GIS-based Habitat Models for Bighorn Sheep Winter Range in Glacier National Park, Montana

GORDON H. DICUS, Glacier National Park, West Glacier, MT 59936, USA

Abstract: I used logistic regression to construct bighorn sheep winter range habitat models for 2 study areas in Glacier National Park (GNP), Montana. During 2 winters, habitat use was described through systematic ground surveys supplemented with focal observations, lasting 1-3 days, of recognizable individual sheep. Available habitat was evaluated using 12 habitat parameters, each measured at a 30-by-30 meter grid-cell resolution with GIS software. For each study area, a set of candidate models was constructed and then validation tested at the other study area. Using habitat parameters common to the best model from each study area, I then pooled all data to construct 2 versions of a final winter range model applicable across GNP. I compared the performance of the final GNP models to that of a regional model (the Smith model GIS application). The GNP models correctly classified 75% and 38% of grid-cells with observed winter use at the 2 study areas. The Smith model GIS application correctly classified 10% and 11% of grid-cells with observed winter use at the 2 study areas. Habitat parameters in the final GNP models were distance-to-escape terrain, snow cover, solar radiation index, slope, and either land-cover type (from a classified satellite image) or horizontal visibility and 2 satellite wavelength-band reflectance values. The final models will be useful to GNP managers for identifying suitable bighorn sheep winter range potentially threatened by conifer encroachment, livestock trespass, exotic plants, and/or illegal hunting pressure.

Key words: bighorn sheep, *Ovis canadensis*, GIS, logistic regression, habitat model, winter range

Considerable bighorn sheep (*Ovis canadensis*) research over the past few decades has focused on creating and improving habitat models. Models can help wildlife managers assess potential reintroduction sites and evaluate habitat improvement options. Initial bighorn sheep habitat models were developed for desert bighorns (*O. c. nelsoni*) (Hansen 1980, Holl 1982, Armentrout and Brigham 1988). Smith et al. (1991) adapted desert bighorn habitat models to address the habitat requirements of Rocky Mountain bighorn sheep (*O. c. canadensis*). The Smith et al. (1991) model (hereafter referred to as the Smith model) was developed from observed habitat use by radio-collared sheep on a 6,900-hectare study area in northeastern Utah, and was intended as a generalized procedure for delineating suitable Rocky Mountain bighorn sheep habitat.

Recent developments in wildlife habitat models have taken advantage of Geographic Information System (GIS) computer software packages. GIS packages, using overlay capabilities and proximity functions, can rapidly and quantitatively assess large land areas to allow objective comparisons of potential habitat (Bleich et al. 1992, Singer and Gudorf 1999). The National Park Service (NPS) used a GIS application of the Smith model (with 8 primary habitat parameters, Table 1) for evaluation of potential reintroduction sites in and adjacent to national parks in the Rocky Mountain region (Johnson 1995, Sweanor et al. 1996, Singer and Gudorf 1999).

Escape terrain – steep, rocky terrain – is a critical bighorn sheep habitat component (Geist 1971, Hansen 1980, Holl 1982, Smith et al. 1988). Able to identify predators at great distances with their excellent eyesight, bighorns evade predators by retreating into escape terrain (Geist 1971). Escape terrain has generally been defined as continuous steep slopes ($\geq 27^{o}$) possessing rocky outcrops and/or cliffs $\geq$1.6 hectares in size and $\geq$15 m in height (Geist 1971, Tilton 1977, Smith et al. 1991). Except for some migration movements, bighorn sheep seldom venture more than 300-500 m from escape terrain (Gionfriddo and Krausman 1986, Wakelyn 1987, Smith et al. 1988). Especially rugged portions of escape terrain function as lambing habitat; the lack of such terrain can be a limiting factor on lamb survival (Geist 1971, Smith et al. 1988, Sweanor et al. 1996).

Horizontal visibility is another important habitat component because it allows bighorn sheep to detect predators at a distance and influences how far sheep are willing to stray from escape terrain (Geist 1971, Risenhoover and Bailey 1980, Krausman 1997). The minimum level of horizontal visibility established by researchers describing suitable bighorn sheep habitat has ranged from 55% to 90% (Smith et al. 1991, Johnson 1995, Sweanor et al. 1996). Even narrow tracts of very low visibility habitat (e.g., thick shrubs or dense timber with horizontal visibility below 30%) can act as barriers to bighorn sheep movement (Risenhoover and Bailey 1980, Smith et al. 1991). Fire influences horizontal visibility and historically played a central role in the maintenance of climax grassland communities. Decades of fire suppression have allowed shrub and conifer encroachment into grassland habitats, degrading bighorn sheep habitat and compromising migratory corridors between seasonal ranges and between subpopulations (Goodson 1980, Wakelyn 1987, Schirokauer 1996).

The availability of adequate forage resources is a basic habitat requirement. Smith et al. (1991) described the forage needs of a bighorn sheep population of 125 animals as 250-300 kg in dry weight of grasses and forbs per hectare; or, as an alternative, 14% canopy cover of grass and forb species. Managers, however, often need to evaluate habitat suitability across large geographic areas for which they do not have accurate estimates of forage quantity. Consequently, most efforts to evaluate or model the suitability of potential bighorn sheep ranges have foregone estimates of forage quantity and focused on the extent of escape terrain and the level of horizontal visibility within or adjacent to grassland habitats (Risenhoover and Bailey 1980, Holl 1982, McCarty 1993, Johnson 1995, Schirokauer 1996, Sweanor et al. 1996).

Some other habitat components of importance to bighorn sheep include water sources, barriers to sheep movements, human disturbance, and presence of domestic livestock (Smith et al. 1991, McCarty 1993, Sweanor et al. 1996, Singer and Gudorf 1999). While free water may act as a limiting factor only in extremely arid sites, most bighorn sheep habitat models have incorporated proximity to free water as a criterion for habitat suitability (Hansen 1980, Holl 1982, Armentrout and Brigham 1988, Smith et al. 1991). Potential barriers to bighorn sheep movement may be natural or man-made and include large rivers and lakes, dense vegetation, non-traversable

Table 1. Smith model GIS application habitat criteria used by the National Park Service in evaluating bighorn sheep habitat in Colorado, Utah, Wyoming, South Dakota, North Dakota and Montana. Additional criteria specified by the Smith model for delineating winter range are also shown. Taken from Sweanor et al. (1996).

Habitat Parameter	Definition
Escape terrain	Areas with slope > 27°, < 85°.
Escape terrain buffer	Areas within 300m of escape terrain and areas < 1000m wide that are bounded on at least 2 sides by escape terrain.
Vegetation density	Areas must have horizontal visibility > 60%.
Water sources	Areas must be within 3.2 km of water sources.
Natural barriers	Areas that bighorn sheep cannot access, e.g., rivers > 2000 cfs, areas with visibility < 30% that are >100 m wide, cliffs with slope > 85°.
Human use areas	Areas covered by human development (e.g., roads, parking lots, and buildings).
Man-made barriers	Areas that cannot be accessed due to man-made barriers, e.g., major highways, wildlife-proof fencing, aqueducts, major canals.
Domestic livestock	Areas must be over 16 km from domestic sheep.

Winter Range – Areas meeting above criteria, with aspect between 120° and 245°, and snow depth <25 cm.

cliffs, wide valleys and plateaus, canals, reservoirs, aqueducts, impassable fencing, major highways and roads, and high-use human development (Smith et al. 1991, Singer and Gudorf 1999). The impacts to bighorn sheep associated with domestic livestock include competition for space and forage, and transmission of disease. The greatest threat is posed by domestic sheep as they are capable of using steep slopes and have the greatest potential for transmitting disease to bighorn sheep (Singer and Gudorf 1999).

I constructed winter range habitat models for Rocky Mountain bighorn sheep on 2 study areas in Glacier National Park (GNP), Montana. Selection of habitat parameters was based on literature review and discussion with colleagues involved in wildlife habitat modeling. Each of 12 habitat parameters (Table 2) was measured at a 30-by-30 m grid-cell resolution using GIS software. I used logistic regression to construct candidate models, and assessed the significance of variable coefficients with likelihood-ratio tests. Candidate model performance was evaluated through validation tests. Using the habitat parameters from the best-performing candidate models, I constructed 2 versions of a final winter range habitat model applicable across GNP. I then compared the prediction accuracies of my final models to the accuracy of the winter range component of the Smith model GIS application used by the NPS in the Rocky Mountain region.

STUDY AREA

The 2 study areas (approximately 4,500 and 6,200 hectares in size) lie entirely within GNP and are situated along the Rocky Mountain Front, a topographically and biologically diverse transition zone between the Continental Divide and the Northern Great Plains. Study area elevation ranges from 1,480-2,830 m and annual precipitation averages 67 cm, about half of which falls as snow. On average, January is the coldest month with a mean minimum temperature of –14 C^O, and July is the warmest month with a mean maximum temperature of 23 C^O (Finklin 1986). Exceptionally strong, warm (chinook) winds are common along the Rocky Mountain Front, especially during winter and spring.

The montane zone along the Rocky Mountain Front typically hosts extensive aspen (*Populus tremuloides*) forests, with wetter sites often supporting black cottonwood (*Populus trichocarpa*). Grasslands, which in GNP occur as a broad band within the montane and subalpine zones, are primarily found on south to west facing slopes and often extend from the montane zone to above treeline. Cool-season bunchgrasses and shrubs dominate these grasslands. Forests of the subalpine zone are dominated by subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and/or lodgepole pine (*Pinus contorta*); lower subalpine forests often have Douglas fir (*Pseudotsuga menziesii*), while higher subalpine forests may hold whitebark pine (*Pinus albicaulis*) or limber pine (*Pinus flexilis*). Avalanche chutes are common on steep, warm slopes within the subalpine zone, are dominated by shrubs and herbaceous vegetation, and are typically associated with long, steep ravines that are moister than adjacent slopes. Along the upper edge of the subalpine zone, subalpine fir, spruce and whitebark pine are stunted and dwarfed by ice-scouring wind or heavy snow accumulation, resulting in sparse "krummholz" forests interspersed with alpine tundra or heath.

The alpine zone in GNP holds sparse vegetation because steep slopes and heavy snow accumulation constrain soil development. The most extensive alpine vegetation is comprised of fellfields dominated by alpine dryad (*Dryas octopetala*), arctic willows (*Salix* species), and alpine varieties of forbs, grasses, and sedges. Fellfields grade into turf on more protected slopes were deeper soils have developed. Dry turf communities are dominated by grasses, sedges, and forbs. Wet turf communities, which often develop below permanent snowfields, support dwarf shrubs, alpine dryad, and arctic willows as well as sedges and forbs. Talus and scree slopes are common in the alpine zone, and hold only very sparse plant cover (typically alpine dryad and some forbs).

METHODS

Ground Surveys

Ten systematic survey routes were established – 5 on each study area. Each route was surveyed once every 12-16 days during January-April of 2000 and 2001. Survey routes followed ridgelines and valley bottoms, using vantage points to scan for sheep with binoculars and spotting scopes. Each study area was broken into survey units on the basis of topography and vantage point perspectives, and each survey unit received survey effort proportionate to its size, ruggedness and vegetation density. Each bighorn sheep group was mapped as a point location, which represented the center of the group. When individual sheep were separated by less than 15-20 m, they were mapped as a single group. When the distance between sheep exceeded 20 m, they were mapped as separate groups. If a large group, with all individuals within 20 m of another sheep, was spread out across a distance of more than 50-60 m, I recorded and mapped the sheep as more than 1 group.

To ensure that sheep use of some cover types was not under-represented, I supplemented systematic surveys with focal observations of individual sheep during daylight hours for 1 to 3 consecutive days. Focal individuals were selected for recognizable traits (horn features or pelage patterns). To the extent possible, tracks in snow were used to infer unobserved movements.

GIS Data Layers

To facilitate the construction and validation of winter range habitat models, I superimposed a grid of 30-by-30 m cells over each study area. To each cell, I assigned values for each of 12 habitat parameters (see Table 2) identified as potentially important components of bighorn sheep habitat (Smith et al. 1991, McCarty 1993, Johnson 1995, Sweanor et al. 1996).

Digital Elevation Models and Digital Line Graphs.--A digital elevation model (DEM) consists of a georeferenced grid-cell layer, with each cell assigned an elevation value. DEMs are constructed at various scales, the most common and useful of which are a 7.5-minute (1:24,000) and a 30-minute (1:100,000) scale. For the purposes of habitat modeling, the 7.5-minute DEM is preferable as it characterizes slope and aspect and delineates escape terrain more accurately than the 30-minute DEM (Johnson 1995). Another product available from the U.S. Geological Survey (USGS) is the digital line graph, a grid-cell layer depicting linear features such as streams and roads.

I used Arc View GIS software to derive several habitat parameter theme layers from a 7.5-minute DEM coverage. I derived slope, aspect, and elevation theme layers in which each 900 m^2 grid-cell in the study areas was assigned a value for each of these parameters. Using the Sweanor et al. (1996) definition of escape terrain (see Table 1), I designated each cell as either meeting or not meeting escape terrain criteria. I then used an Arc View proximity function to generate a theme layer in which each cell was assigned a distance-to-escape terrain value. Similarly, I used a 7.5-minute digital line graph to create a distance-to-water theme layer.

I calculated a solar radiation index for each grid-cell in the study areas. The solar radiation index (SR_i), calculated by the equation shown below, incorporated the latitude (l_i), slope (s_i) and a transformed aspect (ta_i, computed as 180 – aspect, so that south is 0, westerly aspects range from 0 to –180, and easterly aspects range from 0 to +180) for each grid-cell (Kim Keating, USGS, personal communication).

$$SR_i = \cos(l_i)*\cos(s_i) + \sin(l_i)*\sin(s_i)*\cos(ta_i)$$

This solar radiation index is especially helpful because it offers an alternative method of entering aspect into a regression analysis. The traditional measure of aspect (0-360°) is problematic because it is on a circular scale that has no absolute ordering of values (i.e., 360 is not greater than zero). To explore different methods of entering aspect into the modeling of a resource selection function, I also computed a transformed aspect variable, using the equation $TAsp_i = 1000*(\cos(a_i - 45) + 1)$ where a_i is the aspect (on a 0-360° scale) for a given grid-cell (Beers et al. 1966).

Digital Raster Graphic Topographic Maps.--The USGS also produces digital versions of topographic maps. Again, these are georeferenced arrays of grid-cells

Table 2. Habitat parameters used for evaluating bighorn sheep winter range habitat at two study areas in Glacier National Park, Montana. Sources of information are also shown.

Habitat Parameter	Source
Continuous Variables	
Slope (^{o})	USGS digital elevation model
Aspect (^{o}) - cosine transformed	USGS digital elevation model
Elevation (m)	USGS digital elevation model
Distance to escape terrain (m)	USGS digital elevation model
Distance to water (m)	USGS digital line graph
Distance to development (m)	USGS digital raster graphic 7.5-min. map
Distance to livestock (m)	USGS digital raster graphic 7.5-min. map
Horizontal visibility (%)	Field measurement
Solar radiation index	USGS digital elevation model
Vegetation composition index	Satellite imagery – spectral reflectance values
Categorical Variables	
Mid-winter snow cover (Y/N)	Satellite imagery – band 3 & 5 reflectance ratio
Land cover type classification	Satellite imagery – reflectance classification categories

and the finest resolution available is a 7.5-minute (1:24,000) map. Using Arc View GIS software, I selected all areas of human development (buildings, roads and parking lots) within or adjacent to the study areas, and then used a proximity function to assign each 900 m^2 grid-cell a distance-to-human development value. Similarly, taking advantage of an existing GIS theme layer depicting livestock grazing allotments on Blackfeet Indian Reservation lands bordering GNP's eastern boundary, I assigned each grid-cell in the study areas a distance-to-livestock use value. While domestic sheep were prevalent on the Blackfeet Indian Reservation throughout the first half of the 20th century, these grazing allotments have been used only for cattle and horses over the past several decades.

Satellite Imagery.--Also available from the USGS are Thematic Mapper (TM) image data from the Landsat satellite series. These TM images are georeferenced grid-cell layers containing light radiance values. Each grid-cell contains a radiance value for each of 7 wavelength-bands, and each radiance value is stored in binary format, which means the value can range from 0 to 255. While there is some flexibility in selecting a grid-cell size, most users deal with 30-by-30 m grid-cells. Because there is considerable variation in the magnitude of radiance values for the 7 wavelength-bands, it is helpful to transform the radiance values into reflectance values, which are more readily comparable across wavelength-bands. Reflectance values are essentially a calculation of the amount of light radiance detected by the satellite sensors for a given wavelength-band relative to the total amount of light available for that wavelength-band (Carl Key, USGS, personal communication). Furthermore, reflectance value calculations can take topography into consideration, thereby making the reflectance values more representative of vegetative or snow cover differences rather than topographic differences. The following equation calculates a cell by cell reflectance value (R_i) from the radiance value (L_i) and incorporates the eccentricity (d^2, the earth-to-sun distance), sun zenith angle (z_s) and sun azimuth angle (a_s) specific to the TM image being used, as well as the mean upper-atmosphere radiance for each wavelength-band (I_b), and the slope (s_i) and aspect (a_i) for each grid-cell (Carl Key, USGS, personal communication).

$$R_i = (3.1416*L_i*d^2)/(I_b*(\cos(z_s)*\cos(s_i) + \sin(z_s)*\sin(s_i)*\cos(a_s - a_i)))$$

Using this reflectance equation, I calculated topographically-adjusted reflectance values from 6 wavelength-bands (bands 1-5 and band 7) for both a spring (May 23, 1999) TM image and a summer (July 7, 2001) TM image. Some researchers have found TM reflectance values useful in modeling resource selection functions, especially in the absence of vegetation cover type data (Kim Keating, USGS, personal communication). Finally, I used a TM image classification completed by USGS personnel at the Glacier Field Station to assign 1 of 8 land-cover types (Table 3) to each grid-cell within the study areas. Image classification procedures involve an iterative process of grouping cells based on similarities in their reflectance values, and are quite useful in distinguishing among land-cover types (Carl Key, USGS, personal communication).

Most researchers modeling bighorn sheep habitat have specified that suitable winter range must be relatively snow-free; Smith et al. (1991) defined suitable winter range, in part, as areas with snow depths of less than 25 cm. I used TM imagery to characterize snow deposition across my study areas. A ratio of the difference in wavelength-band 3 and 5 reflectance values [(3-5)/(3+5)] performs well in delineating snow cover (Carl Key, USGS, personal communication). I calculated this ratio to accentuate areas covered by snow in 2 TM images -- April 1, 1992 and May 23, 1999. These images were selected from a set of images available at the USGS Glacier Field Station, and were chosen for their clarity (no cloud cover) and a lack of recent snowfall immediately proceeding their date of data capture. For all areas covered by snow in both or either of the 1992 and the 1999 images, I assigned a snowbound value (Yes) to each grid-cell. Conversely, for all areas that were free of snow in both images, I assigned a snow-free value (No) to each grid-cell.

Horizontal Visibility.--To characterize horizontal visibility on my 2 study areas, I assigned visibility values to land-cover types (see Table 3). At least 10 transects were sampled in each land-cover type, then every grid-cell was assigned a horizontal visibility (averaged to the nearest 10%) on the basis of its land-cover type designation. Along 40 m transects at representative sites in each land-cover type on both study areas, I estimated horizontal visibility in 4 cardinal directions at 10 m intervals. Percent horizontal visibility at each representative site was then determined by averaging the 20 estimates collected along the 40 m transect.

Model Development and Testing

Among wildlife researchers, logistic regression has been a popular and effective method for calculating a resource selection function on the basis of a species' presence or absence within sampling units (Walker 1990, Manly et al. 1993, Mace et al. 1998). From a set of values for specified habitat variables at a given sampling unit, the resource selection function then calculates the probability of the species of interest using that sampling

Table 3. Eight land-cover type categories identified in a USGS classification of Thematic Mapper satellite imagery for Glacier National Park, Montana. Associated horizontal visibility percentages, determined through field sampling and averaged to nearest 10%, are also shown.

I.D. #	Land-Cover Type Category	Horizontal Visibility
1	Dry Herbaceous	90
2	Mesic Herbaceous	70
3	Deciduous Tree/Shrub	50
4	Dense, Mesic Coniferous Forest	30
5	Water (Lakes and Rivers)	90
6	Barren Rock/Soil	90
7	Snow (Glaciers and Permanent Snowfields)	90
8	Open, Dry Coniferous Forest	50

unit (Hosmer and Lemeshow 1989, Manly et al. 1993). In this study, the binary response (or dependent) variable is the presence or absence of bighorn sheep within a given 900 m^2 grid-cell as determined through systematic ground surveys. The 12 explanatory (or independent) variables (see Table 2) were selected on the basis of a bighorn sheep habitat model literature review and consultation with colleagues involved in habitat modeling. The logistic regression method is analogous to linear regression, except that instead of constraining the fit of the regression through a least squares method, a maximum likelihood function is employed, and the relationship between the response variable and explanatory variables is non-linear (Hosmer and Lemeshow 1989).

Logistic regression generates a set of coefficients for the explanatory variables, and the regression equation results in an expected probability for each set of explanatory variable values. The probability of an event occurring, in this case the probability that bighorn sheep were present in a given grid-cell, can be expressed as

$$\text{Prob(sheep present)} = e^Z/(1 + e^Z)$$

where $Z = B_O + B_1*X_1 + B_2*X_2 + B_3*X_3 + \ldots + B_K*X_K$. Here, e is the base of the natural logarithm, B_O through B_K are the estimated coefficients, and X_1 through X_K are values of the K explanatory variables for that given grid-cell. The standard measure of a logistic regression model's fit is the likelihood – the probability of the observed results given the set of explanatory variable coefficients. Because the likelihood is a small value (between 0 and 1), most statistical software programs express the measure of a model's goodness-of-fit as –2LL, or –2 times the log of the likelihood. The smaller the value of –2LL, the better the fit of the model.

The interpretation of coefficients in logistic regression is less straightforward than in linear regression. In logistic regression, the coefficient for a given explanatory variable indicates the change in the odds ratio for a 1-unit change in that explanatory variable. The odds ratio is the ratio of the probability that an event will occur to the probability that the event will not occur. The log of the odds ratio (the logit) is equal to Z, the equation containing the coefficients and explanatory variables. Analogous to linear regression, a positive coefficient indicates that as the value of that explanatory variable increases, the odds ratio increases; and a negative coefficient indicates a decrease in the odds ratio as the value of that explanatory variable increases. Coefficients of explanatory variables are assessed with test statistics, which constitute hypothesis tests of the null hypothesis that a coefficient is equal to zero. In logistic regression, the preferred test statistic is the likelihood-ratio (LR) test (Hosmer and Lemeshow 1989).

I used SPSS (Statistical Package for the Social Sciences) software to construct and evaluate the fit of logistic regression models. I began by conducting univariate tests for each explanatory variable using the LR test to assess its significance in explaining the observed values of the response variable. This was accomplished by entering all explanatory variables into a backward-stepwise logistic regression analysis, the first step of which results in an LR test value for each variable. The inclusion of variables into candidate models was based on LR test values using a liberal upper significance limit ($p<0.20$) so that all potentially useful explanatory variables would be included in 1 or more models (Hosmer and Lemeshow 1989). These regression analyses were conducted separately for the data from each study area. Using my knowledge of existing habitat models and my professional judgement, I grouped these potentially useful explanatory variables into a set of candidate models for each study area.

Following model construction, each candidate model was examined for the presence of nonlinear relationships between the explanatory variables and the response variable logit (i.e., the log of the odds ratio). This was accomplished by plotting each continuous explanatory variable against the deviance residuals generated by that model. If no pattern is seen in such a scatterplot, the relationship between that explanatory variable and the response variable logit is approximately linear. A curved pattern suggests the relationship is nonlinear, and that a transformation of the explanatory variable should be considered.

Interactions between variables were considered for each candidate model. Sensible interaction terms were added to the model, and their LR test statistics were examined for significance. Each candidate model was further examined for the presence of explanatory variable values with unusually high influence on the model's coefficients. Predicted probabilities were plotted against leverage and Cook's distance values, both measures of how much the coefficients change when that particular set of explanatory variables is omitted from the regression. To optimize model fit, cases with large leverage or Cook's distance values (>0.2 and >0.6, respectively) were omitted, and the logistic regression model was re-computed (Hosmer and Lemeshow 1989). In addition, each model was examined for the presence of colinearity among explanatory variables. The most obvious sign of colinearity is when coefficients have unusually large values and large standard errors (Hosmer and Lemeshow 1989). Another way to look for colinearity is to enter the response and explanatory variables into a linear regression analysis, and look at standard linear regression statistical measures of colinearity such as tolerance and condition index values (Menard 1995).

Candidate model goodness-of-fit was assessed using the Hosmer and Lemeshow Chi-square statistic and Akaike's information-theory criteria (AIC) statistic (Boyce et al. 2001). A small Hosmer and Lemeshow Chi-square test statistic value resulting in a large significance value (e.g., p >0.5) indicates a well-fit model. The AIC statistic is calculated simply as –2LL + 2*K, where K is the number of explanatory variables in the model (Boyce et al. 2001). A lower AIC value indicates a better model fit. In essence, the AIC statistic penalizes a model that adds variables without gaining a better fit as measured by –2LL (i.e., -2*log-likelihood).

The best way to test the performance of a candidate model, however, is to validate the model with data that were not used in constructing the model. Each of my candidate models was constructed with data from a single study area. This meant that I could validate each candidate model with data from the other study area. The performance of different models was compared through cross tabulations showing the rates of commission and omission. Finally, I compared the predictive accuracy of my best-performing models to the accuracy of the winter range component of the NPS-modified Smith model GIS application.

RESULTS

Ground Surveys

I observed bighorn sheep during 480 observation sessions conducted over the course of 2 winters. Observation sessions occurred at vantage points along 10 survey routes, averaged 39 minutes in duration (range of 20-330 minutes), and amounted to 316.7 hours of total observation time, during which 1,061 sheep group locations were mapped. The average group size was 7 sheep (range of 1-42).

Focal observations involved tracking the movements of a recognizable individual over the course of at least 1 full day and sometimes up to 3 consecutive days. These focal observations typically occurred from survey route vantage points; such that sheep were observed from a distance of 800 m to 2 km, and care was taken to not disrupt normal sheep behavior. A total of 20 focal observation sessions were completed during winter months (Jan-Apr) and in all cases the recognizable individual was in a sheep group (size range of 2-11 sheep). Ten of the focal observations were 1-day sessions, 6 were 2-day sessions, and 4 were 3-day sessions. During all 20 observation sessions, the focal individual remained within the study area and no movements into unexpected habitat types (e.g., dense conifer) were recorded.

To depict bighorn sheep habitat use in a grid-cell layer, I used Arc View GIS software to create a 35 m buffer around sheep group location points, then converted the resulting shape file into a grid layer. Because the GIS software uses a corner of each grid-cell for the reference coordinates, this conversion meant that each sheep group location resulted in a cross-shaped cluster of 12 grid-cells being designated as "sheep present." To assess potential bias against sighting small groups at long distances, I plotted sheep group size against observer-sheep distance. No pattern was discernable, and given the proportional application of survey effort relative to the size, ruggedness and vegetation density of each survey unit, the assumption that all sheep groups had equal probability of detection appeared to have been satisfied.

Candidate Models – Goodness-of-Fit and Colinearity Assessment

On the basis of the Hosmer and Lemeshow Chi-square test and Akaike's information-theory criteria (AIC) statistics, none of my candidate models fit the observed bighorn sheep habitat use data well. All Hosmer and Lemeshow Chi-square test statistic values had very small significance values ($p<0.005$) and all AIC values were quite large. No interaction terms had significant LR test values or offered improvements in model fit, therefore none were included in any of the candidate models.

Although none of the candidate models had large coefficient values or standard errors (signs of colinearity among explanatory variables), I performed a linear regression analysis for each model to examine tolerance and condition index measures of colinearity (Menard 1995). The only explanatory variable displaying a tolerance value (<0.20) or condition index value (>15) indicative of colinearity was horizontal visibility. This is not surprising since horizontal visibility values were assigned to grid-cells by their land-cover type category; therefore, any model that included both these variables would display some colinearity. This colinearity was not problematic, as land-cover type contributed more significantly to model performance than did horizontal visibility.

Model Validation Tests

Validation tests are especially important with models intended for use in prediction (Hosmer and Lemeshow 1989). With each of my candidate models, I performed a validation test using data from the study area not involved in that model's construction. Because the response variable predicted probabilities ranged from 0 to approximately 0.26, my candidate models achieved their best separation of used and unused cell classification using a probability cut-off value of 0.13 – i.e., cases that resulted in a predicted probability of use <0.13 were classified as unused, and cases that resulted in a predicted probability of use >0.13 were classified as used. A common and straightforward means of assessing performance in a validation test is cross tabulation – an assessment of the predicted classification of cells versus the observed classification (Hosmer and Lemeshow 1989). The most common measures obtained from a cross tabulation are the rates of commission and omission. The rate of commission is the percentage of cells correctly classified by the predictive model, including both categories of classification (present/used, and absent/unused). The rate of omission is the percentage of cells incorrectly classified. In addition to recording these measures for each validation test, I calculated the percentage of cells with observed bighorn sheep use that were correctly classified as used (the "rate of positive commission"), and the ratio of all cells classified as used to the number of cells correctly classified as used (the "positive ratio"). I ranked candidate model performance based primarily on the rate of positive commission and the positive ratio.

To derive a single model capable of predicting bighorn sheep winter habitat across all of Glacier National Park (GNP), I pooled the data from both study areas and repeated the logistic regression analysis using the format of my best candidate models. The best candidate models were selected on the basis of validation tests, but model simplicity was also considered. Because there is potential for this final model to be applied at sites outside GNP where the user may not have classified satellite imagery, I examined the effect of replacing the land-cover type variable with 2 satellite reflectance variables in terms of validation test performance. I selected the 2 wavelength-bands (2 and 5) on the basis of LR tests conducted during model construction. This second version of the final model also contained the horizontal visibility variable, which was excluded from the first version because of colinearity with the land-cover type variable.

Finally, I conducted a validation test of the winter range component of the Smith model GIS application. I compared the validation test performance of the Smith model application to that of my 2 final model versions (Table 4). On the basis of positive commission and positive ratio measures from cross tabulations, my final model performed slightly better with the land-cover type variable than with the 2 reflectance variables, and both versions of my final model performed considerably better than the Smith model application.

The values of the constant and coefficients for both versions of my final model are shown in Table 5. Because the land-cover type version of my final model contains a categorical explanatory variable with 8 categories (land-cover type, see Table 3), this equation contains 7 indicator variables. When a categorical explanatory variable is entered into a regression analysis, it is necessary to create indicator variables to identify the category assigned to a particular sampling unit. The number of indicator variables required is 1 less than the number of categories in the explanatory variable because 1 category (either the first or the last) is represented by all zeros.

DISCUSSION

Ground Surveys

Based on observations from ground surveys conducted during winter, bighorn sheep on my 2 study areas appeared to prefer open grassland and rocky habitats to conifer habitats. This generalization was supported by focal observation sessions and opportunistic observation of sheep tracks in snow. During all of my focal observation sessions, the focal individual remained in open habitats and did not venture into forest habitats or into dense, tall shrub habitats adjacent to forest stands. Sheep tracks in snow were infrequently encountered along or near forest edges; these tracks were typically in open grassland and rocky habitats, and occasionally in shrubby and coniferous habitats. Tracks in shrubby sites were generally accompanied by evidence of shrub browsing. On a few occasions, I observed track evidence indicating that bighorn sheep had traveled shrubby, streamside routes through otherwise forested habitat for relatively short distances (50-200 m). These areas typically had only light snow accumulations (<25 cm), and field measurements of horizontal visibility were generally 20-50%. These track observations offer anecdotal evidence that, during winter, most bighorn sheep browsing on shrubs occurred on brushy slopes, in avalanche chutes, and along streams. These sites were characterized by fairly dense shrub canopy cover and were typically located above treeline or immediately adjacent to coniferous forest. During winter, shrubby sites at or above treeline generally had horizontal visibility ≥50%.

Dense and contiguous forest stands tended to have greater snow depths throughout winter than open, wind-swept slopes. Bighorn sheep made very little use of these forest stands until mid- to late-spring and early-summer when the snow cover had either melted or become densely compacted. Observations of tracks, fecal pellets, and occasionally of sheep indicated that during mid- to late-spring and early-summer bighorn sheep sometimes traveled through extensive, contiguous forest as they moved to lambing and/or summer ranges. Most of

Table 4. Validation test performance measures for 2 habitat models developed at Glacier National Park (GNP), Montana, and for the Smith model GIS application. For the 2 GNP models, group classification (sheep present or sheep absent) was based on a 0.13 probability cut-off value. Validation tests were conducted for 2 study areas – Many Glacier and Two Medicine.

Test Area	Commission[a]	Omission[b]	Positive Comm[c]	Positive Ratio[d]
		GNP Model (w/ land-cover type)		
Many Glacier	77.7%	22.3%	75.2%	4.0
Two Medicine	72.0%	28.0%	38.8%	7.0
		GNP Model (w/ bands 2 & 5, and horizontal visibility)		
Many Glacier	77.8%	22.2%	75.3%	4.0
Two Medicine	71.9%	28.1%	37.6%	7.2
		Smith Model GIS Application		
Many Glacier	73.6%	26.4%	10.5%	21.0
Two Medicine	76.6%	23.4%	11.1%	15.1

a – Rate of Commission is the percentage of cells correctly classified as used or unused by the model. For example, if among 100 grid cells observed to be used by sheep, 60 are classified as used and 40 as unused by a predictive model, and among 400 grid cells observed to be unused by sheep, 90 are classified as used and 310 as unused, then the model's rate of commission is (60+310)/500 = 0.74, or 74%.

b – Rate of Omission is the percentage of cells incorrectly classified as used or unused by the model. From the example above, the model's rate of omission is (40+90)/500 = 0.26, or 26%.

c – Rate of Positive Commission is the percentage of cells observed to be used by sheep (i.e., a positive response) that were classified as used by the predictive model. From the example above, the model's rate of positive commission is 60/100 = 0.6, or 60%.

d – Positive Ratio is the ratio of the total number of cells classified (correctly and incorrectly) as used to the number of used cells correctly classified as used. From the example above, the model's positive ratio is (60+90)/60 = 2.5.

this anecdotal evidence of forest travel was seen in lodgepole pine (*Pinus contorta*) forest, where horizontal visibility averaged 30-50%.

Model Goodness-of-Fit and Validation

The goodness-of-fit measures for all candidate models indicated rather poor fit. These poor goodness-of-fit measures were due in part to the very large number of unused sampling units (grid-cells). Even within areas used by bighorn sheep, there were large numbers of "unused" grid-cells with explanatory variable values similar to the "used" cells. This situation makes it difficult for regression techniques to find clear group separation trends in the explanatory variables. It is likely that if sheep habitat use was documented for many consecutive winters so that a high percentage of grid-cells within sheep use areas were labeled as "used," then the regression models' goodness-of-fit measures would improve. At first glance it may appear that model fit might be improved by increasing the size of the sampling unit. However, this would likely exacerbate the dilemma because explanatory variable values would be averaged on a larger scale, which might further diminish any separation trends between "used" and "unused" grid-cells.

Table 5. Explanatory variables and their coefficients, with standard errors, for two models for predicting bighorn sheep winter range in Glacier National Park, Montana.

Model	Variable[a]	Coefficient	Standard Error
GNP Model with land-cover type (LCT)	Constant	- 1.9892	0.1092
	Distance to Escape	- 0.0003	0.00006
	Snow Cover (Y/N)	- 1.0738	0.0325
	Solar Radiation Index	+ 0.00017	0.000011
	Slope (degrees)	- 0.0002	0.000017
	LCT Category 2	- 0.7698	0.0709
	LCT Category 3	- 1.007	0.0781
	LCT Category 4	- 0.3452	0.0567
	LCT Category 5	- 1.9407	0.0958
	LCT Category 6	- 0.0579	0.0079
	LCT Category 7	- 0.4277	0.0701
	LCT Category 8	- 1.4078	0.256
GNP Model with horizontal visibility and TM reflectance	Constant	- 3.5568	0.2114
	Distance to Escape	- 0.0032	0.0001
	Snow Cover (Y/N)	- 1.0327	0.0282
	Solar Radiation Index	+ 0.000164	0.000005
	Slope (degrees)	- 0.00025	0.000016
	Horizontal Visibility (%)	+ 0.0177	0.0008
	Band 2 Reflectance	- 0.000171	0.000013
	Band 5 Reflectance	+ 0.000173	0.000013

a – Explanatory variables: distance to escape terrain; snow cover (binary – yes or no); solar radiation index (computed using slope and aspect); slope (in degrees); land cover type (from a Thematic Mapper satellite image classified into 8 land cover categories, regression analysis defines this variable using 7 binary indicator variables, LCT 2 – LCT 8); horizontal visibility (in percent) was assigned to sampling units through correlation with land cover categories; band 2 and band 5 reflectance values from Thematic Mapper satellite image wavelength bands 2 and 5, adjusting radiance values for the influence of topography.

Although the goodness-of-fit measures for all of the candidate models were rather poor, a measure of greater interest is how well they predict bighorn sheep winter range habitat use. In order to be useful to land managers, the models must do an adequate job of predicting suitable habitat, and this is best assessed through validation tests – i.e., applying the model in an area not used for developing the model and comparing model predictions to known use patterns for that area. The most commonly reported measure of model performance in validation tests is the rate of commission – the percentage of cells correctly classified, which in the case of a logistic regression model involves only 2 classification categories. The rate of commission, however, is sensitive to the relative sizes of the 2 categories and will always favor classification into the larger category, independent of model fit (Hosmer and Lemeshow 1989). For example, in both of my study areas the number of unused cells exceeds the number of used cells by a factor of 10; therefore, a model that correctly classifies a high percentage of unused cells but a very low percentage of used cells still registers a high rate of commission, which as a measure of the model's performance is misleading. To get a more accurate picture of model performance, I examined the rate of positive commission (i.e., the percentage of cells known to be "used" that the model classified as "used") and the positive ratio (i.e., the ratio of the total number of cells classified, correctly and incorrectly, as "used" to the number of cells correctly classified as "used"). Clearly, a model with a high rate of positive commission and a small positive ratio is performing better than a model with a low rate of positive commission and a large positive ratio.

Final Models

While the development and validation of 2 sets of candidate models was critical to the selection of the best models, the overall goal was to derive a final model applicable across all of GNP, and perhaps at sites in other geographic areas. This final model contained the following explanatory variables: distance-to-escape terrain, snow cover, solar radiation index, slope, and land-cover type.

Although resource managers at GNP have ready access to a satellite image classification of land-cover types, land managers elsewhere may have neither vegetation maps nor satellite image classifications. For this reason, and given the wide availability of satellite imagery and its digital radiance values, I also derived a reflectance-value version of my final model using wavelength-band 2 and band 5 reflectance values in place of the land-cover type variable (see Tables 4 and 5).

Explanatory Variables Excluded from Final Models

The 2 final model versions were reached through assessment of model performance in validation tests as well as consideration of model parsimony. The fewer variables in a model, the easier that model is to use and interpret. On the other hand, if these final models were applied to a site outside GNP, it may turn out that they do not contain a parameter important to bighorn sheep winter range habitat suitability at that site.

Horizontal visibility is 1 variable that, although excluded from the land-cover type version of my final model, would quite likely prove to be important at other sites. Horizontal visibility has been identified as a necessary component of bighorn sheep habitat (Risenhoover and Bailey 1980, Krausman 1997). This variable was not included in this version of my final model because of its colinearity with the land-cover type variable, which was used as the basis for assigning horizontal visibility values across the study areas. My second final model version, containing 2 satellite reflectance value variables in place of the land-cover type variable, includes horizontal visibility, which contributed significantly to the model's goodness-of-fit, as evidenced by its large LR test statistic.

Availability of water was identified as an important variable in other habitat models, including the Smith model GIS application (see Table 1). None of the grid-cells in my 2 study areas was >3.2 km from water, which is the maximum distance for habitat suitability established by the Smith model application. The distance-to-water variable was not significant, as measured by the LR test statistic, and was therefore not included in any of my candidate models. Sites with less abundant sources of water than my

GNP study areas would likely find distance-to-water to be an important variable, as might efforts to model bighorn sheep summer range within GNP.

While Smith et al. (1991) identified distance-to-human development as an important factor regarding suitable bighorn sheep habitat, subsequent work has found that it contributes little to habitat suitability assessments (Johnson 1995, Sweanor et al. 1996). Although areas covered by buildings, roads and parking lots clearly offer no essential resources to bighorn sheep, they are generally not detrimental to sheep unless associated with elevated levels of stress and/or mortality (e.g., frequent and sustained human disturbance, unsustainable harvest or roadkill).

Distance-to-livestock is clearly an important parameter of suitable bighorn sheep habitat because of potential competition for forage and space, and especially because domestic sheep are known to pose a significant threat of disease transmission to bighorn sheep (Stelfox 1971, Rowland and Schmidt 1981, Smith et al. 1988). When using the Smith model GIS application to evaluate potential reintroduction sites, the National Park Service has stressed that those reintroduction sites must be at least 16 km from areas used by domestic sheep (Sweanor et al. 1996). While domestic sheep were prevalent along GNP's entire eastern boundary through the first half of the 20th century, grazing allotments along this boundary have been used only for cattle and horses over the last several decades. Although the distance-to-livestock variable did not prove significant in my analysis, cattle and horse trespass into GNP is a management issue of concern regarding spread of exotic plants and competition for forage and space.

Management Implications

One deficiency in the predictive performance of my final models is their limited ability to predict bighorn sheep winter range habitat use on north-facing slopes. The majority of bighorn sheep groups observed during winter were on southerly aspects, and indeed the Smith model GIS application restricts suitable winter range to aspects between 120° and 245° (Johnson 1995, Sweanor et al. 1996). However, my ground surveys documented use of snow-free, north-facing slopes. Although use of these slopes, compared to use of southerly slopes, was infrequent, it occurred throughout the winter. Future investigation into additional variables or modified analyses that would allow more sensitivity in predicting suitable north-facing sites for winter range would be valuable.

Probably the most pressing management concern for bighorn sheep in GNP as well as other sites in the Rocky Mountains is the encroachment of conifers into bighorn sheep habitat, especially low- to mid-elevation winter range areas (Schirokauer 1996). My final models should prove useful to GNP natural resource managers interested in identifying those bighorn sheep winter ranges most threatened by conifer encroachment, as well as historically suitable winter range that has already been fragmented by conifer encroachment. Potential management actions for such sites include prescribed fire and tree thinning.

ACKNOWLEDGMENTS

This paper summarizes a portion of my Master of Science thesis project. Les Marcum, University of Montana Wildlife Biology Program, served as my advisor for that project. Steve Gniadek and Rick Yates, Glacier National Park (GNP), secured project funding and provided many helpful suggestions. Additional funding came from the Rocky Mountain Bighorn Society thanks to the persistence of Bill Pratt. Carl Key and Kim Keating, U.S. Geological Survey, Biological Resources Division, provided guidance in satellite image data processing and the nuances of habitat modeling. Pete Lundberg and Andrika Kuhle, GNP, lumbered across many steep, rocky slopes in helping me accomplish fieldwork.

LITERATURE CITED

ARMENTROUT, D. J., AND W. R. BRIGHAM. 1988. Habitat suitability rating system for desert bighorn sheep in the Basin and Range Province. U. S. Bureau of Land Management Technical Note 384, Denver, Colorado. 19 pp.

BEERS, T. W., P. E. DRESS, AND L. C. WENSEL. 1966. Aspect transformation in productivity research. Journal of Forestry 64: 691-692.

BLEICH, V. C., M. C. NICHOLSON, A. T. LOMBARD, AND P. V. AUGUST. 1992. Preliminary tests of a mountain sheep habitat model using a geographic information system. Biennial Symposium of the Northern Wild Sheep and Goat Council 8:256-263.

BOYCE, M. S., D. I. MACKENZIE, B. F. MANLY, M. A. HAROLDSON, AND D. MOODY. 2001. Negative binomial models for abundance estimation of multiple closed populations. Journal of Wildlife Management 65: 498-509.

FINKLIN, A. I. 1986. A climatic handbook for Glacier National Park. U. S. Dept of Agriculture, Intermountain Research Station Tech Report INT-223.

GEIST, V. 1971. Mountain sheep. Univ of Chicago Press, Chicago IL. 383 pp.

GIONFRIDDO, J. P., AND P. R. KRAUSMAN. 1986. Summer habitat use by mountain sheep (*O. c. mexicana*). Journal of Wildlife Management 50: 331-336.

GOODSON, N. J. 1980. Bighorn sheep in north-central Colorado, past, present and future. Biennial Symposium of the Northern Wild Sheep and Goat Council 2: 190-209.

HANSEN, C. G. 1980. Habitat evaluation. Pages 320-335 *in* G. Monson and L. Sumner, eds. The desert bighorn: its life history, ecology, and management. Univ of Arizona Press, Tucson, AZ. 370 pp.

HOLL, S. A. 1982. Evaluation of bighorn sheep habitat. Desert Bighorn Sheep Council Transactions 26:47-49.

HOSMER, D. W., AND J. LEMESHOW. 1989. Applied logistic regression. John Wiley and Sons, New York, NY. 307 pp.

JOHNSON, T. L. 1995. A test of a habitat evaluation procedure for Rocky Mountain bighorn sheep. Master's thesis. Colorado State University, Ft. Collins. 60 pp.

KRAUSMAN, P. R. 1997. The influence of landscape scale on the management of desert bighorn sheep. Pages 349-367 *in* J. A. Bissonette, editor. Wildlife and landscape ecology: effects of pattern and scale. Springer-Verlag, NY.

MACE, R. D., J. S. WALLER, T. L. MANLEY, K. AKE, AND W. T. WITTINGER. 1998. Landscape evaluation of grizzly bear habitat in western Montana. Conservation Biology 13: 367-377.

MANLY, B. F., L. L. MCDONALD, AND D. L. THOMAS. 1993. Resource selection by animals, statistical design and analysis for field studies. Chapman and Hill, London, England. 177 pp.

MCCARTY, C. W. 1993. Evaluation of a desert bighorn sheep habitat suitability model. Master's thesis. Colorado State University, Fort Collins. 144 pp.

MENARD, S. 1995. Applied logistic regression analysis. Sage Publications, Inc., Thousand Oaks, CA. 97 pp.

RISENHOOVER, K. L., AND J. A. BAILEY. 1980. Visibility: an important factor for an indigenous, low-elevation bighorn herd in Colorado. Biennial Symposium of the Northern Wild Sheep and Goat Council 2:18-27.

ROWLAND, M. M., AND J. L. SCHMIDT. 1981. Transplanting desert bighorn sheep – a review. Transactions of the Desert Bighorn Council 25: 25-28.

SCHIROKAUER, D. W. 1996. The effects of 55 years of vegetative change on bighorn sheep habitat in the Sun River area of Montana. Master's thesis. University of Montana, Missoula MT. 96 pp.

SINGER, F. J., AND M. A. GUDORF. 1999. Restoration of bighorn sheep metapopulations in and near 15 National Parks: conservation of a severely fragmented species. USGS Open File Report 99-102, Midcontinent Ecological Sci. Center, Fort Collins, CO. 391 pp.

SMITH, T. S., J. T. FLINDERS, AND D. W. OLSEN. 1988. Status and distribution of Rocky Mountain bighorn sheep in Utah. Biennial Symposium of the Northern Wild Sheep and Goat Council 6: 5-12.

SMITH, T. S., J. T. FLINDERS, AND D. S. WINN. 1991. A habitat evaluation procedure for Rocky Mountain bighorn sheep in the intermountain west. The Great Basin Naturalist 51:205-225.

STELFOX, J. G. 1971. Bighorn sheep in the Canadian Rockies: a history 1800-1970. Canadian Field Naturalist 85:101-122.

SWEANOR, P. Y., M. GUDORF, AND F. J. SINGER. 1996. Application of a GIS-based bighorn sheep habitat model in Rocky Mountain region National Parks. Biennial Symposium of the Northern Wild Sheep and Goat Council 10:118-125.

TILTON, M. E. 1977. Habitat selection and use by bighorn sheep (*Ovis canadensis*) on a northwestern Montana winter range. Master's thesis. University of Montana, Missoula, MT. 121 pp.

WAKELYN, L. A. 1987. Changing habitat conditions on bighorn sheep ranges in Colorado. Journal of Wildlife Management 51: 904-912.

WALKER, P. A. 1990. Modeling wildlife distributions using a geographic information system: kangaroos in relation to climate. Journal of Biogeography 17: 279-289.