

HABITAT COMPARISONS OF HISTORICALLY STABLE AND LESS STABLE
BIGHORN SHEEP POPULATIONS

by

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Animal and Range Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

November 2008

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November 2008

ACKNOWLEDGEMENTS

This project was made possible through funding from the Joe Skeen Institute for Rangeland Restoration, the Montana chapter of the Foundation for North American Wild Sheep, and Montana Fish, Wildlife, and Parks. Thank you to my graduate committee, Dr. Tracy Brewer, Dr. Jeff Mosley, Keith Aune, and Ray Vinkey. I am especially grateful to Tracy for giving me the opportunity to earn my Masters' degree, and Jeff for his guidance throughout this project. I would like to thank Josh Bilbao for his assistance with my field work and the many, many miles we walked together the past two summers. Special thanks to Eva Strand for her never ending patience and fantastic GIS skills, she had a crucial role in this project. I would like to thank all my fellow graduate students in the basement of Linfield Hall whose listening skills and humor got me through this project. I would like to thank my family and friends for their love and support; I wouldn't have made it through this without all of you. Thank you to Travis Standley for introducing me to Tracy, and supporting me through this experience.

TABLE OF CONTENTS

1. INTRODUCTION	1
2. LITERATURE REVIEW	3
History of Bighorn Sheep in Montana	3
Brief History of Disease Research	5
Habitats Used by Bighorn Sheep	7
Diet Selection	8
Elevation, Slope, and Aspect	9
Escape Terrain	10
Horizontal Visibility	11
Landscape Ruggedness	12
Solar Radiation Index	13
Literature Cited	15
3. HABITAT FEATURES POTENTIALLY LIMITING A BIGHORN SHEEP POPULATION IN WESTERN MONTANA	22
Introduction	22
Materials and Methods	24
Herd Histories	24
Lost Creek	24
Tendoy Mountains	25
Study Areas	25
Approach	29
GIS Sampling	30
Elevation, Slope, and Aspect	32
Landscape Ruggedness	32
Solar Radiation Index	33
Escape Terrain	33
Distance to Escape Terrain	33
Grassland Vegetative Variables	34
Shrub Canopy Cover	35
Graminoid and Forb Frequency	35
Horizontal Visibility	35
Experimental Design and Statistical Analysis	36
Results	38
Summer Ranges	38
Winter Ranges	42
Discussion	43

TABLE OF CONTENTS CONTINUED

Management Implications.....	46
Literature Cited	47
APPENDIX A Maps of the habitat variables using GIS	52

LIST OF TABLES

Table	Page
1. Proportions of land cover types in the summer and winter ranges of the Lost Creek (stable) and Tendoy Mountains (less stable) bighorn sheep populations in western Montana.	37
2. Logistic regression models comparing the Lost Creek (stable) and Tendoy Mountains (less stable) bighorn sheep populations in western Montana.	39
3. Means for habitat variables (\pm SE) for the Lost Creek (stable) and Tendoy Mountains (less stable) bighorn sheep populations in western Montana.	41

LIST OF FIGURES

Figure	Page
1. Summer and winter ranges of the Lost Creek (stable) bighorn sheep population near Anaconda, MT.	27
2. Summer and winter ranges of the Tendoy Mountains (less stable) bighorn sheep population near Dell, MT.....	28

ABSTRACT

Limited research has examined how habitat differences between stable and less stable bighorn populations may influence their success. Understanding these habitat differences may help explain how habitat contributes to bighorn sheep population stability. The objective of the study was to identify potential limiting habitat factors for the Tendoy Mountains bighorn sheep (*Ovis canadensis*) population in western Montana. Habitat variables that were evaluated are unlikely to be influenced by fine-scale weather or disturbance patterns. Land cover, slope, aspect, elevation, landscape ruggedness, solar radiation index (SRI), and distance to escape terrain were measured using GIS. Shrub canopy cover, graminoid and forb frequency, and horizontal visibility were measured in the field. Logistic regression was used to identify habitat differences between the stable and less stable sheep populations in summer and winter. Odds ratios from the logistic regressions were used to identify potential limiting habitat variables for the less stable population. Results from this study indicate that landscape ruggedness ($P < 0.01$) and aspect ($P < 0.01$) in summer ranges, and landscape ruggedness ($P = 0.01$), aspect ($P < 0.01$), and SRI ($P < 0.01$) in winter ranges were the habitat characteristics most likely influencing population stability. Landscape ruggedness and SRI are relatively new habitat metrics that require more research to determine threshold values for bighorn sheep habitat. Results from this study provide initial insights into potential threshold values for landscape ruggedness and SRI for Rocky Mountain bighorns.

CHAPTER 1

INTRODUCTION

Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) are native to the northern Rocky Mountain region and are a highly valued game species (Enk 1999). Bighorn sheep populations dramatically declined and their geographic distribution was greatly reduced in the latter part of the 19th century (Buechner 1960; Geist 1971; Valdez and Krausman 1999; DeCesare 2002). Bighorn sheep in Montana historically occupied all of the larger mountain ranges and most of the smaller, isolated mountain ranges, as well as the Missouri River Breaks terrain (Couey 1950; Buechner 1960). By 1950, bighorn sheep had been extirpated from the Missouri River Breaks terrain and from most of the smaller, isolated mountain ranges east of the continental divide (Couey 1950; Enk 1999; Dicus 2002).

Bighorn sheep are perceived as poor dispersers with strong site fidelity (Geist 1971), which has caused management efforts to focus on reintroducing sheep into unoccupied habitat. Augmentation programs have been implemented as a means of improving the reproductive output and growth of small populations that have experienced die-offs (Enk 1999). However, augmentation programs have had limited success in the western United States (Enk 1999).

Some Montana bighorn sheep populations have been successfully reintroduced. Bighorn sheep were first transplanted in Montana in 1942 (Hoar 1995). In 1950, Couey (1950) estimated there were 1,200 bighorn sheep in Montana. Seventeen isolated

populations, totaling 1,400-1,700 bighorns remained in Montana in 1960 (Buechner 1960). There were approximately 3,100 bighorn sheep in Montana in 1974 (Trefethen 1975). In 2008, there were 49 populations with an estimated 7,185 bighorn sheep in Montana (Carlsen and Erickson, In Press; T. Carlsen pers. comm). However, 14 major die-offs have occurred in Montana since 1984, resulting in losses of bighorn sheep ranging from 75-97% (Carlsen and Erickson, In Press).

Management of Rocky Mountain bighorn sheep has focused on: 1) population demographics, 2) immunological state, and 3) habitat characteristics (K. Aune, personal communication). Demographic targets have been identified for successful populations (Douglas and Leslie 1986; Berger 1990; Smith et al. 1991). Habitats suitable for bighorn sheep have been identified (Risenhoover and Bailey 1985; Zeigenfuss et al. 2000), and bighorn sheep population response to immunological stressors has been documented (Jones and Worley 1994; Monello et al. 2001). Past research has identified domestic sheep (*Ovis aries*) as a potential source of pneumophilic bacteria to bighorn sheep (Martin et al. 1996). However, not all bighorn die-offs are attributed to contact with domestic sheep (Aune et al. 1998; Shackleton et al. 1999).

Limited research has documented how habitat differences between stable and less stable bighorn populations influence their success. Habitat differences may be contributing to the instability of some populations in Montana and other areas in the West. The purpose of this study was to identify potential limiting habitat factors for a less stable Rocky Mountain bighorn sheep population in western Montana.

CHAPTER 2

LITERATURE REVIEW

History of Bighorn Sheep in Montana

Rocky Mountain bighorn sheep are native to Montana and present in many areas across the state; however, bighorn sheep population stability has varied over time. In 1960, Buechner (1960) estimated there were 15,000 to 20,000 wild sheep in the contiguous United States. However, some predict that sheep numbers were likely near 20,000 because many populations were not surveyed at the time of his estimate (Valdez and Krausman 1999). In 1991, approximately 49,000 wild sheep were present in the contiguous United States, and of those, approximately 25,000 were Rocky Mountain bighorn sheep (Valdez and Krausman 1999; DeCesare and Pletscher 2006). Bighorn sheep populations dramatically declined and their geographic distribution was greatly reduced in the latter part of the 19th century (Buechner 1960; Geist 1971; Valdez and Krausman 1999; DeCesare 2002). Major factors for the decline of wild sheep are thought to be a combination of competition with livestock, diseases from domestic livestock, market and sport hunting, and invasion of grasslands by sagebrush and trees (Couey 1950; Buechner 1960; Geist 1971; Aderhold 1972; Enk et al. 2001; Shackleton et al. 1999; Valdez and Krausman 1999).

Bighorn sheep in Montana historically occupied all of the larger mountain ranges and most of the smaller, isolated mountain ranges, as well as the Missouri River Breaks terrain (Couey 1950; Buechner 1960). The first reference to bighorn sheep in Montana

was in the Lewis and Clark journals in 1805 (Couey 1950). By 1950, bighorn sheep had been extirpated from the Missouri River Breaks terrain and from most of the smaller, isolated mountain ranges east of the continental divide (Couey 1950; Enk 1999; Dicus 2002). In addition, the large metapopulations of bighorn sheep along the continental divide had been reduced to small discontinuous remnants (Couey 1950; Schirokauer 1996). Approximately 1,200 bighorn sheep were present in Montana in 1950 (Couey 1950). In 1942, bighorn sheep were first transplanted in Montana, when 11 sheep from the Sun River herd were relocated to the Gates of the Mountains area near Helena (Hoar 1995). In 1960, 1,400-1,700 bighorns remained in Montana (Buechner 1960) and populations increased to approximately 3,100 bighorn sheep in 1974 (Trefethen 1975). Fourteen major die-offs have occurred in Montana since 1984, resulting in losses of bighorn sheep ranging from 75-97% of a given population affected by the die-off (Carlsen and Erickson, In Press). In 2008 in Montana, there were 49 populations totaling 7,185 bighorn sheep (Carlsen and Erickson, In Press; T. Carlsen personal communication, October 2008).

Bighorn sheep are perceived as poor dispersers with strong site fidelity (Geist 1971), so management efforts have focused on reintroducing sheep into unoccupied habitat. Transplant programs have successfully reestablished extirpated populations in several areas of Montana (Buechner 1960; Geist 1971; Aune et al. 1998). In 1991, there were approximately 5,300 bighorn sheep in Montana, largely due to the success of transplant programs (Valdez and Krausman 1999). Local populations of bighorn sheep remain fragmented, despite improving overall numbers (Douglas and Leslie 1999;

DeCesare and Pletscher 2006). Several populations of bighorn sheep in Montana are below minimum viable population estimates of > 100 (Berger 1990) or >125 animals (Smith et al. 1991). Several factors have contributed to unsuccessful translocation attempts including inadequate habitat, competition with other ungulates, diseases from domestic livestock, and human disturbance (Smith et al. 1988; Smith et al. 1991; Shackleton et al. 1999; Johnson and Swift 2000). Reintroductions and supplemental transplants have been a primary tool in bighorn population management in recent decades (Valdez and Krausman 1999; Johnson and Swift 2000; DeCesare and Pletscher 2006).

Brief History of Disease Research

Outbreaks of disease have been identified in bighorn sheep populations for over a century (Buechner 1960). These outbreaks limit the number and distribution of bighorn populations (Valdez and Krausman 1999). Extreme population fluctuations resulting from die-offs have limited the success of conventional wildlife management practices (Enk 1999) and many hypotheses have been proposed to explain disease outbreaks in bighorn sheep (Bunch et al. 1999). Pathogens most commonly associated with disease outbreaks in bighorn sheep have been *Psoroptes* spp., *Protostrongylus* spp., *Pasteurella* spp. and *Mannheimia haemolytica* (Rosen 1981; Jones and Worley 1994; Monello et al. 2001).

Pneumonia is recognized as a major cause of bighorn mortality during most population die-offs (Rosen 1981; Garde et al. 2006). A die-off has been defined as a sudden (<12 months) catastrophic reduction in the population exceeding 50%

(Shackleton et al. 1999). Pneumonia is a disease caused by the pathogen *Pasteurella* spp., and elicits respiratory distress, lethargy, and anorexia and ultimately results in death (Rosen 1981). However, *Pasteurella* spp. infections are not always manifested in disease, and many bighorns may have infections without showing any clinical signs (Rosen 1981; Onderka and Wishart 1988; Dunbar et al. 1990; Wild and Miller 1991). Bighorn sheep infected with pathogenic strains may show no clinical signs, which implies that disease outbreaks may only occur under certain ecological or environmental conditions (Festa-Bianchet 1988; Ryder et al. 1992). Although bighorn conservation is focused on understanding what factors cause *Pasteurella* spp. infections to become pneumonia outbreaks, limited research has shed light on this topic (Aune et al. 1998).

Factors predisposing bighorns to pneumonia may include: lungworm (*Protostrongylus* spp.) or mite (*Psoroptes ovis*) infections, malnutrition, inbreeding, harsh weather conditions, or stress associated with overcrowding (Risenhoover et al. 1988; Belden et al. 1992; Jones and Worley 1994; Schommer and Woolever 2008). Each of these factors may compromise bighorn immunity, and either infection type facilitates the shift from benign to lethal *Pasteurella* spp. infection or enables the establishment of virulent forms that would otherwise be controlled by the immune system (Monello et al. 2001).

Monello et al. (2001) reported that 88% of pneumonia-induced die-offs across the bighorn's geographic range occurred at or within 3 years of peak population numbers; this implies that bighorns' susceptibility to pneumonia may be attributable to density-dependent forces. Changes in normal precipitation and temperature regimes are not

associated with pneumonia outbreaks, but herds found in close proximity to domestic sheep tend to be more susceptible to die-off (Monello et al. 2001; Schommer and Woolever 2008). Large population die-offs associated with scabies (*Psoroptes* spp.) infestations were observed in the late 19th and early 20th centuries (Buechner 1960; Schommer and Woolever 2008). This observation resulted in clinical evidence of scabies in bighorn sheep during die-offs and that these outbreaks occurred following the introduction of domestic sheep (Buechner 1960; Schommer and Woolever 2008). However, not all bighorn sheep die-offs have been located in close proximity to domestic sheep (Foreyt and Jessup 1982; Goodson 1982; Onderka and Wishart 1984; Aune et al. 1998; Shackleton et al. 1999; Rudolph et al. 2007), but it has been noted that the severity of a dieoff is typically more pronounced when contact between domestic sheep and wild sheep occurs (Martin et al. 1996; Aune et al. 1998; Schommer and Woolever 2008).

Habitats Used by Bighorn Sheep

Bighorn sheep inhabit open grasslands (Erickson 1972; Pallister 1974; Risenhoover and Bailey 1985; Shackleton et al. 1999), shrub-steppes (Risenhoover and Bailey 1985; Shackleton et al. 1999), rock outcrops (Erickson 1972; Pallister 1974; Shackleton et al. 1999), cliffs (Risenhoover and Bailey 1985; Shackleton et al. 1999), meadows (Pallister 1974; Shackleton et al. 1999), moist draws (Pallister 1974; Shackleton et al. 1999), stream sides (Pallister 1974; Shackleton et al. 1999), talus slopes (Shackleton et al. 1999), plateaus (Shackleton et al. 1999), deciduous forests (Erickson 1972; Shackleton et al. 1999), clear-cut or burned forests (Erickson 1972; Risenhoover

and Bailey 1985; Shackleton et al. 1999), and conifer forests (Erickson 1972; Pallister 1974; Shackleton et al. 1999). Different habitats meet various bighorn sheep needs, so their use varies daily and seasonally as bighorn requirements for food, security cover, mating and lambing grounds, and thermal regulation change (Risenhoover and Bailey 1985; Risenhoover et al. 1988; Shackleton et al. 1999). Talus slopes, rock outcrops, and cliffs are used for resting, lambing, and security unless they are vegetated; then they become important foraging areas (Erickson 1972; Schirokauer 1996; Shackleton et al. 1999). Deciduous and coniferous forests are used sparingly due to their low horizontal visibility, but open forest stands can be important habitats for foraging and thermal cover (Pallister 1974; Shackleton et al. 1999). Wakelyn (1987) reported that open habitats with high visibility were used most in Colorado regardless of vegetation associations.

Diet Selection

Forbs often contribute the greatest number of species to bighorn diets in winter and spring, however grasses usually dominate bighorn diets based on percent composition (Shackleton et al. 1999; Wagner and Peek 2006). The relative proportions of forbs, grasses, and shrubs that contribute to bighorn diets vary considerably among populations (Pallister 1974; Keating et al. 1985; Shackleton et al. 1999; Wagner and Peek 2006). Therefore, depending on the population, bighorn diets can be dominated by forbs, grasses, or shrubs (Shackleton et al. 1999; Wagner and Peek 2006). Rocky Mountain bighorn sheep diets also change seasonally (Wagner and Peek 2006). Forbs are consumed in the greatest quantities in spring and summer, when these plants are most readily

available (Pallister 1974; Shackleton et al. 1999). Forbs are eaten less frequently in fall and winter after they senesce and decay (Shackleton et al. 1999; Wagner and Peek 2006). Grasses and shrubs are consumed in the greatest quantities in summer and spring, respectively (Pallister 1974; Shackleton et al. 1999). Bighorn sheep generally eat grasses, forbs, and browse in proportion to their availability (Keating et al. 1985; Shackleton et al. 1999; Wagner and Peek 2006).

Elevation, Slope, and Aspect

Previous research has identified slope, aspect, and elevation to be important habitat variables for bighorn sheep (Giest 1971; Shannon et al. 1975; Tilton and Willard 1982; Smith et al. 1991; Johnson and Swift 2000; Zeigenfuss et al. 2000; Dicus 2002; DeCesare 2002; Mooring et al. 2004). Bighorn sheep generally use lower elevation areas in winter and higher elevation areas in summer, because snow levels are usually less at lower elevations (Shackleton et al. 1999). Lower minimum elevation and greater range in elevation were features associated with greater numbers of bighorn sheep in a Colorado population (Wakelyn 1987). Bighorn sheep inhabit defined summer and winter ranges, and spend spring and fall migrating to these seasonal ranges (Geist 1971; Shackleton et al. 1999). Migration among seasonal ranges at different elevations provides important nutritional advantages.

Most bighorn winter ranges include steep south, southwestern, or southeastern-facing slopes, whereas north, east, and west-facing slopes usually dominate bighorn sheep summer ranges (Oldemeyer et al. 1971; Pallister 1974; Shackleton et al. 1999).

Steep slopes appear to be a significant feature even though the severity of the slopes used by bighorn sheep varies between populations (Smith et al. 1991; Johnson 1995; Wakelyn 1987; Shackleton et al. 1999; Singer et al. 2000; Mooring et al. 2004). Seasonal use of different slopes and aspects result in a mosaic of plant communities that provide a variety of foraging opportunities for bighorns (Shackleton et al. 1999).

Escape Terrain

Mountain sheep are often forced to choose between habitat resources such as forage, security cover or terrain, and thermal cover (Festa-Bianchet 1988; Wehausen 1996; Rachlow and Bowyer 1998; Berkley 2005). Bighorn sheep sight predators at great distances and evade them by retreating into steep, rocky terrain (Geist 1971; Risenhoover et al. 1988; Shackleton et al. 1999; Dicus 2002). Escape terrain is defined as areas greater than 0.7 ha in size with continuous steep slopes of ≥ 27 degrees and < 85 degrees, possessing rocky outcrops and/or cliffs (Geist 1971; McCollough et al. 1980; Smith et al. 1991; Schirokauer 1996; Zeigenfuss et al. 2000; DeCesare 2002; Dicus 2002; DeCesare and Pletscher 2006). Bighorn sheep seldom venture more than 300-500 m from escape terrain (Shannon et al. 1975; Gionfriddo and Krausman 1986; Wakelyn 1987; Smith et al. 1988; Dicus 2002), except when an area that is 500-1000 m wide is bounded on at least two sides by escape terrain (Smith et al. 1991). Several studies have concluded that steep escape terrain with adjacent foraging habitats is the primary determinant of bighorn sheep spatial distribution and habitat use patterns (Wakelyn 1987; Risenhoover and Bailey 1985; Smith et al. 1991; Enk 1999).

Bighorn sheep group size increases and foraging efficiency decreases with increasing distance from escape terrain (Risenhoover and Bailey 1980; Rachlow and Bowyer 1998). The amount of escape terrain on a seasonal range is linearly related to the number of sheep present (Wakelyn 1987). The extent and distribution of escape terrain controls the distribution of a bighorn sheep population (Wakelyn 1987; Berkley 2005). The maximum distance that a herd routinely strays from escape terrain determines the amount of habitat available (Wakelyn 1987; Schirokauer 1996). Lambing habitat is comprised of especially rugged portions of escape terrain and the lack of lambing habitat can be a limiting factor on lamb survival (Geist 1971; Smith et al. 1988; Sweanor et al. 1996; Rachlow and Bowyer 1998; Dicus 2002).

Horizontal Visibility

Many bighorn habitat studies or habitat suitability models have highlighted horizontal visibility as a key determinant of bighorn habitat (Risenhoover and Bailey 1980; 1985; Smith et al. 1991; Johnson and Swift 2000; Zeigenfuss et al. 2000). Horizontal visibility allows bighorn sheep to sight predators at a safe distance and influences how far bighorns are willing to stray from escape terrain (Geist 1971; Risenhoover and Bailey 1980; Sweanor et al. 1996; Dicus 2002). The level of horizontal visibility describing suitable bighorn sheep habitat has ranged from 55% to 90% (Smith et al. 1991; Johnson 1995; Sweanor et al. 1996). Bighorn sheep will travel through vegetation types with horizontal visibility as low as 30-50% when migrating between seasonal ranges, however, bighorns prefer vegetation types with horizontal visibility of

60-80% or higher (Dicus 2002). Bighorn sheep in northwestern Montana avoided areas with greater than 75% tree canopy cover, when tree canopy cover was used to indirectly define horizontal visibility (Tilton and Willard 1982). 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).

Landscape Ruggedness

In an effort to quantify escape terrain researchers have used various measures of slope (Smith et al. 1991; Turner et al. 2004), indices of ruggedness (Divine et al. 2000), or a combination of both (McKinney et al. 2003). The first recognized method for quantifying ruggedness was the land surface ruggedness index (LSRI) developed by Beasom et al. (1983). This index assumed that ruggedness is a function of total length of topographic contour lines in a given area. Another terrain ruggedness index was created as an alternative metric using digital terrain data and a Geographic Information System (GIS) (Riley et al. 1999). This index quantified the total elevation change across a given area. However, both of these indices may be strongly correlated with slope, and neither index directly measures the variability in topographic aspect and gradient (Sappington et al. 2007). Therefore, these indices may not clearly distinguish steep, even terrain (high slope and low ruggedness) from steep terrain that is uneven and broken (high slope and high ruggedness) (Sappington et al. 2007).

An ideal measure of ruggedness should contribute to a multivariate representation of topography and incorporate variability in both the aspect and gradient component of

slope (Sappington et al. 2007). Bighorn sheep may perceive ruggedness and slope differently when assessing escape terrain, so it is important to quantify these characteristics independently. Vector ruggedness measure (VRM) directly measures the differences of terrain more independently of slope than did the terrain ruggedness index or the land surface ruggedness index (Sappington et al. 2007). By separating ruggedness from slope, VRM allows these terrain components to be treated as separate variables when quantifying landscapes for habitat analysis (Sappington et al. 2007). Values for VRM can range from 0 (flat) to 1 (most rugged), however, values on natural terrains are rarely > 0.2 (Sappington et al. 2007).

Bighorn adult females perceive escape terrain using both ruggedness and slope (Sappington et al. 2007). Recent studies using VRM concluded both slope and ruggedness to be important factors in seasonal habitat selection and in habitat shifts during parturition (Bangs et al. 2005a; 2005b). Postparturition sites were both steeper and more rugged than preparturition sites in New Mexico, indicating adult females selected escape terrain that offered lambs the greatest ability to evade predators (Bangs et al. 2005b). Predation risk is among the factors driving selection by bighorn sheep for rugged terrain (Berkley 2005).

Solar Radiation Index

Solar radiation interacts with many biological processes that influence wildlife distribution and habitat selection (Keating et al. 2007). A solar radiation index (SRI) that combines latitude, slope, and aspect has been proven to be a significant predictor of

habitat use by bighorn sheep (DeCesare 2002; Dicus 2002). SRI is designed to be proportional to the amount of solar radiation that would theoretically be received in a given area in the absence of factors such as atmospheric interference, cloud or vegetation cover, or shading due to topography (Keating et al. 2007). The index is limited to the domain $-1 \leq \text{SRI} \leq 1$, however, the effect of latitude causes some values not to be possible everywhere (Keating et al. 2007). For example, at 45° latitude, SRI values range between -0.707 and +1 (Keating et al. 2007). SRI may correlate to habitat used by bighorns based on their frequent use of steep, south-facing slopes (Dicus 2002). DeCesare (2002) found SRI to be a stronger explanatory variable than aspect. Dicus (2002) found SRI to have the advantage of being a single continuous variable and believed it should receive more use in future Geographic Information System (GIS) habitat modeling.

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CHAPTER 3

HABITAT FEATURES POTENTIALLY LIMITING A BIGHORN SHEEP
POPULATION IN WESTERN MONTANAIntroduction

Rocky Mountain bighorn sheep are native to Montana and have had varied population stability over time. In 1950, Couey (1950) estimated there were 1,200 bighorn sheep in Montana. An estimated 1,400-1,700 bighorns remained in 1960 (Buechner 1960) and populations increased to approximately 3,100 bighorns in Montana in 1974 (Trefethen 1975). Despite fourteen major die-offs since 1984, resulting in losses of bighorns ranging from 75-97% of a given population affected by the die-off, there were an estimated 7,185 bighorns in Montana in 2008 (Carlsen and Erickson In Press).

Transplant programs have successfully reestablished extirpated populations in several areas of Montana (Buechner 1960; Geist 1971; Aune et al. 1998). However, local populations remain fragmented and small, despite improving bighorn sheep numbers overall (Douglas and Leslie 1999; DeCesare and Pletscher 2006). Several factors have contributed to unsuccessful translocation attempts including inadequate habitat, competition with other ungulates, diseases from domestic livestock, and human disturbances (Smith et al. 1988; Smith et al. 1991; Shackleton et al. 1999; Johnson and Swift 2000).

The Tendoy Mountains Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) herd, in western Montana, has struggled since its inception in 1984. This

population has experienced two die-offs, in which the population was reduced by 75% both times (Aune et al. 1998; C. Fager, personal communication, March 2007).

Additionally, population growth since these die-offs has been extremely slow. This contrasts with a thriving population (Lost Creek) that occupies similar rangeland and open forest habitat in western Montana. The Lost Creek population has only experienced one die-off since its inception in 1967 (R. Vinkey, personal communication, March 2007).

Past research has identified domestic sheep (*Ovis aries*) as a potential source of pneumophilic bacteria to bighorn sheep (Martin et al. 1996). However, not all bighorn die-offs are attributed to contact with domestic sheep (Aune et al. 1998; Shackleton et al. 1999). The Lost Creek and Tendoy Mountains populations have similar histories of contact with domestic sheep in close proximity to seasonal ranges of both populations. Therefore, it is possible that the instability of the Tendoy Mountains population has been induced or partially induced by other factors.

Management of Rocky Mountain bighorn sheep has focused on: 1) population demographics, 2) immunological state, and 3) habitat characteristics (K. Aune, personal communication, November 2007). Demographic targets have been identified for persistent populations (Douglas and Leslie 1986; Berger 1990; Smith et al. 1991). Habitats suitable for bighorn sheep have been identified (Risenhoover and Bailey 1985; Zeigenfuss et al. 2000), and bighorn sheep population response to immunological stressors has been documented (Jones and Worley 1994; Monello et al. 2001). However, limited research has documented how habitat differences between stable and less stable

bighorn populations influence their success. Habitat quality influences reproductive success of bighorn sheep and contributes to the probability of a die-off (Festa Bianchet 1988; Singer et al. 2000). Habitat differences may be contributing to the instability of the Tendoy Mountains bighorn sheep population.

Therefore, we performed a detailed habitat comparison of the Tendoy Mountains and Lost Creek populations to evaluate potential habitat differences. The objective of this study was to identify potential limiting habitat factors for the Tendoy Mountains bighorn sheep population in western Montana.

Materials and Methods

Two bighorn sheep populations, one stable and one less stable, which occupy rangeland and open forest habitats in Montana, have been included in this study: 1) Lost Creek, and 2) Tendoy Mountains. Population stability was characterized for each herd based on the history of the population, including approximate date of inception, number of die-offs, number of transplants, and population trends (Aune et al. 1998; C. Fager, personal communication, March 2007; R. Vinkey, personal communication, March 2007). A stable population was defined as a population with one or less die-offs in 40 years, and less stable was defined as a population with more than one die-off in 40 or less years. A die-off was defined as a sudden (<12 months) catastrophic reduction in the population exceeding 50% of the total population (Shackleton et al. 1999). A stable population also was defined to have a sustained population size of > 125 bighorns, and to have had no population augmentation after the initial transplant.

Herd Histories

Lost Creek Twenty-five bighorns transplanted from the Sun River herd established the Lost Creek bighorn sheep herd in 1967 (Aune et al. 1998). By 1974, more than 80 sheep were present, and despite an aggressive removal program beginning in 1986, the herd had grown to 311 observed sheep in 1991 (Aune et al. 1998). A pneumonia die-off began in September 1991 and the population was reduced by 60% to 116 observed sheep in 1994 (Aune et al. 1998). The population has since rebounded from this die-off, is estimated to contain more than 300 sheep in 2008, and has had no further die-offs (R. Vinkey, personal communication, March 2007). Domestic sheep have occupied lands adjoining the summer and winter ranges of the Lost Creek herd since the herds' inception (i.e., 40⁺ years).

Tendoy Mountains Thirty-six bighorns were initially transplanted into the Tendoy in 1984 from the Rock Creek herd. Fifteen sheep from the Perma-Paradise herd supplemented the Tendoy's herd in 1985 and the herd grew rapidly to 92 sheep by 1988 (Aune et al. 1998). In 1993, a pneumonia epizootic, occurring from September through December, eliminated approximately 75% of the population (Aune et al. 1998). Twenty sheep from Rock Creek again supplemented this herd in 1997, but they did not survive long enough to establish a reproductive herd (C. Fager, personal communication, March 2007). A second die-off occurred in 1999 and the population was again reduced by 75%. In 2002, this herd was supplemented with 30 sheep from the Sun River herd, and grew steadily to 60 sheep by 2004 (C. Fager, personal communication, March 2007). As of

2008 the Tendoy Mountains herd has approximately 100 sheep, including the bighorn sheep that migrate north from Idaho to summer near the year-round resident Tendoy Mountains bighorns. Domestic sheep have occupied lands adjoining the summer and winter ranges of the Tendoy Mountains herd since the herds' inception (i.e., 25⁺ years).

Study Areas

The Lost Creek and Tendoy Mountains bighorn sheep herds occupy rangeland and open forest habitats in western Montana. Topography in these areas is gentle at lower elevations, becoming markedly steeper with increasing elevation, with generally open, flat meadows at the highest elevations. Mountain grassland and sagebrush grassland vegetation occupy low-elevations, with mountain grasslands at mid- to high elevations. Mountain grasslands are dominated by rough fescue (*Festuca campestris* Rydb.), bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), and Idaho fescue (*Festuca idahoensis* Elmer). Sagebrush grasslands are dominated by mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle), bluebunch wheatgrass, and Idaho fescue. Mountain shrub vegetation (e.g., curleaf mountain mahogany (*Cercocarpus ledifolius* Nutt.)) is found around rock and scree outcrops, and deciduous trees (e.g., aspen (*Populus tremuloides* Michx.)) are found near some waterways. Open conifer forest vegetation is found adjacent to dense conifer forest habitats, usually in transition zones between dense forests and mountain or sagebrush grassland vegetation. Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), ponderosa pine (*Pinus ponderosa* C. Lawson), lodgepole pine (*Pinus contorta* Douglas ex Louden), and Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) are the dominant conifers.

Bighorn sheep occupy identifiable ranges in summer and winter (Shackleton et al. 1999), therefore the focus of this study was on those seasonal ranges. Four separate study sites were used: 1) Lost Creek summer range, 2) Lost Creek winter range, 3) Tendoy Mountains summer range, and 4) Tendoy Mountains winter range. The Lost Creek summer range is approximately 20,600 ha and the winter range is about 6,400 ha (Fig. 1). The Tendoy Mountains summer range is approximately 18,400 ha and the winter range is about 7,300 ha (Fig. 2).

The Lost Creek bighorn sheep herd is located 3 km northwest of Anaconda, MT and is located in the Flint Creek and Anaconda/Pintler Mountain Ranges. This herd occupies elevations ranging from 1,600 m to 2,750 m in the summer and 1,700 m to 2,500 m in the winter, with mean annual precipitation of 38 cm (WRCC 2008a). The Lost Creek bighorn sheep herd is located approximately 186 km north of the Tendoy Mountains bighorn sheep herd. The Tendoy Mountains bighorn sheep herd is located 10 km west of Dell, MT in the Tendoy Mountain Range. This herd occupies elevations ranging from 2,000 m to 2,850 m in the summer and 2,000 m to 2,750 m in the winter, with a mean annual precipitation of 24 cm (WRCC 2008b). Both populations are in the Montana Rangeland Resource Unit 43BS –Central Rocky Mountains South Major Land Resource Area (USDA-NRCS 2008). The geologic parent material of the Lost Creek ranges is granitic igneous rocks (Veseth and Montagne 1980). The geologic parent material of the Tendoy Mountains bighorn sheep ranges is predominantly carbonaceous, varying from nearly pure limestone to dolomite (Veseth and Montagne 1980).

Figure 1. Summer and winter ranges of the Lost Creek (stable) bighorn sheep population near Anaconda, MT.

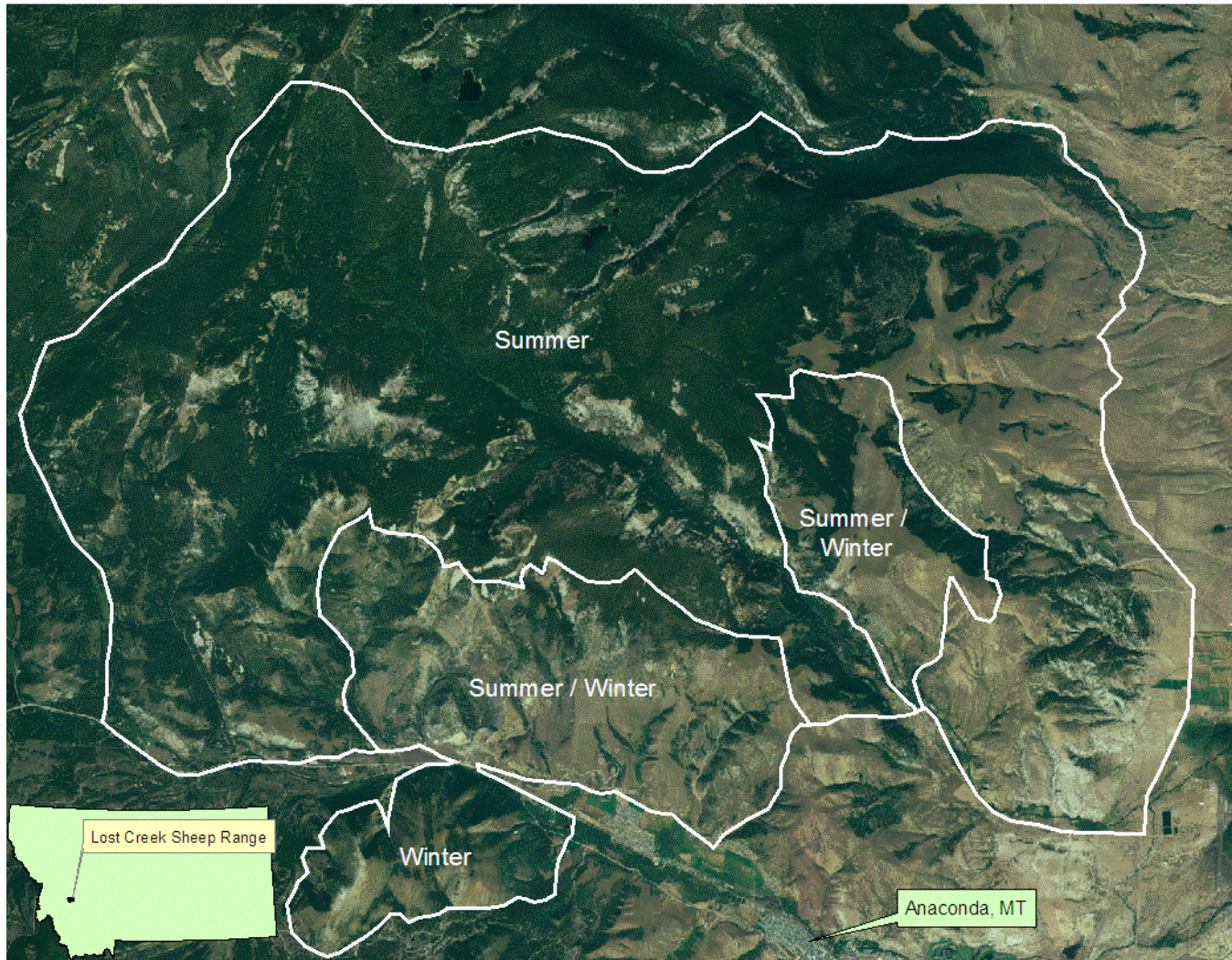
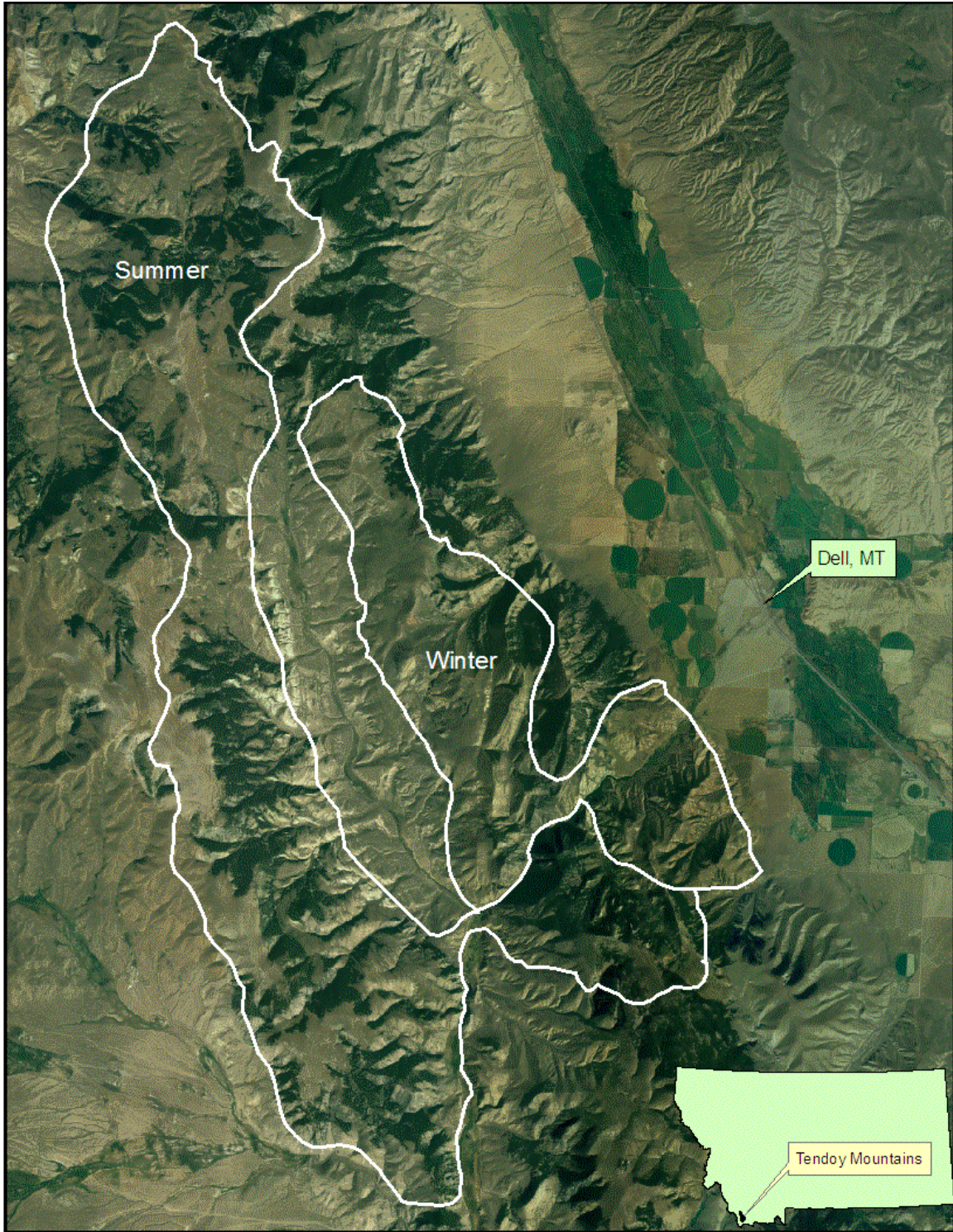


Figure 2. Summer and winter ranges of the Tendoy Mountains (less stable) bighorn sheep population near Dell, MT.



Approach

In Summer 2007 and 2008, I evaluated the spatial and vegetative habitat characteristics of summer and winter ranges of the Lost Creek and Tendoy Mountains populations. The habitat variables that I evaluated are unlikely to be influenced by fine-scale weather or disturbance patterns. The habitat variables selected for sampling are slow to change and generally representative of large-scale temporal and spatial characteristics of these bighorn sheep seasonal ranges, both presently and historically. Land cover, slope, aspect, elevation, landscape ruggedness, solar radiation index (SRI), and distance to escape terrain were measured using a Geographic Information System (GIS). Shrub canopy cover, graminoid and forb frequency, and horizontal visibility were measured in the field.

GIS Sampling

Boundaries of summer and winter ranges of the 2 populations were provided by the Montana Department of Fish, Wildlife, and Parks wildlife biologists for these two areas (C. Fager, personal communication, March 2007, and R. Vinkey, personal communication, March 2007) and were digitized from topographic maps to create seasonal range maps in GIS. Montana GAP Analysis (Fisher et al. 1998) and Canopy 2001 (USGS 2001) satellite derived data were used to characterize land cover of the study sites: 1) in overall summer and winter ranges, and 2) in areas of the summer and winter ranges located within 500 m of bighorn sheep escape terrain. Areas located within 500 m of escape terrain were designated “prime habitat” because bighorn sheep seldom venture more than 500 m from escape terrain (Shannon et al. 1975; Wakelyn 1987; Smith

et al. 1991; Dicus 2002). The proportion of each seasonal range comprised by the prime habitat was quantified.

Land cover of summer and winter ranges was characterized separately into 8 categories: 1) mountain grassland (GAP codes: 3110, 3130, 3140, 3150, 3160, 3170, 3180, 8101), 2) sagebrush grassland (GAP codes: 3318, 3350, 3351, 3352, 3353, 3354), 3) mountain shrub (GAP codes: 3210, 3212, 3213, 3301), 4) open coniferous forest (GAP codes: 4203, 4205, 4208, 4212, 4214, 4223, 4260, 4270, 4290, 4300, 6110), 5) dense coniferous forest (GAP codes: 4203, 4205, 4208, 4212, 4214, 4223, 4260, 4270, 4290, 4300, 6110), 6) deciduous forest (GAP codes: 4101, 6120, 6130), 7) non-forested riparian (GAP codes: 6210, 6310), and 8) rock and scree (GAP codes: 7301, 7400, and 7500, 7800). Open coniferous forest was classified as areas with 20-39% conifer canopy cover, and dense coniferous forest was classified as areas \geq 40% conifer canopy cover. The proportion of summer range and winter range comprised of each land cover type was determined.

Random points distributed across summer and winter ranges (n=200 points/seasonal range) were used to characterize seasonal habitats. Random points distributed across summer and winter ranges in the prime habitats were used to characterize these areas (n=100 points/prime seasonal range). All random points were located a minimum of 60 m apart to ensure independence of sample locations. Random points were generated using the Random function in Arc Macro Language (AML) in Workstation Arc/Info (ESRI 2002). Digital Elevation Models (DEMs) (USGS 2002)

were used to characterize the slope, aspect, elevation, landscape ruggedness, and SRI of each random point.

Elevation, Slope, and Aspect The elevation of each random point corresponded to the elevation value of the 30 x 30-m cell located at that point on the DEM. Aspect and percent slope were calculated for each random point using the elevation values of surrounding cells. Percent slope was calculated with an algorithm and identified as the maximum rate of change in value from its neighbors in a 3 x 3-cell area, and aspect was determined to be the direction of the maximum downhill slope gradient in that area. Aspect was reported in degrees clockwise from due north and then transformed for analysis using a cosine transformation (Brewer 2004).

Landscape Ruggedness Landscape ruggedness was determined using the methods of Sappington et al. (2007). Ruggedness was calculated by decomposing the magnitude of change in the x, y, and z direction within a 3 x 3 cell neighborhood (i.e., 90 x 90-m neighborhood) in a digital elevation model and then estimating the resultant vector 'r'. The landscape ruggedness index was calculated by subtracting the magnitude of the resultant vector divided by the number of cells in the neighborhood from 1. The resulting ruggedness index ranged from 0 in flat areas to 1 in areas with complex, steep terrain. Following Sappington et al. (2007) the ruggedness index was calculated over a 3 x 3 neighborhood to avoid the unrealistic smoothing that is likely to occur using larger neighborhoods. A script for computing landscape ruggedness was accessed for the ArcView program (ESRI 1992-1999) at ArcScripts website: www.esri.com/arcscripts.

Solar Radiation Index Solar radiation index (SRI) was calculated on a cell by cell basis from a digital elevation model following methods suggested by Keating et al. (2007). $SR_i = \cos(l_i) * \cos(s_i) + \sin(l_i) * \sin(s_i) * \cos(ta_i)$, where l = latitude, s = slope, and $ta = 180 - \text{aspect}$. SRI ranges from -1 in areas that receive small amounts of solar radiation to 1 in areas that receive large amounts of solar radiation, such as steep south-facing slopes.

Escape Terrain Escape terrain was defined as areas with continuous slopes > 27 degrees and < 85 degrees, that are ≥ 0.7 ha in size and possessing occasional rock outcroppings and/or cliffs (Geist 1971; McCollough et al. 1980; Smith et al. 1991; Schirokauer 1996; Zeigenfuss et al. 2000; DeCesare 2002; DeCesare and Pletscher 2006; Dicus 2002). To identify potential escape terrain, first areas with slopes ≤ 27 or ≥ 85 degrees were excluded using the raster tools in ArcGIS (ESRI 2002). Then areas that were < 0.7 ha in size were excluded. Lastly, any remaining areas that did not have rock and scree GAP codes (7301, 7400, 7500, or 7800) were excluded. The remaining polygons fulfilled all the criteria necessary to be classified as escape terrain. A 500-m buffer polygon was placed around all of the escape terrain polygons to simulate the distance that bighorns are usually willing to travel from escape terrain (Shannon et al. 1975; Wakelyn 1987; Smith et al. 1991; Dicus 2002).

Distance to Escape Terrain Three-dimensional (vertical and horizontal combined) distances from random points to escape terrain were defined as the shortest straight-line distance from the random point to the feature and also included the additional distance

accrued by following the ups and downs of the undulating terrain along the way. Distance measurements were obtained by summing three-dimensional distance values obtained for each 30-m section of a line between the random point and the nearest escape terrain polygon across the undulating terrain using the SurfaceXsection function in Arc Macro Language (AML) in Workstation Arc/Info (ESRI 2002).

Grassland Vegetative Variables

Shrub canopy cover, graminoid and forb frequency, and horizontal visibility were sampled in early- to mid summer of 2007 and 2008 in the grassland habitat (e.g., mountain grassland and sagebrush grassland vegetation types) of bighorn sheep summer ranges. Shrub canopy cover, graminoid frequency, and horizontal visibility were sampled in mid- to late summer of 2007 and 2008 in the grassland habitat of bighorn sheep winter ranges. Forb frequency was sampled in the summer ranges but not in the winter ranges because forbs are consumed in the greatest quantities in spring and summer, when these plants are most readily available (Pallister 1974; Shackleton et al. 1999), but forbs are eaten less frequently in fall and winter after they senesce and decay (Shackleton et al. 1999; Wagner and Peek 2006). GIS was used to generate 28 random points on each summer range and 25 random points on each winter range. These random points were stratified to the mountain grassland and sagebrush grassland habitats that bighorn sheep use most frequently for foraging. Random points were generated using the sampling tools in Hawth's tools for ArcGIS (Beyer 2008).

Summer ranges were sampled in early- to mid summer in order to capture the frequency of the forb component of their habitat. Winter ranges were sampled in mid- to

late summer when forbs were mostly dried and disintegrated. Global Positioning System (GPS) was used to navigate to the 28 random points on each bighorn sheep summer range and the 25 random points on each bighorn sheep winter range in Summers of 2007 and 2008.

Shrub Canopy Cover Total shrub canopy cover was estimated using the Line Intercept Method (USDA-USDI 1996). At each point, a 50-m transect was aligned due north and south, with the GPS waypoint located at the midpoint of the transect. The horizontal linear length of the vertical projection of shrub foliar cover that intercepts the transect was measured to the nearest centimeter, including all shrub species present.

Graminoid and Forb Frequency Graminoid and forb frequency was measured along the same 50-m transect using the Nested Frequency Method (USDA-USDI 1996). One hundred nested frequency quadrats, located at 0.5-m intervals along the 50-m transect, were sampled at each of the 106 random points. Within each of the 100 quadrats along the transect, graminoid and forb frequency was determined in 5x5-cm, 10x10-cm, 25x25-cm, and 25x50-cm quadrats. The proper size was considered to be the smallest quadrat that sampled a site's most abundant lifeform species at 63-86 % frequency (Curtis and McIntosh 1950). The 10 x 10-cm quadrat met this criterion on the majority of sampling locations.

Horizontal Visibility The staff-ball method was used to estimate horizontal visibility (Collins and Becker 2001). Collins and Becker (2001) found this method to be more precise than either the cover-pole (Griffith and Youtie 1988) or checkerboard target

(Nudds 1977) methods. A tennis ball was mounted on a staff that was driven into the ground at the GPS location. The bottom of the ball was adjusted to 90-cm above the ground (Risenhoover and Bailey 1985) to emulate the level of sight of a bighorn sheep. A circle was walked around the staff with a radius of approximately 20 m. Every 8th step, with my eye located 90 cm above the ground, I looked for the point where the ball and the right side of the staff intersect (Collins and Becker 2001). After completing the circle, horizontal visibility was calculated by dividing the number of times the point of ball/staff intersect was visible by the total number of attempts (e.g., 12 visible/20 total = 60% horizontal visibility) (DeCesare 2002).

A biologically meaningful radius to measure visibility was difficult to select based on variability in historic research. A radius of 20 m was used in previous studies of horizontal visibility (McCarty and Bailey 1992; DeCesare 2002) and corresponds to the diagonal radius of a 30-m x 30-m pixel, which is the spatial scale of my GIS data (DeCesare 2002).

Experimental Design and Statistical Analyses

This was an observational, non-replicated study. The experimental unit was each population's seasonal range (summer range, n=2; winter range, n=2; prime summer range, n=2; prime winter range, n=2). Logistic regression (SAS 2004) was used to identify habitat differences between the stable and less stable bighorn sheep populations in summer and winter. Odds ratios from the logistic regressions were used to identify potential limiting habitat variables for the less stable population. One set of logistic regression models included the GIS habitat variables: landscape ruggedness, SRI, slope,

aspect, elevation, and distance to escape terrain. Logistic regression with the GIS habitat variables compared the overall summer ranges, prime summer range habitat, overall winter ranges, and prime winter range habitat of the two bighorn populations. Another set of logistic regression models included the grassland vegetative variables: horizontal visibility, graminoid frequency, forb frequency, and shrub canopy cover. Logistic regression with the grassland vegetative variables compared the overall summer ranges and the overall winter ranges of the two populations. Population means of each habitat variable were compared using the Wilcoxon rank sums test (Ott 1977). All differences were considered significant at $P \leq 0.05$.

My experimental approach was to compare two populations, one stable and one less stable, that otherwise appear similar. The two populations both occupy rangeland and open forest habitat within the same major land resource area in western Montana. On the edges of their ranges both populations have similar exposure to domestic sheep. Mule deer and elk occupy both areas, but mule deer and elk numbers are not large in either area. If my comparisons of the physical habitat reveal no differences between the two populations, I will conclude that none of the physical habitat characteristics that I compare are likely contributing to population stability of the Tendoy Mountains herd. If differences are found in one or more of the physical habitat features, I will conclude that these habitat features may be contributing to the instability of the Tendoy Mountains population.

Results

Summer and winter ranges of the two bighorn sheep populations have similar proportions of land cover types with a few exceptions (Table 1). Mountain shrub and sagebrush grassland comprise larger portions of the summer ranges in the Tendoy Mountains population, whereas dense conifer forest is more prevalent in the Lost Creek summer and winter ranges. The Tendoy Mountains winter range has a greater proportion of sagebrush grassland. Maps of the GIS habitat variables are in the Appendix.

Summer Ranges

All six GIS habitat characteristics contributed significantly ($P \leq 0.05$; Table 2) in the logistic regression comparing the overall summer ranges of the Tendoy Mountains and Lost Creek populations ($P < 0.01$). Odds ratios and associated confidence intervals in Table 2 indicate that landscape ruggedness is the summer range habitat feature most likely influencing population stability. The less stable population has a higher mean ruggedness value in the overall summer range than the stable population (0.005 vs. 0.0033, respectively; Table 3).

Odds ratios in Table 2 indicate that SRI might also be influencing population stability, however, SRI does not differ between the stable and less stable populations in either the overall summer range ($P = 0.27$) or the prime summer range habitat ($P = 0.99$), averaging 0.655 and 0.655, respectively (Table 3). Odds ratios indicate that aspect also may be influencing population stability. The overall summer range of the less stable population is dominated by northwest-facing slopes, whereas the summer range of the

Table 1. Proportions of land cover types in the summer and winter ranges of the Lost Creek (stable) and Tendoy Mountains (less stable) bighorn sheep populations in western Montana.

Season	Land Cover	Overall Range		Prime Habitat	
		Stable	Less Stable	Stable	Less Stable
Summer	Grassland	23%	23%	9%	20%
	Mountain Shrub	2%	10%	1%	12%
	Sagebrush Grassland	8%	27%	4%	18%
	Non-forested Riparian	0%	0%	0%	0%
	Deciduous Forest	1%	1%	1%	0%
	Rock and Scree	4%	6%	10%	9%
	Open Conifer Forest	6%	10%	8%	11%
	Dense Conifer Forest	56%	23%	67%	29%
	Escape Terrain	9%	10%	22%	19%
Winter	Grassland	36%	39%	24%	35%
	Mountain Shrub	9%	4%	8%	3%
	Sagebrush Grassland	20%	35%	17%	32%
	Non-forested Riparian	0%	0%	1%	0%
	Deciduous Forest	0%	0%	1%	0%
	Rock and Scree	4%	7%	9%	12%
	Open Conifer Forest	5%	5%	9%	5%
	Dense Conifer Forest	26%	9%	32%	12%
	Escape Terrain	11%	11%	25%	21%

stable population is dominated by west-facing slopes ($P < 0.01$; Table 3). Odds ratios also indicate that aspect in the prime summer range may be influencing population stability (Table 2), but aspect in the prime summer range habitat does not differ ($P = 0.71$) between the stable and less stable populations, with the prime summer range of both populations dominated by east-facing slopes (Table 3). Confidence intervals surrounding the odds ratios for elevation, slope, and distance to escape terrain in the overall summer range and prime summer range all include 1.0 (Table 2), indicating that none of these habitat features are limiting population stability. Finally, although shrub canopy cover is greater in the summer range of the Tendoy Mountains population

Table 2. Logistic regression models comparing the Lost Creek (stable) and Tendoy Mountains (less stable) bighorn sheep populations in western Montana.

Range	Variable	<i>P</i> -value	Odds Ratio	Confidence Interval ($\alpha=0.05$)
Summer	Ruggedness	<0.01	>999	$999 \leq 999 \geq 999$
	SRI ¹	<0.01	81.89	$3.48 \leq 81.89 \geq 999$
	Aspect	<0.01	3.75	$1.77 \leq 3.75 \geq 7.96$
	Elevation	<0.01	1.01	$1.00 \leq 1.01 \geq 1.01$
	Slope	0.04	1.03	$1.00 \leq 1.03 \geq 1.07$
	Distance to Escape Terrain	<0.01	1.00	$1.00 \leq 1.00 \geq 1.00$
	Model	<0.01		
Prime Summer	SRI	0.01	189.77	$2.87 \leq 189.77 \geq 999$
	Aspect	0.02	3.65	$1.18 \leq 3.65 \geq 11.23$
	Elevation	<0.01	1.00	$1.00 \leq 1.00 \geq 1.00$
	Slope	0.04	1.02	$1.00 \leq 1.02 \geq 1.04$
	Distance to Escape Terrain	0.04	1.00	$1.00 \leq 1.00 \geq 1.01$
	Model	<0.01		
Winter	Ruggedness	0.05	>999	$11.84 \leq 999 \geq 999$
	SRI	<0.01	354.68	$4.46 \leq 354.68 \geq 999$
	Aspect	<0.01	10.80	$3.47 \leq 10.80 \geq 33.67$
	Elevation	<0.01	1.01	$1.01 \leq 1.01 \geq 1.01$
	Model	<0.01		
Prime Winter	SRI	0.04	277.50	$1.32 \leq 277.50 \geq 999$
	Aspect	0.01	6.99	$1.59 \leq 6.99 \geq 30.73$
	Elevation	<0.01	1.01	$1.00 \leq 1.01 \geq 1.01$
	Model	<0.01		

¹Solar radiation index (SRI)

Table 3. Means for habitat variables (\pm SE) for the Lost Creek (stable) and Tendoy Mountains (less stable) bighorn sheep populations in western Montana.

Range	Variable	Means	
		Stable	Less Stable
Summer	Ruggedness	0.003 (\pm 0.0004)a ²	0.005 (\pm 0.0005)b
	SRI ¹	0.66 (\pm 0.01)a	0.65 (\pm 0.01)a
	Aspect (degrees)	266 (\pm 0.05)a	305 (\pm 0.05)b
	Elevation (m)	2140 (\pm 21)a	2399 (\pm 14)b
	Slope (%)	16.09 (\pm 0.65)a	17.86 (\pm 0.61)b
	Distance to Escape Terrain (m)	1122 (\pm 75)a	833 (\pm 70)b
	Shrub Canopy Cover (%)	9 (\pm 3)a	15 (\pm 3)b
	Graminoid Frequency (%)	63 (\pm 6)a	63 (\pm 4)a
	Forb Frequency (%)	44 (\pm 4)a	56 (\pm 4)a
	Horizontal Visibility (%)	86 (\pm 3)a	88 (\pm 5)a
Prime Summer	Ruggedness	0.004 (\pm 0.0005)a	0.004 (\pm 0.0006)a
	SRI	0.65 (\pm 0.02)a	0.66 (\pm 0.02)a
	Aspect (degrees)	93 (\pm 0.07)a	91 (\pm 0.06)a
	Elevation (m)	2327 (\pm 21)a	2467 (\pm 18)b
	Slope (%)	38.32 (\pm 2.12)a	37.81 (\pm 1.85)a
	Distance to Escape Terrain (m)	142 (\pm 14)a	176 (\pm 16)a
Winter	Ruggedness	0.005 (\pm 0.0006)a	0.006 (\pm 0.0006)b
	SRI	0.72 (\pm 0.01)a	0.66 (\pm 0.01)b
	Aspect (degrees)	248 (\pm 0.04)a	272 (\pm 0.05)b
	Elevation (m)	2008 (\pm 15)a	2296 (\pm 13)b
	Slope (%)	17.79 (\pm 0.60)a	19.20 (\pm 0.58)a
	Distance to Escape Terrain (m)	919 (\pm 65)a	579 (\pm 42)b
	Shrub Canopy Cover (%)	14 (\pm 4)a	20 (\pm 3)a
	Graminoid Frequency (%)	60 (\pm 4)a	65 (\pm 4)a
	Horizontal Visibility (%)	83 (\pm 5)a	93 (\pm 5)a
Prime Winter	Ruggedness	0.006 (\pm 0.001)a	0.008 (\pm 0.001)b
	SRI	0.71 (\pm 0.02)a	0.68 (\pm 0.02)a
	Aspect (degrees)	254 (\pm 0.06)a	98 (\pm 0.06)b
	Elevation (m)	2128 (\pm 21)a	2294 (\pm 19)b
	Slope (%)	39.97 (\pm 1.60)a	42.69 (\pm 1.97)a
	Distance to Escape Terrain (m)	137 (\pm 14)a	143 (\pm 16)a

¹(SRI) Solar radiation index

²Means within rows followed by the same letter are not different ($P > 0.05$).

($P = 0.05$; Table 3), the logistic regression model with the grassland vegetative variables was not significant ($P = 0.11$).

Winter Ranges

Landscape ruggedness, SRI, aspect, and elevation all contributed significantly ($P \leq 0.05$; Table 2) in the logistic regression comparing the overall winter ranges, but slope and distance to escape terrain did not. Odds ratios indicate that landscape ruggedness is the habitat feature in the overall winter range most likely influencing population stability. The less stable population has greater mean ruggedness in its overall winter range than the stable population (0.006 vs. 0.005, respectively; $P < 0.01$; Table 3). SRI is also likely influencing population stability (Table 2), with the less stable population having a lower SRI than the stable population (0.655 vs. 0.722, respectively; $P < 0.01$; Table 3). Aspect appears to influence population stability but much less so than ruggedness and SRI. The overall winter range of the stable population is dominated by south-facing slopes, whereas the overall winter range of the less stable population is dominated by west-facing slopes ($P < 0.01$; Table 3). The small odds ratio for elevation indicates that the elevation of the overall winter range is unlikely affecting population stability (Table 2). None of the grassland habitat vegetative variables differ between the overall winter ranges of the stable and less stable populations (Table 3), and the logistic regression with the grassland vegetative variables in the overall winter ranges was not significant ($P = 0.06$).

Aspect, SRI, and elevation were the only three GIS habitat variables to contribute significantly ($P \leq 0.05$) in the logistic regression comparing the prime winter habitats.

Odds ratios indicate that SRI in the prime winter range may be affecting population stability, however, SRI does not differ between the stable and less stable populations (0.705 vs. 0.684, respectively; $P = 0.23$; Table 3). Aspect also may be influencing population stability (Table 2), with the prime winter habitat of the stable population dominated by southwest-facing slopes and the prime winter range of the less stable population dominated by east-facing slopes ($P = 0.04$; Table 3). The small odds ratio for elevation indicates that this characteristic of the prime winter range is an unlikely influence on population stability (Table 2).

Discussion

Previous research has shown that overcrowding, stress, parasites, and degraded range condition may contribute to the probability of a bighorn sheep die-off (Festa-Bianchet 1988; Singer et al. 2000). Bighorn sheep management has historically focused on population dynamics (Douglas and Leslie 1986; Berger 1990; Smith et al. 1991), immunology (Jones and Worley 1994; Monello et al. 2001), and habitat characteristics of suitable bighorn sheep habitat (Risenhoover and Bailey 1985; Zeigenfuss et al. 2000). Understanding habitat differences that may influence population stability is critical, and this understanding, in conjunction with knowledge regarding other potential bighorn sheep stressors (i.e., predation, disease, competition with other ungulates), is important for managing successful bighorn sheep populations.

Landscape ruggedness of the summer and winter ranges may be limiting population stability of the Tendoy Mountains bighorn sheep herd. The summer and

winter ranges of the Tendoy Mountains herd are both more rugged than those of the Lost Creek herd. Ruggedness values rarely exceed 0.2 in natural terrains (Sappington et al. 2007); therefore, although the extremely small ruggedness values in my study may seem similar, their numerical differences may be biologically meaningful. Adult bighorn ewes perceive the ruggedness and slope of their habitat separately (Bangs et al. 2005a, 2005b; Sappington et al. 2007), making it important to quantify ruggedness independently of slope. Landscape ruggedness is a relatively new metric in bighorn sheep habitat research, and ruggedness values from other studies are unavailable for comparison with my results.

Aspects in the summer and winter ranges may be limiting population stability of the Tendoy Mountains bighorn sheep herd. Northwest-facing slopes dominate the summer range of the Tendoy Mountains herd, west-facing slopes dominate the herd's overall winter range, and east-facing slopes dominate the herd's prime winter range. I hypothesize that bighorns on their summer range in the Tendoy Mountains are not favored by northwestern aspects because the cooler, moister growing conditions on northerly aspects may produce taller, denser vegetation that decreases horizontal visibility for bighorns (Risenhoover and Bailey 1985). The west-facing slopes that dominate the overall winter range of the Tendoy Mountains herd and the east-facing slopes that dominate the herd's prime winter range contrast with the southerly aspects most prevalent in the winter range of the Lost Creek herd and other stable bighorn sheep populations (Tilton and Willard 1982; Gionfriddo and Krausman 1986; Wakelyn 1987; Shackleton et al. 1999). Southerly aspects maximize heat gains from direct and indirect solar radiation, thereby reducing cold stress in bighorns (Geist 1971; Shackleton et al.

1999). Southerly aspects also have less snow cover and more forage available in winter (Oldemeyer et al. 1971; Erickson 1972; Shackleton et al. 1999; Keating et al. 2007).

The amount of solar radiation received in the winter range of the Tendoy Mountains bighorn sheep herd may be limiting the stability of the population. Areas receiving more solar radiation should experience shallower snow depths (Keating et al. 2007) that increase foraging efficiency (Geist 1971), and bighorns' frequent use of steep, south-facing slopes in winter may be correlated with SRI (DeCesare 2002). SRI has been found to be a stronger explanatory variable than aspect (DeCesare 2002), and SRI has the added advantage of being a single continuous variable (Dicus 2002). Like landscape ruggedness, SRI is a relatively new metric in bighorn sheep habitat research, and few studies using SRI have been published. DeCesare (2002) and Dicus (2002) included SRI in their research, but neither author reported actual values to enable me to make comparisons with my data. However, the SRI values for the Lost Creek and Tendoy Mountains winter ranges were similar to those reported by Keating et al. (2007) from a study of winter bighorn sheep habitat in south-central Montana.

My results indicate it is unlikely that elevation, slope, or proximity of escape terrain limits the population stability of the Tendoy Mountains bighorn sheep herd. Similarly, it is unlikely that any of the grassland vegetative features investigated in this study (i.e., horizontal visibility, graminoid frequency, forb frequency, or shrub canopy cover) limit the population stability of the Tendoy Mountains bighorn sheep herd.

Management Implications

Understanding habitat differences between areas occupied by stable and less stable bighorn sheep populations may provide important information for managers of Rocky Mountain bighorn sheep. The objective of this study was to identify physical habitat features that are potentially limiting the Tendoy Mountains bighorn sheep herd in western Montana. Results from this study indicate that landscape ruggedness and aspect in summer ranges, and landscape ruggedness, aspect, and SRI in winter ranges are the habitat characteristics most likely influencing population stability. Landscape ruggedness and SRI are relatively new habitat variables that require more research to determine threshold values for bighorn sheep habitat. Values from my study provide initial insights into potential threshold values for landscape ruggedness and SRI for Rocky Mountain bighorns. My results suggest that landscape ruggedness values of ≥ 0.005 may describe habitat too rugged to support thriving, stable populations of Rocky Mountain bighorns. Additionally, my results suggest that SRI values in winter range may need to exceed 0.655 to support stable populations of Rocky Mountain bighorn sheep. Until more research can better pinpoint threshold values for landscape ruggedness and SRI, my results suggest that future translocations and reintroductions of Rocky Mountain bighorn sheep should be restricted to rangeland and open forest habitats where summer range is dominated by west-facing slopes and winter range is dominated by southerly aspects.

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APPENDIX A

MAPS OF THE HABITAT VARIABLES CHARACTERIZED USING GIS

Figure 3. Elevation in the summer and winter ranges of the Lost Creek (stable) bighorn sheep population.

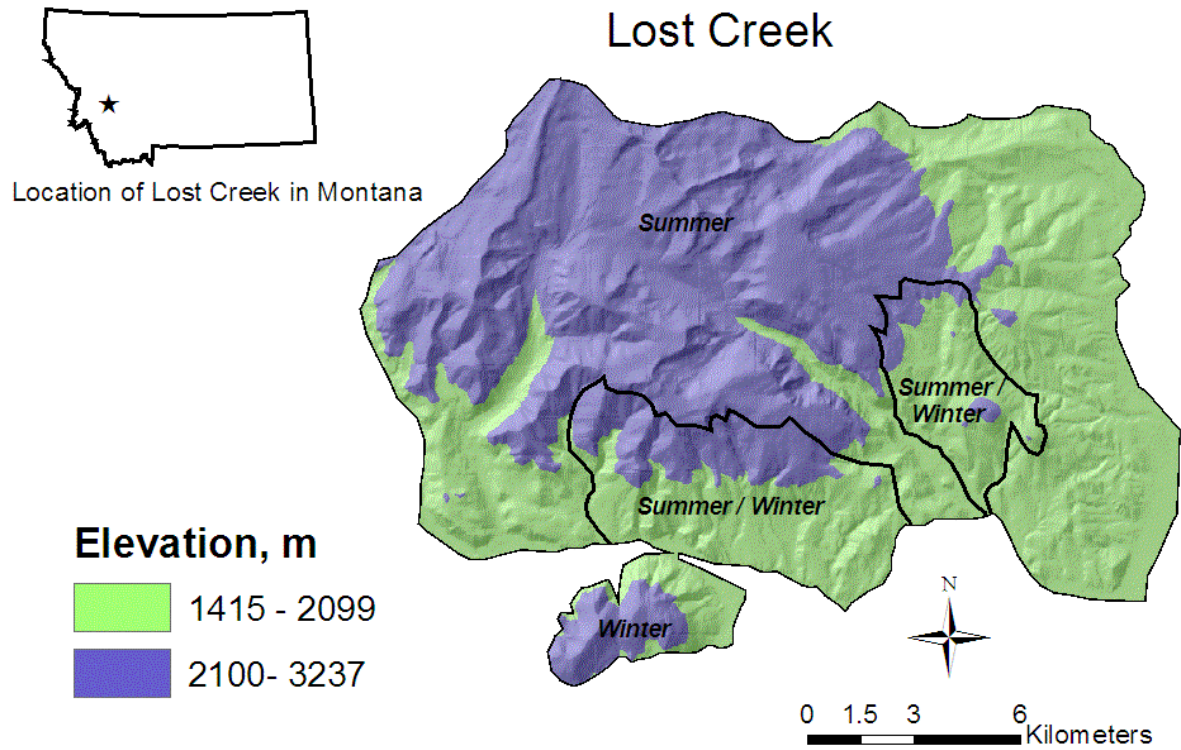


Figure 4. Elevation in the summer and winter ranges of the Tendoy Mountains (less stable) bighorn sheep population.

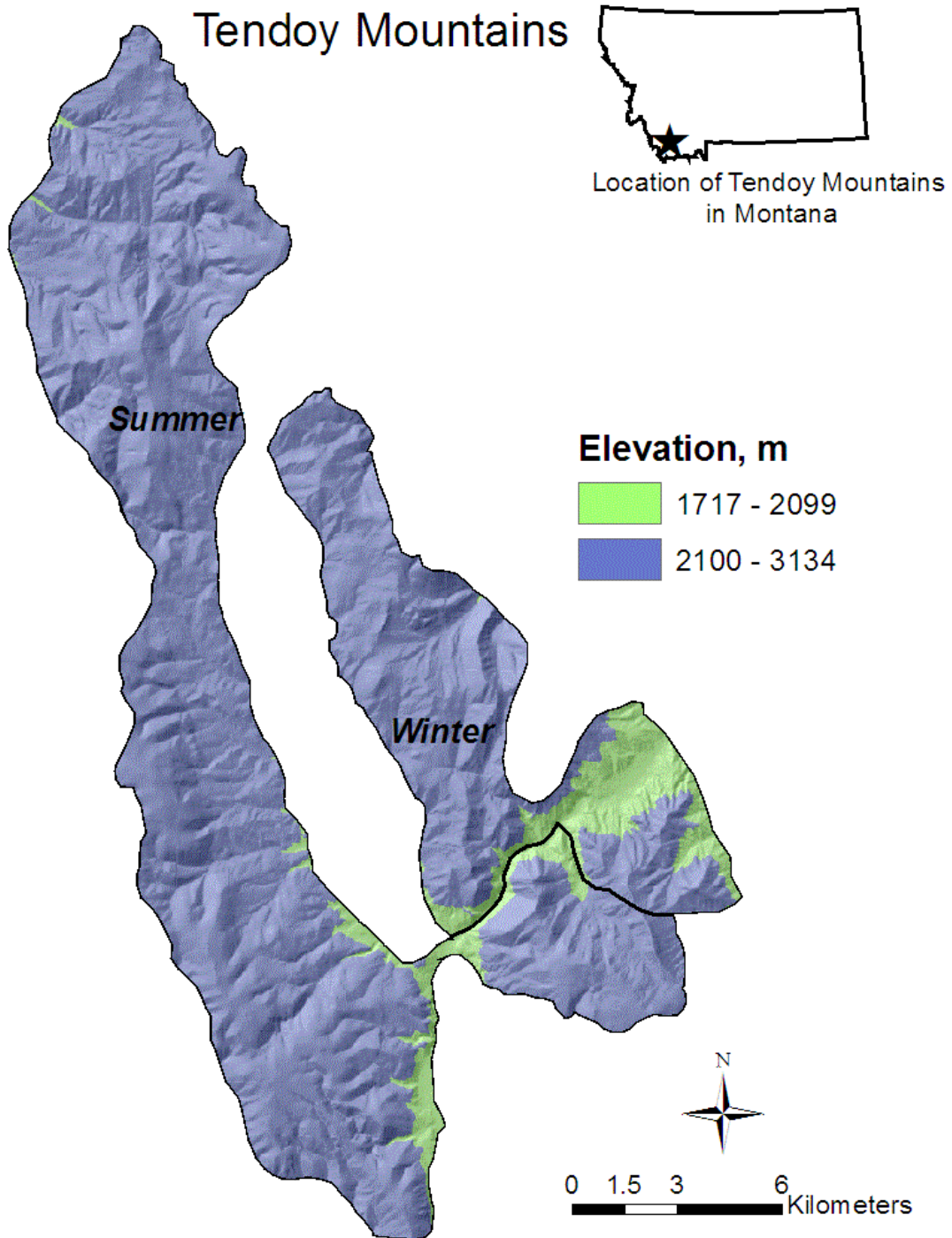


Figure 5. Slope (%) in the summer and winter ranges of the Lost Creek (stable) bighorn sheep population.

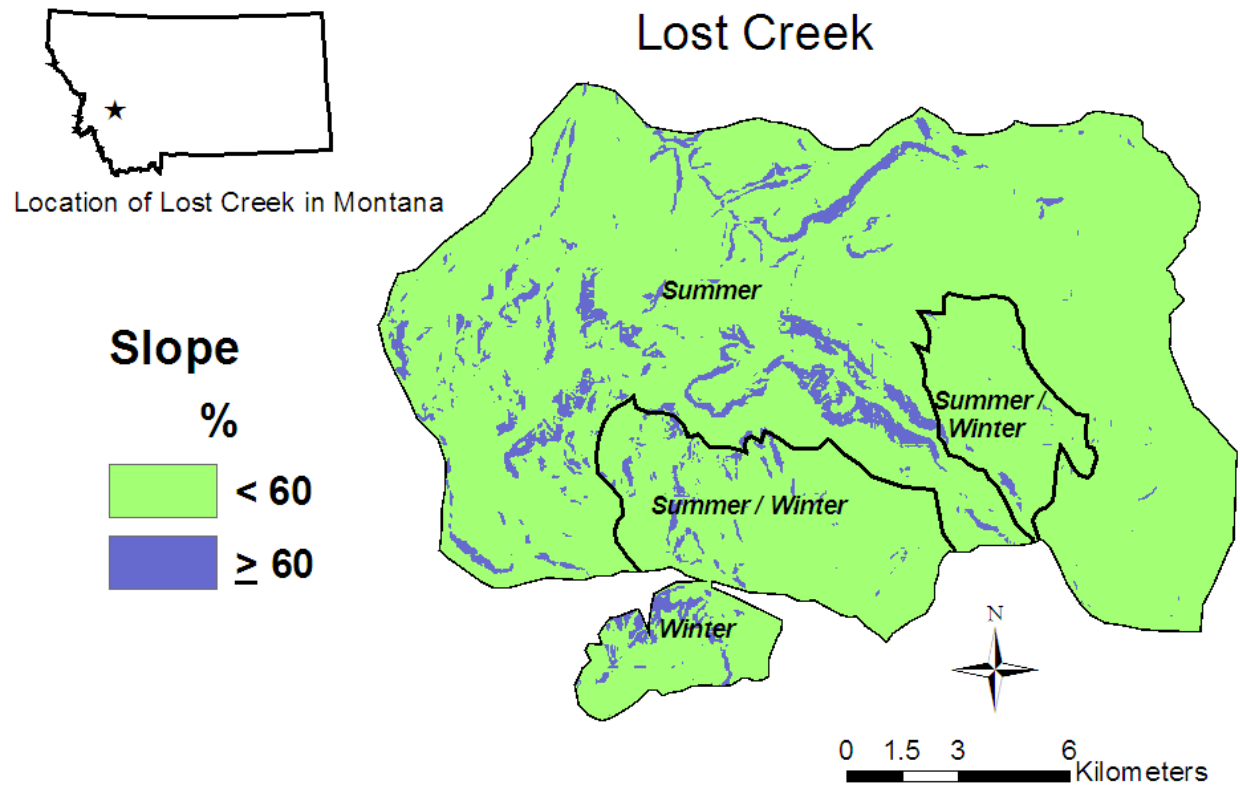


Figure 6. Slope (%) in the summer and winter ranges of the Tendoy Mountains (less stable) bighorn sheep population.

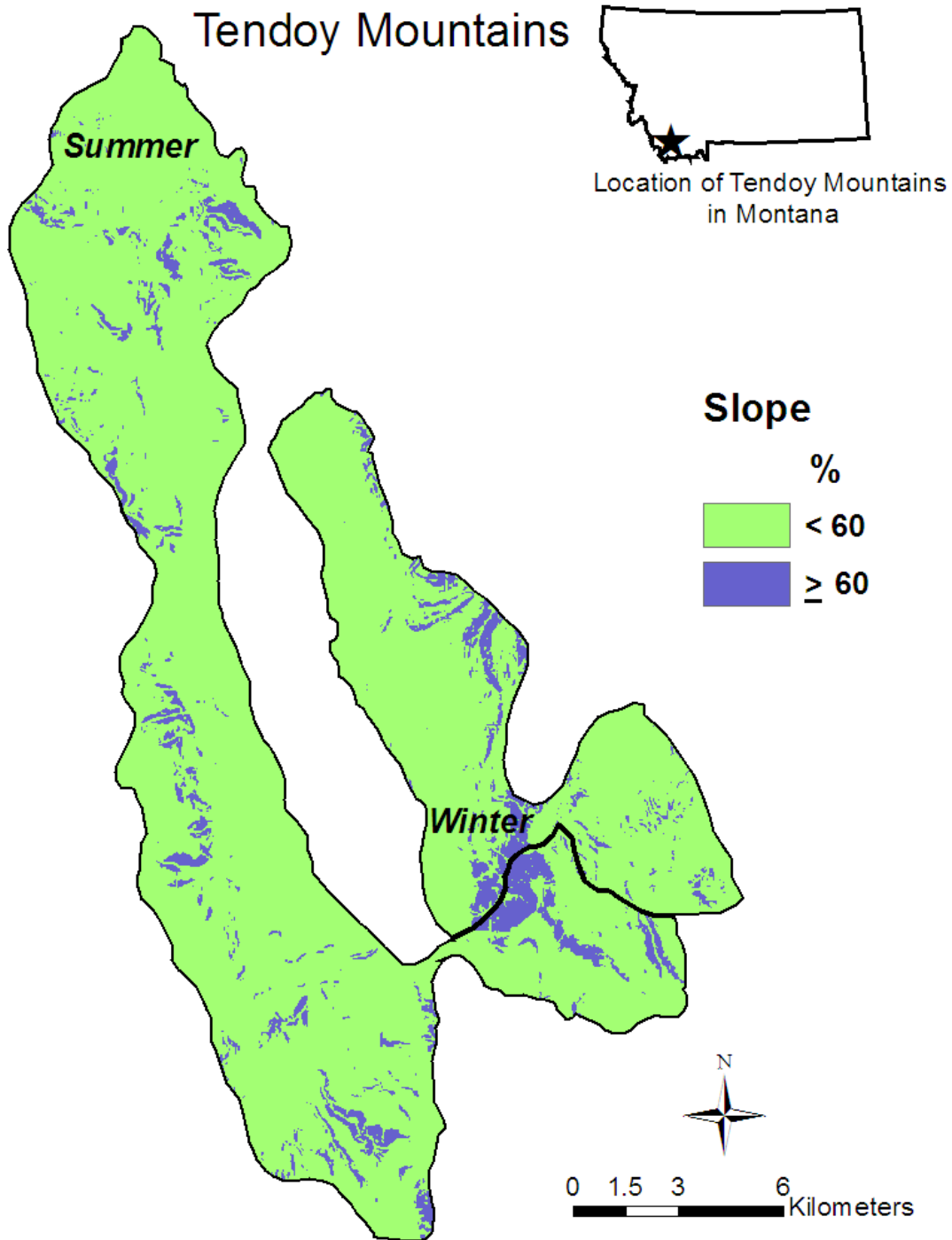


Figure 7. Aspect in the summer and winter ranges of the Lost Creek (stable) bighorn sheep population.

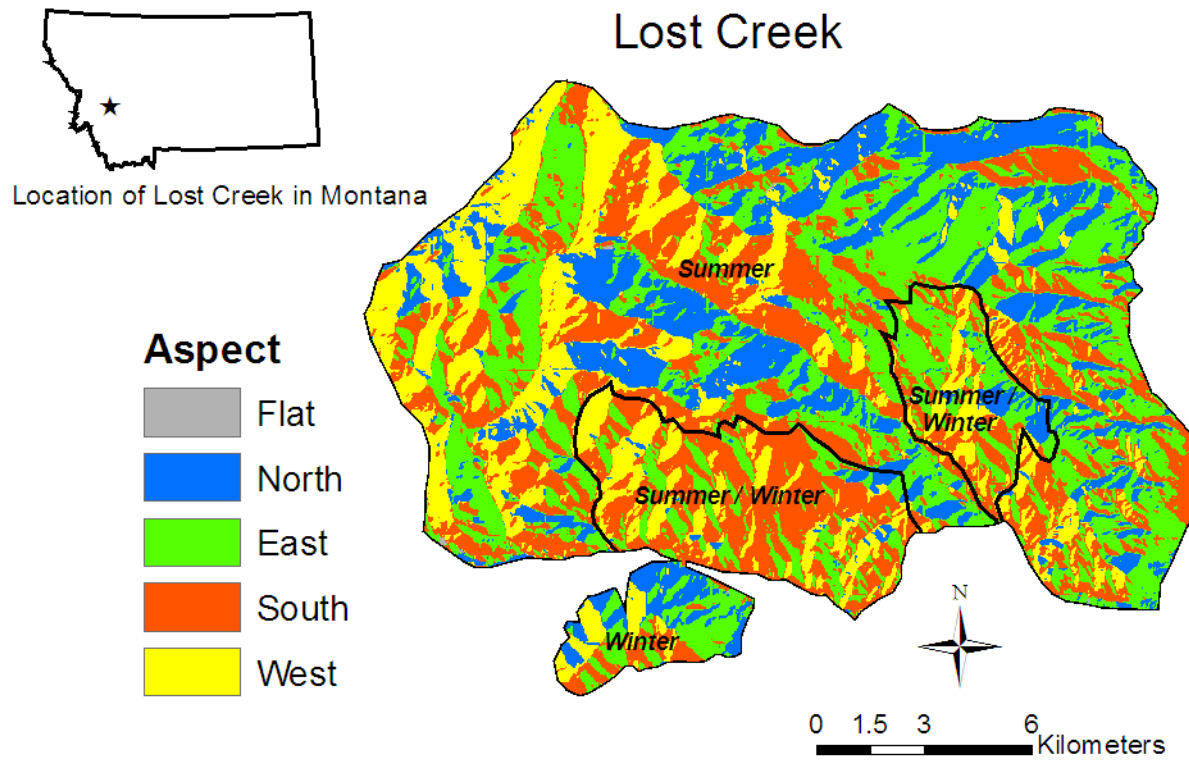


Figure 8. Aspect in the summer and winter ranges of the Tendoy Mountains (less stable) bighorn sheep population.

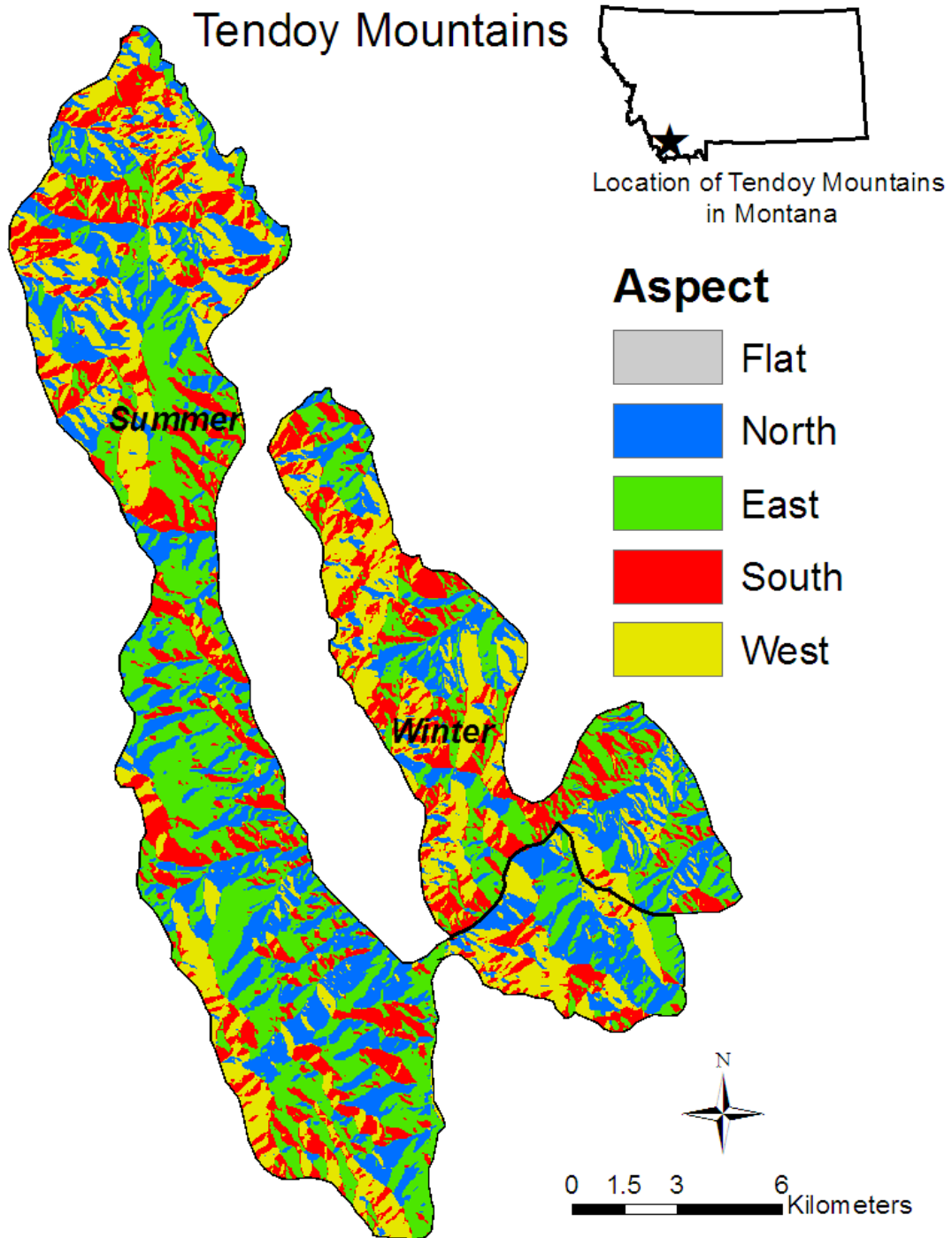


Figure 9. Landscape ruggedness in the summer and winter ranges of the Lost Creek (stable) bighorn sheep population. Ruggedness values ≥ 0.03 are considered “highly rugged”.

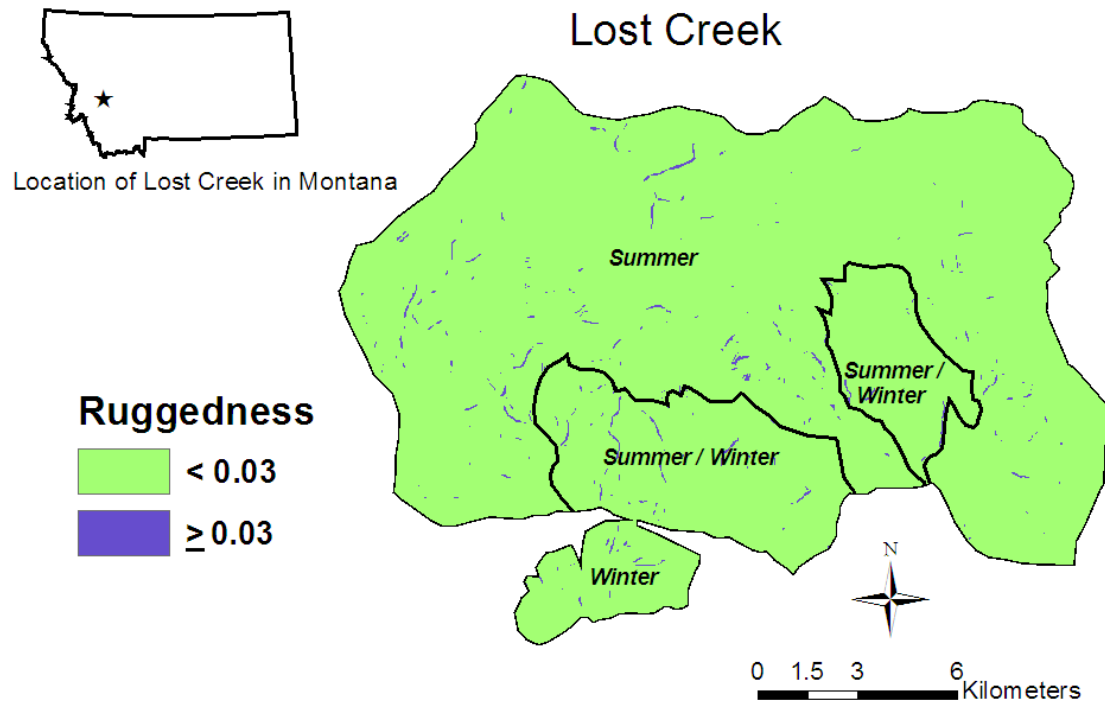


Figure 10. Landscape ruggedness in the summer and winter ranges of the Tendoy Mountains (less stable) bighorn sheep population. Ruggedness values ≥ 0.03 are considered “highly rugged”.

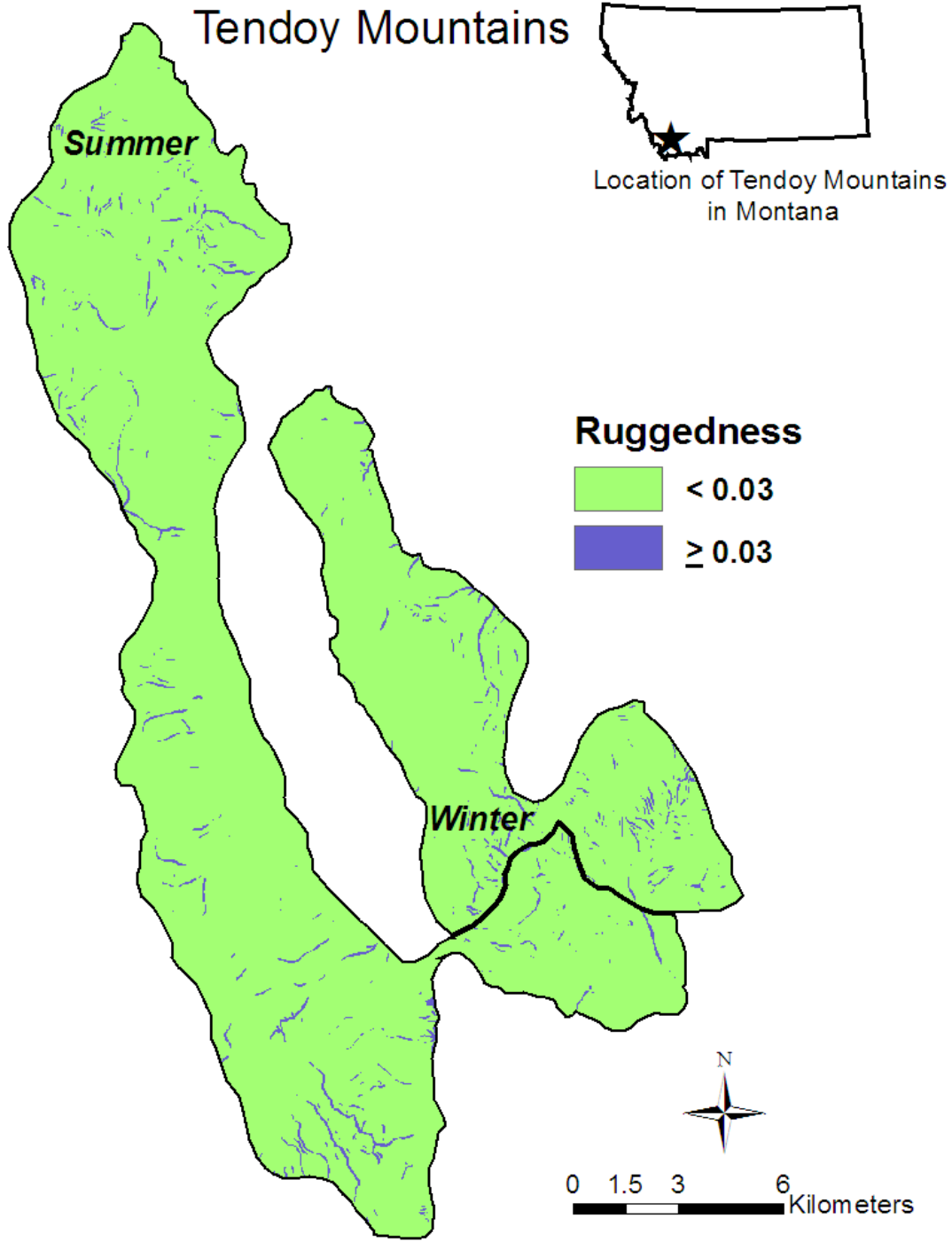


Figure 11. Solar radiation index (SRI) in the summer and winter ranges of the Lost Creek (stable) bighorn sheep population. Solar radiation index values ≥ 0.5 indicate “high” solar radiation.

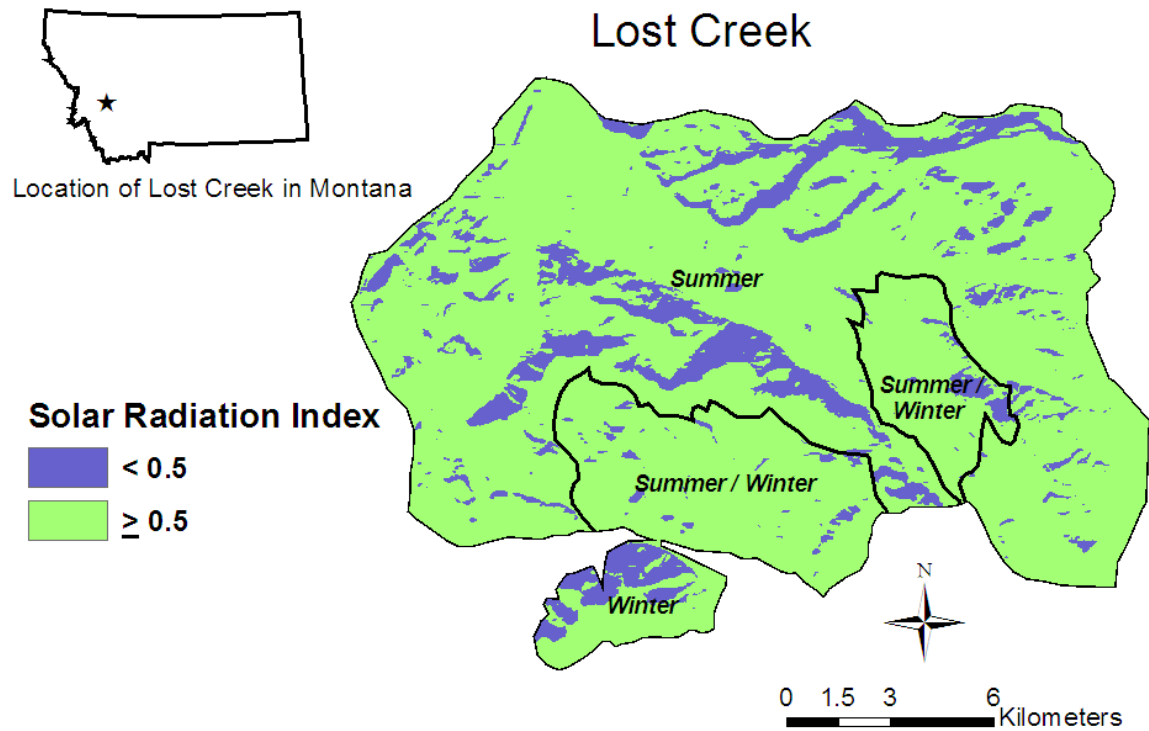


Figure 12. Solar radiation index (SRI) in the summer and winter ranges of the Tendoy Mountains (less stable) bighorn sheep population. Solar radiation index values ≥ 0.5 indicate “high” solar radiation.

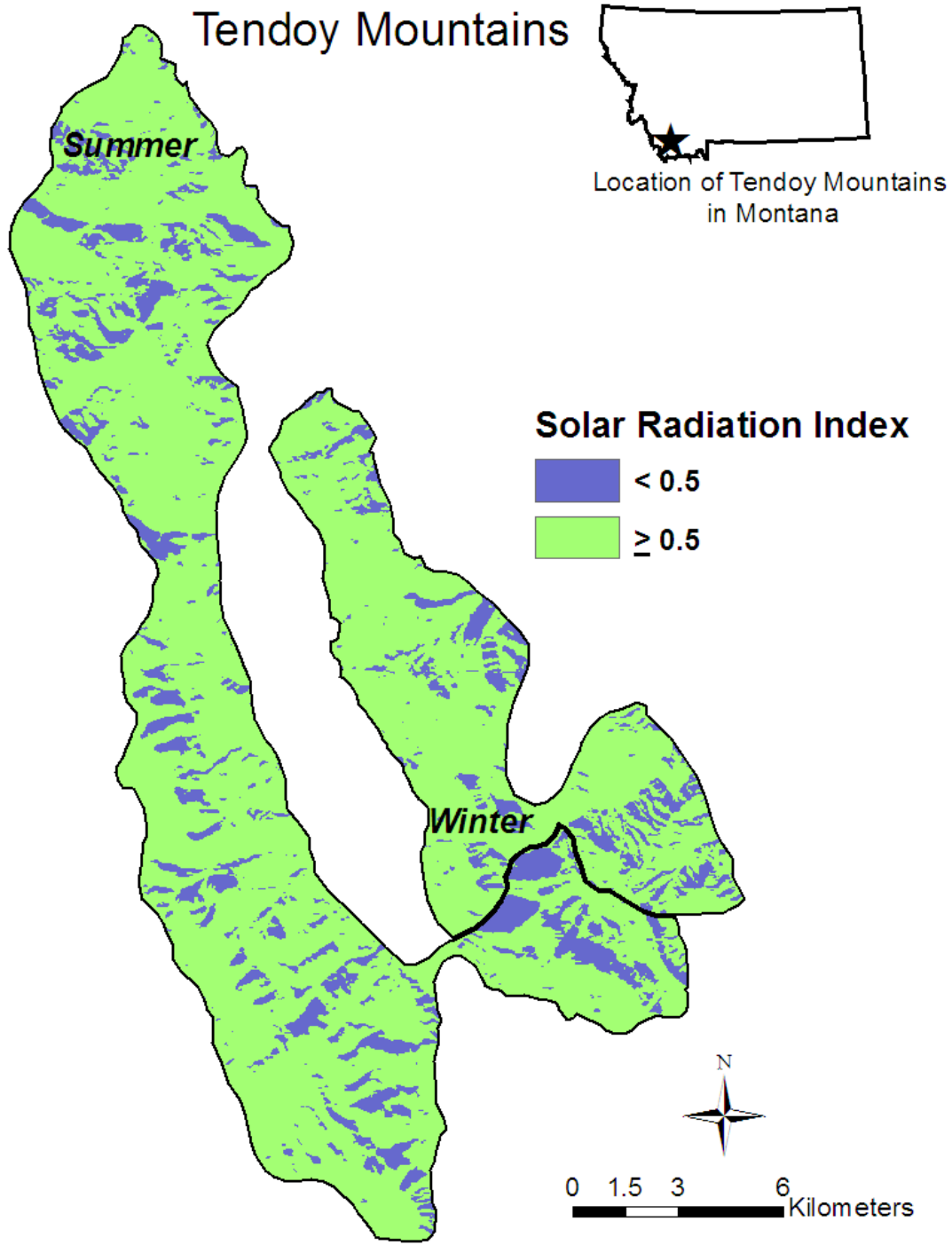


Figure 13. Escape terrain + 500 m buffer in the summer and winter ranges of the Lost Creek (stable) bighorn sheep population.

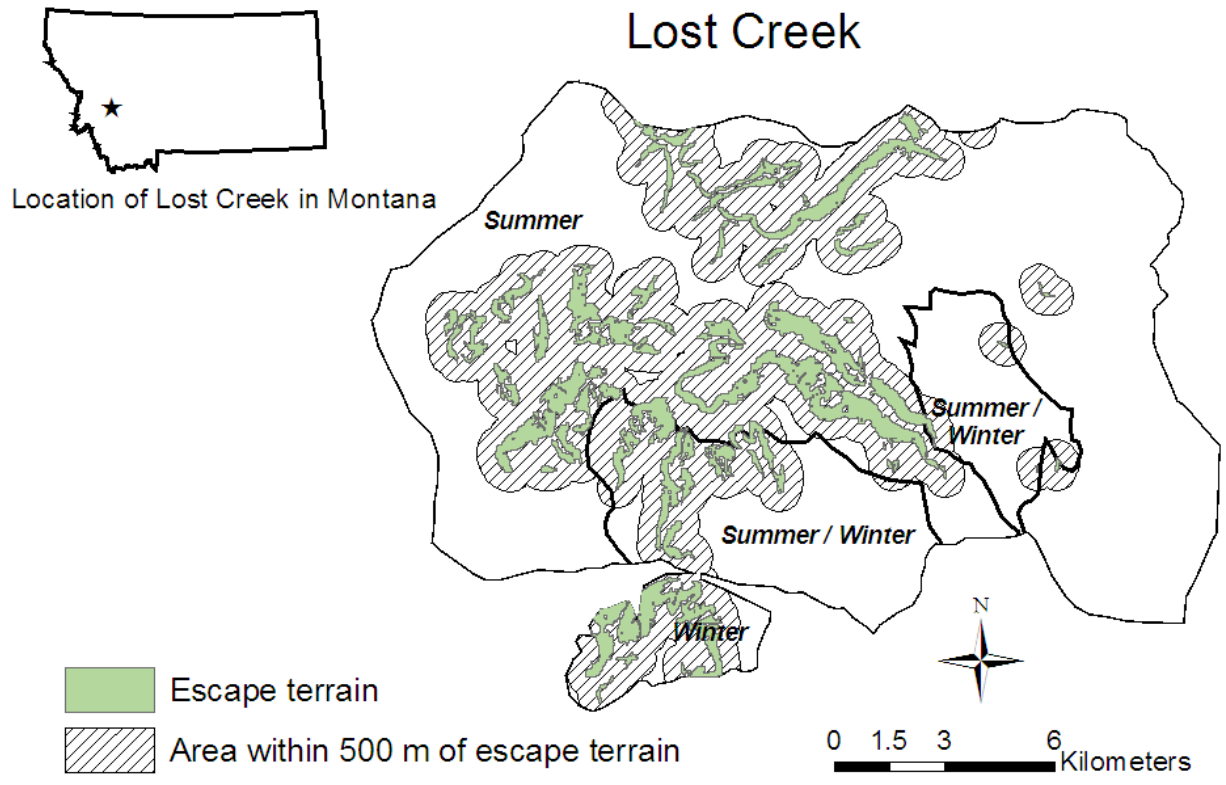


Figure 14. Escape terrain + 500 m buffer in the summer and winter ranges of the Tendoy Mountains (less stable) bighorn sheep population.

