the endangered Nelson's bighorn sheep (*O. c. nelsoni*) were within 3 km of perennial sources of water. Similar results have been reported in other desert areas (Leslie and Douglas 1979), and reintroduction protocol indicates that bighorns should be released into areas within 3.2 km of water sources (Smith et al. 1990, Singer et al. 2000). Notwithstanding the importance of water in parts of the geographic range of bighorn sheep, we did not include it as a variable because there is variation in the detection and quality of water sources. For instance, it may be difficult to detect water sources, such as seeps, when modeling bighorn habitat at a landscape scale. Furthermore, water sources that are easily detected, such as large bodies of water or guzzlers, may be unacceptable to bighorn sheep if there is not adequate escape terrain or visibility. Given the variation in the availability and acceptability of water sources in bighorn habitat, we suggest wildlife managers evaluate water related issues on a site by site basis rather than using distance to water alone. If water sources are lacking in high quality bighorn habitat, wildlife managers may consider installing guzzlers or other water catchments in these areas (Dolan 2006).

When yearlong models for our study areas were extrapolated, they predicted bighorn use correctly >90% of the time. The results, although encouraging, should be interpreted with caution. Even though the Antelope Island model predicted accurately bighorn locations on the Stansbury Mountains, it also classified areas with dense tree cover as having a high probability of use by bighorns, because slope was the only variable considered in that model. Consequently, the amount of high quality habitat predicted by the model was exaggerated (Fig. 7) when compared to habitat classified by the yearlong Stansbury model that included the negative effect of tree cover (Fig. 6). When attempting to construct a model that will predict habitat use over a wide-geographic area, a number of populations with variation in habitat use should be evaluated. At the very least, areas with variation in slope and tree cover should be used to create models. Consequently, models created for Antelope Island would not be able to predict bighorn use effectively at a large scale, because of the homogeneity of the habitat.

The high success of these models could be attributed to the selection of variables that accurately define bighorn habitat use or the influence of habitat conditioning. The Stansbury Mountains population was founded with bighorn sheep from Antelope Island. It follows that bighorns translocated to the Stansbury Mountains may select habitats that are similar to those they used on Antelope Island. We cannot rule out this explanation as to why we were able to extrapolate models with such high success. The alternative explanation is that bighorn sheep select similar slopes and densities of tree cover, and that these variables largely determine habitat use across the range of the species. We recommend the variables used in these models be tested on other bighorn populations throughout North America to validate or disprove their usefulness in modeling habitat.

Although our modeling approach remains untested at a broader scale, we believe it has utility in quantifying and evaluating bighorn sheep habitat over a wide-geographic range. The modeling approach, however, may be improved by considering the effects of scale. There is mounting evidence that scale is important in habitat selection (Gross et al. 1995, Kie et al. 2002) and determining the correct scale for slope, ruggedness, and tree cover for bighorn sheep will likely increase the efficacy of this technique. Additionally, basing models on data collected with GPS collars may improve model accuracy by removing location error and sampling bias that occurs when researchers use locations obtained from other methods. The true relationship between slope, ruggedness, and tree cover may be defined more clearly with GPS tracking.

Finally, domestic sheep are the predominate limiting factor in successfully restoring bighorn sheep to Utah. Since 1966, 17 bighorn populations have been established throughout the state. Declining and failed herds had direct contact or shared seasonal ranges with domestic sheep, whereas growing and successful herds have not associated with domestic sheep (Shannon et al. in review). Singer et al. (2000) found a negative correlation between the success of bighorn populations and their distance to domestic sheep. These authors recommended bighorns and domestic sheep be separated by 20 km (Singer et al. 2000). The presence of domestic sheep negates the suitability of bighorn habitat, and bighorns should not be reintroduced in areas with domestic sheep nearby, regardless of how promising a reintroduction site may appear. By using robust variables in models that accurately define habitat use of bighorns, wildlife managers may select reintroduction sites with adequate bighorn habitat, while still maintaining spatial separation from domestic sheep.

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