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# AN EVALUATION OF GIS-BASED HABITAT MODELS FOR BIGHORN SHEEP WINTER RANGE IN GLACIER NATIONAL PARK, MONTANA, USA

by
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An Evaluation of GIS-based Habitat Models for Bighorn Sheep Winter Range in Glacier National Park, Montana, USA

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I used logistic regression to construct bighorn sheep winter range habitat models for two Glacier National Park (GNP) study areas – one in the Many Glacier valley and one in the Two Medicine valley. During two winters, habitat use was described through systematic ground surveys supplemented with focal observations, lasting 1-3 days, of recognizable individual sheep. Lambing areas were identified through ground surveys conducted from May 1-June 15. Available habitat was evaluated using 14 habitat parameters, each measured at a 30-by-30 meter grid-cell resolution with GIS software.

As a general measure of herd health, composite samples of bighorn sheep fecal pellets were analyzed for levels of fecal nitrogen (FN) and diaminopimelic acid (DAPA). FN content averaged 1.69% and DAPA content ranged from 0.29 to 0.40 mg/g, indicating relatively high quality winter forage.

Candidate models constructed from Many Glacier habitat use data were validated at Two Medicine, and vice versa. Using habitat parameters from the model with the best validation test performance, I constructed two versions of a final GNP winter range model using data pooled from both study areas. 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% of grid-cells with observed winter use at Many Glacier and 38% of grid-cells with observed winter use at Two Medicine. The Smith model GIS application correctly classified 10% and 11% of grid-cells with observed winter use at Many Glacier and Two Medicine, respectively. The GNP models also performed slightly better than the Smith model GIS application in predicting lambing 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 two 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.

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# INTRODUCTION

Bighorn sheep (*Ovis canadensis*) populations in western North America experienced dramatic declines and local extirpations during the late 19th and early 20th centuries due to hunting, competition with domestic livestock for forage and/or space, and diseases transmitted from domestic sheep (Cowan 1940, Buechner 1960, Stelfox 1971). While bighorn sheep have been successfully re-established on some former ranges, many reintroduction efforts have languished due to: inadequate quantities of seasonal ranges; severe competition with other wild ungulates or with domestic sheep, cattle and goats; diseases acquired from domestic sheep; improper juxtaposition of key habitat components; and human harassment (Rowland and Schmidt 1981, Smith et al. 1988). Considerable research over the past few decades has focused on creating and improving bighorn sheep habitat models, which can help wildlife managers assess potential reintroduction sites as well as evaluate habitat improvement options. Initial models were developed for desert bighorn sheep (*O. c. nelsoni*) (Hansen 1980, Holl 1982, Armentrout and Brigham 1988). Smith et al. (1991) adapted existing desert bighorn sheep habitat models to address the habitat requirements of Rocky Mountain bighorn sheep (*O. c. canadensis*). As part of a regional bighorn sheep restoration program, the National Park Service (NPS) used a modified application of the Smith et al. (1991) model 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).

In this thesis I present winter range habitat models constructed for Rocky Mountain bighorn sheep on two study areas in Glacier National Park (GNP), Montana. Selection of habitat variables was based on literature review and discussion with colleagues involved in wildlife habitat modeling. Candidate models were constructed via logistic regression, and the significance of variable coefficients was examined with likelihood ratio tests. I assessed the goodness-of-fit of candidate models using Akaike's information-theory criteria (AIC) and the Hosmer and Lemeshow Chi-square test (Hosmer and Lemeshow 1989, Movsas et al. 1997, Boyce et al. 2001). Candidate model performance was evaluated through validation tests -- each model, developed from a single study area, was validated by assessing its accuracy in predicting habitat use on the study area not included in that model's development. Using the habitat variables from the best-performing candidate models, I constructed two versions of a final winter range model applicable across GNP. I then compared the prediction accuracies of my final models to the accuracy of the winter range component of the NPS modified application of the Smith et al. (1991) model. The remainder of this introduction summarizes the historical distribution of bighorn sheep in North America, population viability concerns, important bighorn sheep habitat components, features and tests of existing bighorn sheep habitat models, and the recent history of bighorn sheep in GNP.

## Historical Bighorn Sheep Distribution in North America

Historic accounts indicate that bighorn sheep inhabited nearly all steep habitats in mountains, foothills, river breaks and prairie badlands in western North America. Following dramatic population declines during the late 19th and early 20th centuries, historic bighorn sheep metapopulations have been reduced to small, isolated groups existing in a highly fragmented distribution (Singer and Gudorf 1999). While estimates of the number of bighorn sheep present in the western United States prior to 1850 range from 500,000 to 2 million (Seton 1929, Wishart 1978, Valdez 1988), estimates of current bighorn sheep numbers range from 35,000 to 45,000 (Hoefs 1985). From the 1870's through the 1890's, rampant hide and meat hunting extirpated many small, easily accessible bighorn sheep populations. From the turn of the 20th century through the 1950's, bighorn sheep appear to have been heavily impacted by domestic sheep due to competition and disease transmission (Buechner 1960, Stelfox 1971). Because domestic sheep are capable of using steep slopes and arid ranges, they can exert considerable competitive pressure on bighorn sheep for forage and space. Diseases, primarily pneumonia and scabies, carried by domestic sheep with few ill effects have been frequently implicated in widespread bighorn sheep die-offs (Buechner 1960, Goodson 1982). Indeed, it has become a priority in both the management of extant bighorn sheep populations and the planning of future reintroduction efforts to maintain complete separation between bighorn sheep ranges and domestic sheep (Goodson 1982, Smith et al. 1991, Sweanor et al. 1996, Singer and Gudorf 1999).

Within the state of Montana, bighorn sheep historically occupied all of the larger mountain ranges and most of the smaller, isolated mountain ranges, as well as the river-breaks terrain along the Missouri River (Couey 1950). By the middle of the 20th century, bighorn sheep had been extirpated from the river-breaks terrain of the Missouri River and from most of the smaller, isolated mountain ranges east of the continental divide; and the continuity among metapopulations along the continental divide had been significantly reduced (Couey 1950). As in other western states, efforts to reintroduce bighorn sheep into formerly occupied ranges in Montana have had varying levels of success (Janson 1974).

## Bighorn Sheep Population Viability

Adapted to exploit climax grassland communities, bighorn sheep are characterized by relatively long life spans, low reproductive rates, slow maturation, and social mechanisms that pass home ranges and migration routes from one generation to the next (Geist 1971, Singer and Gudorf 1999). Expansion of bighorn sheep populations into unoccupied ranges is limited by their gregarious social system and their habit of learning traditional home ranges and migration routes from older members of the herd (Geist 1975). Occupying grassland habitat patchily distributed within the forest biome, bighorn sheep are not uniformly distributed across the landscape. For species with such naturally fragmented distribution, the metapopulation concept has been central to the thinking of researchers and managers for the past two decades. A metapopulation is a set of subpopulations of a given species that are geographically separated, but that remain interconnected through the processes of immigration, emigration and/or recolonization (Lande and Barrowclough 1987). Historically, bighorn sheep probably occurred in subpopulations occupying discrete patches of steep, rocky terrain separated by forests or flat areas (Schwartz et al. 1986, Bleich et al. 1990). These subpopulations, however, were connected across large landscapes by emigration and immigration, which allowed gene flow between subpopulations (Luikhart and Allendorf 1996). Migration movements of up to 18 km (11 miles) by bighorn rams are common, and movements of 50 km (31 miles) have been recorded (Geist 1971, Thorne 1979, Cochran and Smith 1983, Festa-Bianchet 1986). Provided that no migration barriers exist, subpopulations separated by up to 50 km may potentially form a metapopulation (Dunn 1993, Singer and Gudorf

1999). In the modern landscape of western North America, connectivity between subpopulations is threatened by expanding human development – such as housing and resort development, canals, reservoirs, interstate highways, and recreational activities (Bleich et al. 1996). A loss of connectivity can lead to isolation of the subpopulations. The reduction or elimination of immigration into a given subpopulation leads to inbreeding, which has been shown to decrease growth rates, increase neonate mortality, and increase susceptibility to disease (Skiba and Schmidt 1982, Ralls and Ballou 1983). Inbreeding potential is positively correlated with the distance between subpopulations and inversely related to subpopulation size (Gilpin 1987).

One idea that has grown out of the metapopulation approach is a minimum viable population (MVP) size. Shaffer (1987) defined an MVP as the smallest, isolated population having at least a 95% probability of surviving at least 100 years. Examining empirical data from 122 bighorn sheep populations in the southwestern United States, Berger (1990) found that populations with less than 50 sheep rapidly went extinct, and that only populations with over 100 sheep persisted for more than 70 years. In the development of a habitat evaluation procedure for Rocky Mountain bighorn sheep, Smith et al. (1991) recommended an MVP of 125 sheep. However, populations of 50 sheep or less may persist if the habitat quality of seasonal ranges remains high and travel corridors allowing gene flow with other populations are maintained (Krausman 1997). Thus, persistence of small bighorn sheep populations may be associated more with subpopulation connectivity and management activities than with an MVP (Goodson 1994).

## Important Bighorn Sheep Habitat Components

Bighorn sheep inhabit open, grassland habitats in mountainous terrain. Able to identify predators at great distances with their excellent eyesight, bighorn sheep evade predators by retreating into steep, rocky terrain (Geist 1971). Escape terrain is the most critical bighorn sheep habitat component (Geist 1971, Shannon et al. 1975, Hansen 1980, Wilson et al. 1980, Holl 1982, Wakelyn 1987, Smith et al. 1988). Escape terrain has generally been defined as continuous steep slopes of 27-degrees or greater and possessing rocky outcrops and/or cliffs greater than 1.6 hectares (4 acres) in size and at least 15 m (49 ft) in height (Geist 1971, Tilton 1977, McCollough et al. 1980, Smith et al. 1991). Except for some migration movements, bighorn sheep seldom venture more than 300-500 m (984-1,640 ft) from escape terrain (Shannon et al. 1975, Gionfriddo and Krausman 1986, Wakelyn 1987, Smith et al. 1988). According to Risenhoover and Bailey (1980), bighorn sheep group size increased and foraging efficiency decreased with increasing distance from escape terrain. 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 as it allows bighorn sheep to sight predators at a safe 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). There is, however, general agreement among these studies that although bighorn sheep will travel through vegetation types with horizontal visibility as low as 30-50% when migrating between seasonal ranges, they display clear preference for vegetation types with horizontal visibility of 60-80% or higher. Researchers using tree canopy cover to indirectly define horizontal visibility found that bighorn sheep avoided areas with greater than 75% tree canopy cover (Tilton and Willard 1982, Hughes 1997). Even narrow tracts of very low visibility habitat (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. Most of the grasslands along Montana's Rocky Mountain Front were created and maintained by wildfires (Stelfox 1971, Arno and Gruell 1986). Fire in grassland habitats tends to increase nutrient content and production of herbaceous vegetation by removing dead material and stimulating new growth (Hobbs and Spowart 1984, Seip and Bunnell 1985, McWhirter et al. 1992, Smith et al. 1999, Ruckstuhl et al. 2000). Decades of aggressive fire suppression have allowed shrubs and conifers to encroach into mid-elevation grasslands along the Rocky Mountain Front (Arno and Gruell 1986, Schirokauer 1996). Although the frequency of stand replacing fires along the eastern side of present day Glacier National Park was one fire every 10 to 19 years during the 18th and 19th centuries and the first third of the 20th century, no stand replacing fires have occurred over the past 65 years (Barrett 1993, Barrett 1997). The encroachment of shrubs and conifers into grassland habitats associated with fire suppression reduces the amount of suitable bighorn sheep habitat and compromises migratory corridors between seasonal ranges and between different subpopulations (Goodson 1980, Wakelyn 1987, Schirokauer 1996). Small, prescribed fires can mimic natural, historic conditions along grassland perimeters; however, given the strong winds so common along the Rocky Mountain Front, the use of prescribed fire is not very practical.

As alluded to earlier, 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 kilograms (551-661 pounds) in dry weight of grasses and forbs per hectare (2.47 acres); or, as an alternative, 14% canopy cover of grass and forb species. Bighorn sheep forage requirements have also been described in terms of forage abundance, with an emphasis on continuous distribution, without any effort to quantify minimum requirements (Miller and Gaud 1989, Risenhoover and Bailey 1985). Managers, however, often need to evaluate habitat suitability across large geographic areas for which they do not have accurate estimates of forage quantity or distribution. 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, Hughes 1997).

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). Water may be available to bighorn sheep as free (running or standing) water, dew, preformed in forage, or through oxidative metabolism (Turner and Weaver 1980). 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). Although some desert bighorn sheep herds have been documented to inhabit sites with no permanent sources of free water (Watts 1979, Krausman and Leopold 1986), it is well accepted that bighorn sheep require free water availability in lambing areas (Smith et al. 1991, Singer and Gudorf 1999).

Potential barriers to bighorn sheep movement may be natural or man-made and include large rivers and lakes, dense vegetation, non-traversable cliffs, wide valleys and plateaus, canals, reservoirs, aqueducts, impassable fencing, major highways and roads, and high-use human development (Smith et al. 1991). While bighorn sheep are known to occasionally swim across rivers and lakes (Cowan 1940), large rivers and lakes, canals, reservoirs and aqueducts likely act as barriers to everyday movements on seasonal ranges (Smith et al. 1991, Singer and Gudorf 1999). As discussed earlier, predator avoidance instincts cause bighorn sheep to avoid dense vegetation. Although desert bighorn sheep are known to make migration movements across wide valleys, the need for nearby escape terrain for predator avoidance generally keeps bighorns away from wide valleys and plateaus (Geist 1971, Krausman 1997). Major highways and roads also can act as movement barriers, and although bighorn sheep may become habituated to human activity and may forage on cultivated lawns and gardens (Riggs 1977), high-use developed areas on or adjacent to suitable habitat result in a reduction of available habitat (Smith et al. 1991, Johnson 1995).

Human disturbance to bighorn sheep can result in increased energy expenditure, lowered foraging efficiency, and higher heart and metabolic rates (MacArthur et al. 1979, Stockwell and Bateman 1991, Bleich et al. 1994). The most obvious response to human disturbance is escape behavior or flight, but less obvious physiological responses also cause detrimental energetic costs and likely occur even in bighorn sheep that appear to be well habituated to human activities (Ostovar 1998). Bighorn sheep appear to habituate most readily to vehicles along roadways, while the greatest sources of disturbance appear to be low-flying aircraft and hikers (Ostovar 1998, Singer and Gudorf 1999). Decreased reproductive success has been documented in ungulate populations exposed to chronic human disturbance (Joslin 1986, Yarmoloy et al. 1988, Harrington and Veitch 1992). Finally, as discussed earlier, 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). Simultaneous habitat use by bighorn sheep and cattle and/or horses is generally minimal because cattle and horse use of lower-elevation bighorn winter ranges typically occurs during summer when bighorn sheep have moved up to higher-elevation summer ranges. Nevertheless, cattle and horses may impact the habitat quality of bighorn sheep winter range by reducing forage availability (McCarty 1993).

## Bighorn Sheep Habitat Models

With the increasing interest in restoring bighorn sheep populations to historic ranges from which they were extirpated, much work has focused on creating and improving sheep habitat models. Initial models were developed for desert bighorn sheep and identified seven primary habitat parameters: natural vegetation, topography, precipitation, evaporation, water availability, existing bighorn sheep use, and human impacts (Hansen 1980, Holl 1982, Armentrout and Brigham 1988). Smith et al. (1991) adapted desert bighorn sheep habitat models to address the habitat parameters of Rocky Mountain bighorn sheep. 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. This model focused on elevation, slope, escape terrain, horizontal visibility as determined by tree and shrub canopy cover, and the amount of grass, forb, and shrub cover (Smith et al. 1991).

Recent developments in bighorn sheep habitat models have taken advantage of Geographic Information System (GIS) computer software packages. GIS packages can rapidly and quantitatively assess large land areas to allow objective comparisons of potential habitat (Singer and Gudorf 1999). Additional GIS capabilities include evaluating the influence of particular habitat criteria on model predictions of suitable habitat, and identifying areas for potential habitat improvement (e.g., reduction of forest encroachment into grasslands, protection of travel corridors, development planning, etc.). Analysis of Landsat satellite images and digitized aerial photographs can quantify temporal changes in vegetative composition and identify areas where conifer or shrub encroachment into grasslands may be degrading the forage or visibility component of bighorn sheep winter range (Risenhoover and Bailey 1980, Schirokauer 1996). GIS-based habitat models use overlay capabilities and proximity functions to delineate suitable habitat based on user-defined habitat parameter criteria (Smith et al. 1991, Bleich et al. 1992).

Some researchers have used a pattern recognition (PATREC) model as a systematic, mathematical method of qualifying habitat suitability by assigning high- and low-use "conditional probabilities" to specific habitat parameter criteria (Kling 1980, Holl 1982, Smith et al. 1991). Typically, these conditional probabilities are based on animal densities observed by local and regional biologists and/or through field survey work. There are potential problems with associating animal density with habitat quality. Van Horne (1983) summarized three ways in which such habitat quality conclusions may be inaccurate: 1) summer density-habitat associations may be meaningless if winter conditions dictate survival, or vice versa; 2) fluctuations in biotic and abiotic resources may mean that current densities reflect short-term changes in environmental conditions; and 3) high-densities of subordinate animals in poor-quality "sink" habitats may occur due to territorial behavior of dominant animals, or the influence of predators or humans (e.g., harvest, high use, or development).

While some researchers evaluating bighorn sheep habitat models have described habitat use by deploying radio telemetry collars on a sample of animals (Bleich et al. 1992, McCarty 1993), others have described habitat use through aerial and/or ground surveys of populations with no radio-collared individuals (Wakeling and Miller 1990, Haas 1991, Schirokauer 1996). Although weather conditions (i.e., falling snow, low cloud ceiling) dictate the days during which surveys can be conducted and surveys are limited to daylight hours, sound study designs using systematic surveys can provide an objective description of bighorn sheep habitat use with biases minimized (Wakeling and Miller 1990). Sources of potential bias include observer expectancy, and variation in sightability due to sheep activity (e.g., bedded versus feeding or moving) or to habitat type (e.g., rugged, convoluted rocky areas; open grassy slopes; ridge tops; areas with a conifer or aspen overstory canopy).

As habitat models are developed, their usefulness depends on validation through performance tests (Berry 1986, Chalk 1986). Bleich et al. (1992) used aerial telemetry data from a reintroduced population of desert bighorn sheep on a 13,000-hectare study area to test predictions of the model developed by Hansen (1980). Focusing on the habitat parameters of topography, vegetation, and water availability, these authors concluded that the Hansen model has value for reintroduction site evaluation although they found that sheep avoided moderate slopes predicted as suitable by the model (Bleich et al. 1992). In assessing three desert bighorn sheep models, Haas (1991) compared suitable habitat predictions with her own aerial and ground surveys of a reintroduced sheep population; gridding the approximately 10,000-hectare study area into 1 $km^2$ units, she found that the models correctly predicted sheep presence/absence for 70% of the grid units. McCarty (1993) examined the Armentrout and Brigham (1988) desert bighorn sheep habitat model applied at a micro-habitat scale (20-m radius circular plots) and a macro-habitat scale (square km plots), using radio telemetry to gather sheep locations on an 11,000-hectare study area. McCarty (1993) found that sheep habitat selection was better correlated with habitat parameter indices measured at the micro-habitat scale than at the macro-habitat scale, and identified topographic ruggedness, distance to escape terrain, and visibility as the parameters that best explained observed sheep locations.

While a modified GIS application of the Smith model (using eight primary habitat parameters, Table 1) has recently been used to assess potential reintroduction sites in Rocky Mountain Region National Parks (Sweanor et al. 1996, Hughes 1997, Singer and

Gudorf 1999), I am aware of only two efforts to test the accuracy of suitable bighorn sheep habitat predictions generated by this Smith model application. Johnson (1995) evaluated the Smith model's suitable habitat predictions at eight reintroduction sites in Colorado. The reintroduction sites, of which four were successful and four were failures, ranged in size from 260 to 52,500 hectares. The Smith model predicted no suitable habitat at six sites, and 18 hectares and 65 hectares of suitable habitat at two of the successful sites (Johnson 1995). The model's poor performance was largely a result of the use of small scale (1:250,000) USGS digital elevation models, which reduced the ability of a GIS package to accurately identify escape terrain (Johnson and Swift 1999). Johnson (1995) improved the Smith model's performance slightly by reducing the horizontal visibility parameter criteria from >80% to >60%, and the human use area buffer parameter criteria from 150 m to zero. Schirokauer (1996) applied the Smith model to a 42,000-hectare study area in the Sun River drainage in Montana; however, having collected only a small number of sheep locations in limited ground surveys, he was not able to critically evaluate model performance.

### Bighorn Sheep in Glacier National Park

While accounts of bighorn sheep in and around Glacier National Park (GNP) pre-date the park's establishment in 1910, demographic information is sparse and difficult to interpret. As the east side of present day GNP was opened to mining in the late 1800's, bighorn sheep were exposed to heavy hunting pressure. Prior to the establishment of GNP in 1910, the Many Glacier valley – one of GNP's primary winter range areas and the site of the mining-based, historic townsite of Altyn – may have supported semi-commercial

**Table 1. Habitat criteria used in Smith model GIS application.**

This application was 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 and lambing range are also shown. These habitat criteria were 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 added stipulations that aspect be between 120° and 245°, and that snow depth be less than 25 cm.

**Lambing Range** – Areas meeting above criteria, with added stipulations that aspect be between 45° and 315°, and that a water source be within 1 km. In addition, any area meeting all of these criteria must be at least 2 hectares (4.9 acres) in size.

hunting operations (Riggs 1977). Another potential influence on bighorn sheep numbers and distribution during the early part of the 20th century was domestic sheep, which are known to transmit disease, particularly pneumonia, to bighorn sheep. While sheep ranching was prevalent on the Blackfeet Indian Reservation, bordering the east side of GNP, and in the Badger-Two Medicine area, just south of GNP, I could not find published information regarding sheep grazing allotments in these areas. The earliest park-wide bighorn sheep population estimates were made in 1917 and 1918, with estimates ranging from 1,500 to 2,000 sheep (Bailey and Bailey 1918, Seton 1927). These estimates, however, employed inappropriate assumptions on the park-wide extent of suitable bighorn sheep habitat and the rate of population growth, and relied on second-hand sheep observations that very likely resulted in duplication of counts (Keating 1985a).

The first concerted efforts to estimate ungulate populations in GNP through systematic survey counts began in the early 1920's. As the culmination of a three-year effort, GNP staff estimated a 1924 park-wide population of 1,111 bighorn sheep. Again, however, this estimate very likely included duplicate counts because it used surveys from both summer and winter range areas (Keating 1985a). Adjustment of this 1924 estimate, by discarding summer range counts, and of the 1917 Seton estimate, by removing unsuitable habitat from the park-wide extrapolation, resulted in park-wide estimates of 475 to 600 bighorn sheep (Keating 1985a). Fluctuations in survey effort and timing make park-wide comparisons between historic and current bighorn sheep numbers very difficult. After 1940, organized, park-wide survey counts had a reduced geographical coverage, and by the 1960's the park-wide survey effort had collapsed.

The one location in the park where survey effort has been relatively complete and comparable is the Many Glacier valley. In Many Glacier, the core bighorn sheep winter range area abuts and overlaps with the access road and developed area; as a result, bighorn sheep are readily observable and have been regularly tallied. In 1917, a GNP ranger reported 207 bighorn sheep at Many Glacier (Bailey and Bailey 1918). Coming soon after the establishment of GNP, which curtailed a period of heavy hunting pressure, this 1917 count may reflect a post-overexploitation irruption rather than a higher historic carrying capacity (Keating 1985a). Artificial winter feeding of bighorn sheep at Many Glacier began in February of 1920 and continued until 1937 (Riggs 1977). From the initiation of artificial feeding in 1920 until the first recorded epizootic die-off of bighorn sheep in 1927, Many Glacier mid-winter counts averaged 157 bighorn sheep (Keating 1985a). From 1928 through 1936, Many Glacier mid-winter counts averaged 103 bighorn sheep (Keating 1985a). The Many Glacier bighorn sheep herd experienced its second recorded epizootic die-off during the winter of 1936-37 (Riggs 1977). As in the 1927 die-off, approximately 30 bighorn sheep deaths were documented in 1937, although the disease responsible for these deaths was not recorded (Riggs 1977). The highest bighorn sheep counts at Many Glacier in recent years have occurred in late April and early May, which is the time of the spring concentration of bighorn sheep on core winter range areas (Geist 1971). Although mixing of ram groups and ewe groups is limited, both sexes gather on the slopes of Altyn Peak and Mount Henkel in the spring, and high counts have ranged from 95 to 105 bighorn sheep (GNP wildlife records). Since 1937, only two epizootic die-offs have been recorded; they occurred during the winters of

1955-56 and 1983-84, and each involved less than 10 bighorn sheep mortalities, with pneumonia being the suspected cause of death (Keating 1985a).

The survey counts summarized by Keating (1985a) are the only existing records of historic bighorn sheep numbers in GNP. If sex and age classification data were collected during GNP bighorn sheep surveys from the 1920's through the 1960's, this information has not survived. Keating (1985b) summarized sex and age ratios based on surveys conducted in the mid-1970's and the mid-1980's. At Many Glacier, based on three total sheep counts ranging from 49 to 76 sheep, ratios were 32-46 lambs and 34-146 rams per 100 ewes (Keating 1985b). If the one, oddly low ram ratio from Many Glacier is disregarded, then the adjusted figure becomes 126-146 rams per 100 ewes. At Two Medicine, based on a total sheep count of 60 sheep, ratios were 45 lambs and 127 rams per 100 ewes (Keating 1985b).

Information on bighorn sheep distribution in GNP is very limited. As discussed by Keating (1985a), a map overlay from 1939 (based on 1934-1939 surveys) depicting park-wide bighorn sheep winter range has survived, although no thorough description of methods and considerations still exists. While most of the winter range polygons delineated on this overlay coincide with known current bighorn sheep winter range sites, there are several anomalies. It is unknown whether these anomalies represent bighorn sheep summer or fall range, speculation on potential bighorn sheep winter range, or winter ranges no longer occupied by bighorn sheep. A few of the polygons from this 1939 map seem quite unrealistic as sheep winter range either because of forest cover and shallow slopes or because of heavy snow accumulation. Other, more plausible polygons may have been affected by forest encroachment as a result of fire exclusion or by hunting pressure. In addition to a long winter hunting season on the Blackfeet Indian Reservation, there is undoubtedly some bighorn sheep hunting that occurs inside the park boundary. In fact, in January of 2000, during a routine sheep survey for this project, two illegal hunters were observed removing the head from a full-curl ram approximately one-half mile inside the park boundary. Park rangers later apprehended the two perpetrators, and subsequent investigation revealed that three full-curl rams had been shot inside the park.

In summary, bighorn sheep appear to still occupy most of the winter range areas they occupied in the 1930's (Keating 1985a, GNP wildlife records), although fire exclusion very likely has degraded lower elevation portions of these winter ranges and hunting pressure continues to impact sheep on winter ranges along GNP's boundary. Prior to the onset of this study, no systematic bighorn sheep surveys had occurred since the mid-1980's. Fairly regular, incidental bighorn sheep counts occurred during the 1990's at Many Glacier, mostly during the spring concentration (late April-early May). Occasional late winter incidental counts were made during the 1990's in the Two Medicine area. The sex and age classified counts I conducted during the winters of 1999-2000 and 2000-2001 provide excellent baseline data regarding current bighorn sheep population status on GNP's two primary winter range areas. The winter range habitat models presented here will assist GNP natural resource managers in identifying: 1) small, peripheral winter range areas in need of future surveys to determine current bighorn sheep status; 2) areas where conifer encroachment is degrading current or historic bighorn sheep winter range; and 3) areas where hunting pressure may be excluding sheep from suitable winter range habitat.

## STUDY AREA DESCRIPTION

The two study areas are situated along the Rocky Mountain Front, a topographically and biologically diverse transition zone between the Continental Divide and the Northern Great Plains, and both lie entirely within Glacier National Park (GNP) (Figure 1). One study area, 4,518 hectares in size, is in the northeast portion of GNP in the Many Glacier valley, approximately 18 km (11 miles) northwest of the town of Saint Mary. The other study area, 6,276 hectares in size, is in the southeast portion of GNP in the Two Medicine valley, approximately 10 km (6 miles) west-northwest of the town of East Glacier. The two study areas are separated by approximately 37 km (23 miles). The Many Glacier study area is comprised of Mount Henkel, Altyn Peak, and Apikuni Mountain, plus portions of Allen Mountain, Grinnell Point, and Mount Wilbur, and part of the Swiftcurrent Creek valley bottom, and ranges in elevation from 1,480-2,775 m (4,855-9,105 ft) (Figure 2). The Two Medicine study area is comprised of Spot Mountain, Scenic Point, and Bison Mountain, plus portions of Mount Henry, Appistoki Peak, Red Mountain, and Rising Wolf Mountain, and part of the Two Medicine Creek valley bottom, and ranges in elevation from 1,575-2,830 m (5,168-9,285 ft) (Figure 3).

### Climate

Glacier National Park's climate is transitional between northern maritime and northern continental, and is influenced by Pacific storm systems from the west and by arctic air masses from the north (Finklin 1986). Most of the moisture from Pacific storms falls west of the Continental Divide, while cold arctic air masses moving south from continental Canada typically remain east of the Continental Divide. As a result the east side of the park is typically drier and cooler than the west side. On average, January is the coldest month, with a mean minimum temperature of –14 C$^{O}$ (7 F$^{O}$) in the Saint Mary and East Glacier townsites, and –11 C$^{O}$ (12 F$^{O}$) in the West Glacier townsite (Finklin 1986). The mean maximum temperature in July, the warmest month, is 23 C$^{O}$ (74 F$^{O}$) in Saint Mary and East Glacier, and 26 C$^{O}$ (78 F$^{O}$) in West Glacier (Finklin 1986). While temperatures generally decrease with gains in elevation, temperature inversions (in which valley temperatures are cooler than high-elevation temperatures) frequently occur during summer nights and winter days.

While annual precipitation on the east and west sides of the park is similar, precipitation levels generally decrease from south to north. East of the Continental Divide, East Glacier receives an average of 76 cm (31 in) of annual precipitation and Lake Sherburne, just east of Many Glacier, receives an average of 59 cm (23 in) of annual precipitation (Finklin 1986). About half of this annual precipitation falls as snow between November and March.

Compared to the lower elevations west of the Continental Divide, the park's east side receives more sunshine and higher winds, with exceptionally strong, warm (chinook) winds occurring in winter and spring. Prevailing wind direction is from the west to southwest. Because of warmer, less windy winters and cloudier, more humid summers, the west side of the park provides a more temperate climate for vegetation. Severe temperature fluctuations on the park's east side are especially detrimental to woody plants with living tissue above ground (Lesica 2002).

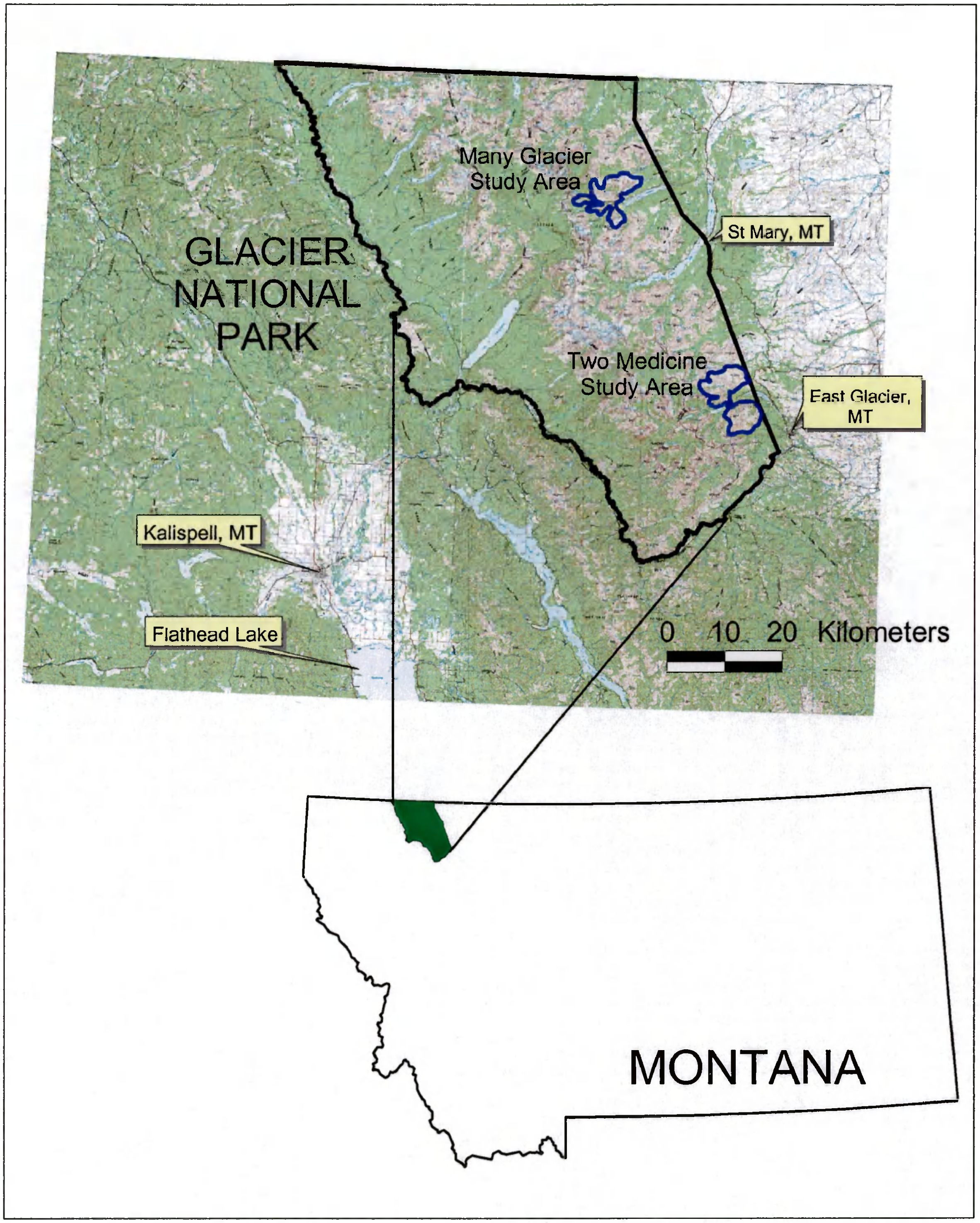

Figure 1. Overview of study areas in Glacier National Park, which is located in northwest Montana near the city of Kalispell.

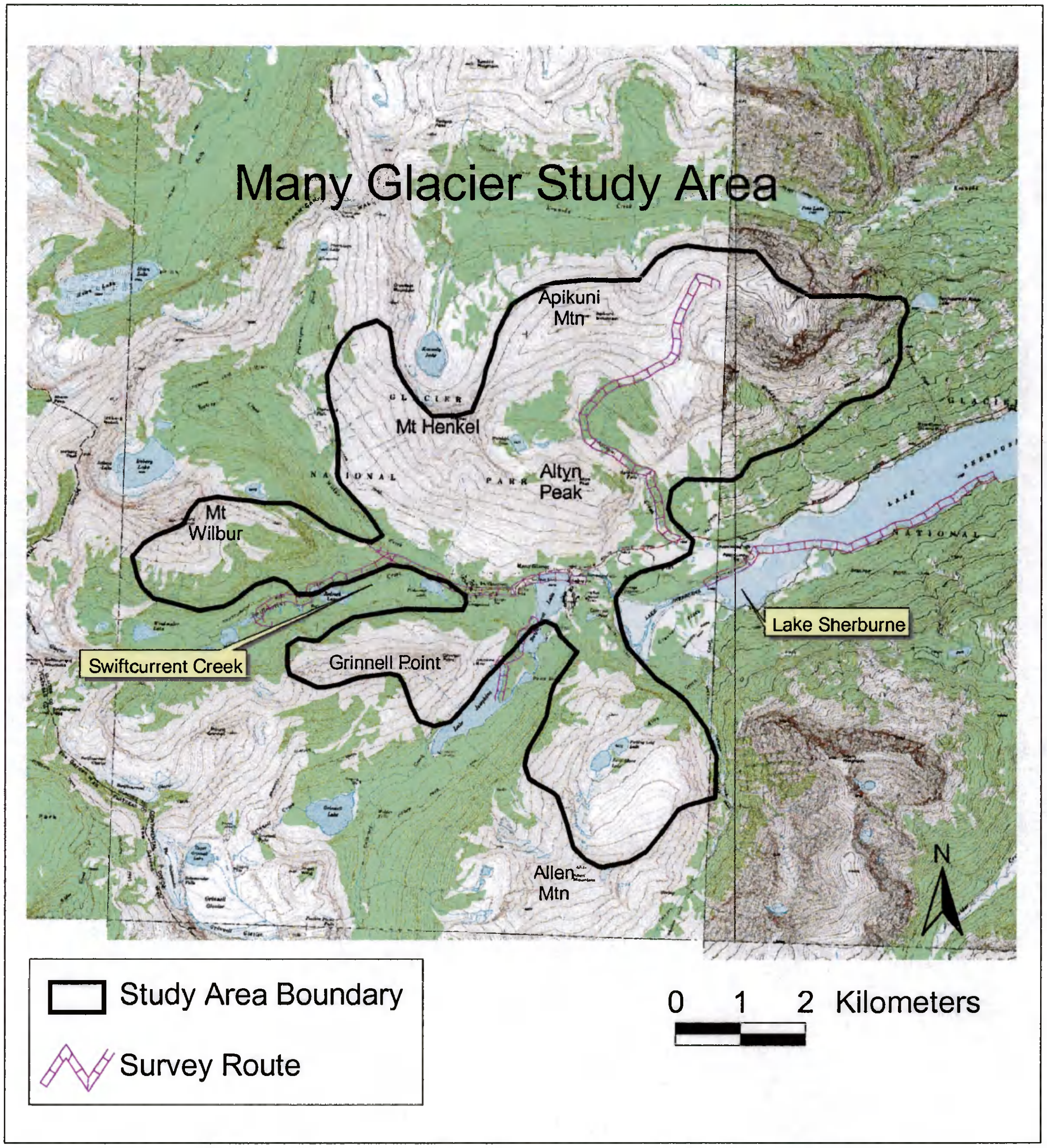

Figure 2. Detailed view of the Many Glacier study area in Glacier National Park, Montana.

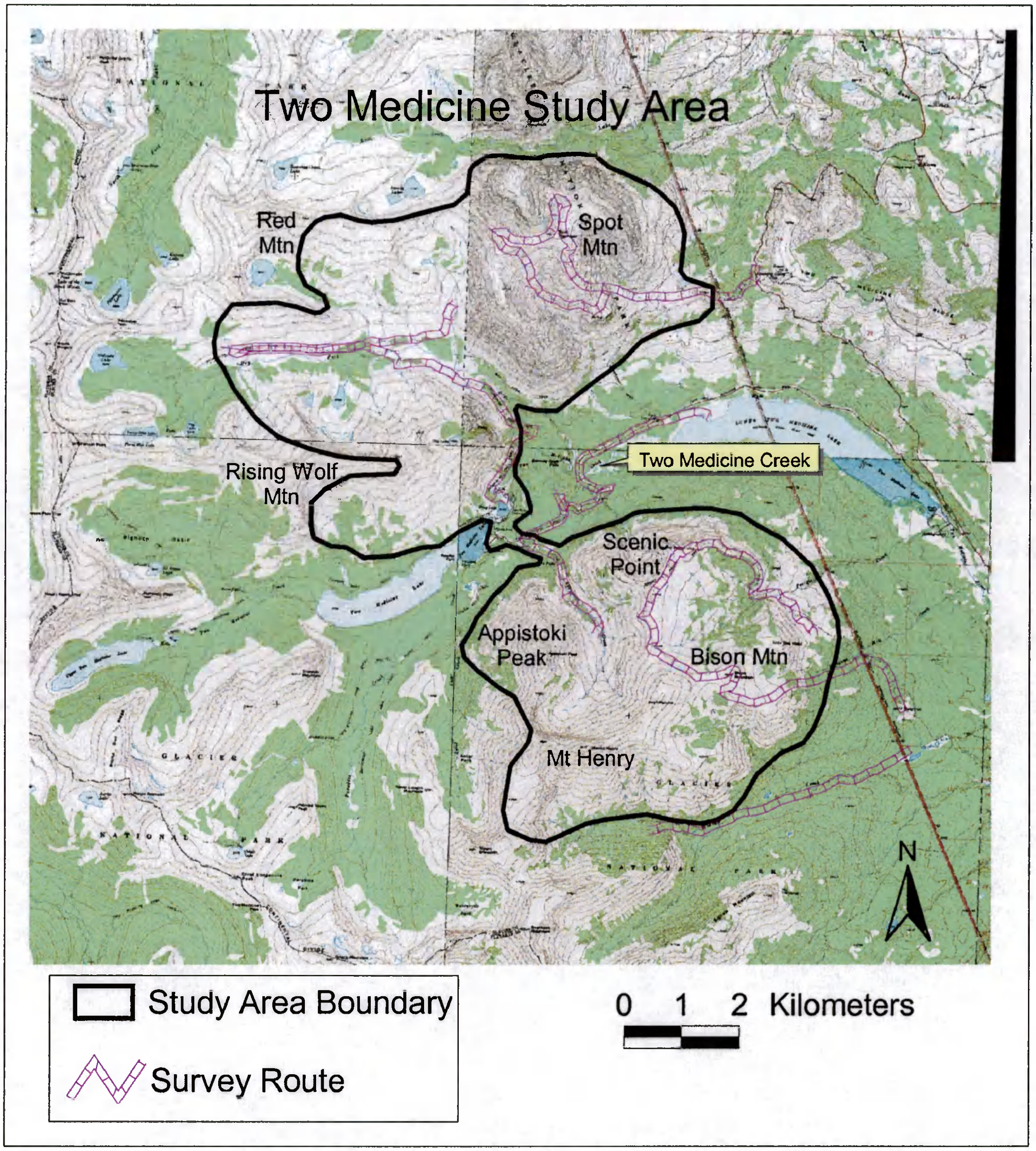

Figure 3. Detailed view of the Two Medicine study area in Glacier National Park, Montana.

## Geology

The geologic formations in Glacier National Park (GNP) are made up primarily of limestone and dolomite sedimentary rocks of the Belt Series (800 million to over 1 billion years old), with 70-100 million year old deposits of shaly mudstones (Raupp et al. 1983). These ancient sedimentary rock formations went through overthrust uplifting 65-70 million years ago. Evidence of this folding and uplifting is visible along the many sheer mountain faces, as is evidence of minor intrusions of igneous rock. GNP was almost entirely covered by huge valley glaciers during the last ice age, and the mountains and valleys display ample evidence of the carving action of ice and water. The massive lateral and terminal moraines left behind by the last ice age are responsible for the many long finger lakes found in the park. The 40 or so glaciers currently remaining in the park have been shrinking for the past 150 years, and their role as sources of disturbance to vegetation and soil has been taken over by spring snowmelt run-off, avalanches, rock slides, and wind (Lesica 2002).

## Fire History

Although GNP's east side has not experienced a large-scale fire since 1936, presettlement fires occurred frequently and were a major force controlling vegetative succession and landscape diversity (Barrett 1997). The strong winds common along the East Front influence fire regimes by contributing to dead fuel loading (from blowdowns and winter kill), desiccating fuels during the summer fire season, stunting tree growth (making the tree canopy more susceptible to fire), and accelerating fire spread (Barrett 1997). Furthermore, occasional extreme fire weather can cause stand replacement fires irrespective of stand age, elevation, aspect or terrain shape (Johnson and Wowchuck 1993). While organized fire suppression efforts began around the turn of the 20th century, they did not become truly effective until about 1940 (Arno 1980). The fire suppression efforts since 1940 have significantly increased the fire interval and prevented numerous fires that would have occurred in grassland, aspen (*Populus tremuloides*) and coniferous forest habitats under more natural conditions (Barrett 1997). Prior to 1940, small to moderate size fires were common and spread in disjunct patterns, resulting in an average stand size of less than 20 hectares for both single- and multi-age forest stands (Barrett 1997).

Lightning ignition of fires is rare on GNP's east side, and even most pre-1900 fires were likely started by humans; indeed, Native Americans throughout the region are known to have commonly ignited fires in grasslands and forests (Barrett and Arno 1982). Between 1700 and 1940, fire intervals ranged from 1-40 years, and the mean fire interval was 10 years while the fire cycle (the time required to burn an area equal in size to the entire study area) was 200 years (Barrett 1993, Barrett 1997). The current 60 year long fire interval is unprecedented and is causing the forest mosaic to age more uniformly, which may decrease spatial and compositional diversity (Romme and Knight 1982). Fire suppression may be allowing conifers to encroach into previously unforested terrain along GNP's east side, as well as exacerbating stand decadence caused by insects, blister rust (*Chronartium ribicola*), root rots and windfall (Barrett 1997). As fuel loads accumulate, these alterations to landscape succession may contribute to larger and more intense wildfires.

## Vegetation

Glacier National Park (GNP) hosts a rich diversity of vegetation. This diversity is due primarily to GNP's large elevation gradient, which results in vegetation changes comparable to the changes encountered when traveling north in the Northern Hemisphere at a fixed elevation. Lesica (2002) identified three life zones in GNP -- the Montane, Subalpine, and Alpine Zones. These life zones are roughly delineated by elevation: the Montane Zone occurs between 915-1,675 m (3,000-5,500 ft); the Subalpine Zone occurs between 1,525-2,285 m (5,000-7,500 ft); and the Alpine zone occurs above 1,980 m (6,500 ft). The following vegetative description is taken largely from A Flora of Glacier National Park, Montana (Lesica 2002).

The Montane Zone along GNP's east side typically hosts extensive aspen forests whose sparse canopies promote a lush understory of shrubs and tall forbs and grasses; wetter sites often support black cottonwood (*Populus trichocarpa*). Grasslands, which occur in a broad band within the Montane and Subalpine Zones along GNP's east side, 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. Although exotic plants and noxious weeds are a concern within GNP's grasslands, they currently have very limited distribution across bighorn sheep habitats. Forests of the Subalpine Zone are the most common habitat in GNP and 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*), western larch (*Larix occidentalis*) and white pine (*Pinus monticola*), while higher subalpine forests may hold whitebark pine (*Pinus albicaulis*). In many areas along

GNP's east side, lower subalpine forests extend down to valley bottoms, except on warm slopes that tend to support grasslands. 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. Within the Subalpine Zone, fire has influenced forest composition and structure, resulting in extensive lodgepole pine stands on gentle, warm slopes and extensive brush fields on steep, warm slopes. Infrequent fires at higher elevations within the Subalpine Zone are important in maintaining whitebark pine stands. Also instrumental in shaping subalpine forests are disease and insects. Finally, 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.

Although nearly one-third of GNP is above treeline, the Alpine Zone 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. Finally, talus and scree slopes are common in the Alpine Zone. On these steep slopes, rocks and sparse soil is constantly shifting downhill; plant cover is very sparse, with alpine dryad and some forbs managing to take hold.

# METHODS

## Ground Surveys

Ten systematic survey routes (see Figures 2 and 3) were established on Glacier National Park's two primary bighorn sheep winter ranges, the Many Glacier and Two Medicine valleys. Each route was surveyed once every 12-16 days during January - April of 2000 and 2001. Also, during May - June of 2000 and 2001, surveys for lambing areas were conducted in both valleys. Survey routes followed ridgelines and valley bottoms, using vantage points to scan for sheep with binoculars and spotting scopes. Each winter range was broken into survey areas on the basis of topography and vantage point perspectives, and each survey area received survey effort proportionate to its size, ruggedness and vegetation density. Bighorn sheep groups were 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 20-25 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 one 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 one to three 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. A standardized data form (Appendix A) was used to record group size, sex/age composition, activity, and landscape cover type for all sheep group locations. Bighorn sheep were observed with 10x binoculars and 15-

45x spotting scopes, and all sheep group locations were mapped on 7.5-minute USGS quadrangle maps.

## Fecal Pellet Sampling

At least once a month during mid- to late-winter (January through March), composite fecal pellet samples were collected by sub-sampling one or two fecal pellets from each of 10-15 fresh pellet groups. Composite samples were collected only from observed bighorn sheep groups, with separate samples collected from high-elevation and low-elevation sites. Samples were kept frozen until shipped to the lab. Lab analysis (performed by Washington State University's Wildlife Habitat Nutrition Laboratory) involved oven drying and grinding of fecal pellets, followed by the Kjeldahl analysis method to determine percent fecal nitrogen and fecal diaminopimelic acid (DAPA) content (Hodgman et al. 1996). Fecal nitrogen has been shown to be positively correlated with forage intake, dietary protein, and digestibility (Hebert and Lake 1986, Irwin et al. 1993, Kucera 1997). Fecal levels of DAPA, a component of the cell walls of rumen bacteria, serve as an index of rumen bacterial population levels and thus of the intake of digestible energy (Kucera 1997). For all composite fecal samples, three replicates of fecal nitrogen analysis were conducted. Due to budget constraints, only a single DAPA analysis was conducted for each composite fecal sample.

Diet composition was estimated through microhistological analysis, which involved identification of plant fragments viewed at 100X magnification, with 150 fields of view examined for each sample (Kasworm et al. 1984, Wikeem and Pitt 1992). Although microhistological analysis may overestimate graminoid and underestimate forb portions of diets, the technique generally yields accurate rankings of dietary components (Wikeem and Pitt 1992).

## GIS Data Layers

Geographic Information System (GIS) software packages are powerful tools useful for spatial analysis of habitat structure and configuration across a landscape. Much recent bighorn sheep habitat modeling work has taken advantage of the overlay capabilities and proximity functions of GIS packages (Smith et al. 1991, Johnson 1995, Schirokauer 1996, Sweanor et al. 1996). To facilitate the construction and validation of winter range habitat models on my two study areas, I superimposed a grid of 30-by-30 m cells over each study area. The Many Glacier study area contained 50,196 of these 900 $m^2$ cells, while the Two Medicine study area contained 69,736 cells. To each cell, I assigned values for each of 14 habitat parameters (Table 2) identified as potentially important components of bighorn sheep habitat (Haas 1991, Smith et al. 1991, McCarty 1993, Johnson 1995, Sweanor et al. 1996).

### *Digital Elevation Models and Digital Line Graphs*

Digital elevation model (DEM) data are arrays of elevation values referenced to a geographic coordinate system such as a Universal Transverse Mercator (UTM) projection. DEM data consists of a grid of cells spaced at regular intervals, with each cell assigned an elevation value; they are produced by and available from the U.S. Geological Survey (USGS). 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

**Table 2. Habitat parameters for bighorn sheep winter range habitat models.**

Habitat parameters used for evaluating bighorn sheep winter range habitat in the Many Glacier and Two Medicine study areas. Sources of information for each habitat parameter are also shown.

| Habitat Parameter | Source |
|---|---|
| *Continuous Variables* | |
| Slope (%) | USGS digital elevation model |
| Aspect (°) - 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 |
| Succulent vegetation density index | Satellite imagery – spectral reflectance "greenness" |
| Vegetation moisture index | Satellite imagery – spectral reflectance "brightness" |
| *Categorical Variables* | |
| Mid-winter snow cover (Y/N) | Satellite imagery – band 3 & 5 reflectance ratio |
| Land cover type classification | Satellite imagery – reflectance classification categories |

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, Johnson and Swift 1999). Another product available from the USGS is the digital line graph, an array of regularly spaced grid cells depicting linear features such as streams and roads.

I used Arc View GIS software to derive several habitat parameter values from a 7.5-minute DEM coverage of Glacier National Park. I derived slope, aspect, and elevation values so that 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 (Yes) or not meeting (No) escape terrain criteria. This escape terrain designation layer than allowed me to use an Arc View proximity function to generate a theme layer in which each cell was assigned a distance-to-escape-terrain value. I performed a similar operation using 7.5-minute digital line graphs, which allowed me to assign a distance-to-water value to each cell in the study areas.

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 degrees, 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 the aspect of each grid cell into modeling regression techniques. The traditional measure of aspect (0-360 degrees) 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 degree scale) for a given cell (Beers et al. 1966). Within the resulting range (0-2000) of *TAsp* values, a southwest aspect had a value near zero, a southeast and northwest aspect had a value around 1,000 and a northeast aspect had a value near 2,000.

### *Digital Raster Graphic Topographic Maps*

The USGS also produces digital versions of topographic maps. Again, these are arrays of grid cells 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 GNP data 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 image data from the Landsat satellite series. These TM images are arrays of regularly spaced grid cells containing values for light wavelength irradiance, with grid cells referenced to a geographic coordinate system. Each grid cell contains a radiance value for each of seven 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 seven 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 (irradiance) 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 irradiance for each wavelength band ($I_b$), and the slope ($s_i$) and aspect ($a_i$) for each 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 six wavelength bands (bands 1-5 and band 7) for both an early spring (May 23, 1999) TM image and a mid 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). To explore other potentially useful numerical variables derived from satellite imagery, I used the same six wavelength bands from these two TM images to calculate "greenness" and "brightness" through the tasseled cap transformation (Crist and Cicone 1984). Mace et al. (1998) found "greenness" (an index to succulent vegetation density) and "brightness" (an index to vegetation moisture content) useful in modeling grizzly bear (*Ursus horribilis*) habitat. Finally, I used a TM image classification completed by USGS personnel at the Glacier Field Station to assign one of eight land cover types (Table 3) to each 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 vegetation types (Carl Key, USGS, personal communication).

Most researchers modeling bighorn sheep habitat have specified that suitable winter range habitat must be relatively snowfree; Smith et al. (1991) defined suitable winter range, in part, as areas with snow depths of less than 25 cm (10 in). 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 two TM images, one from April 1, 1992 and one

**Table 3. Land cover type categories from a USGS satellite image classification.**

Eight land cover type categories identified in a USGS classification of Thematic Mapper satellite imagery for Glacier National Park, Montana, were applied to the Many Glacier and Two Medicine study areas. Associated percentages of horizontal visibility at 30 m were determined through field sampling.

| 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 |

from 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), a lack of recent snowfall immediately proceeding their date of data capture, and their appropriateness for discerning the snowpack extent in late winter and in early spring. 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 snowfree value (No) to each grid cell.

### *Horizontal Visibility*

Horizontal visibility is a critical component of bighorn sheep habitat because it allows early detection of predators so that sheep may retreat to escape terrain (Geist 1971, Risenhoover and Bailey 1980, Krausman 1997). While bighorn sheep generally prefer open habitats, they will use open forest stands that are close to escape terrain (Geist 1971, Shannon et al. 1975, Tilton and Willard 1982). To characterize horizontal visibility on my two study areas, I assigned visibility values to land cover types identified in a USGS classification of a Thematic Mapper satellite image (see Table 3). At least ten transects were sampled in each land cover type, then every grid cell within each study area was assigned a horizontal visibility (averaged to the nearest 10%) on the basis of its land cover type designation. Field measurements of horizontal visibility were made along 40 m transects at representative sites in each land cover type on both study areas; at 10 m intervals along each transect, visibility percentages were estimated in four cardinal directions. I estimated visibility percentages by estimating what percentage of a field assistant (assuming the posture of a bighorn sheep) was visible at a distance of 30 m.

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 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 14 explanatory (or independent) variables (Table 2) were selected on the basis of a bighorn sheep habitat model literature review and consultation with professionals involved with 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 value 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 probability of an event not occurring is simply

$$\text{Prob(sheep absent)} = 1 - \text{Prob (sheep present)}.$$

A plot of the expected probabilities against the "logit" (the equation containing the explanatory variables and their coefficients, shown as Z above) takes on the characteristic S-shaped logistic curve. The expected probability value is on a scale of 0 to 1, and can be interpreted as the probability that the response variable will equal 0 or 1 given the set of explanatory variable values. 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 straight-forward than in linear regression. In logistic regression, the coefficient for a given explanatory variable indicates the change in the odds ratio for a one-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, which can be written as: Prob(event)/(1 – Prob(event)). The log of the odds ratio (the logit), as mentioned above, 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 coefficient 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). The LR test is computationally intensive as it estimates the logistic regression model with each variable eliminated in turn in order to compare the log-likelihood of the reduced model (without a given variable) to the log-likelihood of the full model (with all variables). The LR test statistic value is obtained by dividing the log-likelihood of the reduced model by the log-likelihood of the full model. Typically, when constructing a model, a test statistic significance level is established as the basis for including a variable (in a forward stepwise selection process) or removing a variable (in a backward stepwise selection process).

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 a model 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 one or more candidate 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. In regression analyses, residuals represent the difference between predicted values and observed values. In logistic regression, a model's overall deviance (i.e., the –2LL value discussed earlier) is equal to the sum of the squared deviance residuals. If no pattern is seen in a scatterplot of a continuous explanatory variable against the deviance residuals, 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 likelihood ratio 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 (greater than 0.2 and greater than 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, Frid 2000).

Candidate model goodness-of-fit was assessed using a Chi-square statistic and Akaike's information-theory criteria (AIC) statistic (Movsas et al. 1997, Boyce et al. 2001). Because a logistic regression model's expected response variable values are probabilities while observed values are either 0 or 1, a traditional Chi-square goodness-of-fit test performs poorly. For example, given a classification cut-off value of 0.5, expected response values of 0.01 and 0.49 both result in the response variable being classified as a 0 for each set of explanatory variable values. A Chi-square test, which would compare the expected value classifications of 0 to observed values of 0, can not distinguish between the unambiguous response value of 0.01 and the ambiguous response value of 0.49. Hosmer and Lemeshow (1989) developed a partial solution to this problem by grouping the response variable expected probabilities into ten groups (e.g., 0-0.09, 0.1-0.19, 0.2-0.29, etc.), which allows an assessment of the logistic regression model's performance across the full range of expected response values. Compared to a traditional Chi-square goodness-of-fit test, the Hosmer and Lemeshow goodness-of-fit test has greater sensitivity in evaluating where, across the range of expected response variable values, miss-classifications are occurring. Like a traditional Chi-square test, a large Hosmer and Lemeshow Chi-square test statistic value results in a low significance value, reflecting the low probability of that outcome – this is not a desirable logistic regression model output. The better a model performs, the more closely the expected response variable values match observed response variable values – that is, the higher the outcome probability. Therefore, a small Hosmer and Lemeshow Chi-square test statistic value and a large significance value indicate a well-fit model. With logistic regression, Akaike's information-theory criteria (AIC) statistic is calculated simply as –2LL + 2*K, where K is the number of explanatory variables in the model (Movsas et al. 1997, 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 – i.e., either an entirely new set of data, or a subset of the original data that was withheld during model construction. 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 application.

# RESULTS

## Ground Surveys

I observed bighorn sheep during 480 observation sessions conducted over the course of two winters (Jan-Apr of 2000 and 2001). Observation sessions occurred at vantage points along ten survey routes (see Figures 2 and 3), averaged 39 minutes in duration (range of 20-330 minutes), and amounted to 316.7 hours of total observation time. Within the Many Glacier study area, 246 observation sessions were completed, with 592 sheep group locations mapped. The average bighorn sheep group size observed at Many Glacier was 7.1 (range of 1-57 sheep). Within the Two Medicine study area, 234 observation sessions were completed, with 469 sheep group locations mapped. The average bighorn sheep group size observed at Two Medicine was 5.6 (range of 1-42 sheep). Over the course of two springs (May-Jun 2000 and 2001), 143 observation sessions were completed, with an average duration of 44 minutes (range of 20-170 minutes), and amounting to 100.9 hours of observation. Within the Many Glacier study area, 125 observation sessions were completed, with 206 sheep group locations mapped. The average group size observed at Many Glacier during spring was 6.8 sheep (range of 1-55). Within the Two Medicine study area, 18 observation sessions were completed, with 42 sheep group locations mapped. The average group size observed at Two Medicine during spring was 6.4 sheep (range of 1-28).

From the winter (Jan-Apr) observation sessions, an analysis of unduplicated sheep counts indicated a minimum of 85 sheep on the Many Glacier winter range, and a minimum of 185 sheep on the Two Medicine winter range. At Many Glacier, sex/age ratios were 133 rams per 100 ewes, and 59 lambs per 100 ewes. At Two Medicine, there were 122 rams per 100 ewes, and 46 lambs per 100 ewes.

Focal observations involved tracking the movements of a recognizable individual over the course of at least one full day and sometimes up to three 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). Eight of the focal observations were conducted in the Many Glacier study area; of these, 3 lasted one day, 2 lasted two days, and 3 lasted three days (Figure 4). Twelve of the focal observations were conducted in the Two Medicine study area; of these, 7 lasted one day, 4 lasted two days, and 1 lasted three days (Figure 4). 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.

All bighorn sheep location data were entered into a Microsoft Access database. Each location point represented the center of a bighorn sheep group (group size ranged from 1-57 sheep). To depict bighorn sheep habitat use in a grid cell layer, I used ArcView GIS software to create a 35 m buffer around sheep 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 twelve 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

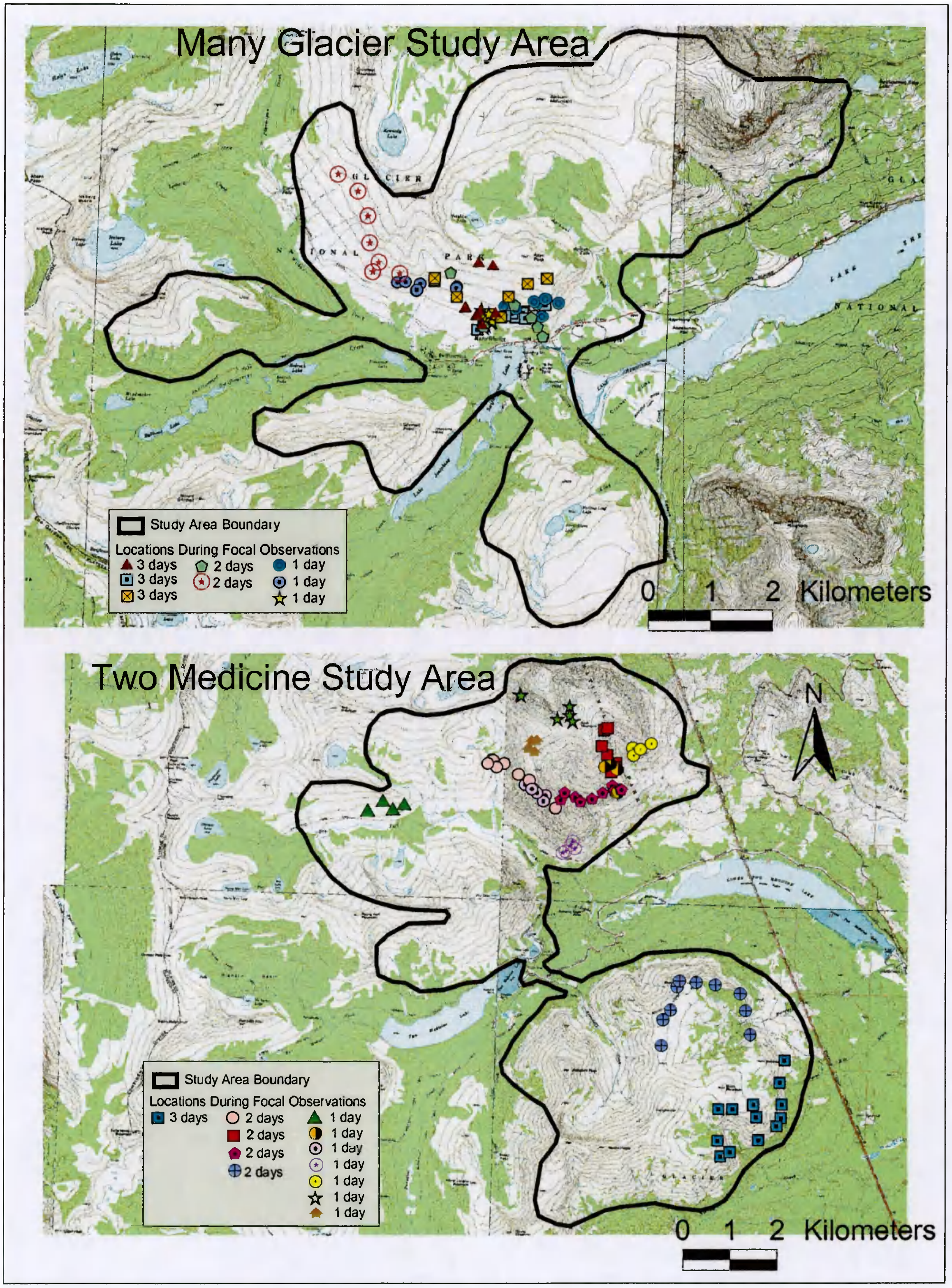

Figure 4. Locations of bighorn sheep groups followed during 1-3 day focal observation sessions conducted during winter in the Many Glacier (top) and Two Medicine (bottom) study areas.

was discernable, and given the proportional application of survey effort relative to the size, ruggedness and vegetation density of each survey area, the assumption that all sheep groups had equal probability of detection appeared to have been satisfied.

### Fecal Pellet Sampling

Eleven composite fecal samples were collected, seven from the Two Medicine study area and four from the Many Glacier study area, and analyzed for levels of fecal nitrogen (FN) and diaminopimelic acid (DAPA) (Table 4). Among the Two Medicine samples, four were collected at high elevations (2,280-2,800 m) while three were collected at low elevations (1,620-2,130 m). All four of the Many Glacier samples were collected at low elevations (1,500-2,000 m). For the 12 replicates from 4 composite fecal samples collected at Many Glacier, the average FN content was 1.617%. The 12 replicates from 4 high elevation Two Medicine composite fecal samples resulted in an average FN content of 1.685%, and the 9 replicates from 3 low elevation Two Medicine composite samples gave an average FN content of 1.693%. I found no significant differences among FN values from the three collection areas revealed by *t* statistic tests for independent samples.

Lab analysis from 4 low elevation Many Glacier samples, 3 low elevation Two Medicine samples, and 4 high elevation Two Medicine samples resulted in average DAPA levels of 0.294 mg/g, 0.400 mg/g and 0.288 mg/g, respectively. The low elevation Two Medicine DAPA values were larger than either the low elevation Many Glacier DAPA values ($t = 7.145$, 5 df, $p = 0.001$) or the high elevation Two Medicine DAPA values ($t = 3.149$, 5 df, $p = 0.025$).

Six fecal samples from the Two Medicine study area and 4 from the Many Glacier study area were analyzed for diet components. At Two Medicine, bighorn sheep diets consisted, on average, of 43.8% grasses, 29.9% forbs, 16.1% sedges/rushes, 6.5% shrubs, 2.6% trees, and 1.1% mosses. At Many Glacier, bighorn sheep diets consisted, on average, of 48.0% grasses, 24.6% sedges/rushes, 15.4% forbs, 5.2% shrubs, 5.4% mosses, 1.2% trees, and 0.2% lichens. A complete list of forage species and estimated percentages for each composite fecal sample is presented in Appendix B.

### 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 – that is, all Hosmer and Lemeshow Chi-square test statistic values had very small significance values and all AIC values were quite large (Tables 5 and 6). 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, Frid 2000). 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

**Table 4. Fecal nitrogen and diaminopimelic acid levels in sheep fecal pellets.**

Bighorn sheep fecal pellets collected during winter on the Two Medicine (TM) and Many Glacier (MG) study areas were analyzed for fecal nitrogen (FN, in percent content) and diaminopimelic acid (DAPA, in milligrams per gram). Elevation class refers to whether the composite pellet sample was collected at low or high elevation.

| **Sample I.D.** | **Average FN (%)** (Replicates = 3) | **DAPA (mg/g)** (Replicates = 1) | **Elevation Class** |
|---|---|---|---|
| TM1 | 1.680 | 0.2611 | High elev. |
| TM2 | 1.903 | 0.2641 | High elev. |
| TM3 | 1.527 | 0.2551 | High elev. |
| TM4 | 1.630 | 0.3711 | High elev. |
| TM5 | 1.813 | 0.3701 | Low elev. |
| TM6 | 1.630 | 0.4251 | Low elev. |
| TM7 | 1.637 | 0.4041 | Low elev. |
| MG1 | 1.517 | 0.2801 | Low elev. |
| MG2 | 1.540 | 0.2931 | Low elev. |
| MG3 | 1.693 | 0.3051 | Low elev. |
| MG4 | 1.719 | 0.2981 | Low elev. |

**Table 5. Goodness-of-fit measures for Two Medicine candidate models.**

The set of logistic regression candidate models developed for the Two Medicine study area were evaluated for goodness-of-fit using Akaike's information-theory criteria (AIC) and Hosmer and Lemeshow Chi-square test statistics. Ranking of models was based primarily on AIC values.

| Rank | Model | HL Chi-Sq[a] | AIC[b] | Explanatory Variables[c] |
|---|---|---|---|---|
| 1 | TM1<br>W/ C[d] | 140.774 | 23,684 | DistEscp, DistStock, SnowCovr, Slope, TAspect, LandTyp (8 cat), 99Band2 |
| 2 | TM2<br>W/ C | 124.240 | 23,687 | DistEscp, DistStock, SnowCovr, Slope, TAspect, LandTyp (8 cat) |
| 3 | TM3<br>W/ C | 31.616 | 24,120 | DistEscp, SnowCovr, Slope, TAspect, LandTyp (8 cat), 99Band2 |
| 4 | TM4<br>W/ C | 31.616 | 24,124 | DistEscp, SnowCovr, SolarNdx, Slope, TAspect, LandTyp (8 cat) |
| 5 | TM5<br>No C[e] | 29.262 | 24,138 | DistEscp, SnowCovr, SolarNdx, Slope, TAspect, LandTyp (8 cat), 99Band2 |
| 6 | TM6<br>No C | 27.447 | 24,185 | DistEscp, SnowCovr, Slope, TAspect, LandTyp (8 cat), 99Band2 |
| 7 | TM7<br>W/ C | 97.540 | 24,125 | DistEscp, SnowCovr, Slope, TAspect, LandTyp (8 cat) |
| 8 | TM8<br>No C | 33.893 | 24,148 | DistEscp, SnowCovr, SolarNdx, Slope, LandTyp (8 cat), 99Band2 |
| 9 | TM9<br>No C | 35.292 | 24,140 | DistEscp, SnowCovr, SolarNdx, Slope, TAspect, LandTyp (8 cat) |
| 10 | TM10<br>W/ C | 33.216 | 24,150 | DistEscp, SnowCovr, SolarNdx, Slope, LandTyp (8 cat) |

**a** – Hosmer and Lemeshow Chi-square test statistic. For all models here, degrees of freedom = 8 and $p < 0.0005$.

**b** – Akaike's information-theory criteria statistic (= -2LL + 2(# explanatory variables)).

**c** – Explanatory (or dependent) variables: DistEscp = distance to escape terrain; DistStock = distance to livestock grazing allotment; SnowCovr = snow cover category (either snow bound or snowfree); SolarNdx = index of solar radiation (derived from slope and aspect); Slope = slope angle; TAspect = transformed aspect; LandTyp = land cover type classification (based on 8 categories of a satellite image classification); 99Band2 = wavelength band 2 reflectance values (determined from a Thematic Mapper satellite image).

**d** – indicates that regression equation includes a constant.

**e** – indicates that regression equation contains no constant.

**Table 6. Goodness-of-fit measures for Many Glacier candidate models.**

The set of logistic regression candidate models developed for the Many Glacier study area were evaluated for goodness-of-fit using Akaike's information-theory criteria (AIC) and Hosmer and Lemeshow Chi-square test statistics. Ranking of models was based primarily on AIC values.

| Rank | Model | HL Chi-Sq[a] | AIC[b] | Explanatory Variables[c] |
|---|---|---|---|---|
| 1 | MG1 W/ C[d] | 156.174 | 10,621 | DistEscp, DistDvlp, SnowCovr, SolarNdx, Slope, TAspect, LandTyp (8 cat) |
| 2 | MG2 W/ C | 146.564 | 10,629 | DistEscp, DistDvlp, SnowCovr, Slope, TAspect, LandTyp (8 cat) |
| 3 | MG3 W/ C | 168.640 | 10,908 | DistEscp, DistDvlp, SnowCovr, SolarNdx, Slope, LandTyp (8 cat) |
| 4 | MG4 No C[e] | 196.575 | 10,925 | DistEscp, DistDvlp, SnowCovr, SolarNdx, Slope, TAspect, LandTyp (8 cat) |
| 5 | MG5 No C | 214.776 | 10,997 | DistEscp, DistDvlp, SnowCovr, SolarNdx, Slope, LandTyp (8 cat) |
| 6 | MG6 W/ C | 101.480 | 12,433 | DistEscp, SnowCovr, SolarNdx, Slope, TAspect, LandTyp (8 cat) |
| 7 | MG7 No C | 166.485 | 12,445 | DistEscp, SnowCovr, SolarNdx, Slope, TAspect, LandTyp (8 cat) |
| 8 | MG8 W/ C | 50.758 | 12,530 | DistEscp, SnowCovr, Slope, TAspect, LandTyp (8 cat) |
| 9 | MG9 W/ C | 186.727 | 12,576 | DistEscp, SnowCovr, SolarNdx, Slope, LandTyp (8 cat) |
| 10 | MG10 No C | 115.971 | 12,594 | DistEscp, SnowCovr, SolarNdx, Slope, LandTyp (8 cat) |

**a** – Hosmer and Lemeshow Chi-square test statistic. For all models here, degrees of freedom = 8 and $p < 0.00005$.

**b** – Akaike's information-theory criteria statistic (= -2LL + 2(# explanatory variables)).

**c** – Explanatory (or dependent) variables: DistEscp = distance to escape terrain; DistDvlp = distance to development (roads, buildings); SnowCovr = snow cover category (either snow bound or snowfree); SolarNdx = index of solar radiation (derived from slope and aspect); Slope = slope angle; TAspect = transformed aspect; LandTyp = land cover type classification (based on 8 categories of a satellite image classification).

**d** – indicates that regression equation includes a constant.

**e** – indicates that regression equation contains no constant.

contributed more significantly to model performance than did horizontal visibility. Because only 15% of the grid cells at each study area were classified as land cover types (dense conifer, open conifer, and deciduous tree/shrub) with horizontal visibility below 60%, when horizontal visibility was included in a model without the land cover type variable, it did not contribute significantly to that model's fit.

### 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). Likewise, 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 conducted validation tests and recorded the performance measures described above for the 10 candidate models from each study area (Table 7).

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 model from each study area was selected primarily on the basis of the validation tests, but model simplicity was also considered. Although the best Two Medicine model (see Table 7) included the transformed aspect variable, I chose to leave this variable out of the final model because it did not offer clear improvement to model performance, and because aspect is incorporated in the solar radiation index variable. Because there is potential for this final model to be applied at sites outside GNP where the user may not have access to a vegetation map or classified satellite imagery, I examined the effect of replacing the land cover type variable with two satellite reflectance variables in terms of validation test performance. I selected the two wavelength bands (bands 2 and 5) on the basis of likelihood-ratio 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, employing the winter range criteria described in Table 1, I conducted a validation test of the Smith model GIS application at both of my study areas. I compared the validation test performance of the Smith model application to that of my two final model versions (Table 8). 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 two reflectance variables, and both versions of my final model performed considerably better than the Smith model application. Given the availability of the GNP land cover type layer and its slightly better performance compared to the reflectance values, I focused on the land cover type version of the final model. A visual assessment of the extent of predicted winter range habitat use further conveys the superior performance of my final model in comparison to the Smith model application (Figures 5 and 6).

The values of the constant and coefficients for both versions of my final model are shown in Table 9. 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. Regression software programs automatically create these indicator, or "dummy" variables. The number of indicator variables required is one less than the number of categories in the explanatory variable because one category (either the first or the last) is represented by all zeros. As means of illustration, imagine a categorical variable with four categories. The software would create three indicator variables (I1, I2 and I3), which would allow the four categories to be represented as follows: category A is represented by I1=0, I2=0, I3=0; category B is represented as I1=1, I2=0, I3=0; category C is represented as I1=0, I2=1, I3=0; and category D is represented as I1=0, I2=0, I3=1. As explained in Table 9, I specified that

**Table 7. Validation test performance measures for candidate models.**

Logistic regression models developed at the Two Medicine study area were validated using survey results from the Many Glacier study area, and vice versa. Ranking of models was based on cross tabulations of observed versus predicted presence/absence of bighorn sheep within each sampling unit (a 900 $m^2$ grid cell). Group classification was based on a 0.13 probability cut-off value. Model names (TM1, MG1, TM2, etc.) correspond to model names in Tables 5 and 6.

| Rank | Model | Commission[a] | Omission[b] | Positive Comm[c] | Positive Ratio[d] |
|---|---|---|---|---|---|
| | | Two Medicine Models Validated at Many Glacier | | | |
| 1 | TM4 | 76.4% | 23.6% | 66% | 4.5 |
| 2 | TM3 | 75.5% | 24.5% | 66% | 4.7 |
| 3 | TM10 | 77.1% | 22.9% | 60% | 4.7 |
| 4 | TM6 | 76.1% | 23.9% | 50% | 5.4 |
| 5 | TM9 | 79.8% | 20.2% | 37% | 5.5 |
| 6 | TM5 | 80.0% | 20.0% | 36% | 5.5 |
| 7 | TM7 | 84.6% | 15.4% | 22% | 5.4 |
| 8 | TM8 | 79.0% | 21.0% | 33% | 6.2 |
| 9 | TM1 | 82.6% | 17.4% | 12% | 10.3 |
| 10 | TM2 | 90.6% | 9.4% | 1% | 8.9 |
| | | Many Glacier Models Validated at Two Medicine | | | |
| 1 | MG9 | 71.4% | 28.6% | 39% | 7.2 |
| 2 | MG6 | 73.1% | 26.9% | 34% | 7.3 |
| 3 | MG10 | 72.5% | 27.5% | 35% | 7.5 |
| 4 | MG7 | 74.8% | 25.2% | 30% | 7.5 |
| 5 | MG8 | 76.0% | 24.0% | 27% | 7.6 |
| 6 | MG2 | 84.8% | 15.2% | 7% | 11.0 |
| 7 | MG1 | 84.6% | 15.4% | 6% | 12.1 |
| 8 | MG4 | 82.9% | 17.1% | 7% | 13.0 |
| 9 | MG3 | 81.0% | 19.0% | 9% | 13.3 |
| 10 | MG5 | 85.2% | 14.8% | 2% | 30.6 |

**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.

**Table 8. Validation test performance measures for final and Smith models.**

Validation tests were conducted for two final models developed at Glacier National Park, Montana, and for the Smith model GIS application. For the two final models, group classification was based on a 0.13 probability cut-off value. The Smith model GIS application was taken from Sweanor et al. (1996).

| Test Area | Commission[a] | Omission[b] | Positive Comm[c] | Positive Ratio[d] |
|---|---|---|---|---|
| | | Final 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 |
| | | Final 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.

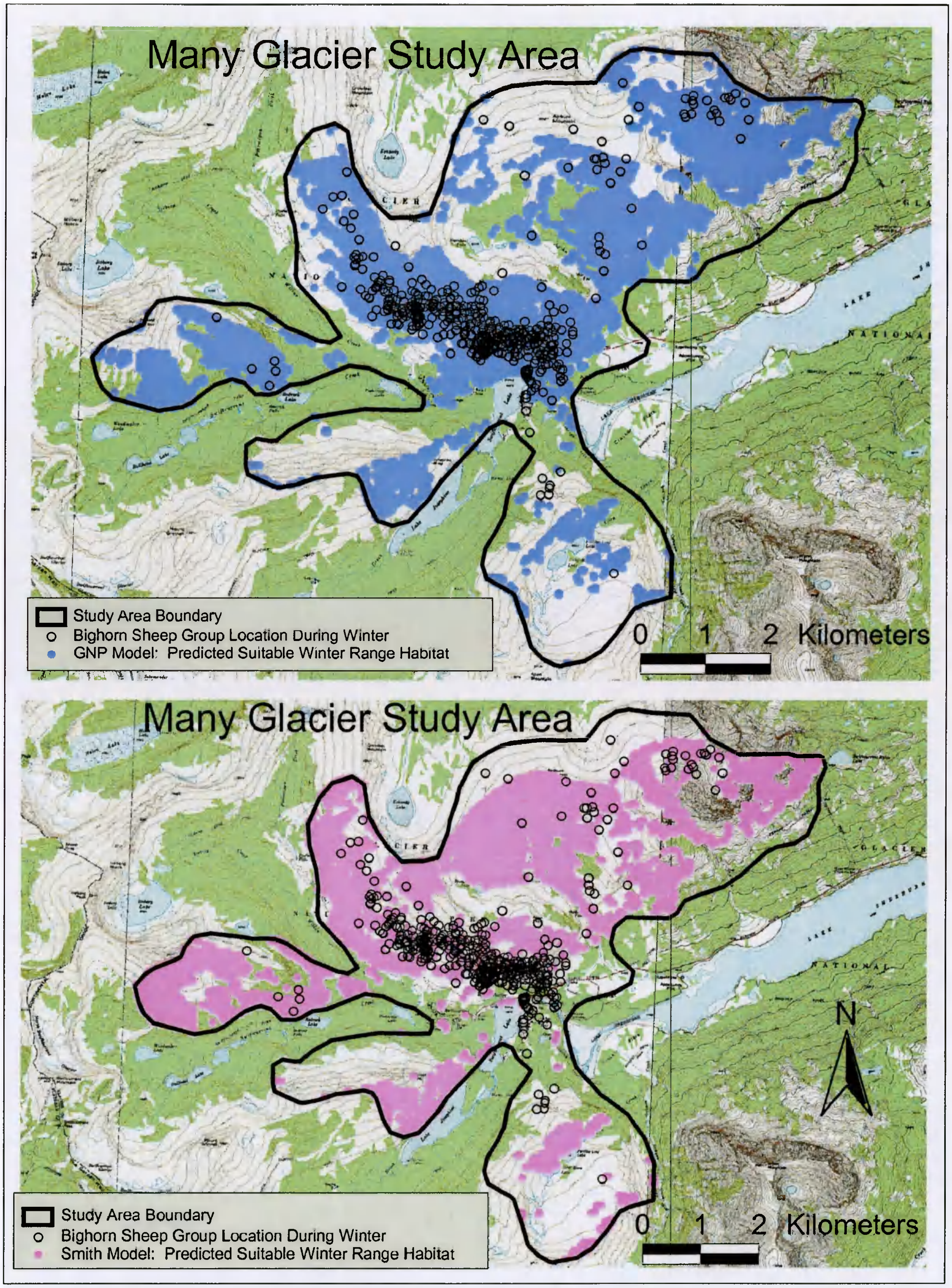

Figure 5. The extent of suitable winter range habitat within the Many Glacier study area as predicted by a model developed in Glacier National Park (top) and by a GIS application of the Smith model (bottom). Bighorn sheep group locations during winter are also shown.

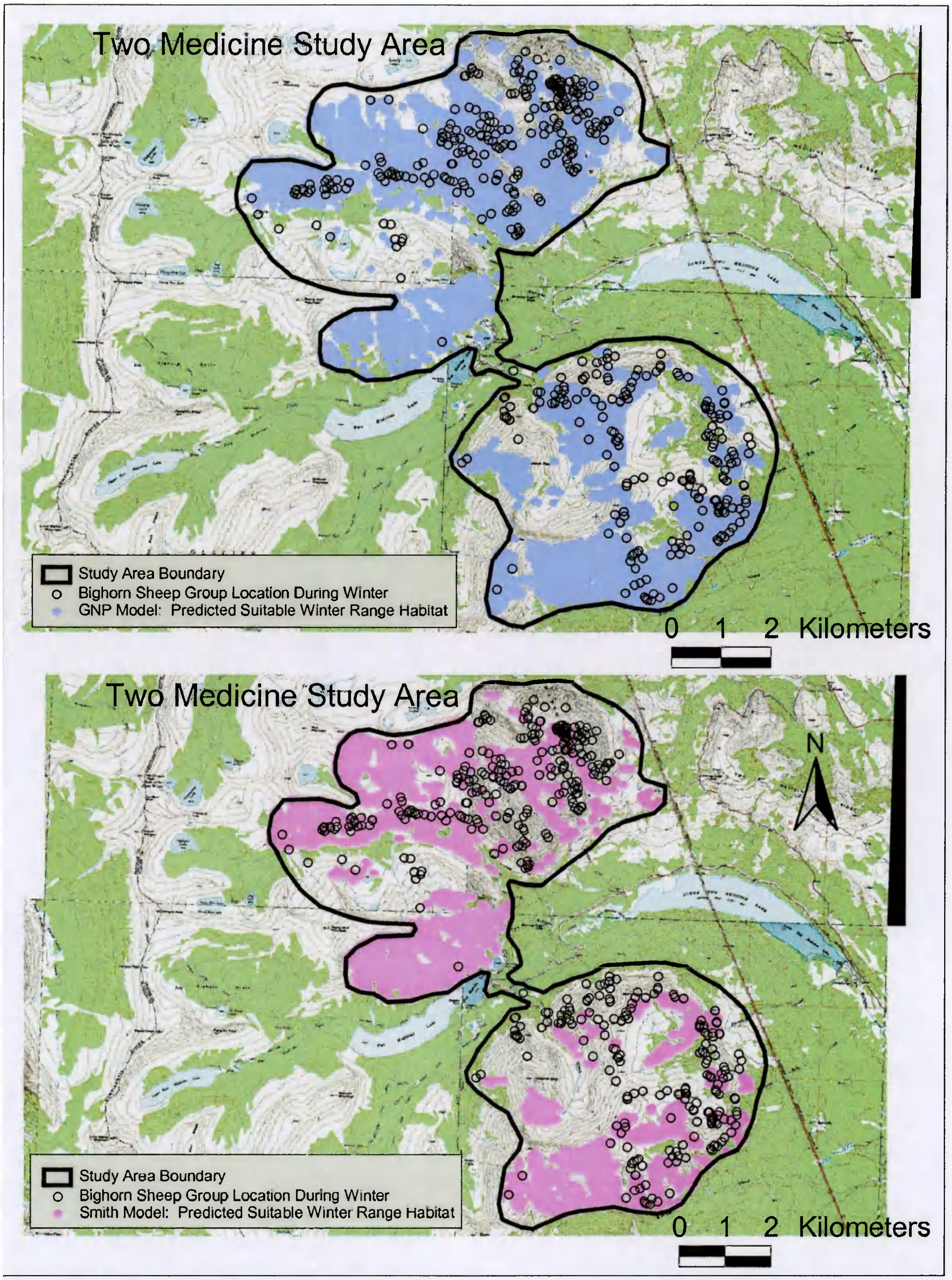

Figure 6. The extent of suitable winter range habitat within the Two Medicine study area as predicted by a model developed in Glacier National Park (top) and by a GIS application of the Smith model (bottom). Bighorn sheep group locations during winter are also shown.

**Table 9. Components of final models.**

Explanatory variables and their coefficients, with standard errors, for two versions of a final logistic regression model for predicting bighorn sheep winter range in Glacier National Park, Montana.

| Model | Variable[a] | Coefficient | Standard Error |
|---|---|---|---|
| **Final 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 |
| **Final 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.

land cover type category 1 (dry herbaceous) be represented by all zeros; therefore, the equation contains no coefficient for category 1.

## Consideration of Lambing Locations

The construction of logistic regression models describing bighorn sheep lambing areas was impractical because of the limited number of lamb locations documented during two springs (May 1–June 15) of ground surveys. However, winter range model criteria offer a basis from which to further define lambing area characteristics (Smith et al. 1991, Sweanor et al. 1996). The Smith model application employs the criteria shown in Table 1, with a broadening of the range of acceptable aspects (45°-315°) and a narrowing of the acceptable distance to water (not more than 1 km). In addition, any areas identified by these criteria must be at least 2 hectares in size.

Bighorn sheep ewes generally seek out rugged terrain for lambing to maximize security from predation on new born lambs, and require relatively easy access to water or new vegetation growth (i.e., moist areas) (Geist 1971, Smith et al. 1988, Singer and Gudorf 1999). To look at lambing area predictions, I used only two criteria – escape terrain and snowpack extent. I accomplished this by running the land cover type version of my final winter range model without the snowfree restriction, then removed all grid cells that were covered by snow in the May 23, 1999 TM satellite image. I also narrowed the definition of escape terrain to slopes greater than 35° so as to emphasize steep, rugged slopes. I did not restrict cells on the basis of distance to streams because of the availability of moisture from emergent vegetation as the snowpack melts. And I did not place any restrictions on aspect, because I have observed bighorn ewes lambing on north-facing slopes in GNP. A visual assessment indicated that these criteria worked well, and did a slightly better job than the Smith model application in predicting lambing areas (Figures 7 and 8).

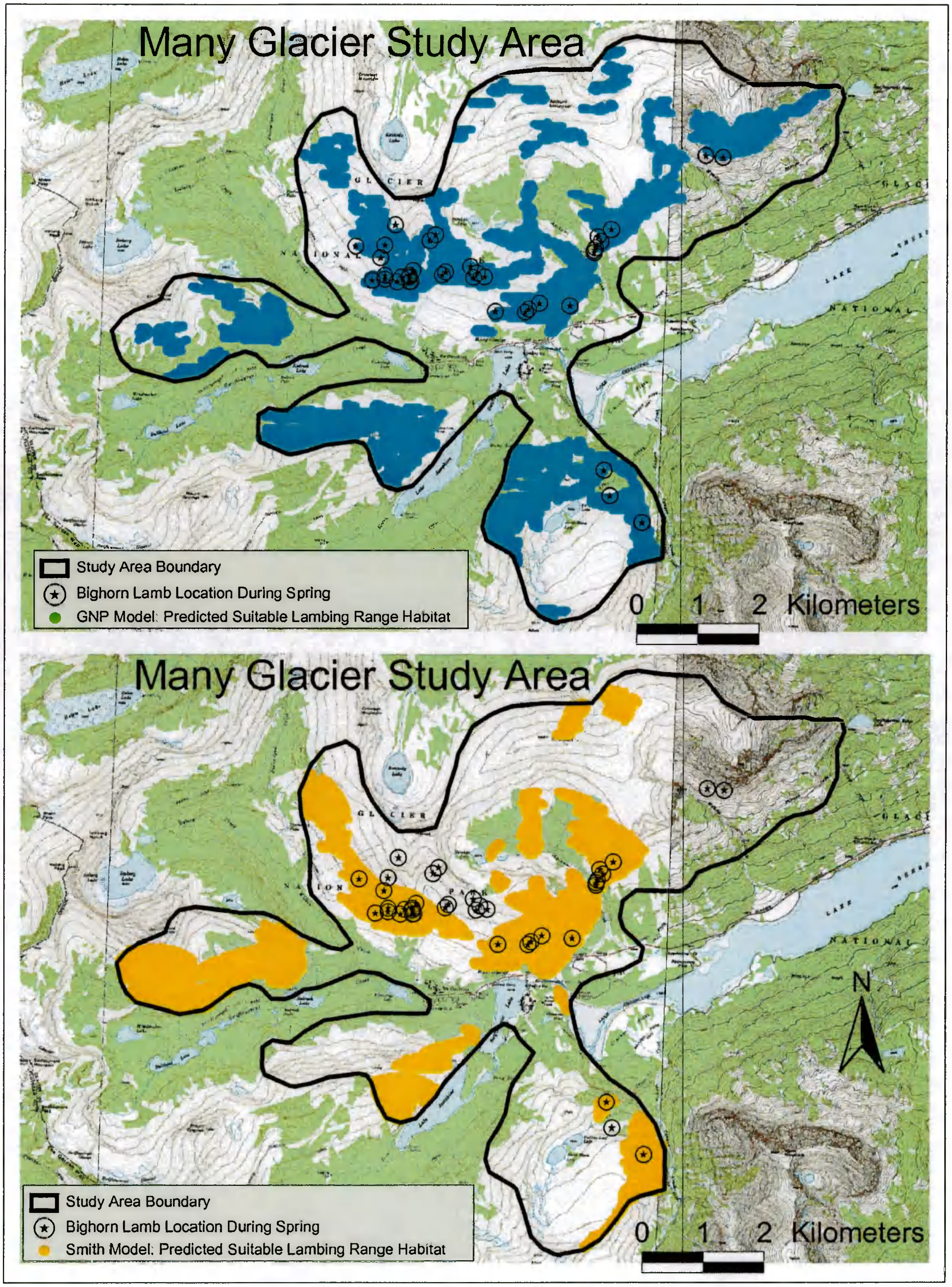

Figure 7. The extent of suitable lambing range habitat within the Many Glacier study area as predicted by a model developed in Glacier National Park (top) and by a GIS application of the Smith model (bottom). Bighorn sheep lamb locations during spring are shown.

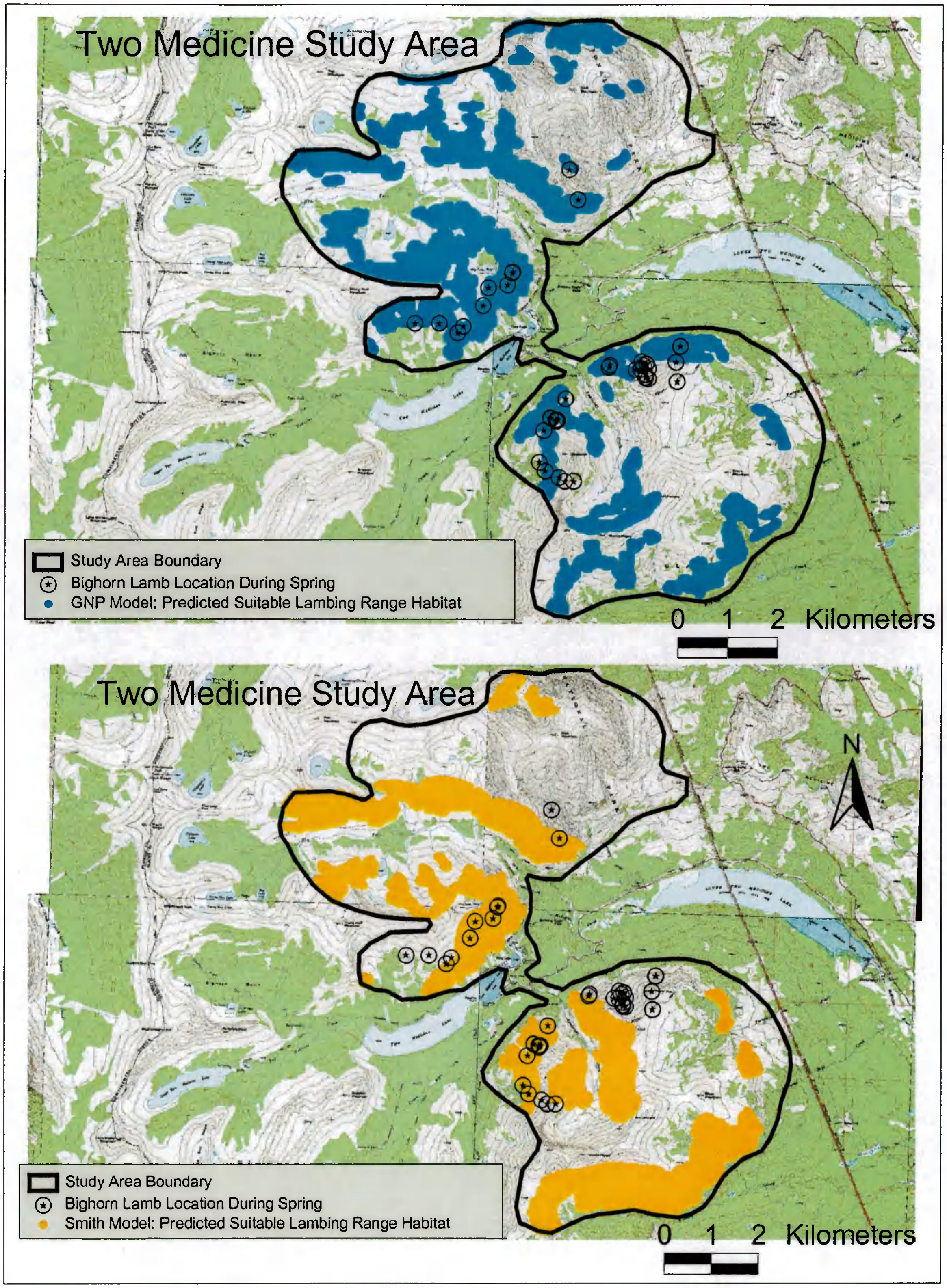

Figure 8. The extent of suitable lambing range habitat within the Two Medicine study area as predicted by a model developed at Glacier National Park (top) and by a GIS application of the Smith model (bottom). Bighorn sheep lamb locations during spring are shown.

# DISCUSSION

## Bighorn Sheep Surveys

Based on observations from ground surveys conducted during winter, bighorn sheep on my two study areas appeared to prefer open grassland and rocky habitats to conifer habitats. This generalization was supported by focal observation sessions, opportunistic observation of sheep tracks in snow, and fecal pellet diet analysis results. 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. Shrubby sites at or above treeline, with the absence of leaves, generally had horizontal visibility $\geq$ 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 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 late spring and early summer bighorn sheep sometimes traveled through extensive, contiguous forest as they moved to lambing and/or summer ranges. Most of this anecdotal evidence of forest travel was seen in lodgepole pine (*Pinus contorta*) forest, where horizontal visibility averaged 30-50%.

Field observations regarding sex/age classification counts and disturbance to bighorn sheep may be of general interest. While careful ground surveys provide fairly thorough sex/age ratio data, it is difficult to account for duplication among surveys conducted on consecutive days when summarizing sex/age data across large areas. The spring concentration -- which on my study areas began in mid-April and peaked in early May, and occurred on core winter range areas as well as peripheral areas where snow cover melted off quickly – offered the best opportunity to acquire sex/age ratio data for a large portion of a given herd over a relatively short survey time period. The earliest that I observed a new lamb during this study was the 8th of May, and my observations indicated that most lambing occurred from mid-May through the first week of June. Although considerably more time intensive than aerial surveys, ground surveys appeared to result in far less disturbance to bighorn sheep compared to aerial surveys. During aerial surveys over Glacier National Park (GNP), bighorn sheep typically attempted to flee from the airplane (a Cessna 185); as the airplane circled, sheep tended to bunch into tight groups, and sometimes broke off running in a new direction. In addition, aerial surveys appeared to be much less effective than ground surveys at locating sheep groups on low-elevation slopes where vegetative cover is denser and/or the rocky terrain is more rugged.

Finally, while ground surveys allowed me to document some lambing areas, the expanding availability of habitat as snow cover melted made it quite difficult to achieve thorough surveys of all potential lambing areas. Some ewes probably move several kilometers from their winter ranges to lambing areas. I observed bighorn sheep ewes lambing on north-facing slopes, and indeed the lambing range application of my final model predicted large areas on north-facing slopes to be suitable lambing terrain (see Figures 7 and 8). More ground surveys would be required to document which of these predicted slopes are used for lambing.

**Fecal pellet sampling**

In terms of annual variation, winter fecal nitrogen (FN) levels are the lowest and most constant, while spring FN levels are the highest and most variable (Hebert et al. 1984). Published winter FN levels for bighorn sheep have ranged from 0.96-1.58%, with values of 0.96-1.16% coming from herds experiencing declines attributed to poor diet quality (Hebert et al. 1984, Irwin et al. 1993). Irwin et al. (1993) suggested that FN levels below 1.3% may indicate winter diets deficient in protein and energy. The FN levels of 1.62-1.69% recorded from my composite fecal samples suggest that bighorn sheep herds, at least during the winters of 2000 and 2001, had access to high quality winter forage on the Many Glacier and Two Medicine core winter ranges.

One problem with fecal nitrogen as a correlate of diet quality is that protein-complexing tannins tend to reduce nitrogen digestibility, resulting in over-estimation of diet quality from the fecal nitrogen index (Holechek et al. 1982, Hobbs 1987). However, high-tannin forages must comprise over 25% of the diet before the fecal nitrogen correlation to dietary nitrogen is affected (Leslie and Starkey 1985). Winter diets comprised principally of cured grasses are virtually free of tannins (Irwin et al. 1993). Hebert and Lake (1986) found that ungulate diet quality, even for browsing species, is well indexed by fecal nitrogen.

While I could find no published documentation of winter diaminopimelic acid (DAPA) levels for bighorn sheep, Hebert and Lake (1986) assessed fecal DAPA levels for spring, summer and fall for captive and free ranging bighorn sheep herds in south-central British Columbia. Hebert and Lake (1986) reported that while annual variation in DAPA levels were strongly correlated with annual FN levels, DAPA levels did not closely match digestible energy throughout the year. However, Hebert and Lake (1986) suggested that DAPA can serve as an index of digestible energy during periods of plant dormancy. The lowest bighorn sheep fecal DAPA levels reported by Hebert and Lake (1986) occurred in December, after the fall green-up in vegetation, and averaged 0.311 mg/g. Summer levels averaged 0.515 mg/g and spring levels spiked to 0.856 mg/g (Hebert and Lake 1986).

The DAPA levels recorded on my study areas suggest normal levels of digestible energy for the winter vegetation dormancy period. The fact that low elevation Two Medicine samples generated significantly higher DAPA levels than low elevation Many Glacier samples may reflect a lower density, more dispersed (and perhaps more selective) pattern of bighorn sheep foraging relative to the Many Glacier site. The core area of the Many Glacier winter range, from which most fecal pellets were collected, experiences consistent winter use and highly concentrated spring use. The significant difference between low elevation Two Medicine DAPA levels and high elevation Two Medicine

DAPA levels is likely a result of higher vegetation density and diversity at lower elevations.

Other studies involving microhistological analysis of fecal pellet samples to estimate bighorn sheep forage use revealed fairly similar breakdowns of diet components. Keating et al. (1985) found that winter bighorn sheep diets consisted of 54-59% grasses, 6-7% forbs, and 35-41% shrubs/trees in the upper Yellowstone valley. Bighorn sheep winter diets in the Sun River areas along Montana's Rocky Mountain Front averaged 48-65% grasses, 12% forbs, and 23-42% shrubs/trees (Kasworm et al. 1984). And for a captive herd in British Columbia, Wikeem and Pitt (1992) reported an average winter diet of 70% grasses, 11% forbs, and 19% shrub/tree browse.

In comparison to these other studies, microhistological analysis of winter diet components from my two GNP study areas resulted in similar use of grasses (60-73%), greater use of forbs (16-30%) and less use of shrubs/trees (6-10%) (see Appendix B). The greater use of forbs probably reflects the abundance of alpine forbs and sedges in the upper elevations of the GNP winter ranges. The same appeared to be true for sedges, which in the summaries above were included with grasses -- bighorn sheep winter diets on my two GNP study areas averaged 16-25% sedges while the other studies reported that sedges comprised only 2-5% of the winter diet.

Shrubs comprised an average of 6.0% (range of 0-23.1%) of the bighorn sheep winter diet on my study areas, while conifers comprised an average of 1.7% (range of 0-5.8%) (see Appendix B). The shrub component of the winter diet was dominated by wolf willow (*Elaeagnus commutata*), with Oregon grape (*Berberis repens*) and red-osier dogwood (*Cornus stolonifera*) comprising minor portions in some samples. Douglas fir

(*Pseudotsuga menziesii*) dominated the conifer component of the winter diet (see Appendix B). Field observations indicated that wind-stunted trees and saplings growing in isolation or in small clumps within grassland habitats offered the most common opportunities for bighorn sheep to browse on conifers.

## Model Goodness-of-Fit and Validation

The goodness-of-fit measures for all candidate models indicated rather poor fit – AIC values were quite large and the Hosmer and Lemeshow Chi-square values were large enough that all significance levels were <0.0005 (see Tables 5 and 6). I suspect that 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.

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 two classification categories. The rate of commission, however, is sensitive to the relative sizes of the two 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 validation test performance is a bit 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. Similarly, if considering two models with equal rates of positive commission, the model with the smaller positive ratio is the better performer.

## Final Models

While the development and validation of two sets of models was critical to the selection of the best models, the overall goal was to derive one or two models applicable across all of Glacier National Park (GNP), and perhaps at sites in other geographic areas. To achieve this goal, I selected the best model from each study area and then averaged the coefficients from these two models to formulate a single model. The best performing Many Glacier model (model MG9; see Tables 6 and 7) contained the following explanatory variables: distance to escape terrain, snow cover, solar radiation index, slope, and land cover type. The best performing Two Medicine model (model TM4; see Tables 5 and 7) contained the following explanatory variables: distance to escape terrain, snow cover, solar radiation index, slope, transformed aspect, and land cover type. Because the inclusion of the transformed aspect variable did not produce a clear improvement in model fit (slightly smaller AIC and Hosmer and Lemeshow Chi-square test statistic values; see Table 5) compared to the model without transformed aspect (model TM10), and because aspect is incorporated in the solar radiation index variable, I identified models MG9 and TM10 as the best predictive models from which to derive the land cover type version of my final model (see Tables 8 and 9). 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 8 and 9).

## Explanatory Variables Excluded from Final Models

The two final model versions were reached through assessment of their 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. In reviewing the literature for validation tests of bighorn sheep habitat models, I examined the variables found to explain sheep habitat use by various authors (Table 10).

Horizontal visibility is one variable that, although excluded from the land cover type version of my final model, would quite likely prove to be significant at other sites. Horizontal visibility has been identified as a very important 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. In the context of this final model version, the role of horizontal visibility in explaining bighorn sheep winter range habitat use patterns can be deduced from the role of the land cover type variable. My second final model version, containing two 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 significantly large likelihood-ratio test statistic.

Availability of water is another variable identified as significant in other habitat models, including the Smith model application (see Table 1). None of the grid cells in my two study areas was greater than 3.2 km from water, which is the maximum distance

**Table 10. Summary of bighorn sheep habitat model validation tests.**

A comparison of habitat variables found to be useful in explaining bighorn sheep habitat use in model validation tests conducted by various authors. The sub-species involved and the state in which the validation test was conducted are also shown.

| Authors (model tested) | Habitat Variables | | | | | Sub-species (study area state) |
|---|---|---|---|---|---|---|
| | Vegetation | Topography (Escape Terrain) | Water Availability | Horizontal Visibility | Human Disturbance | |
| Haas 1991 (Armentrout & Brigham 1988; and Hansen 1980) | X | X | X | | X | Desert bighorn (Utah) |
| Bleich et al. 1992 (Hansen 1980) | X | X | X | | | Desert bighorn (California) |
| McCarty 1993 (Armentrout & Brigham 1988) | | X | | X | | Desert bighorn (Colorado) |
| Johnson 1995 (Smith et al. 1991) | | X | X | X | | Rocky Mtn bighorn (Colorado) |
| Schirokauer 1996 (Smith et al. 1991) | | X | | X | | Rocky Mtn bighorn (Montana) |
| Dicus 2002 thesis (Smith et al. 1991) | X | X | | X | | Rocky Mtn bighorn (Montana) |

for habitat suitability established by the Smith model application. The distance to water variable was not significant, as measured by the likelihood-ratio 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 a significant variable, as might efforts to model bighorn sheep summer range within GNP.

While Smith et al. (1991) identified distance to 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). As an explanatory variable in Many Glacier models, distance to development displayed statistical significance. However, this proved to be an artifact of the presence of buildings and roads immediately adjacent to the core winter range in the Many Glacier valley. This variable had a negative coefficient, indicating that as distance to development increased, probability of sheep use decreased. This is counter to expectations and merely reflects the fact that as you move away from the core winter range, you also happen to move away from development.

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 (Buechner 1960, Stelfox 1971, Rowland and Schmidt 1981, Smith et al. 1988). When using the Smith model application to evaluate potential reintroduction sites, the

National Park Service has stressed that those reintroduction site 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 common along the park's east side and competition for forage and space is a management issue of concern.

## Suggestions for Future Research

The most obvious deficiency in the predictive performance of my models lies in 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 snowfree, north-facing slopes. Although use of these slopes, compared to use of southerly slopes, was infrequent, it occurred throughout the winter. In addition, use of north-facing slopes for lambing was noted, and while the lambing range application of my final models successfully predicted some of these areas, it also predicted large portions of north-facing slopes where no lambing activity was observed. Future investigation into additional variables or modified analyses that would allow more sensitivity in predicting suitable north-facing sites for both winter range and lambing 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 currently suitable bighorn sheep winter range 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.

Finally, more information is needed on the migration movements of bighorn sheep in GNP. Very little is known about rates of emigration and immigration for the various herds in the park, or what levels of genetic exchange currently occur. Based on anecdotal evidence, it is likely that adequate connectivity exists among GNP's herds for them to function as a metapopulation. Furthermore, it is likely that there is adequate connectivity with herds in Waterton Lakes National Park across the international boundary in Alberta, Canada. It seems unlikely, however, that adequate connectivity with populations to the south, in the Sun River area, exist to allow metapopulation function in that direction. For the future management of these bighorn sheep herds, it would be extremely helpful to accurately identify migration routes, both among seasonal ranges of a single herd and between separate herds.

**Appendix A.** Standardized data form used to record group size, sex/age composition, activity, and cover type for all sheep groups observed during ground surveys in the Many Glacier and Two Medicine valleys of Glacier National Park, Montana, during January – May of 2000 and 2001.

**SHEEP SURVEY FORM**

**Reference Map by Date, Obs & Time**

**Date** **Observer**

**CODES**

| Sex/Age | Cover Type | Activity | |
|---|---|---|---|
| **A)classI ram** | **1)grass/forb** | **1)feed** | **4)stand alert** |
| **B)classII ram** | **2)shrub** | **a)grass** | **5)run** |
| **C)classIII ram** | **3)conifer** | **b)shrub** | **a)predator** |
| **D)classIV ram** | **4)talus** | **c)conifer** | **b)human** |
| **E)female** | **5)rock** | **d)unknown** | **c)no obs cause** |
| **F)lamb-of-year** | **6)snowfield** | **2)bedded** | For 5a/b, incl. i.d. & |
| **G)yearling** | **7)unknown** | **3)walk** | est. distance |

**Obs Location**

**Sheep Locations:**

| Time | Map Ref Code | Number in Group | Sex/Age | Activity | Cov Type | | Weather | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Temp | Wind | Cloud | Precip |
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**Appendix B.** List of forage species identified by microhistological analysis of bighorn sheep fecal pellets from winter range study areas in Glacier National Park. Numbers represent estimated percentage of diet.

***Two Medicine Study Area*:**

| | Plot ID | | | | | | |
|---|---|---|---|---|---|---|---|
| **Plant species** | *TM1* | *TM2* | *TM3* | *TM4* | *TM5* | *TM6* | **Average** |
| Antennaria spp. | 1.2 | 0.4 | 0.5 | 3.4 | | | 0.92 |
| Arabis spp. | | | | | | 0.4 | 0.07 |
| Arnica spp. | | 0.7 | 0.2 | | | | 0.15 |
| Artemisia spp. | 1.7 | 0.7 | 1.9 | 1 | 4.5 | | 1.63 |
| Astragalus spp. | 0.7 | 0.9 | 0.6 | 2.9 | 2.7 | 1.6 | 1.57 |
| Cerastium spp. | | | 1.6 | 0.7 | | | 0.38 |
| Descurainia spp. | | | 3.3 | 1.2 | 1.6 | | 1.02 |
| Draba spp. | | 0.4 | 0.3 | 1.7 | 1.4 | | 0.63 |
| Erigeron spp. | | | 1.3 | 3.1 | 0.2 | | 0.77 |
| Lupinus spp. | 6.9 | 3.5 | 1 | 8.2 | 5.4 | 10.5 | 5.92 |
| Penstemon spp. | | | 3.2 | | | | 0.53 |
| Polygonum spp. | | | | | 1 | | 0.17 |
| Rumex acetosa | | 0.7 | 1 | 0.7 | | | 0.40 |
| Silene/Arenaria spp. | 9.1 | 18.1 | 20.7 | 6.5 | 10.3 | | 10.78 |
| Stellaria spp. | | | 1.3 | | | | 0.22 |
| Trifolium/Medicago/Melilotus | | 0.2 | 1.3 | | | | 0.25 |
| Cruciferae spp. | 0.7 | 0.2 | | | | | 0.15 |
| Monocot forb | | | | 3.4 | | | 0.57 |
| Other forbs | 4.4 | 5.2 | 5.1 | 1.4 | 2.2 | 2.9 | 3.53 |
| **TOTAL FORBS** | 24.7 | 31 | 43.3 | 34.2 | 29.3 | 15.4 | 29.65 |
| Agrostis spp. | 1.3 | 5.2 | 2.6 | 0.7 | | 2.1 | 1.98 |
| Alopecurus spp. | 0.7 | 3.8 | 2.9 | 0.7 | 2.2 | 2.1 | 2.07 |
| Bromus spp. | 0.7 | | 0.6 | | | 0.8 | 0.35 |
| Calamagrostis purpurascens | 8.1 | 14.3 | 15 | 22.2 | 6.1 | 13.9 | 13.27 |
| Danthonia spp. | | 0.3 | | | 0.6 | | 0.15 |
| Deschampsia spp. | 3.7 | 1 | 0.6 | 1.4 | 8 | 1.6 | 2.72 |
| Elymus spp. | 6.8 | 7 | 0.3 | | 2.2 | 4.5 | 3.47 |
| Festuca spp. | 13.6 | 5.9 | 2.2 | 1.7 | 3.2 | 4.1 | 5.12 |
| Koeleria macrantha | | | 2.6 | 2.1 | 1.9 | | 1.10 |
| Phleum alpinum | | | | | 1.6 | | 0.27 |
| Poa spp. | 7.5 | 9 | 3.8 | 4.1 | 7.7 | 9 | 6.85 |
| Stipa spp. | 5.4 | 4.2 | 2.9 | 3.4 | 1 | 0.8 | 2.95 |
| Trisetum spp. | 4.4 | 0.3 | | | 2.6 | | 1.22 |
| Other Grasses | 4.4 | 3.1 | 1.9 | 1 | 0.3 | 2.9 | 2.27 |
| **TOTAL GRASSES** | 56.6 | 54.1 | 35.4 | 37.3 | 37.4 | 41.8 | 43.77 |
| Carex capillaris | | | 1.9 | | 1.3 | | 0.53 |
| Carex spp. | 6.8 | 5.6 | 13.1 | 9.9 | 18 | 15.2 | 11.43 |
| Juncus spp. | | 2.1 | 3.8 | 2.4 | 9 | | 2.88 |
| Kobresia spp. | 2.4 | 1.4 | 1.3 | 1 | 1 | | 1.18 |
| **TOTAL SEDGE/RUSH** | 9.2 | 9.1 | 20.1 | 13.3 | 29.3 | 15.2 | 16.03 |
| Cornus stolonifera | | 1 | | 0.7 | | | 0.28 |
| Elaeagnus commutata | 6.1 | 0.3 | | 4.8 | 0.6 | 22.7 | 5.75 |
| Berberis repens | | 0.7 | | | 0.6 | | 0.22 |
| Shrub | | 0.3 | | | | 0.4 | 0.12 |
| Shrub stem | | | | 1 | | | 0.17 |
| **TOTAL SHRUBS** | 6.1 | 2.3 | | 6.5 | 1.2 | 23.1 | 6.53 |
| Juniperus spp. | | | | | | 0.4 | 0.07 |
| Pseudotsuga menziesii | 2.4 | 0.7 | | 5.5 | 1 | 3.3 | 2.15 |
| Salix spp. Leaf | | | | 1.4 | | 0.8 | 0.37 |
| **TOTAL TREES** | 2.4 | 0.7 | | 6.9 | 1 | 4.5 | 2.58 |
| Moss | 1 | 2.8 | 0.6 | 1 | 1.3 | | 1.12 |

**Appendix B.** List of forage species identified by microhistological analysis of bighorn sheep fecal pellets from winter range study areas in Glacier National Park. Numbers represent estimated percentage of diet.

***Many Glacier Study Area***:

| | Plot ID | | | | |
|---|---|---|---|---|---|
| **Plant species** | *MG1* | *MG2* | *MG3* | *MG4* | **Average** |
| Arabis spp. | | 0.3 | | 0.7 | 0.25 |
| Arnica spp. | | | 0.3 | | 0.08 |
| Artemisia spp. | | 0.3 | | 0.3 | 0.15 |
| Astragalus spp. | 3 | 0.8 | 2.2 | 0.6 | 1.65 |
| Draba spp. | | 0.6 | | | 0.15 |
| Erigeron spp. | 1.4 | | 0.2 | | 0.40 |
| Lupinus spp. | 4.4 | 5.2 | 10.2 | 1.1 | 5.23 |
| Monarda fistulosa | 1.4 | 1.8 | | | 0.80 |
| Penstemon spp. | | | | 0.3 | 0.08 |
| Potentilla spp. | 0.4 | | | | 0.10 |
| Silene/Arenaria spp. | 3.9 | 2.2 | | 10.3 | 4.10 |
| Composite hair | 0.4 | | | | 0.10 |
| Other forbs | 1.8 | 0.9 | 4.1 | 2.3 | 2.28 |
| **TOTAL FORBS** | 16.7 | 12.1 | 17 | 15.6 | 15.35 |
| Agrostis spp. | 3.5 | 4.6 | 1.3 | | 2.35 |
| Alopecurus spp. | 1.4 | | 0.6 | | 0.50 |
| Bromus spp. | 1.1 | 3.1 | 1.9 | 1.4 | 1.88 |
| Calamagrostis | 37.8 | 16.6 | 19.7 | 0.6 | 18.68 |
| Deschampsia spp. | 2.5 | | 1.6 | 2.3 | 1.60 |
| Elymus spp. | 2.8 | | 7 | 0.8 | 2.65 |
| Festuca spp. | 8.8 | 8.9 | 7 | 1.7 | 6.60 |
| Koeleria macrantha | 4.2 | 0.6 | 1 | | 1.45 |
| Phleum alpinum | | | 0.6 | | 0.15 |
| Poa spp. | 8.8 | 8.6 | 5.7 | 4.6 | 6.93 |
| Stipa spp. | 3.9 | 1.5 | 11.5 | | 4.23 |
| Trisetum spp. | 0.4 | | | | 0.10 |
| Other Grasses | 0.7 | 1.5 | 1.3 | | 0.88 |
| **TOTAL GRASSES** | 75.9 | 45.4 | 59.2 | 11.4 | 47.98 |
| Carex capillaris | | 2.8 | 0.6 | 11.2 | 3.65 |
| Carex spp. | 1.1 | 21.8 | 9.5 | 19.2 | 12.90 |
| Juncus spp. | | 3.7 | 2.5 | 14.6 | 5.20 |
| Kobresia spp. | | | | 6.3 | 1.58 |
| Luzula spp. | | 0.9 | | 4.3 | 1.30 |
| **TOTAL SEDGE/RUSH** | 1.1 | 29.2 | 12.6 | 55.6 | 24.63 |
| Amelanchier alnifolia stem | 2.1 | | | | 0.53 |
| Cornus stolonifera | | 1.2 | | | 0.30 |
| Elaeagnus commutata | | 4.8 | 1.6 | 1.4 | 1.95 |
| Berberis repens | 2.5 | 1.8 | 1.3 | | 1.40 |
| Vaccinium spp. Leaf | 1.4 | | 1.3 | | 0.68 |
| Shrub | | 0.6 | | | 0.15 |
| Shrub stem | | | | 0.6 | 0.15 |
| **TOTAL SHRUBS** | 6 | 8.4 | 4.2 | 2 | 5.15 |
| Pseudotsuga menziesii | | 2.2 | 1 | 0.6 | 0.95 |
| Salix spp. Leaf | | | | 1.1 | 0.28 |
| **TOTAL TREES** | | 2.2 | 1 | 1.7 | 1.23 |
| Moss | 0.3 | 2.5 | 6 | 12.9 | 5.43 |
| Lichen | | | | 0.8 | 0.20 |

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