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Spatial Analysis of Bighorn Sheep Movement in the Radium Hot Springs Area, British
Columbia: Modelling and Management

by

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Abstract

Bighorn sheep (*Ovis canadensis*) are a blue-listed (vulnerable) species in British Columbia. I used compositional analysis on GPS telemetry data collected from a sample of bighorn sheep at Radium Hot Springs, British Columbia, to assess a habitat suitability index (HSI) movement corridor model previously developed for this study area. I also developed an empirical model using resource selection functions (RSFs), and then compared the predictive abilities of the two models using a withheld set of data. The ability of the HSI summer model to predict sheep movement routes was limited because most sheep migration events were rapid movements through poor quality habitat. The RSF model had better prediction success of sheep occurrence in summer than did the HSI model. I provide management recommendations for the Radium herd, including a series of proposed sites for re-introduction of fire on low and mid-elevation sites.

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List of Symbols, Abbreviations and Nomenclature

Symbol	Definition
AIC	Akaike's Information Criterion
ATS	Advanced Telemetry Systems
BIOB	Bighorn In Our Backyard
DNA	Deoxyribonucleic Acid
ESRI	Environmental Systems Research Institute, Inc
GIS	Geographic Information System
GPS	Global Positioning System
HSI	Habitat Suitability Index
km	Kilometre
MANOVA	Multivariate Analysis of Variance
MCP	Minimum Convex Polygon
PDOP	Position Dilution of Precision
RIC	Resources Inventory Committee
RMS	Root Mean Square
RSBSWG	Radium-Stoddart Bighorn Sheep Working Group
RSF	Resource Selection Function
RSPF	Resource Selection Probability Function
SAS	SAS Institute Inc.
VHF	Very High Frequency

Chapter One: General Introduction

In south-eastern British Columbia, forest encroachment into grassland habitats is a serious issue for biodiversity conservation and for the integrity of bighorn sheep (*Ovis canadensis* (Ramey 1999)) habitat and movement corridors (Davidson 1994, Demarchi et al. 2000, Gray 2001, Gayton 2004). Conifer in-growth due to fire suppression on sheep winter ranges has reduced forage opportunity (Davidson 1994) and increased the risk of spread of disease by concentrating sheep in a reduced area (Schwantje 1988). Consequently, the identification and restoration of movement corridors of bighorn sheep is an important conservation measure for this species because of the implications for seasonal migration, gene flow between populations, and occasional dispersal (Risenhoover et al. 1988, Tremblay 2001, Demarchi et al. 2000, Dibb 2004, Tremblay and Dibb 2004). This is a particularly important consideration for the Radium Hot Springs bighorn sheep herd due to the location of this herd near the northern limit of sheep distribution in the southern B.C. Rockies (and therefore having few neighbouring populations with which to exchange genes or animals), and the relative rarity of open habitats in Rocky Mountain ecosystems at this latitude (Achuff et al. 1984, Gray 2001).

Managers of Kootenay National Park have recognized a series of problems relating to bighorn sheep management, including loss of winter range through urban development and forest encroachment, loss of intermediate range habitats from fire suppression, and unprecedented levels of bighorn sheep – motor vehicle collisions due to shifting patterns of winter range selection (Tremblay and Dibb 2004, Dibb 2006). It therefore is important for

park managers and for managers of cooperating jurisdictions to learn more about the locations and seasons of use of movement corridors, to understand the characteristics of corridors used by sheep, and to be able to predict and test the response of bighorn sheep to various management scenarios for movement corridors.

Bighorn sheep are currently on the British Columbia blue list of terrestrial vertebrates that are classified as “vulnerable”, and have a provincial conservation status ranking of “S2S3” or “imperilled/vulnerable” (BC Conservation Data Centre 2006). Two recognized ecotypes occur in British Columbia: Rocky Mountain Bighorn Sheep and California Bighorn Sheep, totalling approximately 7,000 animals province-wide (Blood 2000, Demarchi et al. 2000). These two ecotypes are distributed broadly in western North America and comprise an estimated 40,000 animals (Valdez and Krausman 1999, Demarchi et al. 2000). A subspecies, the Desert Bighorn (*O. canadensis nelsoni*), occurs in the south-western United States and has an estimated population of 23,000 (Valdez and Krausman 1999). These population totals establish bighorn sheep as one of the rarest ungulates in North America, and current numbers are greatly diminished from estimates for the pre-European settlement period, which range from approximately 500,000 to 4,000,000 (Seton 1909, Valdez and Krausman 1999). Many causes have been implicated in this population decline, including competition and disease from domestic livestock, unregulated hunting, loss and alienation of winter habitat, habitat fragmentation, increased vehicle access, and conifer encroachment into native grasslands (Buechner 1960, Stelfox 1971, Valdez and Krausman 1999, Demarchi et al. 2000).

Bighorn sheep are habitat specialists, relying on rugged, open forest and grassland habitat with shallow snow cover (Demarchi et al. 2000, Singer et al. 2000b, Singer et al. 2001). This results in a geographic range that is naturally fragmented (Bleich et al. 1990, Bleich et al. 1996, Decesare and Pletscher 2006). In British Columbia suitable ranges are restricted to areas with the driest climates (Hudson et al. 1976, Shackleton 1999, Blood 2000). However, dispersal of bighorn sheep between populations or to new habitats has rarely been recorded (Ramey II 1995, Bleich et al. 1996, Jorgenson et al. 1997, Gross et al. 2000) even though such movement is expected to have benefits, including rescue of local populations from extirpation, maintenance of genetic diversity, and response to climate change (Chetkiewicz et al. 2006). In some ranges rams temporarily visit other sheep ranges during the rut (Geist 1971, Forbes and Hogg 1999), behaviour that may have benefits for gene flow (Festa-Bianchet 1991).

Individual sheep develop home ranges through knowledge transmitted from older animals, rather than through juvenile dispersal (Geist 1999). Most bighorn sheep use several seasonal ranges and follow traditional migration routes between seasonal ranges (Geist 1971, Singer et al. 2000c, Krausman and Bowyer 2003). In some areas sheep in spring historically followed newly emerging vegetation up from lower elevations to the alpine (Smith 1954, Festa-Bianchet 1988b, Demarchi et al. 2000, Krausman and Bowyer 2003), but forest in-growth into these intermediate ranges has caused sheep to spend more time concentrated on limited winter ranges (Davidson 1994, Demarchi and Demarchi 1994). Conservation of historic migratory routes and habitats of bighorn sheep is crucial because the behavioural limitations of this species make it unlikely to find new routes or habitats

once old ones have been lost. This tendency towards “sedentariness”, in which static or declining herds become less migratory and over-concentrated, is a major obstacle to bighorn sheep conservation because it leads to increased risk of predation and disease, seasonal deficiencies in forage, and prolonged exposure to harassment by humans (Risenhoover et al. 1988, Singer et al. 2001).

Habitat modelling methods, including habitat suitability index (HSI) models and resource selection function (RSF) models, can be adapted to modelling movement corridors (Tremblay 2001, Chetkiewicz et al. 2006). Where field data is lacking for a species of interest in a particular area, HSI models can be developed in which model parameters, such as terrain and vegetation characteristics, are estimated through information from other study areas or through expert opinion (Gough and Ruston 2000, Tremblay 2001). However, RSF models, based on animal location data and using ratios of resources used to resources available to an animal, have also become widely used (Manly et al. 2002, Alldredge and Griswold 2006, Thomas and Taylor 2006). These models are well suited to adaptive management approaches in which management experiments are used to test model predictions, resulting in an on-going cycle of model improvement and active management (Walters 1986, Sinclair 1991, Osko et al. 2004). Chetkiewicz et al. (2006) recommended the use of probabilistic RSFs for modelling corridors as an important alternative to conventional categorical representations of corridors, habitat patches, and matrix.

The Radium Hot Springs area at and near Kootenay National Park provided a unique opportunity to investigate the use of movement corridors by bighorn sheep. Tremblay

(2001) developed a movement corridor GIS model, based on an HSI approach, but its predictions were not tested. In addition, there was a strong management emphasis on bighorn sheep ecosystems at Kootenay National Park (Parks Canada 2000) and, as Wildlife Specialist for Kootenay, Yoho and Banff National Parks, I was well positioned to conduct such an investigation.

In this thesis my overall objectives were to validate the existing movement corridor model developed by Tremblay (2001), to develop and assess a new RSF model of movement corridors based upon GPS telemetry data collected from a sample of Radium Hot Springs bighorn sheep, and to interpret model outputs and assumptions in the context of management of the Radium bighorns. The latter objective was intended to lead to informed management recommendations to benefit conservation of this herd. I also present the corridor model with the intent to eventually test its general applicability beyond the immediate study area, and in order to learn whether it could provide insights into meta-population dynamics of bighorn sheep in south-eastern B.C. and adjacent Alberta. I also wished to provide recommendations for future research and monitoring. Detailed information on basic ecology of the Radium bighorns has been provided as part of a linked but separate study (Dibb 2006). Response of bighorn sheep to active management events such as restoration treatments has been reported in Dibb and Quinn (in press).

I use a definition of “migration” following that of Berger (2004, pg. 321), that migration is a “seasonal round-trip movement between discrete areas not used at other times of the

year”. By contrast, “dispersal”, or “emigration”, is a one-way trip beyond the individual’s previous home range or territory.

Chapter Two: Literature Review

In this chapter I provide background information necessary to develop a bighorn sheep habitat and/or movement corridor model for the Radium Hot Springs study area. This information includes contextual information on the Radium Hot Springs herd, life history and ecological characteristics of the species relevant to model development, and an overview of approaches to model development and validation. In view of my objective to develop practical and well-supported management recommendations, I provide a review of adaptive behaviour of bighorn sheep, because these behaviours are of central importance in the ability of this species to respond to management actions. I also present a historical overview of bighorn sheep and rangelands management in south-eastern British Columbia as additional context for management recommendations.

2.1 Bighorn Sheep Ecology and Life History

2.1.1 Aggregation into Herds, Subpopulations and Metapopulations

Bighorn sheep are gregarious animals, although patterns of aggregation vary seasonally and from one area to another (Geist 1971, Lenarz 1979, Krausman and Shackleton 2000). To avoid confusion in referring to groups of sheep, I modified the terminology proposed by Festa-Bianchet (1986) and Demarchi et al. (2000) based on the organization of female groups as the fundamental units. At the smallest scale, a “herd” is comprised of a group of ewes, their offspring, and associated rams occupying a discrete winter range (Festa-Bianchet 1986). A “subpopulation” consists of two or more herds that share a common summer range (Luikart and Allendorf 1996, Demarchi et al. 2000). A “metapopulation” consists of two or more subpopulations (Bleich et al. 1996) and typically occurs over large

geographic areas. Luikart and Allendorf (1996) used mitochondrial-DNA variability of Rocky Mountain bighorn sheep to infer the presence of large-scale metapopulations separated by zones of little gene flow; all BC and Alberta herds were assigned to a single metapopulation. Under this terminology the Radium bighorn sheep are considered a “herd” because all animals share a common winter range.

2.1.2 Radium Bighorn Sheep Population Dynamics

Radio-telemetry data (Dibb 2006) indicate that the Radium herd appears to be a relatively discrete unit with little recent evidence of linkage to other sheep herds. However, some interchange of animals with adjacent herds was reported in the early 1970s (Stelfox 1978). The Radium bighorn sheep herd through most of the 20th century was characterized by gradual increases to approximately 150 to 250 animals, followed by sudden die-offs reducing the population to 20 to 50 animals on roughly 25 year cycles (Stelfox 1978, Poll et al. 1984, Stelfox et al. 1985, Demarchi et al. 2000, Tremblay 2001, Tremblay and Dibb 2004). At the time of my study the herd was estimated at 160 to 200 animals (Tremblay and Dibb 2004, Dibb 2006). The Radium herd is embedded within a bighorn sheep metapopulation that, in the East Kootenay region, consists of approximately 33 winter range locations each holding about 15 to 300 animals (Demarchi et al. 2000).

A major source of mortality in the Radium herd through the 20th century was periodic all-age die-offs caused by respiratory disease epizootics (Stelfox et al. 1985). Schwantje (1988) found that these die-offs were preceded by high population densities, heavy competition for forage, contact with domestic sheep, severe winter weather, high lungworm

levels, and low mineral levels in some sheep. The reduction of high density herds by using them as source populations for transplant programs may be a means of preventing die-offs (Demarchi and Demarchi 1994). The Radium herd was used as a source for transplants 6 times between 1986 and 1994, totalling 145 animals, and again in 2005 when 25 animals were removed (Demarchi et al. 2000, Parks Canada, unpublished data).

A shift in winter range use by the Radium herd occurred around 1990 (Demarchi and Demarchi 1994, Dibb and Tremblay 2004) and resulted in the sheep frequently crossing highway 93/95 just south of the village of Radium Hot Springs to access patches of habitat within or near the village (Dibb 2006). This has led to increased levels of highway mortality, with 32 known sheep-vehicle collisions from 2002 to 2004 (Dibb 2006). In addition, 3 railway kills were recorded during the same period (Dibb 2006).

Among marked sheep at Radium Hot Springs vehicle collisions are the most common cause of mortality (Dibb 2006). Other causes of death recorded for marked and unmarked Radium sheep include predation, disease, falls, and unknown causes (Parks Canada, unpublished data).

2.1.3 Seasonal Ranges and Migration Corridors

A fundamental aspect of bighorn sheep life history is the use of distinct seasonal ranges with regular migrations between these ranges (Geist 1971). Migrations may be vertical as well as horizontal, and migration distances of up to 70 km have been reported for some bighorn sheep populations (Smith 1954, Krausman and Shackleton 2000). Except in the

case of sedentary populations, bighorn sheep use at least 2 seasonal ranges, including summer and winter ranges (Krausman and Shackleton 2000), although some authors have reported as many as 6 distinct seasonal ranges (Geist 1971). Transitional ranges between winter and summer ranges have also been reported (Smith 1954, Davidson 1994, Demarchi et al. 2000) and may play a role in preventing over-use of winter ranges (Demarchi et al. 2000). At Radium Hot Springs, B.C. Dibb (2006) found evidence of distinct winter, lambing, and summer ranges, but very little use of transitional ranges.

Fryxell et al. (1988) presented three hypotheses to explain the greater abundance of migratory ungulates than sedentary ones in grassland ecosystems. First, the food supply is expected to be greater because migratory animals have access to a larger area. For bighorn sheep, Hebert (1973) and Festa-Bianchet (1988b) reported that vertical movements in spring and summer prolonged access to nutritious emerging vegetation. Second, migration could prevent over-grazing of critical habitat through seasonal rotation of habitats. For example, Risenhoover et al. (1988) found that lack of migratory behaviour in bighorn sheep could lead to seasonal deficiencies in forage quality and quantity. Third, migratory ungulates may be able to avoid predators for at least a portion of the year. Bighorn ewes commonly migrate to secure terrain when giving birth to lambs, even at the expense of diminished forage opportunity (Festa-Bianchet 1988a, Rachlow and Bowyer 1998, Bangs et al. 2005). Migration is also important to bighorn sheep to obtain access to mineral sources (Stelfox et al. 1985, Festa-Bianchet 1988b), to promote gene flow through migration to other sheep ranges (Geist 1971, Epps et al. 2005) and to discover new habitats (Risenhoover et al. 1988, Bleich et al. 1996).

I found little information in the literature describing daily movements of bighorn sheep or characteristics of movement corridors. Lawson and Johnson (1982) reported that sheep moved continually while foraging, implying that movement routes may have much in common with habitat areas. Woolf et al. (1970) identified two general types of bighorn sheep movements: foraging movements and directional movement to a specific location. Foraging movements were relatively slow and meandering, and were interrupted frequently as animals stopped to feed. Direct movements were rapid and purposeful, and sheep only occasionally stopped to look around. Stelfox (1976b) reported that in areas with suitable intermediate habitat, sheep travelled slowly during spring migration and foraged on their way upslope. However, movements during fall migration may be more rapid (Geist 1971).

In general, bighorn sheep prefer travelling through areas with high visibility and within or close to steep, rocky terrain (Geist 1971, Becker et al. 1978, Martin and Stewart 1980, MacCallum 1991). Although bighorn sheep prefer travelling across open areas, they have been reported to move quickly through closed forests when necessary (Geist 1971, Lawson and Johnson 1982). Other impediments to bighorn sheep movement were documented by Smith et al. (1990) and include large water bodies, steep cliffs, wide (> 1 km) valleys, high fencing, major highways, and centres of human activity. Tremblay (2001) modelled potential movement corridors for bighorn sheep and incorporated zones of influence of human disturbance as well as inherent habitat quality, visibility, and proximity to escape terrain. However, this same author noted that sheep in her study area were habituated to humans and that psychological barriers to sheep movement appeared to be minimal.

In summary, there appears to be little evidence that sheep strongly prefer a different set of landscape characteristics for movement than they do for habitat and, indeed, the distinction between habitat and movement routes is blurred because sheep tend to forage as they move. Sheep may, however, travel rapidly through unsuitable habitat as part of a traditional migration route.

2.1.4 Dispersal and Exploratory Movements

Dispersal is a mechanism for animal populations to avoid or reduce the probability of inbreeding depression and enables individual animals to avoid crowded ranges and intense competition (Martins et al. 2002). Dispersal also can provide a means by which animals can colonise vacant ranges (Singer et al. 2000b, Woodroffe 2003). Dispersal is predominantly male-biased in polygynous ungulates (Martins et al. 2002). Translocation of animals, as a form of artificial dispersal, has been advocated by some wildlife managers for conservation of species that are poor dispersers (Singer et al. 2002b, Woodroffe 2003).

Male bighorn sheep have a greater tendency than females to explore new ranges (U.S. Fish and Wildlife Service 2003), perhaps driven by the need to find breeding opportunities. However, bighorn sheep generally show reluctance to disperse from their home ranges, thus making them unlikely to colonise unoccupied habitat (Geist 1971, Bleich et al. 1990, Singer et al. 2000a, Singer et al. 2000b). Species that are poor dispersers are likely to have difficulty recovering from population declines and are more susceptible to extinction than good dispersers (Woodroffe 2003). No emigration was detected among bighorn rams at

Sheep River, Alberta, in a study in which 360 sheep of both sexes were marked over a nine year period (Festa-Bianchet 1991). Some of these rams left their native group to rut in other ranges, but they generally returned after the rut.

The lack of direct evidence of dispersal in bighorn sheep is corroborated by a pattern of increasingly small, isolated, and sedentary bighorn populations in which apparently suitable habitats are not colonised (Risenhoover et al. 1988). This situation in part may be due to loss of traditional migration routes, whether through failure of collective memory as populations declined or due to creation of barriers or filters to bighorn movement.

Krausman et al. (1999) observed that bighorns, once extirpated, lose their “adaptive plasticity”. These authors believed that the colonisation ability of bighorns has been suppressed due to human disturbance, competition, and the high degree of specialization of this species. However, Geist (1999) suggested that high quality bighorn sheep phenotypes, such as could be expressed in reintroduced populations, are more likely to disperse.

Douglas and Leslie (1999) noted that habitat generalists and species with high fecundity are usually better at colonising unoccupied habitat than habitat specialists with low fecundity like bighorn sheep. While sheep have made very few, if any, substantial unaided range extensions in North America in recent decades (Geist 1971, Singer et al. 2000b), it is possible that some mechanism for doing so exists, given that sheep colonised much of mountainous North America after the last ice age (Geist 1999). Many authors believe that North American sheep were much more continuously distributed and numerous prior to European contact (e.g., Seton 1909, Valdez 1988 cited in Krausman and Shackleton 2000).

Geist (1971) speculated on possible mechanisms by which sheep could colonise new ranges. He noted that wild sheep in Asia had made sudden, long distance (up to 500 km) movements involving at least part of a population, in response to catastrophic events such as droughts. Geist (1971) also observed that groups of younger rams occasionally would go on excursions into timbered valleys. He believed that such a group of young rams could wander into new, suitable habitat, retain memory of it, and in a later year be followed into the new habitat by young ewes. However, Geist (1971) also reported that such an occurrence had never been observed. McCann (1956) hypothesized that emigrations to vacant ranges in pristine North America may have occurred as a result of “population pressure” when local populations became overabundant. Western North America formerly consisted of more continuous open habitats, and sheep then could have colonised adjacent habitats so long as they were connected, or nearly connected, to currently occupied habitats.

The European ibex (*Ibex capra capra*) is a mountain ungulate that has many social and behavioural characteristics in common with bighorn sheep. This species declined to less than 100 individuals in the European Alps by the beginning of the 19th century but has since increased to approximately 40,000 individuals among more than 100 broadly distributed populations in Italy, France, Switzerland, Germany, Slovenia, and Austria (Stuwe and Nievergelt 1991, Maudet et al. 2002). Most or all of these newly established populations were the result of reintroductions from captive herds or wild populations rather than natural dispersal from extant populations (Stuwe and Nievergelt 1991, Girard et al. 1999). However, some transplanted herds increased the extent of their occupied range as their numbers increased (Stuwe and Nievergelt 1991).

At very localized scales, sheep have expanded their ranges into newly reclaimed coal mine sites (MacCallum and Geist 1998), although these reclaimed sites were immediately adjacent to and highly visible from occupied sheep habitat (B. MacCallum, personal communication). Sheep have also made small range shifts to take advantage of immediately adjacent forest thinning and burning projects (Arnett et al. 1998, Dibb and Quinn, in press).

Bleich et al. (1996) hypothesized that exploratory behaviour was a necessary precursor to the colonisation of new ranges by females. An exploratory movement into vacant habitat would precede the incorporation of such habitat into seasonal migrations that, in turn, could be followed by an emigration event. Lambs born following their mothers' emigration to a new range would be likely to establish home ranges there.

More recently, Singer et al. (2000b) reported on the extreme rarity of dispersal events in bighorns, referring partially to evidence from mitochondrial DNA differences measured between bighorn populations occupying nearby mountain ranges. Restricted movements of ewes, in particular, were inferred from this study. The conservative dispersal behaviour of female bighorn sheep implies that metapopulation dynamics are driven along matrilineal lines (Bleich et al. 1996).

2.1.5 Factors Influencing Habitat Selection

The basic elements of habitat for mountain sheep include presence or proximity of steep, rugged terrain, relatively arid conditions, and open habitat with good visibility such as alpine areas, grasslands and shrub-steppes (Nichols and Bunnell 1999, Krausman and Shackleton 2000, Krausman and Bowyer 2003). Such conditions occur in much of western North America and, indeed, mountain sheep formerly were much more continuously distributed across the mountains of western North America, and in some areas with broken terrain east of the mountains (McCann 1956, Buechner 1960). Climate, elevation, and latitude vary greatly across mountain sheep range, and consequently vegetation communities used by mountain sheep also vary greatly from north to south and from low elevations to high elevations (Krausman and Bowyer 2003). Considered at the scale of western North America and over thousands of years, mountain sheep appear to have had the ability to adapt to a wide range of climatic and vegetation types (Shackleton 1999), although most ranges occurred within relatively stable ecosystems (Geist 1971). However, the ability of mountain sheep to adapt rapidly to local habitat changes is constrained by the species' tendency to use traditional habitats (Geist 1971). Key factors to consider in habitat selection by bighorn sheep include climatic variation, broad patterns of vegetation cover, terrain, and human activity (Tremblay 2001).

2.1.5.1 Climate

Ranges used by Rocky Mountain bighorn sheep are characterized by relatively arid conditions (Krausman and Shackleton 2000), particularly in their winter range. The critical snow depth, as suggested by Stelfox (1976b), is from 30 to 54 cm depending on animal age

and size. Winter ranges are selected in low snowfall areas by choosing some combination of low elevation, southerly aspects, and wind-swept areas (Shackleton et al. 1999, Krausman and Bowyer 2003). Snow crusts caused by freeze-thaw cycles can be a particularly severe constraint on bighorn winter foraging (Shackleton et al. 1999, Demarchi et al. 2000).

2.1.5.2 Vegetation Cover and Visibility

The physical structure of plant communities may be of more importance to bighorns than species composition (Shackleton et al. 1999). Open habitats with high visibility, such as grasslands and shrub-steppe communities, enable bighorns to detect predators more easily (Krausman and Shackleton 2000). Risenhoover and Bailey (1985) found that preferred habitats of bighorn sheep at their study area in Colorado were most strongly correlated with visibility and forage density. Some sites with an abundance of forage species favoured by sheep but with poor visibility were used only occasionally. Bighorn sheep have varying needs for vegetative cover depending on whether they are foraging, resting, lambing, or seeking thermal regulation (Krausman and Bowyer 2003). Closed forests are rarely used, although sheep sometimes exploit patches of trees as a means of obtaining thermal cover (Geist 1971).

A lack of detailed vegetation inventory exists for the Radium study area. For this reason, and in order to develop a model with applicability beyond the study area, I focussed on selecting vegetation variables that are readily available from broad-scale forest cover mapping. Characteristics of a small portion of the historic bighorn sheep winter range

within the study area are provided in Gray (2001). Plant communities within Kootenay National Park are described in Achuff et al. (1984) although the scope of this report includes little winter range and only about half of summer range of the Radium herd. Page (2004, 2005) provides a detailed description of plant communities and their response to ecosystem restoration activities in the Redstreak restoration area.

Demarchi et al. (2000) described winter range in British Columbia as consisting of undisturbed climax grasslands dominated by bunchgrasses or rough fescue, although forbs and shrubs, as well as grasses, are eaten. Summer forage consists mainly of alpine and subalpine plants, including sedges, grasses, and forbs. Shackleton et al. (1999) concluded that bighorns consumed grasses, forbs and shrubs in roughly similar proportions to their availability.

2.1.5.3 Terrain

Krausman and Bowyer (2003) compiled a review of general topographic characteristics of the habitat of all sub-species of bighorn sheep. Terrain features used by bighorns include steep or gentle slopes, broken cliffs, rock outcrops, canyons and adjacent benches, and mesa tops. Escape terrain consists of steep, broken areas at slopes between 27° and 85° (Smith et al. 1999, Demarchi et al. 2000). Foraging areas are rarely far from escape terrain, although males generally will venture further from steep areas than will females (Geist and Petocz 1977, Morgantini and Hudson 1981, Corti and Shackleton 2002). Escape terrain is a particularly important component of lambing range that females seek out during parturition (Geist 1971, Becker et al. 1978, Bangs et al. 2005). Smith et al. (1999) found that 90% of

all bighorn sheep activity in their study area occurred within 300 m of escape terrain.

Numerous studies (summaries in Shackleton et al. 1999, Krausman and Shackleton 2000, Tremblay 2001) have found that bighorn sheep favour steep slopes over flat terrain.

Few wildlife species in North America exploit a greater range of elevations than bighorn sheep, with desert bighorns ranging from below sea level in southern California to greater than 4000 metres in some south-western mountain ranges (Krausman and Shackleton 2000). California and Rocky Mountain ecotypes range between about 450 and 3000 metres, while in the Rocky Mountains of southern Canada bighorn range from about 800 to 2800 metres (Holroyd and Van Tighem 1983, Poll et al. 1984, Tremblay 2001, Tremblay and Dibb 2004). In most populations lower elevations are selected in winter to avoid deep snowpacks.

Bighorn sheep exploit a variety of topographic aspects in order to maintain optimal thermal conditions and to maximize forage availability, abundance and quality (Tremblay 2001).

Among Rocky Mountain bighorn sheep, south or south-west aspects are commonly chosen in winter due to warmer temperatures and shallower snowpacks (Stelfox 1976b, Dibb 2006). Aspect choice appears to be more variable in summer; Stelfox (1976b) reported that bighorns tended to use south and east aspects in May and June, south and west aspects in July and August, and shift towards north aspects in late summer and fall to take advantage of plant growing conditions at moist sites.

Shackleton (1999) and Demarchi et al. (2000) reviewed the habitat requirements of Rocky Mountain bighorn sheep in British Columbia. They characterized the terrain preferences of this subspecies in winter as low elevation slopes with southerly aspects close to rocky escarpments or talus slopes. However, a small number of herds in south-eastern British Columbia were described as distinct ecotypes using different winter range selection strategies: one such ecotype winters on windswept alpine and subalpine ridges, and another winters in exposed mid-elevation, south-facing grassland slopes. All Rocky Mountain bighorns in B.C. use alpine areas and subalpine meadow/forest complexes in summer (Shackleton 1999, Demarchi et al. 2000).

Access to salt and trace minerals may be important for some populations of Rocky Mountain bighorn sheep, particularly in spring and early summer (Wishart 1978, Shackleton 1999, Shackleton et al. 1999). At Radium Hot Springs, B.C., bighorn sheep, particularly females and young, make periodic brief excursions from their alpine summer range to low elevation mineral sources (Dibb 2006). Geist (1971) included a “salt lick range” among the 6 seasonal ranges he described for bighorn rams in Banff National Park, noting that the rams moved large distances to access the licks in late spring or early summer. Geist (1971) also described instances of bighorn ewes making short excursions from summer range to nearby salt licks. Geist (1971) hypothesized that mineral acquisition in spring and early summer helps sheep alleviate deficits acquired during winter foraging and is related to the needs of bone growth, pelage replacement, and lactation.

2.1.6 Social Organization

Bighorn sheep are generally gregarious animals with a tendency towards grouping of same-sized animals (Geist 1971). Due to size differences between adult males and females, all-male groups are usually separate from groups of females and juveniles, but all groups come together during the rut. Group sizes vary greatly according to season, age-sex class(es), and predation risk, and may range from 2 to greater than 100 animals (Krausman and Shackleton 2000).

2.1.6.1 Group Cohesion

Group integrity is an important consideration in habitat modelling using radio-telemetry data because spatial autocorrelation of location data may occur if study animals are members of the same group (Aebischer et al. 1993, Garshelis 2000). There are considerable differences reported in the literature regarding the constancy of membership in bighorn sheep social units (Krausman et al. 1999).

Geist (1971) reported that mountain sheep, particularly females, in Banff National Park formed cohesive seasonal home range groups. Female sheep showed strong site fidelity to maternal home ranges and therefore had a tendency to associate frequently with the same animals. Decesare and Pletscher (2005, 2006) investigated this phenomenon in western Montana using a modified nearest neighbour spatial analysis of radio-marked sheep locations and concluded that, for their study area, there was a lack of independence of relocations among individuals. These authors therefore pooled data within each identifiable sub-herd and used these sub-herds as the sampling unit. Distinct groups of

female bighorns in south-western Alberta overlapped in distribution seasonally and ewes from different groups mixed freely during overlap (Festa-Bianchet 1986, 1991). However, these sheep tended to remain with their own group when the groups subsequently separated.

By contrast, bighorn sheep in other studies have exhibited little constancy of group membership (Smith 1954, Buechner 1960, Woolf et al. 1970). Leslie and Douglas (1979) reported that persistent family groups or home range groups were not evident in their Nevada study area. These authors concluded that group integrity was weakened at high population densities, whereas at low population densities group integrity may be favoured as part of an adaptive strategy to maintain vigilance from predators. Boyce et al. (1999) described two types of group behaviour: cohesive maternal home-range groups characterized by strong fidelity in seasonal habitat use and, within such a seasonal grouping, ephemeral groups of related or non-related animals that aggregate temporarily on a day to day basis. Factors that may influence group cohesion include seasonal behavioural considerations such as rutting and lambing, and use of risky versus secure terrain with the latter favouring smaller groups.

2.1.6.2 Sexual Segregation

In many species of ungulates, males are larger than females and the two sexes are spatially segregated except during the breeding season (Geist 1971, Ruckstuhl and Neuhaus 2001, 2002). Numerous hypotheses have been developed to explain the mechanisms behind sexual segregation (e.g., Shank 1979, Ruckstuhl 1998, Perez-Barberia and Gordon 1999,

Mysterud 2000, Bon et al. 2001, Ruckstuhl and Neuhaus 2002, Von Hardenberg et al. 2003), and considerable debate has ensued (e.g., Mooring et al. 2003, Neuhaus and Ruckstuhl 2004).

The “activity budget” hypothesis, in which sexual segregation is driven by the need to group in order to synchronize foraging and rumination activities, has been proposed as a proximate cause of segregation in ungulates (Ruckstuhl 1998, Ruckstuhl and Neuhaus 2005). However, segregation likely is influenced by other environmental and behavioural factors (Bon et al. 2005, Main and du Toit 2005). For bighorn sheep, a reasonable body of evidence suggests the importance of predation risk in shaping social structure (Geist and Petocz 1977, Morgantini and Hudson 1981, Bleich et al. 1997, Corti and Shackleton 2002, Mooring et al. 2003). Body size may affect the susceptibility of a group of animals to predation and thus influence the security of the terrain chosen (Ruckstuhl 1998).

Regardless of the identity of the underlying mechanisms, segregation of age-sex groups is a fundamental aspect of social organization and has important implications for habitat selection and for habitat model development. Furthermore, understanding of the specific needs of each sex in sexually segregated species is crucial to effective conservation (Ruckstuhl and Clutton-Brock 2005).

2.2 Historical Management of Bighorn Sheep in South-Eastern British Columbia

2.2.1 East Kootenay Region

During the late 1800s sheep populations in the East Kootenay region reportedly declined due to over-hunting in an era of few regulations and no enforcement (Blood 2000). Herds increased after approximately 1910 when bighorn hunting was closed or restricted. By the early 1920s the total number of bighorn sheep in the region was estimated to have peaked at nearly 5000 animals (Davidson 1994).

A series of epizootic all-age die-offs, believed to have been associated with contact with domestic sheep, occurred at approximately 25-year intervals for which the earliest record is 1924 (Schwantje 1988, Davidson 1994). Subsequent population recovery was insufficient to return populations to their pre-die-off levels, so the overall population trend in the 20th century was downward, to approximately 2000 animals by the late 1980s (Davidson 1994) and between 1400 and 1800 in 2002 (I. Teske, personal communication).

By the 1950s the B.C. Forest Service was employing fencing in some areas to separate domestic livestock from bighorn winter ranges (Demarchi 1988). In the late 1960s recommendations were made to improve winter range by reducing numbers of competing livestock or by using burns and seeding to enhance habitat (Smith and Demarchi 1969), although the extent to which these recommendations were followed is unclear.

Substantial habitat management programs did not begin until the 1970s after another major die-off and further deterioration of range condition from overgrazing (Blood 2000). Sport-hunting groups helped to support some of these initiatives, which included securement of critical bighorn winter ranges. A sheep recovery project was initiated in 1982 with objectives pertaining to disease research, habitat enhancement, habitat monitoring, bighorn sheep health treatments, and bighorn sheep translocations (Davidson 1994). Between 1982 and 1988, this program completed habitat enhancement treatments including prescribed fire, thinning, slashing, seeding and nitrogen fertilization on about 2000 ha of winter and spring range. Some sheep populations were treated with anti-parasite drugs and had their diets supplemented with trace minerals. Additionally, a sheep transplant program took place in order to restock traditional ranges where populations had been severely reduced, and to reduce the potential for disease outbreak by reducing high density source herds. However, these treatments and enhancement projects were rarely evaluated in a rigorous manner, and assessment of their benefits has been largely speculative (Demarchi and Demarchi 1994).

In 1994 the provincial Wildlife Branch developed a bighorn sheep enhancement plan for the East Kootenay region (Demarchi and Demarchi 1994). This plan made specific recommendations for research, wildlife management area designation, habitat acquisition, habitat enhancement, translocations, access management, and hunting regulations. The plan recommended the establishment of a “Rocky Mountain Bighorn Management Council” to serve as a liaison between the public and the provincial Wildlife Branch. It

also recommended improved public education and participation in bighorn research and management.

By 2003 the provincial ministry of Water, Land and Air Protection estimated that most bighorn sheep populations were stable or declining, with only those in the Elk Valley and at Radium Hot Springs increasing (I. Teske, personal communication). This agency set population recovery goals to increase total sheep numbers to 1700 by 2005 and 2300 by 2010. Other management goals were to protect remaining range, restore degraded range, prevent die-offs, reduce predation impacts, and maintain hunting opportunities for large rams including fertilization of critical ranges to promote forage production and help produce large rams quickly (I. Teske, personal communication).

2.2.2 Radium Hot Springs and Kootenay National Park Herd

Cowan (1943, cited in Poll et al. 1984) reported that in 1922 the Radium herd experienced a major die-off, recovering to about 30 animals by 1930 and to about 140 by 1938. A second die-off occurred during 1941-42. The Radium herd gradually increased to about 175 animals by 1966, at which time a third die-off occurred, reducing the herd to 40 animals (Stelfox 1976a). Numbers have gradually increased since then, and the Radium herd avoided the 1980s die-off that affected herds elsewhere along the Rocky Mountain Trench in the East Kootenay region (Schwantje 1988, Parks Canada, unpublished data). The Radium herd was used as a source population for herd augmentation or reintroduction efforts elsewhere in the East Kootenay region and northern United States in the 1980s; this may have kept the Radium population low enough to avoid the range deterioration and

crowding associated with the onset of pneumonia-lungworm induced die-offs (Davidson 1994).

2.2.2.1 1970 and 1988 Management Planning, Kootenay National Park

The Kootenay National Park Provisional Master Plan of 1970 (Parks Canada 1970) set in place a systematic program for reporting on the current state of the park and plans for development and other activities in the future. This plan introduced a national parks zoning system that designated certain lands for special protection. However, none of the special areas in this planning cycle were within the park's unique, semi-arid grassland/open forest ecosystems that are highly important for bighorn sheep and other species of plants and animals (Parks Canada 1970). The trans-boundary seasonal migrations of the sheep were recognized explicitly and "close liaison with outside agencies and individuals" was recommended.

The 1970 plan refers to the pneumonia lungworm die-off of the Radium herd in 1967 and notes the apparent cyclical nature of the disease. The suggestion is made that the disease is a natural mechanism for preventing high-density herds from damaging their ranges. This is in spite of evidence dating back to at least 1870 that domestic sheep introduce potentially lethal exotic disease to mountain sheep (Brooks 1923). No specific management actions for bighorn sheep were proposed in this plan.

Kootenay National Park's 1988 Management Plan (Canadian Parks Service 1988) gave bighorn sheep a high profile, and sheep were explicitly mentioned in 1 of the 6 important

natural history themes: “the wildlife populations that are representative of the Western Ranges, particularly the Sinclair Canyon – Redstreak Bench bighorn sheep band and the Mount Wardle goat herd” (Canadian Parks Service 1988, p. 13). The Parks Service’s zoning system was defined in detail and included a large “special preservation” area in south-western Kootenay National Park created in part to protect bighorn sheep habitat. The plan included a management objective to “manage the park on an ecological basis; cooperating and coordinating resource management and research with the other mountain national parks, and with provincial agencies and private interests managing adjacent lands” (Canadian Parks Service 1988, p. 30). The two main wildlife management problems identified in the plan were highway mortality and “the effects of adjacent land management on wildlife”.

Resource management goals introduced in the 1988 plan included the use of prescribed or random ignition fire to maintain natural vegetation, and active pursuit of provincial government cooperation in coordinated approaches to management of trans-boundary wildlife, particularly bighorn sheep. A knowledge deficiency on the effect of stress resulting from human contact and development on bighorn sheep was identified.

2.2.2.2 The 1990 Bighorn Sheep Cooperative Management Plan

In 1990 the Canadian Parks Service and the British Columbia Wildlife Branch jointly developed a management plan for the Radium-Stoddart bighorn sheep (Stelfox 1990). The plan was intended to prevent recurrent die-offs such as those that occurred in the 1940s and 1960s. The plan notes “the Canadian Parks Service normally does not interfere with

natural processes but strongly supports the need for joint and manipulative management of this herd to ensure their policies do not negatively impact on adjoining lands” (Stelfox 1990, p. 4).

The plan included management objectives to: (1) optimize population abundance, stability and health within the winter range carrying capacity; (2) maintain critical habitats including migratory corridors, mineral licks, and wetlands; (3) minimize development and deterioration of critical ranges; (4) provide a mechanism for future joint management actions; (5) provide for cooperation in monitoring, research, habitat enhancement, enforcement, capture and transplant, public relations and public education. Winter range carrying capacity was recognized as a key factor limiting sheep population levels. The extent to which lambing ranges, mineral licks and intermediate range areas were limiting factors was considered to be unknown and required future study.

2.2.2.3 Current Management of the Radium Bighorn Sheep

The 2000 management plan for Kootenay National Park (Parks Canada 2000) is intended to guide the overall direction of the park for 10 to 15 years. Adaptive management and the precautionary principle are explicitly recognized as important aspects of the plan.

The 2000 plan contains several objectives that pertain to bighorn sheep management. The plan also contains several key actions for wildlife monitoring, research, and public education with potential application to management of bighorn sheep. A summary of

relevant management plan goals, objectives, key actions, and zoning decisions is presented in Table 1.

While the 1988 and 2000 management plans have provided broad direction, in practice bighorn management since 1997 has been coordinated through the activities of “Bighorn in Our Backyard” (BIOB), a public education, stewardship, and monitoring initiative (Osprey Communications 2003, 2004, 2005, Dubois et al. 2004), and through the Radium-Stoddart Bighorn Sheep Working Group (RSBSWG), a multi-agency and stakeholder committee which guides management of the Radium bighorns (Dibb 2004).

Within the BIOB project, bighorn sheep are used as an ambassador species for the whole suite of rare plants, animals and ecological communities that are dependent on dry grassland and open forest ecosystems. The BIOB project takes a four-pronged approach to conservation of grassland/open forest ecosystems by focusing on education and outreach, stewardship, research and restoration, and sustainable community development to address issues on critical winter range (Osprey Communications 2003). The first three years of the BIOB project (1997-2000) endeavored to raise the level of ecological literacy within the community and to build stewardship through a program of education, outreach and citizen monitoring activities. This fostered broad understanding and support within the community for conservation measures for bighorn, and set the stage for research and restoration activities that began in 2001 (Dubois et al. 2004).

The Radium-Stoddart Bighorn Sheep Working Group has been the primary vehicle for planning and implementing a series of three restoration projects that have occurred since 2001 on provincial crown and national park land in the Radium-Stoddart area. The success of these initiatives can be attributed, in part, to the inclusive composition of the RSBSWG. Membership in this committee includes Parks Canada, three B.C. government agencies, the Village of Radium Hot Springs, the Ktunaxa-Kinbasket Tribal Council, Slokan Forest Products, the Columbia Basin Fish and Wildlife Compensation Program, the East Kootenay Wildlife Association, and the B.C. Southern Guide Outfitters Association.

2.3 Wildlife Habitat and Movement Modelling

2.3.1 Habitat Modelling Overview

Models, broadly defined as “abstractions or simplifications of real-world systems” (Nichols 2001, pg. 12), are encountered widely in natural resource management. However, one of the challenges of modelling is to interpret model outputs appropriately given their limitations and assumptions. Conroy (1993), in reference to models used in resource management, observed that many users of models treat model predictions as if they are fact. Other potential misuses of models include acceptance of model outputs only when they seem to make sense, the tweaking of parameters to make the model fit the data, and the discarding of model predictions that appear to make no sense at all (Conroy 1993). Starfield (1997) advised that models be thought of as hypotheses, experiments, or problem-solving tools. In this context models are developed to represent the current best understanding of the system, but with clearly stated assumptions that themselves can be converted into testable hypotheses.

Conroy (1993) reported that models have two main purposes: 1) assist managers in making better decisions, and 2) improve understanding of the system under investigation. He then offered the following criteria for assessing the usefulness of a model as an adaptive management tool:

- Realism. Provisional understanding of the system is represented by a biological theory or hypothesis.
- Precision. The model can explain and predict real world phenomena.
- Testable predictions. Alternative management schemes can be predicted and tested.
- Feedback mechanism. Falsification of model predictions is used to modify the model.

Shenk and Franklin (2001) described three broad classes of applied models:

- Theoretical models are developed in the absence of empirical data, but suggest causal relationships and other mechanisms for explaining the system's behaviour and are useful for generating suites of alternative hypotheses. Model relationships and parameterization are commonly based on expert opinion (Tremblay 2001). For wildlife-habitat studies, such models build upon a general conceptual framework and are not necessarily tied to local study areas (Dettki et al. 2003).
- Statistical (or empirical) models use empirical data to make inferences and test competing hypotheses. White (2001) described statistical models as those

models that define parameters from data. In wildlife habitat studies these models are developed using locally derived data and typically have limited power when extrapolated to other areas (Boyce et al. 2002, Dettki et al. 2003).

Dettki et al. (2003), in investigating the performance of a theoretical and a statistical model in assessing moose habitat suitability, recommended the use of statistical models to fine-tune the assumptions used in theoretical models.

White (2001) noted the usefulness of fitting theoretical models to data in a hybrid approach.

- Decision-theoretical models attempt to predict a system's response to possible management scenarios and thus are amenable to adaptive management approaches (Nichols 2001). These models typically assess a set of management objectives and options in an iterative procedure to arrive at an optimal or, at least, a "wise" solution, and may be based upon Bayesian inference methods or optimization methods such as dynamic programming (Nichols 2001, Williams et al. 2002).

Nichols (2001) categorized resource management models according to their intended use.

Thus, theoretical uses of models investigate system responses under specific hypotheses but without any comparison of model outputs to actual data. In empirical model applications, model predictions are compared with data in order to assess competing hypotheses.

Finally, in decision-theoretic uses, models predict the consequences of hypotheses about system behaviour in order to derive optimal or wise solutions.

I consider process-based approaches, including spatially explicit and individual-based models, to be a 4th class of model. Here population processes such as birth, death and reproduction, as well as animal location, are simulated at the level of individual animals (Turchin 1998, Williams et al. 2002). These models require a greater understanding of life history processes but are able to model variation in the use of space within a landscape, and can be useful for predicting animal distribution and abundance in that the mechanisms of animal distribution are modelled and so may improve understanding of the underlying processes. Individual-based models are well suited to investigations of species that exhibit solitary or territorial behaviour and for investigation of small populations (Gough and Rushton 2000). An individual-based model that includes the spatial location of individuals on the landscape is also “spatially explicit” (DeAngelis et al. 2001).

Recent discussions of modelling in the wildlife management literature emphasize the formulation of *a priori* hypotheses and the incorporation of experimental design and management considerations rather than application of models that are strictly theoretical or statistical. Nichols (2001) stated that empirical manipulations done “just to see what happens” are rarely as useful from a scientific perspective as manipulations conducted to test model-based predictions. However, theoretical and statistical models are still widely in use, both as standalone models, as hybrids, and as part of decision-theoretical models or information-theoretic (Burnham and Anderson 1998) methods (see 2.3.1.3 below). Overall, parallel advances in the last several decades in development of information theory and in computing power provide ecological modellers with the tools to substantially improve the rigor of model selection and development (Burnham and Anderson 1998).

I provide additional review below on the types of models that are either assessed or constructed as part of this thesis.

2.3.1.1 Theoretical Habitat Suitability Models

Habitat suitability index (HSI) models are widely used in wildlife and forest management and are examples of theoretical modelling approaches because the underlying relationship between habitat suitability and each variable used in the model is assumed and commonly is based on expert opinion (Tremblay 2001). Gough and Rushton (2000) categorized HSI models as belonging to the class of “associative” models, which they defined as top-down, “black-box” models that determine relationships between the distribution of species and various environmental features without explicitly modelling population processes such as birth, death and dispersal. These models were contrasted with “process-based” models (see section 2.3.3), including individual-based models, that simulate population processes in the hope that “the distribution of the animals will arise as an emergent property” (Gough and Rushton 2000).

In HSI modelling, hypothetical relationships between the habitat and the wildlife species of concern are developed, usually guided by expert opinion. Model variables are identified, scaled to values ranging between 0 and 1, and relative importance coefficients are assigned (Morrison et al. 1998). Assumptions are formulated about the functional relationships of the variables and guide the procedure used to combine the model variables, i.e., define the way that variables are logically or mathematically combined to produce an overall habitat

value at each point in the study area (Tremblay 2001). The factors are combined using functions such that the assigned habitat suitability value also ranges between 0 and 1 (Morrison et al. 1998, Store and Kangas 2001). A GIS application can be used to manage, produce, analyse and combine spatial data describing the habitat factors.

2.3.1.2 Statistical or Empirical Habitat Models

Boyce et al. (2002) define resource selection functions (RSF) as models that produce values proportional to the probability of use of a resource but do so with statistical rigor because the models are developed using data rather than expert opinion. Manly et al. (2002) provide a guide to the use of RSFs in studying animal selection of food, habitat and other resources. The basic approach in resource selection studies is to compare the use of resources by animals to the availability of those resources on the landscape.

Manly et al. (2002) provided some useful definitions pertaining to RSF models. The use of a resource is defined as the amount of that resource used by an animal or a population of animals in a certain, fixed period of time. Resource availability is defined as the amount of that resource accessible to the animal(s) in that same period of time. When resource use is disproportionate to resource availability, then the usage is “selective”. “Preference”, on the other hand, refers to the likelihood that a resource will be selected given equal availability to other resources.

RSF models can be derived from presence/absence (used vs. unused) data, but this can be problematic in telemetry studies because absence of telemetry data for an area or resource

does not necessarily indicate lack of use. It is usually easier to obtain presence/available (used vs. available) data (Boyce et al. 2002). Manly et al. (2002) have proposed three designs for resource selection studies using used versus available data. In Design I the available and used resource units are both defined for the whole population of animals being studied. In Design II the available resource units are assumed to be the same for the whole population of animals but the used units are identified at the individual level. Finally, in Design III both available and used resource units are identified for individual animals. Boyce et al. (2002) and Howlin et al. (2003) discuss methods for evaluating how well RSF models based on presence/absence or presence/availability data predict the location of animals on a landscape. Typically, the RSF modeller will need to use a withheld sub-sample of data to evaluate predictive success (see section 2.3.6).

McDonald and Manly (2001) recommend a set of principles for use in empirical modelling, one of which is “do not over-fit the data”. They note that over-fitting occurs when some of the random variation in the data is accounted for by model variables. Thus, some of these variables may not really be related to resource selection and the model may be weak when used with new data. Here, RSF modelling can be combined with some method of model selection such as Akaike’s Information Criterion (AIC) to choose a model that explains much of the variation with only a compact set of variables (McDonald and Manly 2001).

2.3.1.3 Information-Theoretic Methods

Information-theoretic approaches are presented by Franklin et al. (2001) as alternatives to traditional null hypothesis testing of competing hypotheses or models. These methods are

commonly used as integral parts of the RSF methods described above, but information-theoretic methods emphasize that a set of *a priori* hypotheses should be developed based on biological and management considerations. These hypotheses are expressed using some underlying statistical model, such as linear regression, and then appropriate sets of data are collected in order to assess the hypotheses. AIC is used to compare and rank the competing hypotheses based on goodness-of-fit testing and parsimonious use of model parameters; in other words, the models with the combination of best fit of model to the data and fewest parameters will be highest ranked. An additional tool, the “Akaike weights”, can be used to assess how good (or likely) the various models are relative to each other.

Advantages of statistical model selection include the following (Franklin et al. (2001):

- It avoids the arbitrary limitations of null hypothesis testing and significance levels;
- The use of multiple working hypotheses can prevent the bias introduced when managers or biologists propose a single hypothesis guided by their individual biases.
- The approach provides an objective means of analyzing a range of *a priori* hypotheses.

Burnham and Anderson (1998) caution against modelling with a large number (> 50) of ecological variables in the “blind hope” that the method sorts out the significant variables. This strategy reportedly uncovers spurious correlations, particularly if the number of cases (samples) is small relative to the number of variables. Burnham and Anderson (1998) also

provide the caveat that the method can only select the best model from the set provided; good models cannot be selected if none are included among the candidate set.

2.3.1.4 Compositional Analysis

Aebischer et al. (1993) discussed problems associated with typical analyses of animal radio-telemetry data to determine habitat use. These problems included:

- Non-independence of successive radio-telemetry locations for individual animals;
- Non-independence of data when pooled across individuals from distinct age-sex classes or other groups (animals from different groups may behave or select habitat differently);
- In typical interpretations of radio-telemetry data an animal's avoidance of one habitat type can lead to apparent preference of other habitat types;
- Animals may be aggregated into age-sex classes or other groups and there may be differences in habitat use between groups;
- Difficulties with the definition of available habitat; usually available habitat is determined within the total study area which may include areas not available to an animal.

Compositional analysis was proposed to resolve the above issues (Aebischer et al. 1993).

Habitat use is expressed on an individual animal basis as the proportion of that individual's trajectory (movement path) or home range in each habitat type (Erickson et al. 2001).

Habitat preference is determined using pair-wise comparison of the use:availability ratios

for all habitat types to rank habitats from least to most preferred, thereby avoiding potentially confusing references to absolute preference. Additionally, habitat use can be determined at two scales to reconcile the difficulty in defining availability: selection of a home range from within the study area, and selection of habitat use within the individual's home range (Aebischer et al. 1993).

2.3.1.5 Autocorrelation of Location Data in Habitat Selection Modelling

The importance of autocorrelation in habitat selection studies has been a controversial topic (Otis and White 1999). In part this controversy arises because of the conflicting needs of eliminating autocorrelation in order to satisfy assumptions of independence in statistical hypothesis testing, and maintaining autocorrelation in order to detect the biological signal of interest (De Solla et al. 1999, Cushman et al. 2005, Fortin and Dale 2005, Borger et al. 2006). Aebischer et al. (1993), in discussing the application of compositional analysis to radio-telemetry data (see 2.3.4 above), recommended that independence of data pooled across individuals could be achieved by using independent animals in the radio-marked sample; i.e., animals that were not continually members of the same flock, herd, or other grouping. However Millsaugh et al. (1998) argued that an animal's biology and life history stage should be used to determine spatial independence for animals that group. These authors made a distinction between biologically independent animals that form groups to exploit a resource, such as herding ungulates, and animals that are biologically dependent upon group members, such as parent-offspring groups and obligatory cooperative predators.

Commonly used methods for eliminating autocorrelation from animal location data are to subsample the data or to collect data only at sufficiently long time intervals that autocorrelation is predicted not to occur (Swihart and Slade 1985, Garton et al. 2001, Kenward 2001). White and Garrott (1990) recommended a rule of thumb by which statistical independence of radio-telemetry data is achieved by selecting time intervals between successive locations such that the study animal has sufficient time to move anywhere within its home range. These approaches have been criticized on the grounds that eliminating actual or potential autocorrelated data may also limit the scope of biological inferences that can be made from these data (De Solla et al. 1999). Fortin and Dale (2005) recommended using all available data and learning to use the lack of independence as an avenue for investigation of the spatial structure of ecological phenomena.

2.3.2 Model Assessment Procedures

Model assessment is an essential part of ecological modelling that occurs subsequent to the initial building of a model (Williams et al. 2002). Depending on the type and purpose of model, there may be several different phases to the assessment.

Verification is the process of determining whether the model is structured correctly and performs as expected. Verification tasks could include checking that the model algorithms work properly, that the computer code correctly implements the algorithms, and that model performance is consistent with data used in development (Johnson 2001, Williams et al. 2002).

Validation occurs subsequent to verification, and typically assesses model predictions in relation to real-world data that was not used in model development (Mayer and Butler 1993). Johnson (2001) summarized criteria for model validation; his list included precision, generality, realism, accuracy, robustness and resolution. He also noted that models, as imperfect characterizations of the real world, never can be truly validated; however, they can be invalidated. With this in mind, validation should be viewed as an iterative process in which either confidence in a model increases with more testing or the model is shown to be invalid. Model validation can be considered a form of scientific hypothesis testing; the model represents a testable hypothesis that we set out to disprove (Williams et al. 2002).

Sensitivity analysis is a model assessment procedure in which a model's input values, parameters, and even structural features are changed systematically in order to explore the model's response (Johnson 2001, Williams et al. 2002). Sensitivity analyses may be used to identify: (1) crucial parameters that require particular care in their estimation; (2) insignificant parameters that can be eliminated from the model; and (3) inputs that contribute most to output variability (Hamby 1994).

Garshelis (2000) agreed that habitat models are essentially hypotheses in need of testing. However, he argued that the relationships between habitat and animal populations expressed in such models are unlikely to be exactly correct, and therefore habitat models could not be "rejected" or "accepted" according to conventional hypothesis testing

approaches. Garshelis (2000) therefore questioned the appropriateness of terms such as “validate” and “verify” in the context of assessing habitat suitability models.

Johnson (2001) proposed an alternative terminology for model assessment, which he called “Evaluation Methods” based on a set of validation techniques described by Mayer and Butler (1993).

- Subjective assessment. Use of expert opinion and other subjective tests.
- Visualization techniques. Use of plots, graphs, time series comparisons and other visual displays of model results and real world observations; this also is a subjective technique.
- Measures of deviation. When actual data and model predictions can be paired by time, location, treatment, etc. various measures, such as RMS error, can be used to quantify differences.
- Statistical tests. A variety of statistical measures, such as t-tests, contingency tables, and correlation coefficients comparing model versus actual results.

Statistical tests of model performance need to use a different set of data than was used in model development in order to assess the predictive validity of the model (Power 1993, Johnson 2001), although practical limitations of time and money frequently prevent researchers from acquiring such independent data (Boyce et al. 2002). However, Mladenoff et al. (1999) tested a spatial model of gray wolf habitat suitability using an independent sample of data collected subsequent to model development. These researchers used compositional analysis (Aebischer et al. 1993) to assess wolf use of habitat probability

classes from the original model; in particular, habitat classes were ranked based on how strongly they were selected for in relation to availability within the study area. Mladenoff et al. (1999) calculated Wilks' lambda (λ), a test statistic used in multivariate analysis, to test whether overall wolf habitat use was significantly different from random.

Boyce et al. (2002) recommended spatially explicit RSF model evaluation using *k*-fold cross validation, a method in which a portion of the original data is withheld using a *k*-fold partitioning scheme. Under this method, the study area is classified into an arbitrary number of categories based on values of the RSF model. Withheld data are then used to construct frequency tables of RSF scores within each RSF model category. According to these authors, a "good" model would be indicated if a high correlation exists between frequencies of RSF scores and the values of RSF categories, a relationship which they recommended be tested using a Spearman-rank correlation.

Howlin et al. (2003) provided a variation on the method of Boyce et al. (2002). These authors also regressed the frequency of withheld data points occurring in each model category against the expected frequency as predicted by the model, but did not use a *k*-fold partitioning scheme. Instead, Howlin et al. (2003) recommended withholding many small blocks of data within either the geographic extent of the study area or within the time frame of the study area. However, as these authors imply, the choice of scheme for withholding data depends on the objectives of the study. The best predictive ability of a model being assessed using this method would result in a linear regression line with a slope not significantly different from 1 and intersecting the origin. Predictive abilities of the model

under validation can be rated as “good”, “acceptable”, or “unacceptable” depending on the value and the 95% confidence interval of the slope of the validation regression (see section 3.7).

2.3.3 Movement Modelling: Least-Cost Path Analysis

Least-cost path methods, closely related to permeability models and friction models, implement graph theory to model animal movements across a landscape (Chetkiewicz 2006, Dreilisma et al. 2007). These are raster-based GIS models that consider energetic costs and mortality risks that animals are subject to as they travel (Ray et al. 2002). Each raster cell is assigned a value that represents its relative permeability to movement by the target organism, based on such variables as terrain, habitat suitability, human disturbance, and mortality risk. Least-cost algorithms can then derive optimal solutions for travel between designated starting and ending points. Least-cost path models have been used to identify dispersal and migration corridors between protected areas or important habitat patches (Walker and Craighead 1997, Callaghan et al. 1998, Ray et al. 2002, Osborn and Parker 2003).

Tremblay (2001) identified two limitations of these cost-surface approaches. She pointed out that the need to identify known starting and ending points for the analysis may prove unwieldy when modelling corridors between a large number of habitat patches. In addition, the models may be based on the assumption that high quality habitats will be selected for movement, and therefore may be poorly suited for predicting travel routes through poor quality habitat. Ray et al. (2002) suggested that these models are frequently limited in

utility because of insufficient information on animal habitat use for accurate modelling and because of the subjectivity of estimates of permeability. In addition, the difficulty of representing narrow features in raster format can lead to errors in least-cost path models, such as the formation of non-existent “shortcuts” across barriers (Rothley 2005).

Chetkiewicz et al. (2006) observed that most least-cost models were parameterized with habitat information derived from the literature or from expert opinion, and rarely were validated. These authors suggested that multivariate RSF models could be used to provide cost surfaces that would better characterize habitat suitability and, therefore, would provide better measures of functional landscape connectivity.

Chapter Three: Methods

3.1 Study Area

The study area encompasses 543 km² in the Stanford and Brisco Ranges of the Rocky Mountains near Radium Hot Springs in south-eastern British Columbia, and is centred on 50° 38' N, 116° 0' W. This area extends from the community of Windermere in the south to the community of Spillimacheen in the north, and is bounded to the west by the Columbia River and to the east by the Kootenay River valley (Figure 1). I defined the study area as the minimum convex polygon (MCP) enclosing all telemetry points collected from all study animals from 2002 through 2004. Elevations range from just below 800 m at the Columbia River to nearly 2,800 m at the highest summits of the mountain ridges. Approximately one-third of the study area is within Kootenay National Park, with most of the rest occurring on B.C. provincial crown lands. Important areas of winter range also occur on private, municipal, and First Nations lands in the Columbia Valley.

Climate is characterized by a transition from low precipitation and relatively warm conditions in valley bottoms to higher precipitation and cool temperatures at higher elevations (Achuff et al. 1984). Mean annual temperatures range from approximately 5.0°C near the valley bottom at Radium Hot Springs to 1.6°C at Sinclair Pass at 1370 m elevation (Janz and Storr 1977). Mean annual precipitation is 366 mm at the Kootenay West Gate near Radium Hot Springs, and is 608 mm at Sinclair Pass. No climate data were available from alpine regions within the study area, but mean annual temperatures are expected to be lower than at lower elevations and mean annual precipitation amounts are expected to be higher (Achuff et al. 1984).

Four biogeoclimatic zones occur within the study area: Interior Douglas Fir (IDF) and Montane Spruce (MS) in the valley bottoms, Engelmann Spruce – Subalpine Fir (ESSF) at mid-elevations, and alpine tundra (AT) at higher elevations (Meidinger and Pojar 1991). Lower elevation forests are dominated by Douglas fir (*Pseudotsuga menziesii*), white spruce (*Picea glauca*), and aspen (*Populus tremuloides*) and are interspersed with patches of grassland (Achuff et al. 1984). Upper elevation forests are dominated by white spruce, Engelmann spruce (*P. engelmannii*) and hybrids of these two species, and by subalpine fir (*Abies lasiocarpa*). Stands of alpine larch (*Larix lyallii*) and whitebark pine (*Pinus albicaulis*) also occur at some high elevation sites. Seral forests of lodgepole pine (*P. contorta*) occur after fire, except near tree-line. Tree-line occurs at approximately 2,300 m. Plant communities in the alpine tundra zone form a fine scale mosaic in which microclimate variations produce marked changes in dominant species (Achuff et al. 1984). However, much of the alpine zone consists of unvegetated rock outcroppings, cliffs, talus and scree.

Wildlife mortality records from Kootenay National Park (Parks Canada, unpublished data) suggest that cougars (*Puma concolor*), and coyotes (*Canis latrans*) are the main predators of bighorn sheep in the study area. Other large and medium-sized predators include wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), black bears (*U. americanus*), wolverines (*Gulo gulo*), lynx (*Lynx canadensis*), bobcats (*L. rufus*), and golden eagles (*Aquila chrysaetos*). Approximately 7,000 permanent human residents occupy the Columbia Valley along the western edge of the study area, including about 700 permanent residents of the village of

Radium Hot Springs. However, there is additionally a large population of seasonal residents and a growing tourism industry. Provincial Highways 93 and 95 cross the study area east-west and north-south respectively. While human settlement is centred on the Columbia Valley, recreational activities occur broadly throughout the study area, in part using access created by a network of logging and mineral roads. Some high elevation watersheds and ridge crests remain relatively difficult to access. On provincial lands trophy hunting of full curl bighorn rams occurs under a general open season in the fall, and harvest levels in the provincial wildlife management unit that includes the study area average around 3% annually (I. Teske, personal communication).

3.2 Capture

Sheep were captured on their winter range at Radium Hot Springs, B.C. and fitted with GPS radio collars each year from 2002 through 2005. The capture team captured study animals by darting with immobilization drugs. The capture team searched winter range areas for groups of sheep located in gentle terrain and away from hazards such as highways, rivers, and cliffs. I generally selected adult sheep that appeared to be in good physical condition and I chose animals of both sexes in order to be able to investigate sex differences in habitat selection. However, I avoided selecting rams less than about two-thirds curl because of concerns that neck growth could result in tightening of radio-collars, and avoided selecting full-curl rams because these animals could have been legally hunted and therefore might have been subject to unnaturally high levels of mortality. These constraints led to a selection split of approximately two-thirds ewes and one-third rams. Where practical, I avoided capturing more than one animal from the same group in order to reduce the chances that collared animals would have strong associations with each other. Immobilization of free-ranging sheep was carried out using a combination of Xylazine-Ketamine, or occasionally using Xylazine-Telazol or Ketamine-Medetomidine.

Several samples and measurements were collected from all study animals at the time of capture, except where high or increasing levels of animal alertness precluded it. The capture team collected faecal pellets for parasite load testing, and blood samples for disease testing and archival purposes for future DNA studies. Animal age was estimated by counting horn annuli and assessing tooth wear and eruption. Processing of animals, including time required for immobilization to take effect, usually required 25 to 55 minutes,

after which reversal agents were administered. The Parks Canada wildlife veterinarian (Dr. Todd Shury) and/or a biologist with experience capturing and handling several hundred bighorn sheep (Ian Ross, ARC Wildlife) attended captures. Capture and handling methods are described in more detail by Kinley (2002, 2003) and Dibb (2006).

The Parks Canada Agency Animal Care Committee under Research and Collection Permits LLYK02-01, LLYK02-35, LLYK03-15, LLYK04-02, and KOONP-2005-3518 approved animal capture and handling methods. Methods were consistent with British Columbia standard methods for live animal capture and handling (RIC 1998). Additional details on methods were provided in a Parks Canada Animal Care Committee Animal Utilization Protocol submission that accompanied the above-noted research permits.

I captured and radio collared 40 sheep (25 females and 15 males) in 4 sessions (Table 2). However complete sets of data for entire study years were not available for all study animals. In 2005 a ram (id M309) went missing in September 2005 and his collar was never recovered despite aerial and road-based telemetry searches spanning approximately 200 km north-south and 60 km east-west. Two other rams (id M003 and M005) and 4 females (id F102, F204, F209, and F303) died prior to the planned date of collar removal. The GPS function of three radio-collars in 2002 (id F004, F007, and F011) malfunctioned, resulting in data loss.

Estimated age of sheep at time of capture ranged from 2.5 to 10.5 years for females ($\bar{X} = 5.0 \pm 0.54$ yr) and 4.5 to 7.5 years for males ($\bar{X} = 6.2 \pm 0.26$ yr). In 2002 collars were

initially deployed on 8-13 January and removed from study animals on 24 October 2002. However, I deployed 1 collar on 4 March 2002 to replace a study animal that had died shortly after capture. Additionally, the collar release mechanism did not function on 2 collars; these collars had to be removed by free-range darting at a later date, and one of these collars continued to collect data until its removal. For the 2003 field season, 7 collars were deployed on 16-18 December 2002, and 3 collars were deployed on 3 March 2003. All collars on surviving animals were removed on 1-3 December 2003. In 2004, collars were deployed on 4 non-consecutive days in March 2004 and were removed on non-consecutive days in either late October or late November 2004. I removed collars from 2 rams earlier than planned in the fall of 2004 because the collars appeared to be getting tight, although no decline in animal condition or changes in behaviour were observed. In 2005, collars were deployed on 7-11 February and released in early November, except for 2 collars that were removed on January 30, 2006. The GPS function of all collars in 2003, 2004 and 2005 appeared to work properly. One ram and 1 ewe from year 1, M002 and F007 respectively, had to be immobilized to remove their collars because the collar release mechanisms failed. While immobilized, both these animals were fitted with new radio collars and so participated in year 2 of the study as well. However, the GPS function had failed on F007's collar in April 2002, so 2003 is the only year for which I have a complete data set for this animal. M002, who was easily recognizable because of distinctive horn damage, was also selected for capture and radio-marking in 2004 and 2005, and so I have acquired 4 years of data from this animal. No other attempts were made to recapture individuals for more than one study year.

Over the 4 years I obtained GPS locations on 89% of scheduled attempts and, of those, 86.4% were 3-dimensional locations (3D) and 13.6% were two-dimensional (2D). In total, I obtained 62,174 2D and 3D locations over 9,647 animal-days of operation (Table 2).

3.3 Data Collection Procedures

All study animals were fitted with GPS radio collars (Model G2000, Advanced Telemetry Systems, Isanti, Minnesota, USA) with a VHF transmitter as well as a 12-channel Garmin (Olathe, Kansas, USA) GPS engine and weighing approximately 950 g. I programmed these collars to log GPS location data on a 12 month schedule, at least covering the period from just prior to study animals leaving their winter range in spring to just after the animals return to their winter range in the fall. In the first year of the study (2002) the collars were programmed to attempt to collect points every 8 hours and 30 minutes from December through March, and at 4 hour and 15 minute intervals during the rest of year. This schedule was based on the assumption that sheep would travel more during spring, summer and fall, and therefore more frequent sampling would be beneficial during those periods in order to record use of movement routes. Based on the 2002 results I altered the schedule in years 2 through 4 (2003-05) to collect points at intervals of 12 hours and 48 minutes from November through April, and at intervals of 2 hours and 8 minutes in other months. Once animals had returned to their winter range I released the collars using a remote release mechanism, recovered the collars, and downloaded data from the collar's GPS memory to a computer using a serial port cable. I then returned the collars to the manufacturer for refurbishment before deployment the next year. Thus, there was a period of approximately

two months each winter during which no animals wore radio collars, except for those animals whose collar release mechanism malfunctioned and so collar removal was delayed.

The radio collar VHF function was programmed to be active from 0800 hours to 1700 hours local standard time each day. I attempted to receive VHF signals from each study animal at least once per week in order to check for mortality signals and GPS function status through a coded pulse pattern. I attempted to visually locate each animal periodically in order to verify that the collars were not causing injury to the sheep, to collect group composition data, and to verify reproductive status of any collared ewes. VHF telemetry was also used to triangulate animal locations periodically as a source of backup data in case of failure of collar GPS function. In practice, the lack of access and the complexity of terrain in the study area made it difficult to obtain accurate VHF fixes on study animals except when the animals were close to highways (i.e., mainly while on their winter range).

All GPS location data was collected subsequent to the removal of the Selective Availability feature of the US military global positioning system. Consequently, horizontal positional accuracy is expected to be within 10 metres of the true location 95% of the time under clear tracking conditions (Geographic Data B.C. 2001). There may be decreases in accuracy in areas where the sky view is obstructed by terrain features or forest cover. D'Eon et al. (2002) investigated GPS radio-telemetry error in mountainous terrain in south-eastern British Columbia and found mean location errors of 28.2 m (n = 487) for 2-D fixes and 9.1 m (n = 5712) for 3-D fixes; I expected similar location errors in this study.

I considered the potential for systematic bias of GPS fix-rates in different habitat types due to effects of habitat attributes such as terrain and forest cover. I contributed two ATS GPS radio-collars to a cooperative GPS-bias study spanning study areas of several wildlife research projects in the Central Rocky Mountains (Hebblewhite et al. 2006). Fix rates of GPS radio-collars produced by three different manufacturers were tested at sites in an approximately 19,000 km² area in Banff, Yoho and Kootenay National Parks, Peter Lougheed Provincial Park and Kananaskis Country Provincial Recreation Area, and included tests within my study area. Hebblewhite et al. (2006) stratified sites by canopy cover, elevation, slope, and aspect, and then calculated for each land-cover class the proportion of successful fix attempts. These authors then reported on GPS habitat bias for the Central Rocky Mountains including my study area. They found that ATS radio-collars identical to those used in my study had achieved an average fix rate success of 94.1% over all habitat types tested, and that the lowest fix rate success for any habitat type was 90.2% for closed conifer forest. For more details on these methods see Hebblewhite et al. (2006).

GPS telemetry data was downloaded from radio collars using Advanced Telemetry Systems' (ATS) WinCollar software (Advanced Telemetry Systems 2004). The data from all collars was merged into a single file, and some basic manipulations (addition of fields, data censoring, distance calculations), were performed using Microsoft Excel 2000 (Microsoft Corporation 1999). I performed spatial analyses using ArcGIS 9.0 (ESRI 2005) and ArcView 3.3 software (ESRI 2002). I also used the Animal Movements extension of ArcView 3.3 (Hooge and Eichenlaub 1997) and Hawth's Analysis Tools extension of

ArcGIS (Beyer 2005). I conducted statistical tests using SAS 9.1 software (SAS Institute 2005). Details of these analyses are provided below.

Inaccuracy of GPS locations can result in miscalculation of animal habitat use (Frair et al. 2004). GPS location data can be screened for positional accuracy either by eliminating points collected under 2-dimensional (2D) satellite geometry, or by eliminating points on the basis of position dilution of precision (PDOP) (D'Eon and Delparte 2005). However, for some analyses, omitting locations may systematically introduce bias into the remaining data. Thus, the researcher faces a trade-off between assuring location accuracy of the GPS data and the likelihood of creating bias (D'Eon and Delparte 2005). For most analyses I included only 3-dimensional (3D) GPS points with PDOP values of less than 6.0, as recommended by B.C. Resource Inventory Committee standards (Geographic Data B.C. 2001) to ensure precision of locations, since the results of Hebblewhite et al. (2006) indicate low potential for habitat bias in my study area. However, for analyses involving selection of a subset of "movement" points this limitation was too restrictive and I instead followed the recommendation of D'Eon and Delparte (2005) to use 3D and 2D points with PDOP values of less than 10.0. These authors reported that, in their study area in southeastern British Columbia, the PDOP limit of 10 removed major outliers from their data, but resulted in only a 1-3% loss of data, a reduction they felt was a practical alternative to more aggressive data reduction procedures. For development of RSF models I used a subset of the telemetry data consisting of one point per animal per day to maintain independence of consecutive observations (Erickson et al. 2001). Since bighorn sheep are mainly diurnal (Geist 1971, Sayre and Seabloom 1994, Shackleton et al. 1999) I chose to use location

points collected during daylight hours when sheep were likely to be moving or foraging, in order to emphasize selection of habitat for these purposes. Therefore, I selected the first location point after 9:00 a.m. standard time each day for each animal provided that point met the location accuracy constraints; otherwise I tested the next point for that day, and so on.

3.4 Initial Delineation of Movement Routes

In order to derive an approximate, diagrammatic estimation of movement routes I considered sequences of telemetry points within a GIS and converted point sequences into polylines for each study animal in years 2002 to 2004. I initially included all telemetry points, regardless of expected spatial accuracy, but then eliminated low precision points if they appeared to be outliers; i.e., points whose distance from other points in a movement sequence was biologically infeasible given movement rates of bighorn sheep. I used visual interpretation of these data to derive a network of 27 location nodes at which many polylines intersected, mainly at mountain peaks, intersections of ridge crests, mineral licks, and valley bottom sites well used by sheep, with an average of about 5 km separating consecutive nodes. I constructed separate networks for males and females.

I estimated the extent to which a route (edge) between nodes functioned for sheep movement by tallying the number of telemetry point sequences that traversed more than half the edge at an average straight-line speed of at least 1 km per hour. This categorization into “high-speed” and “low-speed” movement (corresponding to “directed” and “foraging” movements reported by Woolf et al. (1970)) was necessary because movements in core

habitat areas typically were very small, irregular in direction, and, in some habitat patches, numbered literally thousands of polyline segments that were impractical to count. Instead, these core habitat areas were identified using 95% fixed kernel density functions for each sex independently. The tallying of “high-speed” movements, on the other hand, was intended to capture movement outside of core habitat patches represented by the kernel density functions. The threshold of 1 km per hour was chosen because this appeared to be the approximate limit separating movements typical within core habitats from movements between core habitats.

I depicted the relative use of each route on a movement route diagram by constructing edges with line thickness proportional to the number of movement events. Movement routes were simply depicted as the shortest line segment between 2 nodes, even though sheep sometimes followed markedly non-linear paths. I categorized movement events as “summer”, extending from mid-May through October, and “winter”, extending from November through mid-May. Return trips between 2 nodes were counted as 2 trips.

3.5 Validation of Habitat Suitability Model

Tremblay (2001) developed habitat models and corridor maps for bighorn sheep, grizzly bear, and elk in the Radium Hot Springs area using an HSI approach. Her bighorn sheep model consisted of habitat, disturbance and movement routines that were ultimately combined into a map of bighorn corridor values (Figure 2). The habitat routine used wildlife suitability ratings that had been developed and mapped by previous workers using

field sign and information from relevant literature from elsewhere in North America. Both summer and winter habitat values were calculated.

Tremblay's disturbance "routine" was intended to account for alienation effects that human activity could have on bighorn sheep habitat use. Consequently, she identified human disturbance features within her study area and then applied a disturbance coefficient to a zone of influence around each feature. Disturbance coefficients and zones of influence were derived from the literature, personal observations, and key informant interviews. The movement routine incorporated the availability of escape terrain and good visibility into the model. Escape terrain coefficients were assigned values based on distance from slopes greater than 80%. Visibility coefficients were derived from estimates of forest canopy closure. Final "corridor values" were calculated as the product of the habitat value, disturbance coefficient, and movement coefficient, and were mapped for both summer and winter. These map products were then interpreted somewhat subjectively into maps of potential corridors, combining the corridor value maps with the author's personal observations, key informant interviews, and information in the literature.

To validate Tremblay's (2001) model, and to test for non-random use of the landscape by sheep, I used bighorn sheep GPS telemetry data from 2002 to 2004. Telemetry data was pooled for both sexes because Tremblay's (2001) model did not differentiate corridor use by sex. I calculated spatial utilization of resources to determine, for each study animal, the number of telemetry points in each of Tremblay's (2001) HSI classes. I also determined the relative proportions of these classes within each animal's individual home range and

within the overall study area. I calculated utilization:availability ratios, and then applied compositional analysis (Aebischer et al. 1993, Mladenoff et al. 1999) to compare use to availability for each of Tremblay's 5 summer (May through October) corridor value classes (very low, low, moderate, high and very high). Compositional analysis required a log-ratio transformation of the habitat utilization:availability data in order to achieve linear independence of the habitat class proportions and thereby allow application of a broader range of statistical tools (Mladenoff et al. 1999). I did not test Tremblay's winter corridor value model based on findings reported in Dibb (2006) that the Radium bighorn sheep in winter (November through April) rarely moved outside the village of Radium Hot Springs and its immediate surroundings (see also section 4.2).

Compositional analysis assumes that each study animal represents an independent measure of habitat use within the population, an assumption that Aebischer et al. (1993) felt was questionable for gregarious species (Aebischer et al. 1993). However, Millspaugh et al. (1998) reported that animals that group to exploit a resource are biologically independent, as opposed to animals such as predators that hunt cooperatively in packs and therefore are inherently dependent on each other. Given that some degree of controversy remains, I decided to further explore the group structure and gregariousness of bighorn sheep.

In the Radium study area I observed sheep consistently in large groups in winter, but in summer found them in smaller groups whose numbers and membership were highly variable from day to day (Parks Canada, unpublished data). To test for the independence of collared study animal locations I used software application "ASSOCI" (Weber et al. 1998).

This application assessed whether pairs of radio-marked individuals demonstrated association by meeting user-specified thresholds for spatial separation and temporal threshold. Here spatial separation was calculated as the Euclidean distance between telemetry points recorded at the same time for each individual, and temporal threshold was the percentage of occasions during which the separation of the two individuals exceeded the spatial threshold. I explored the social organization of the Radium bighorn sheep in summer by using several different combinations of threshold values, with consideration given to the average rate of travel between successive telemetry points by all animals. In particular I wished to determine whether the population behaved in summer as a cohesive herd, in which case compositional analysis, according to some authors, could be ruled out as an appropriate method for assessing habitat selection, and to determine whether certain pairs of individuals were highly correlated in space and time.

In determining which threshold values to use I considered that the average rate of movement between successive telemetry points (2002-2004) of all study animals in summer was 92.4 ± 0.9 metres/hour (S.D. = 146.0), that the horizontal extent of individual groups of sheep in summer (determined through visual observation) typically was less than 200 m, and that pairs of corresponding points between paired individuals did not always match perfectly in time but could be ± 2 hours. I chose 400 metres as the maximum spatial threshold to indicate association, with a temporal threshold of 50%. Thus, the overall definition of association was for 2 radio-collared sheep to be within 400 metres of each other for at least 50% of their temporally matched location points in a study year.

I performed the compositional analyses by using the BYCOMP program (Ott and Hovey 1997) within SAS statistical software (SAS Institute 2005). BYCOMP first employs a multivariate analysis of variance (MANOVA) and calculates the Wilks' Lambda (λ) statistic to determine whether sheep use of corridor classes differed from random. Next, for use determined to be non-random, BYCOMP ranked corridor classes in order of sheep preference, and calculated levels of significance for preference differences between ranks using a t-test. When comparing preference of pairs of classes I considered $p < 0.05$ to represent significant differences.

I assessed corridor value class selection at 2 spatial scales in order to investigate the possible effects of an arbitrary definition of study area (Aebischer et al. 1993). First, I considered selection at the home range scale in which availability was determined within the minimum convex polygon (MCP) home range of each animal. Then, I considered selection at the study area scale in which availability was determined within the intersection of the telemetry study area (MCP of all location points of all study animals) and Tremblay's (2001) study area. This latter step was necessary because Tremblay's (2001) study area also incorporated habitat models for grizzly bear (*Ursus arctos*) and elk (*Cervus elaphus*) and was not optimally configured for bighorn sheep. Consequently, her study area did not coincide perfectly with the RSF model study area. A map of her model's summer corridor values is shown in Figure 3.

I repeated the analyses using: 1) all 3D points with PDOP values < 6.0 , and 2) "movement points", in which I selected points with PDOP values < 10.0 and for which the straight line

rates of travel from the previous point and to the next point were $> 100 \text{ m hr}^{-1}$. The use of “movement points” was intended to assess use of the landscape when sheep are actually traveling, as opposed to when they may be foraging or resting.

One potential problem with compositional analysis arises when one or more study animals do not utilize all habitat types, resulting in an invalid value (0) in the numerator or denominator of the log-ratio transformation (Aebischer et al. 1993). Aebischer et al. (1993) recommend two possible solutions: 1) habitat categories can be merged together such that each animal makes at least some use of each new category, or 2) a small positive value, less than the value of the smallest recorded non-zero utilization, can be substituted for the zero corresponding to the non-utilized habitat category. I used both of these approaches in order to explore whether there were differences in habitat class ranking.

3.6 Statistical Model of Sheep Habitat

Tremblay's (2001) model incorporated several habitat variables intended specifically to reflect suitability of habitat for sheep movement; these variables included human use disturbance coefficients, disturbance zones of influence, visibility, and proximity to escape terrain. However, these variables have been reported elsewhere in the literature as being important factors not just in travel route selection, but also more generally in habitat selection. For example, Sweaner et al. (1996) and Demarchi et al. (2000) incorporated escape terrain, escape terrain buffers, visibility (vegetation density), and human use areas into their definitions of landscape feature requirements for bighorn sheep habitat mapping. Smith et al. (1999) found that 90% of all bighorn sheep activity in their study area occurred

within 300 m of escape terrain. Risenhoover and Bailey (1985) found that preferred habitats of bighorn sheep were most strongly correlated with visibility and forage density. Responses of bighorn sheep to human activity, as reported in the literature, are more variable, but several researchers have reported that human activity negatively affected selection of foraging habitat (e.g., Hamilton et al. 1982, King and Workman 1986, Papouchis et al. 2001).

These considerations indicate that definitions of terrain and human activity factors built into Tremblay's (2001) corridor model may be equally suitable for modelling habitat generally. Therefore, I developed an empirical habitat model using all GPS telemetry data meeting precision criteria, and compared the ability of this model to predict sheep occurrence to that of Tremblay's (2001) model as another means of assessing the validity of Tremblay's (2001) model within the Radium study area.

I developed a statistical model by using logistic regression to derive resource selection functions (RSF) from use/availability data (Manly et al. 2002). This process produces relative probabilities of occurrence of bighorn sheep throughout the study area as a function of a particular set of measured predictor variables (Manly et al. 2002). I used a "Design II" approach (Thomas and Taylor 1990) in which the use of resources was measured for individual study animals but availability was measured at the scale of the entire study area. I obtained resource selection probability functions (RSPFs) using

$$w(x) = \frac{\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_i x_i)}{1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_i x_i)} \quad (1)$$

where $w(x)$ is the probability of use, x_i are data values for individual predictor variables, β_0 is a constant, and β_i represent coefficients of the predictor variables.

I considered 24 biologically relevant predictor variables for model development, organized broadly into two categories: vegetation variables and terrain variables. A list of variables and their sources is provided in Table 3. Use data consisted of 4,053 GPS telemetry location points from May through October in 2002, 2003, and 2004 and included a maximum of one point per animal per day. Availability data consisted of 4,000 randomly located points within the entire study area generated by Hawth's Analysis Tools extension (Beyer 2005) to ArcGIS (ESRI 2005). I extracted habitat attributes from digital data layers using ArcGIS (ESRI 2005). Spatial resolution for all digital data was 30 m.

I used the SAS "LOGISTIC" procedure (SAS Institute 2005) to run logistic regression using maximum likelihood estimation (Tabachnick and Fedell 2001, O'Rourke et al. 2005) for calculating variable coefficients. I tested for the occurrence of highly correlated predictor variables in two ways. First, I used Pearson correlation coefficients (procedure "CORR", SAS Institute 2005) between pairs of variables to identify highly correlated pairs. I assumed collinearity if correlations were $> |0.7|$ and retained the variable that explained the most deviance when run in a univariate model. Second, I followed a procedure described by Allison (1999) to identify situations in which no pair of variables is highly correlated, but several variables considered together are highly interdependent. I ran my model through the SAS regression procedure with collinearity options specified (procedure "REG, SAS Institute 2005), and then used the variables' tolerance values as measures of

collinearity. Although there is no generally accepted cut-off level for tolerance values, I considered elimination of variables with tolerance values below 0.4, following the procedure of Allison (1999). I also ran univariate logistic regressions to identify and eliminate variables with weak predictive ability, and then used a reduced set of variables to develop *a priori* candidate models (Franklin et al. 2001) based on the two broad categories of variables and on combinations from the two categories.

I compared the resulting set of candidate models using the AIC (Burnham and Anderson 1998, Franklin et al. 2001). This criterion takes the form

$$AIC = -2\{\log_e(L_m)\} + 2K \quad (2)$$

where L_m is the maximized likelihood for the fitted model and K is the number of variables.

I ranked the competing models by increasing order of AIC and used the highest ranking model or models for subsequent comparison to the Tremblay (2001) model. I calculated the Akaike weight (w_i) for each candidate model (Burnham and Anderson 2003) and used this to assess the relative likelihood of each of the candidate models being the best model of the set. I also used AIC values and the AIC differences to assess whether there was sufficient support for the top ranked model to exclude lower ranked models from further consideration and to consider the possible need for model-averaging. In particular, I followed the Burnham and Anderson (2003) rule of thumb that models for which $\Delta_i \leq 2$ cannot be ruled out as the best model.

To facilitate comparisons, I reclassified this model (hereafter referred to as the “RSF” model) to the same number of classes used by Tremblay (2001) in her model (hereafter

referred to as the “HSI” model). Thus, while the model output at any point in the study area was a value between 0 and 1.0, this output was reclassified to a discrete value from 1 to 5 representing 5 classes (“very low”, “low”, “moderate”, “high” and “very high”). Class break points were set such that the RSF model had the same relative proportions of area within each class. For example, if 1.0% of the study area was rated “very high” according to the HSI model, then I set the “very high” class break point for the RSF model so that the highest ranking 1.0% of the study area according to this model was classed as “very high”.

3.7 Comparison of HSI and RSF Models

I used GPS telemetry data from 9 animals radio-collared in 2005 to compare the relative performances of the HSI and RSF models. These data were not used in development of the RSF model in order to avoid the biases inherent in testing a model with the same data used to develop it (Johnson 2001, Williams et al. 2002). I used a subset of the 2005 telemetry data consisting of only those points that occurred within the intersection of the two study areas.

I used compositional analysis (Aebischer et al. 1993) to investigate the sheep use of habitat classes of both models and to compare the rank order of classes. I also used t-tests to test for significance of differences between classes. I tested each model at both spatial scales; i.e., with availability defined first at the scale of individual home ranges and then at the scale of the entire study area. I repeated these analyses after collapsing the “high” and “very high” habitat classes of each model into a single class to remove any effects of small sample sizes within the “very high” class.

I also applied the “sample validation method” of Howlin et al. (2003) in order to obtain some absolute measures of the predictive abilities of the two models. For each model I used approximately 10,000 random points within the intersection of the two study areas to define availability. From this set of points I generated 20 percentiles, or “bins”, based on the values of the model at all points. By summing the model’s predicted probability of occurrence at each point within a bin, and then scaling according to the number of points in the “used” sample, I determined an “expected count” of used points in each bin. I then took a sample of 1057 telemetry points (maximum one point per day per animal) and assigned each point to the bin corresponding to the model value at that point; this determined the “observed count” for the sample validation used dataset. I used simple linear regression of the observed count on the expected count, and then assessed the predictive ability of the model based on the slope and 95% confidence intervals of slope using Table 4 from Howlin et al. (2003). I used SAS procedure ROBUSTREG (SAS Institute 2005) to explore the effects of highly influential and outlier points on the linear regression.

3.8 Restoration Recommendations

I considered the possible need for ecosystem restoration along bighorn sheep spring and fall movement corridors, based on interpretation of the corridor delineation and modelling results. I first used a GIS to identify a set of candidate polygons based on terrain and vegetation attributes. In particular, I mapped polygons that had south-west, south, or south-east aspects, slope angles of greater than 15° , and elevations between 800 and 2000 m. I then selected from those polygons areas with forest canopy closure of greater than 50%, on

the assumption that sites with suitable terrain but with thick forest cover would be the best candidates for restoration treatments such as thinning or prescribed burning. Of all polygons meeting these criteria, I identified those polygons along active, heavily used corridors as the highest restoration priorities, and those along relatively infrequently used corridors or adjacent to historic winter range as secondary priorities.

I also considered the need to maintain sheep access to historic winter range at Stoddart, Shuswap, and Windermere Creeks south of Radium Hot Springs. I located this winter corridor by using telemetry point sequences from several rams that travelled it, and interpolated between points by using terrain features, by connecting forest openings, and by avoiding agricultural lands.

Chapter Four: Results

4.1 Initial Delineation of Movement Routes

All study animals except 1 exhibited migratory behaviour, moving between winter range in the Columbia River valley bottom and summer range in alpine areas of the Brisco or Stanford ranges (Figure 4). Study animal M005 was killed on highway 93/95 on August 1st 2002 having never moved to the high country. The area within and immediately adjacent to the village of Radium Hot Springs comprised most of the winter range, including the village itself, the Radium Springs Golf Course, the “Mile Hill” on highway 93/95, a small area just north of the Radium village, and adjacent portions of KNP east to the Radium Hot Springs pools. Five of 7 rams in 2002 and 2003 made brief winter excursions as far south as Stoddart or Windermere Creeks; in 2004 most ram radio collars were removed in October and so early to mid-winter movements of these animals were not recorded. No marked females were recorded using areas south of the Mile Hill in winter, or making any winter movements of more than 2 km, although I observed several unmarked ewe-lamb groups at Stoddart Creek, approximately 7 km south of the core winter range near Radium village.

In summer, all study animals selected habitats either in the Brisco Range north of highway 93, or in the Stanford Range south of highway 93. Of 14 females, 11 used only the Brisco Range, 1 exclusively used the Stanford Range, and 2 used both. Of 8 males, 2 used the Brisco Range and 6 used the Stanford Range. There was little spatial overlap of summer habitat use by males and females, illustrated through the 95% kernel density functions

depicted in Figures 5 and 6. In the Brisco Range, females tended to use habitats south of Mt. Kindersley, while rams used habitats north of Mt. Kindersley in the Mt. Crook area. In the Stanford Range, ram use was concentrated on Kimpton Ridge and the south ridge of Mt. Sinclair, whereas the small amount of female use recorded was mainly on the north ridge of Mt. Sinclair.

Sheep sometimes made rapid movements of several km in 2 to 6 hours between habitat patches or seasonal ranges, especially in summer. Frequently travelled routes typically linked winter range to lambing or summer range, or linked summer range to mineral sites (Figures 5 and 6). Visual observation of groups of sheep throughout the summer confirmed that these animals frequently visited two sites to obtain minerals: the salt shed at the Parks Canada Highways Service Centre compound, and the highway 93 roadside approximately 12 km east of Radium Hot Springs village. Lambing sites, as inferred from telemetry data and visual observation of sheep, occurred mainly on west and south aspects in the Brisco Range, in steep terrain < 300 m below tree line. Most movement routes were along ridge crests, and along steep, indistinct ridges or slopes that represented the most direct routes from alpine terrain to valley bottom sites.

4.2 Validation of Habitat Suitability Model

Between November and the end of April, sheep nearly always remained within a small (< 6 km²) area of winter range. Therefore there was insufficient data available to assess the “winter corridor values” map derived by Tremblay (2001). I therefore limited model validation to the summer corridor values map of Tremblay (2001).

The results of testing for animal independence using application ASSOCI (Weber et al. 1998) are summarized in Table 5 as animal pair-wise percentage association values in each year from 2002 to 2004. The overall mean association between individual bighorn sheep was 6.2%, and only 1 pair of sheep out of 85 possible pairs was classified as associated (within 400 m of each other at least 50% of the time). Increasing the spatial threshold to 800 metres increased the overall mean association to 9.2% but still only 1 pair of sheep were found to be associated. Although spatial and temporal thresholds in these analyses are somewhat arbitrary, these results indicate that bighorn sheep in summer act largely independently of one another and do not occupy their habitat as 1 or several discrete units. I therefore proceeded with compositional analysis of Tremblay's (2001) classification using individual animals as the sample units.

Tremblay's (2001) classification scheme for her corridor value surface resulted in a high proportion of the study area (67.0%) being classified as very low corridor value and only a small proportion classified as very high (0.8%), with the remaining classes falling in between (Table 6). Some individual animals were not recorded within the "very high" class, therefore I executed the compositional analysis using both substitution of a small value for zero and collapsing Tremblay's classes 4 and 5 into a single category.

At the scale of individual home ranges I found evidence that bighorn sheep use of the HSI model's probability classes was significantly non-random both when I used all 5 classes but replaced utilization values of zero with a very small non-zero number ($\lambda = 0.14$, $F = 25.37$,

$p < 0.001$, Table 7) and when I collapsed the high and very high classes into a single class ($\lambda = 0.14$, $F = 36.66$, $p < 0.001$, Table 8). In the latter case, sheep showed a preference for the moderate class over all other classes and the combined high and very high class ranked above the low and very low classes. Although the very low class was ranked higher than the low class, the difference was not significantly different than random. In the case where all five classes were retained, results were similar except that the very high class was ranked lowest of all classes, with this difference being significant at $p < 0.05$ when the very high class was compared to either the moderate or high classes.

Similarly, at the scale of the entire study area bighorn sheep exhibited selection for corridor value classes both when I used all 5 classes but replaced utilization values of zero in the very high class with a very small non-zero number ($\lambda = 0.12$, $F = 31.51$, $p < 0.001$, Table 9), and when classes 4 and 5 were collapsed into a single class ($\lambda = 0.13$, $F = 41.85$, $p < 0.001$, Table 10), and class rankings were similar to the previous example, including that the very high class again was ranked lowest.

Given that the very high corridor value class occurs over such a small portion of the study area, further results in this section are reported for analyses with combined high/very high classes. Overall, considering both scales of analysis, the moderate class is the most strongly selected for, followed in order by the high/very high class, the very low class, and the low class. Selection differences between the low and very low classes generally were not significant to $p < 0.05$ but differences in selection between other classes were significant to $p = 0.05$.

I obtained similar results when the analyses were repeated on a subset of sheep GPS points that included only points associated with substantial sheep movement as calculated from successive point locations. For these movement points sheep exhibited selection for corridor value classes both at the individual home range scale ($\lambda = 0.13$, $F = 27.84$, $p < 0.001$, Table 11) and at the scale of the entire study area ($\lambda = 0.065$, $F = 57.40$, $p < 0.001$, Table 12). At the home range scale sheep preferred the moderate class to very low or low classes and preferred the high/very high class to low; all other differences among class preferences were not significant to $p < 0.05$. At the study area scale sheep preferred the moderate class relative to all others, and preferred the high/very high class to very low. Other differences among class preferences were not significant to $p < 0.05$.

Table 13 summarizes all compositional analyses, showing the rank order of sheep preference for the various classes, including identification of significant versus non-significant differences among consecutive classes.

4.3 Statistical Model of Sheep Habitat

I ranked a set of 7 candidate models on AIC after initial screening of variables for collinearity and predictive power. Model “Terrain + Vegetation 2” was the top ranked model (Table 14). The second ranked model, “Terrain + Vegetation 3”, had an AIC difference of 3.8 from the top ranked model, providing weak evidence that the top model was not the best candidate in the set (Burnham and Anderson 2003). The Akaike weights of 0.869 and 0.131 for the top and second ranked models respectively indicated that the top

ranked model was 6.63 times more likely than the second ranked model to be the actual top model of the set. I therefore chose the “Terrain + Vegetation 2” RSF model as the basis for comparison of statistical modelling with Tremblay’s (2001) approach.

The logistic regression equation for the “Terrain and Vegetation 2” model was as follows:

$$w(x) = 1 / (1 + \exp(-0.6387 + 0.0293[\text{slope}] - 0.000326[\text{dem}] - 0.0132[\text{dem300sd}] - 0.4929[\text{aspect3}] + 0.1167[\text{greenness}] + 0.0251[\text{crownclosure}] - 0.00415[\text{rad_may}])) \quad (3)$$

This model indicated that compared to random locations within the study area, sheep locations were associated with the following attributes: lower slope angles, lower greenness values, open forest canopy, higher elevation, greater vertical terrain complexity, higher solar radiation values in May, and easterly aspects. I reclassified the model’s raster output to 5 classes and adjusted break points between classes to facilitate comparisons with the HSI model. A map showing the RSF model in 5 classes is shown in Figure 7.

4.4 Comparison of HSI and RSF Models

For the RSF model, at the scale of individual home ranges, compositional analysis (Aebischer et al. 1993) using 2005 data provided evidence that sheep selected for habitat value classes in a non-random manner. This was the case both when I retained all 5 habitat classes for the compositional analysis ($\lambda = 0.083$, $F = 11.12$, $p = 0.02$, Table 15), and when the high and very high classes were collapsed into a single class ($\lambda = 0.084$, $F = 18.12$, $p =$

0.004, Table 16). For the 4 class analysis, habitat classes were ranked in the order expected; in other words, the “high” class was the most preferred, followed by “moderate”, “low”, and “very low” in order. Differences in class preference were all significant to $p < 0.05$. The results were similar for the 5 class analysis except that preference for the “very high” class was not significantly different than for the “moderate” or “high” classes. Similar results were obtained at the study area scale (Tables 17 and 18).

The HSI model exhibited generally weaker correspondence between class and ranking, although significant selection occurred overall at the individual home range scale both with 5 habitat classes ($\lambda = 0.026$, $F = 37.44$, $p = 0.002$, Table 19) and with 4 classes ($\lambda = 0.032$, $F = 49.65$, $p < 0.001$, Table 20). However, in the 5 class analysis both the “moderate” and “high” classes were significantly more preferred than the “very high” class and the “high” class was not significantly more preferred than the “moderate” class. Differences between the “low” and “very low” classes were not significant. Similar results were obtained for analysis at the study area scale (Tables 21 and 22). Test statistics from all compositional analyses are summarized in Table 23.

Using the sample validation method of Howlin et al. (2003) I determined the numbers of expected (random) points and used (telemetry) points in each percentile bin for each model (Table 24). In the case of the RSF model I found a linear regression equation for expected versus used counts of:

$$\text{Used} = -73.626 + 2.393 * \text{Expected} \quad (4)$$

($F = 29.58$, $p < 0.001$, $R^2 = 0.622$, Figure 8).

The slope of 2.393 had upper and lower 95% confidence intervals of 1.531 and 3.273 respectively. Despite large confidence intervals, this fits the “acceptable” predictive ability category of Howlin et al. (2003) because the slope was greater than 1 and the confidence interval excludes 0 and 1. I also repeated the linear regression after eliminating the three regression points corresponding to the three highest ranked bins, which regression robustness testing found were highly influential points. Although these points represent real data, their prominence may be exaggerated because the RSF model was based on several spatial layers with discrete values which, when combined in logistic regression, produced large numbers of model points in the highest ranking categories. The linear regression equation for this subset of points was:

$$\text{Used} = -5.790 + 0.734 * \text{Expected} \quad (5)$$

$$(F = 25.47, p < 0.001, R^2 = 0.629, \text{Figure 9})$$

with the slope 95% confidence intervals of 0.440 and 1.028, corresponding to “good” model predictive ability (Howlin et al. 2003) because the confidence interval excluded 0 but included 1. The F statistics for both linear regression tests on the RSF model indicate that overall the linear regression models explain a significant portion of the variation in the data. The R^2 values suggest that just over 60% of the variation in the RSF used value can be explained by this variable’s linear relationship to the RSF expected value.

Using the same procedure on the HSI model I derived a linear regression equation of

$$\text{Used} = 23.499 + 0.556 * \text{Expected} \quad (6)$$

$$(F = 4.53, p = 0.047, R^2 = 0.201, \text{Figure 10})$$

and slope confidence intervals of 0.44 and 1.07. This corresponded to model predictive ability of “good”, although the model barely achieves significance at the $p = 0.05$ level and the R^2 values suggest that only 20% of the variation in the HSI used value can be explained by this variable’s linear relationship to the HSI expected value. Linear regression robustness testing identified 5 points that were either outliers (1) or highly influential (4). When these points were removed from the regression I derived the following equation:

$$\text{Used} = 11.671 + 0.187 * \text{Expected} \quad (7)$$

$$(F = 2.85, p = 0.115, R^2 = 0.180, \text{Figure 11})$$

The slope in this regression had confidence intervals of -0.031 and 0.405 , values that correspond to “unacceptable” predictive ability because the confidence interval includes 0 (Howlin et al. 2003). The F statistics for both linear regression tests on the HSI model, being at or somewhat below $p = 0.05$, indicate marginal ability of the regression tests to explain a significant portion of the variation in the data; the R^2 values suggest that only about 20% of the variation in the HSI used value can be explained by this variable’s linear relationship to the HSI expected value.

4.5 Restoration Recommendations

I completed the selection of candidate polygons for restoration using the criteria described in section 3.8. These polygons are shown in Figures 12 and 13.

Chapter Five: Discussion

5.1 Validation of Habitat Suitability Model

One of my primary objectives was to validate the HSI movement corridor model developed by Tremblay (2001). However, there are no absolute measures of the validity or predictive ability of an HSI or use-availability model, nor is there a single combination of validation measures that could be applied to all models for all purposes (Mayer and Butler 1993). I chose two model assessment methods, compositional analysis (Aebischer et al. 1993) and the sample validation method (Howlin et al. 2003) that are suited to my particular problem because of issues including independence of use:availability ratios, the use of arbitrary definitions of study area, ease of computation, and the ability to distinguish between poor, acceptable, and good model predictive ability.

Association testing indicated that the Radium bighorn sheep did not aggregate in summer into cohesive herds with constant membership. Weber et al. (1998), applying the same methods I used but with thresholds of 200 m and 70%, found mean associations of 11% and 16% for two herds of radio-collared elk (*Cervus elaphus*) and concluded that these animals were organized as “gregarious aggregations” whose “structure and composition were relatively dynamic over even brief time periods” (Weber et al. 1998, pg. 7). A similar description applies to the social organization of the Radium bighorn sheep during summer. I speculate that the differing levels of spatial independence reported among bighorn sheep herds in North America is a result of differences among study areas in such influences on

animal grouping as size and proximity of habitat patches, herd size, habitat quality, and predation pressure.

At both scales considered, i.e., selection of a home range within the study area and selection of habitat within a home range, sheep selection of HSI model classes was significantly different from the proportions available within the landscape. Nonetheless, this model appears to have considerable limitation when applied to the Radium Hot Springs study area. Compositional analyses indicate a weak correspondence between the rank order of habitat classes and the rank order of preference by study animals. Linear regression testing using the sample validation method produced variable results ranging from “unacceptable” to “good” depending on whether outlying points were excluded from the regression. R^2 values for these tests indicate relatively weak ability of the regression tests to explain the observed data.

I argue that the theoretical HSI movement corridor model developed by Tremblay (2001) is better suited for characterizing general habitat selection by bighorn sheep than for characterizing movement corridors specifically. Tremblay's (2001) model calculates corridor values based on model parameters that assume that sheep will select open habitats for movement. However, in the Radium Hot Springs study area open habitats were generally available only near the valley floor and above tree-line. Consequently corridor models based on open terrain selection are poorly suited for predicting locations of corridors between major seasonal ranges. Use:availability ratios derived from occurrence of summer telemetry points within Tremblay's 5 corridor model classes demonstrate this

(Table 6). Ratios derived from movement telemetry points for the three highest ranking classes (moderate, high, very high) were all lower than the corresponding ratios derived from all telemetry points. The use:availability ratio for the lowest ranking class (very low) was higher for movement points than for all points. Additionally, compositional analyses of Tremblay's habitat classes in relation to summer telemetry data show more significant differences in selection between classes than do corresponding compositional analyses using movement points only (Tables 8, 10, 11, 12, 13).

I observed few substantial differences between outputs of compositional analyses conducted at individual home range scales versus at the scale of the entire study area. Thus, the apparent lack of conformance of sheep habitat selection with the HSI model does not appear to be a function of scale.

Tremblay's (2001) definitions of habitat classes in her HSI model resulted in less than 1% of the study area being categorized as "very high" corridor value. For management purposes, such a restrictive definition of the "very high" category is unlikely to be useful. In view of the small extent of this category, and the likelihood that in model assessment only a small number of telemetry points would fall in this category, it is appropriate to merge the "high" and "very high" classes into a single category. Indeed, the "very low" category defined by Tremblay comprises 67% of the study area and sheep selected the "low" category (21% of study area) nearly in proportion to its availability. Although any definitions of class boundaries are arbitrary, it could be argued that Tremblay's definitions were weighted too heavily towards the low ranking categories. It may be difficult to

convince managers of the conservation value of “very low” importance habitat, even though in my study sheep spent 41% of their time in such habitat. This is an example of a problem that Garshelis (2000) identified with use:availability studies: how to define available habitats. It is typically assumed that animals have free and equal access to all available habitats, although this assumption may only hold if availability is defined for each animal individually, as was done in my study for compositional analyses at individual home range scales. However, there remains the problem that low ranking habitats, if large in area, may be crucial to meeting the life requirements of a population of animals even if these habitats are selected less than in proportion to their occurrence. Thus, caution is needed in interpretation of model outputs for management purposes, especially if such models are based on relatively long seasons that might obscure the selection of very specific habitats over a short time period (Garshelis 2000) to meet a specific life requisite (e.g., lambing). If sufficient data exist, it may be advisable to model selection over several shorter time periods rather than over one long season or even an entire year.

Tremblay (2001) modeled winter habitat and movement on the assumption that bighorn sheep at Radium could have several distinct winter ranges, with corresponding movements in between, as found by Geist (1971) for a study area in Banff National Park, Alberta. Telemetry monitoring of the Radium herd, however, found only scant evidence of such ranges or movements (Dibb 2006). In fact, the Radium sheep were found to be confined for nearly 8 months each year to approximately 10 km² of winter range within or near the village of Radium Hot Springs, with only occasional, brief, and unpredictable movements of a small number of animals to the Stoddart Creek, Shuswap Creek, or Windermere Creek

winter ranges 7 - 16 km south of the village. This intensive use of a small winter range area over a prolonged period may be, in part, an optimal foraging strategy that allows these animals to acquire forage resources efficiently (MacArthur and Pianka 1966). However, bighorn sheep habituated to urban areas may have increased risk of disease transmission, collisions with motor vehicles, harassment by dogs and humans, and consumption of toxic plants (Rubin et al. 2002, Tremblay and Dibb 2004, Dibb and Quinn, in press). Although benefits for sheep conservation would likely accrue from reducing habituation to the Radium village area through habitat restoration and other means, it appears unlikely that this would result in use of a set of temporally distinct winter ranges with regular migrations between them, as reported by Geist (1971). Stelfox (1978) and Stelfox et al. (1985), in field studies of the Radium herd between 1966 and 1985, prior to abandonment of traditional winter range, did not report any evidence of temporally distinct winter ranges. In any case, it was not practical to assess Tremblay's model of winter corridor values for bighorn sheep because sheep exhibited very little migratory behaviour in winter during my study.

5.2 Initial Delineation of Movement Routes

Sexual segregation in summer leads to strongly different patterns of habitat selection and movement corridor use by the two sexes (Figures 5, 6). Nearly all female sheep use summer habitats north of Sinclair Creek (Dibb 2006). These habitats are accessed by the south ridges of Mt. Berland, John McKay Ridge, and East Sinclair Ridge, and along the ridge crest connecting Transmitter Peak to Mt. Kindersley. Some of the most heavily used summer habitats are traversed by the popular Kindersley-Sinclair hiking trail. The

importance of this area for lambing and lamb rearing justifies monitoring human activity and taking measures to protect sheep from human disturbance, discussed below in the “Recommendations” chapter. Several lambing sites were located up to 40 km north of Radium Hot Springs and were reached largely via lower slope and valley bottom travel, rather than by ridge systems. This suggests the possibility that sheep access to these sites in future could be impaired by human developments near the foot of the Brisco Range between the communities of Edgewater and Harrogate. In addition, these journeys to northern lambing sites placed the sheep at risk of coming into contact with domestic sheep ranches, and thereby being exposed to potentially lethal pathogens (Foreyt and Jessup 1982, Foreyt 1989, Gross et al. 2000).

Most rams used summer habitats south of Sinclair Creek in the Kimpton Ridge area, although several used habitats north of Sinclair Creek near Mt. Crook. The southern ranges were accessed only from the north, via Kimpton Ridge, or from the west, via Redstreak Mountain. No movement was recorded directly between these summer ranges and the historic winter ranges at Stoddart, Shuswap, and Windermere Creeks. Several study rams also made occasional visits to the historic winter ranges at Stoddart, Shuswap, and Windermere Creeks, traveling south from Radium mainly along valley bottom routes and adjacent rocky knolls, and in proximity to known domestic sheep ranches.

Both sexes made periodic migrations from summer range to valley bottom mineral sites and back to summer range. One and possibly both of the two main mineral sites are artificial. One site is the road salt shed in the Parks Canada highways compound at McKay Creek;

the other is a site along highway 93 near Sinclair Pass for which it is not certain if the mineral source is natural or is the residue from heavy applications of de-icing salt during winter. Stelfox (1978) and Stelfox et al. (1985) reported that mineral licks of the Radium herd occurred at Stoddart Creek and along lower Sinclair Creek. These authors did not record sheep obtaining minerals at the compound salt shed or at Sinclair Summit along highway 93. Sheep patterns of mineral use likely have changed in the past 3 decades due to increased availability of artificial salt sources. However some road salts have ferrocyanides or other inorganic chloride salts added as anti-caking agents and are considered toxic (Environment Canada 2006); the effects of repeated consumption of such substances by bighorn sheep is unknown, although no evidence of negative health effects was reported by Dibb (2006).

5.3 Statistical Model of Sheep Habitat

Using RSF modelling I found that, during summer, bighorn sheep selected habitat that was characterized by more open forest structure, higher elevation, and greater terrain complexity than were randomly selected points within the study area, consistent with results from other bighorn sheep habitat studies (Risenhoover and Bailey 1985, Smith et al. 1990, Johnson and Swift 2000, Tremblay 2001). Sheep also selected easterly aspects, lower greenness values, and lower steepness (slope). Sheep selected easterly aspects mainly during July, August and September, when males selected easterly aspects 34.0% of the time and females 23.1% of the time out of a total of 8 aspect classes (Dibb 2006). Delayed plant phenology on northerly and easterly aspects enables sheep to extend their access to nutritious, emerging food plants (Festa-Bianchet 1988b). However the north-

south trend of mountain ranges in the Radium study area results in little occurrence of north aspects. It appears that the selection of easterly aspects in summer overrode the selection of warm south and west aspects in May, June, and October. The selection of habitats with low greenness values corresponds to selection for less dense vegetation communities, likely offering greater visibility for predator detection. The apparent selection of lower slope angles was more surprising, given the tendency of sheep in other study areas to prefer habitat within or close to escape terrain (Johnson and Swift 2000, McKinney et al. 2003). However, bighorn sheep at Radium Hot Springs remain on their low elevation, flat winter ranges within or near the village of Radium Hot Springs until mid to late May; thus, by using Tremblay's definition of "summer" as from May 1st to October 31st, up to a month of low slope angle locations are collected for each study animal.

It was beyond the scope of this study to develop separate RSF models for male and female sheep, but this would be a worthwhile future project if data collection continues for several more years and leads to a large enough sample of each sex for RSF model development and compositional analyses. Enough data may already exist to test the hypothesis that ram segregation from ewes in summer is driven by differences in habitat selection rather than by a tendency toward social segregation. Sex-specific models developed for individual seasons could be important for management because they could predict the occurrence of animals in relation to key life history events; for example, the location of female lambing ranges, and male concentration areas during the fall ram harvest season.

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5.4 Comparison of HSI and RSF Models

Based on discussions provided above, it is most appropriate to compare compositional analyses for the two models using all telemetry points (i.e., not using just those points meeting the criteria of “movement” points), with the “high” and “very high” classes merged into a single class, and using definitions of availability at the scale of individual animal home ranges. Using these assumptions, the RSF model had a perfect correspondence between rank order based on use, and predicted rank order; in other words, the “very low” class was the least preferred, followed by the “low” class, and so on. In addition, the differences in selection between classes were all significant to $p \leq 0.05$. On the other hand, for the HSI model the “low” class was ranked lower than the “very low” class (although the difference was not significant to $p = 0.05$), and the combined “high” class was not selected to a significantly higher degree than was the “moderate” class. On this basis I conclude that the RSF model fits the telemetry data better than does the HSI model.

Comparisons of model performance using the sample validation method of Howlin et al. (2003) were less clear. However, F statistics suggested that linear regression tests run on the RSF model can explain a significant ($p < 0.001$) portion of the variation in the data, whereas corresponding tests run on the HSI model were, in one case, not significant to $p = 0.05$ and, in the other case, were barely significant to this level.

I attribute the RSF model’s performance to the following factors:

- (1) The model was developed using data specific to the Radium study area, unlike the HSI model that incorporated parameters derived from bighorn sheep studies elsewhere in western North America.
- (2) The Radium study area, relative to most other bighorn sheep study areas, was characterized by thick forest cover and the presence of artificial, urbanized habitats whose use may not be predicted by models based on idealized habitat preferences of sheep. The RSF model incorporated data that represented the whole spectrum of habitats actually used by sheep and, according to Hebblewhite et al. (2006) likely were not strongly biased according to forest cover.
- (3) The RSF model used several variables that were not available or were not used in development of the HSI model.
- (4) The HSI approach has several weaknesses, including its reliance on expert opinion, and the subjective manner in which variables are chosen and weighted. The RSF approach is mathematically more robust.

The advantages of the RSF modelling approach in characterizing the Radium study area specifically, however, could weaken the model's ability to predict habitat use in other areas. This model should be applied cautiously to other areas, particularly to study areas that are far enough removed to be influenced by a substantially different set of environmental conditions. Ideally a more general RSF model could be developed or assessed using data collected from several sheep populations.

5.5 Data Collection and Study Design Considerations

Sample size limitations in this study made it necessary to pool data from both sexes of animals and from several years of the study. This approach also allowed direct comparisons between the RSF and HSI models because the HSI model was developed without consideration of sex differences in habitat selection. Pooling data across years may obscure differences resulting from annual variation in environmental conditions, but may result in a model that is less skewed by one year of unusual conditions and therefore is better suited for long-term management purposes.

One limitation of habitat modelling in the Radium Hot Springs study area at present is the lack of availability of a comprehensive forest cover spatial database at an appropriate resolution and covering the entire study area. Tremblay (2001) also encountered this problem in her HSI modelling in the Radium study area. Validation confirmed that, in general, the RSF model adequately predicted the occurrence of independent bighorn sheep locations; however, I believe that model performance could be improved with use of a better forest cover layer. In particular, 1:20,000 coverage of the entire study area, and the availability of a large suite of forested and non-forested cover variables are needed. Such coverage is expected to be available in 2007 under the British Columbia Vegetation Resources Inventory (Sandvoss et al. 2005).

5.6 Migration

Migratory behaviour among marked animals in the Radium bighorn sheep herd was common during my study, although 1 marked animal did not migrate, and groups of

unmarked rams were frequently observed near Radium Hot Springs in summer (Parks Canada, unpublished data) and may have been sedentary animals. Poor visibility along seasonal migration routes due to forest encroachment in the study area is of concern because of the potential for such insecure migration corridors to be abandoned by sheep (Risenhoover et al. 1988). Continued fire suppression in the ranges of the Radium bighorn sheep will exacerbate this problem. Although the specific implications for individual fitness of abandonment of migration routes are unknown, as are the fitness consequences of habituated sheep relying on artificial habitats in urban areas, migration is crucial to maintenance of large, mobile and wild sheep populations (Risenhoover et al. 1988, Epps et al. 2005). While continued efforts are needed to maintain and restore critical winter range, maintaining connectivity between sheep seasonal ranges should also be a management priority.

According to migration theory (Hedenstrom 2003), selection should favour migration if it increases reproductive success (Baker 1978). Reproductive success, in turn, is affected by forage quality and availability, and by predation risk (Nicholson et al. 1997, Fryxell and Sinclair 1988). In British Columbia, horn growth, as a correlate to nutrition, has been shown to be greater in migratory herds than in non-migratory ones (Hebert 1973, Wehausen and Ramey II 2000). Nonetheless, bighorn sheep may choose to abandon their seasonal migrations if deteriorating habitat quality reduces the nutritional advantages or if migration becomes too risky due to predation (Festa-Bianchet 1988b, Risenhoover et al. 1988). In the Radium Hot Springs study area sedentary behaviour of bighorn sheep likely would lead to increased levels of highway strikes and increased pressure on limited winter

range, in addition to possible decreased nutritional intake. The maps of habitat and movement routes in this thesis will provide pertinent information for fire and vegetation management planning. The reliance of bighorn sheep on traditional migration routes (Geist 1971) suggests that current migration routes, even if degraded because of forest in-growth, are the logical places to begin restoration programs. Some recommended areas for treatment are mapped in Figures 12 and 13, and are based on interpretation of RSF model outputs, sheep terrain and vegetation structure preferences, and proximity to current or historic migration routes.

5.7 Dispersal

I did not detect any dispersal of animals from the Radium Hot Springs study area, a result that is not surprising in view of the relatively small sample size of marked animals and the rarity of dispersal events reported from other studies of this species (Geist 1971, Bleich et al. 1996, Gross et al. 2000). In addition, I did not select study animals from the young ram age-sex classes that were most likely to disperse (Geist 1971). Several long distance movements of up to 40 km from Radium Hot Springs did occur, but these were either exploratory movements by rams that did not result in contact with other herds, or travel by females to lambing sites. In all such cases the animals subsequently returned to the Radium Hot Springs area. However, Stelfox (1978) reported that in 1972 at least 1 bighorn tagged in Radium had been seen in a group of sheep at Golden, B.C., more than 90 km from Radium, and that it was likely that the entire group of sheep had originated in Radium. Sheep had not previously been observed in the Golden area. A herd of sheep still persisted at that location at the time of my study (Parks Canada, unpublished data). Tremblay

(2001), based on interviews with knowledgeable persons, reported that an individual sheep, recognizable because of a distinctive injury, had been observed both at Radium and in the Mitchell Range. I could not find other evidence of movement of sheep between the Radium area and other sheep ranges.

In spite of the infrequency of dispersal among wild sheep, conservation in the long-term requires consideration of avenues for dispersal between herds because sheep are patchily distributed in what some authors have proposed is a metapopulation structure (Bleich et al. 1996, Demarchi et al. 2000). In a metapopulation structure movement between subpopulations is needed in order to promote genetic diversity and to recover from local population declines and extirpations (Singer et al. 2000b, Chetkiewicz et al. 2006). In Kootenay National Park a herd of bighorn sheep persisted in the Mitchell Range east of the Kootenay River until at least the early 1970s (Stelfox 1978) but this herd has been functionally extirpated since the 1980s (Parks Canada, unpublished data). Large wildfires that burnt portions of this range in 2003 may have created suitable sheep habitat, but sheep presently may be unwilling to travel the 10 km through thick forest cover to reach the Mitchell Range from the Radium Hot Springs area. Similarly, conifer encroachment in the Brisco and Spillimacheen Ranges has further isolated the Radium sheep from the next populations to the north near Golden and to the south at Columbia Lake.

Although little information is available on characteristics of dispersal routes of bighorn sheep, dispersing animals are likely to apply some of the same decision rules in selecting dispersal routes as they do in selecting habitats for residency (Chetkiewicz et al. 2006). A

validated, regional-scale model of bighorn sheep habitat suitability could help to identify potential linkages between herds and thus provide further guidance to forest management planning.

Management and conservation of long-distance migratory species is challenging in part because such species are likely to be dependent on a mix of land jurisdictions. The challenge is even greater for species such as bighorn sheep that have adaptive behavioural limitations, and, therefore, may be poorly equipped to respond to loss or disruption of traditional habitats or movement routes (Risenhoover et al. 1988, Singer et al. 2000a). Detailed knowledge of migratory movements is a critical component of conservation planning (Thirgood et al. 2004). This thesis provides new information on the migratory movements of bighorn sheep at Radium Hot Springs and, in conjunction with other information sources and with a program of active management, provides an opportunity to restore connectivity between seasonal ranges and to other sheep ranges in the East Kootenay region.

Chapter Six: Recommendations

6.1 Model Improvements and Extensions

1. Re-run the RSF model based on new forest cover mapping, when available. Forest cover mapping is expected to be available in 2007 at improved resolution (1:20,000) than older mapping, available for the entire Radium study area, and with more attributes relevant to bighorn sheep habitat selection. For example, classification of vegetated and non-vegetated lands above tree-line would allow distinctions to be made between bare rock, ice, talus, moraine, and several classes of alpine vegetation classes, distinctions that the current model cannot make.
2. Collect more movement points through additional animal-years of sampling and by increasing the sampling frequency of GPS collars during migration periods.
Develop a movement RSF model based on these.
3. Develop separate RSF habitat models for male and female sheep, and for several shorter seasons rather than for one May through October summer period.
4. Acquire movement/habitat telemetry points from other sheep ranges and use these to develop and test a regional RSF model of sheep habitat/movement. Such data may become available because other agencies in south-eastern B.C. and south-western Alberta are currently monitoring radio-collared animals as part of habitat studies and to monitor the success of transplant programs. Larger scale models of bighorn sheep habitat/movement could then be used as an input into forest management and land use planning initiatives.
5. Use GPS telemetry data to model bighorn sheep lambing sites.

6.2 Management Recommendations

1. Continue to monitor a sample of bighorn sheep at Radium Hot Springs to measure the response of sheep to completed and future habitat restoration measures. Use monitoring results to plan and conduct restoration activities in an adaptive management approach.
2. Plan and conduct additional restoration work within critical winter range, focussing on areas immediately adjacent to occupied habitat and emphasizing treatment of areas within or near escape terrain. Monitor changes in levels of sheep use of artificial habitats within the village of Radium Hot Springs and in rates of crossing highway 93/95 on the mile hill.
3. Re-introduce fire to potential mid-elevation intermediate habitats along seasonal migration routes including the south slope of Mt. Berland, the south slope of McKay Ridge, and the west slope of Redstreak Mountain (Figure 12). Also consider re-introducing fire to the north side of Stoddart Creek to improve habitat connectivity between the historic Stoddart Creek winter range and ram summer habitats along Kimpton Ridge. Monitor changes in sheep use of these areas and changes in average dates of migration above and below certain elevations.
4. Use forest thinning and/or burning to maintain a secure corridor for sheep between winter range at Radium and historic winter ranges at Stoddart, Shuwsap, and Windermere Creeks (Figure 13).
5. Use forest thinning and/or burning to maintain secure linkages south of the study area to connect the Radium herd to the Columbia Lake herd. Also consider

opportunities to improve linkages between the Radium herd and the Mitchell range to the east.

6. In upcoming park management and zoning processes recognize the unique importance of the Kindersley-Sinclair trail area for ewe-lamb groups in summer. Management options for this area include a zoning designation as a “Zone 1” special preservation area or environmentally sensitive site, public education, seasonal restrictions on dog use, and possible seasonal restrictions on off-trail travel.
7. Take measures to reduce the risk of contact between domestic and wild sheep. Areas of highest risk have been identified by comparing locations of sheep migration routes and habitats to locations of known domestic sheep ranches (Dibb 2006). Measures to reduce risk of contact have been discussed by other authors (Zehnder and Adams 2002) and include double fencing of domestic sheep pastures, and incentives to ranchers to remove their herds.
8. Study of bighorn sheep movements in the Radium Hot Springs area has shown that these sheep access road salt as a mineral source at the Parks Canada salt shed and along roadways (Dibb 2006). Parks Canada, provincial government and local government highway maintenance operators need to select road de-icing salts that do not have ferrocyanides or other toxic additives.
9. Rates of road kill among the Radium bighorn sheep were reported at up to 10% of the population annually (Dibb 2006), and recent evidence of a population decline (Parks Canada, unpublished data) may indicate that these mortality rates are not

sustainable. The following measures could help to reduce highway mortality of sheep on the “mile hill” of highway 93/95 just south of Radium Hot Springs:

- a) Reduce traffic speed
- b) Provide fencing and an underpass, taking advantage of natural terrain features, on the mile hill. An opportunity will be created when/if the highway is upgraded to 4 lanes.
- c) Use alternative de-icing salts that will not attract sheep to the roadway.
- d) Continue habitat restoration measures east of the highway so that sheep have less need to use artificial habitats in Radium village, and therefore less need to cross the highway.

10. Protect lambing sites from human development and activity through appropriate use of land use zoning and human use management tools.

11. Large rams occur mainly in the park during hunting season (Dibb 2006). Managers responsible for regulating the provincial hunt should consider that disturbance associated with concentrated hunting on limited fall range outside the park could further concentrate the rams on in-park habitats.

Table 1. Summary of Kootenay National Park Management Plan statements pertaining to bighorn sheep management (Parks Canada 2000)

	Target	Plan Section #
Strategic Goal	Natural processes maintain the long-term composition and structure of vegetation communities	3.10.1
Objective	Maintain and restore the role of fire...	3.10.2
Key Actions	Restore... 50% of the estimated long term fire cycle	3.10.2(6)
Strategic Goal	Viable populations of native wildlife	3.11.1
Objectives	Maintain ... and restore habitat quality and connectivity for wildlife...	3.11.2
	Restore long-term patterns of behaviour, distribution and abundance of ungulates	3.11.2
Key Actions	Reduce wildlife highway mortality rate...	3.11.3(12)
	Restore important movement corridors at major pinch points [including Sinclair Canyon]	3.11.3(16)
	Encourage the protection of rare ecosystems in the Columbia Valley	3.11.3(22)
Objectives	Cooperate [with others] to maintain a viable sheep population in the region.	5.14.1
Zoning	Dry Gulch – Stoddart Creek Zone 1 (“Special Preservation”) area created to preserve... major winter and summer ranges for bighorn sheep	9.2

Table 2. Summary of radio-collar deployment dates and fix success.

Year	ID	Date On	Date Off	Period of Data Collection (Days)	Total Fix Attempts	Total Fixes	Fix Success Rate	Fixes			3D% of Attempts	3D Fixes PDOP > 6.0 (Cal Yr)	Notes
								3D	2D	3D% of Fixes			
2002	F001	08-Jan-02	21-Aug-02	225	1036	941	91%	816	125	86.7%	78.7%	736	Collar Malfunction at End
2002	M002	08-Jan-02	11-Mar-03	426	1891	1547	82%	1165	382	75.3%	61.6%	896	Collar didn't release; stayed on
2002	F004	10-Jan-02	24-Oct-02	256	1222	451	37%	418	33	92.7%	34.2%	408	Collar Malfunctioned
2002	M005	10-Jan-02	01-Aug-02	204	923	804	87%	683	121	85.0%	74.0%	625	Highway Mortality Aug 1/02
2002	F006	10-Jan-02	24-Oct-02	287	1392	1264	91%	1103	161	87.3%	79.3%	982	As planned
2002	F007	11-Jan-02	16-Dec-02	90	324	170	52%	142	28	83.5%	43.8%	158	Collar malfunctioned
2002	M008	11-Jan-02	29-Nov-02	311	1592	1213	76%	891	322	73.5%	56.0%	771	As planned
2002	F009	12-Jan-02	24-Oct-02	285	1386	1231	89%	1036	195	84.2%	74.8%	956	As planned
2002	F010	13-Jan-02	24-Oct-02	284	1382	1188	86%	960	228	80.8%	69.4%	842	As planned
2002	F011	04-Mar-02	24-Oct-02	96	461	232	50%	222	10	95.7%	48.2%	210	Collar malfunctioned
				2464	11609	9041	78%	7436	1605	82.2%	64.1%	6584	2002 Total
					9602	8188	85%	6654	1534	81.3%	69.3%	5808	2002 excluding 3 malfunctioning collars
2003	F007	16-Dec-02	02-Dec-03	352	2166	2051	95%	1857	194	90.5%	85.8%	1723	As planned
2003	M002	11-Mar-03	02-Dec-03	264	1992	1821	91%	1567	254	86.1%	78.6%	1540	As planned
2003	M101	16-Dec-02	02-Dec-03	352	2153	1734	81%	1340	394	77.3%	62.2%	1202	As planned
2003	F102	16-Dec-02	24-Mar-03	99	183	182	99%	166	16	91.2%	90.7%	132	Highway Mort March 24-03
2003	F103	17-Dec-02	02-Dec-03	351	2147	2024	94%	1817	207	89.8%	84.6%	1682	As planned
2003	F104	17-Dec-02	02-Dec-03	351	2147	1977	92%	1782	195	90.1%	83.0%	1602	As planned
2003	M105	18-Dec-02	02-Dec-03	350	2147	1777	83%	1415	362	79.6%	65.9%	1268	As planned
2003	M106	18-Dec-02	02-Dec-03	349	2153	1431	66%	907	524	63.4%	42.1%	789	As planned
2003	F107	11-Mar-03	01-Dec-03	265	1994	1743	87%	1488	255	85.4%	74.6%	1383	As planned
2003	F108	11-Mar-03	02-Dec-03	265	1993	1946	98%	1849	97	95.0%	92.8%	1746	As planned
				2998	19075	16686	87%	14188	2498	85.0%	74.4%	13067	2003 Total
2004	M002	08-Mar-04	22-Oct-04	227	2357	1964	83%	1549	415	78.9%	65.7%	1372	Collar removed early - irritation
2004	F202	09-Mar-04	30-Nov-04	266	2798	2521	90%	2210	311	87.7%	79.0%	2043	As planned
2004	F203	09-Mar-04	08-Nov-04	244	2547	2121	83%	1785	336	84.2%	70.1%	1606	Highway Mortality Nov. 8, 2004
2004	F204	09-Mar-04	13-Jul-04	125	1217	1171	96%	1091	80	93.2%	89.6%	1023	Unknown Mort in alpine (fall?) July 13, 2004.
2004	F205	18-Mar-04	30-Nov-04	257	2777	2489	90%	2145	344	86.2%	77.2%	1947	As planned
2004	M206	18-Mar-04	20-Oct-04	216	2335	1856	79%	1466	390	79.0%	62.8%	1340	Collar removed early - irritation
2004	M207	18-Mar-04	30-Nov-04	256	2776	2683	97%	2494	189	93.0%	89.8%	2268	As planned
2004	M208	30-Mar-04	17-Nov-04	232	2609	2375	91%	2066	309	87.0%	79.2%	1846	As planned
2004	F209	30-Mar-04	17-May-04	48	226	210	93%	190	20	90.5%	84.1%	181	Mort from natural causes (disease/poor health)
				1871	19642	17390	89%	14996	2394	86.2%	76.3%	13626	2004 Total
2005	M002	10-Feb-05	30-Jan-06	268	2960	2767	93%	2503	264	90.5%	84.6%	2291	Collar did not release - darted and recollared
2005	F205	07-Feb-05	04-Nov-05	270	2553	2266	89%	1933	333	85.3%	75.7%	1805	As planned
2005	F301	07-Feb-05	04-Nov-05	271	2560	2347	92%	2081	266	88.7%	81.3%	1938	As planned
2005	F302	07-Feb-05	30-Jan-06	358	2969	2918	98%	2794	124	95.8%	94.1%	2658	Collar did not release - darted and recollared
2005	F303	07-Feb-05	14-Apr-05	67	257	243	95%	234	9	96.3%	91.0%	220	Destroyed after injured by vehicle, Mile Hill
2005	F305	08-Feb-05	04-Nov-05	270	2557	2318	91%	2080	238	89.7%	81.3%	1945	As planned
2005	F306	08-Feb-05	06-Nov-05	272	2583	2475	96%	2278	197	92.0%	88.2%	2160	As planned
2005	F307	08-Feb-05	04-Nov-05	270	2557	2485	97%	2364	121	95.1%	92.4%	2253	As planned
2005	M308	09-Feb-05	03-Nov-05	268	2542	2091	82%	1636	455	78.2%	64.4%	1457	As planned
2005	M309	10-Feb-05	Not removed										Not removed; sheep not found
				2314	21539	19910	92%	17903	2007	89.9%	83.1%	16727	2005 Total
				9647	69857	62174	89.0%	53741	8433	86.4%	76.9%	49228	Grand Total

Table 3. List of GIS predictor variables considered for bighorn sheep habitat modelling

Description	Source
Elevation from digital elevation model	* NTDB and TRIM databases
Slope aspect in 8 classes of 45 degrees and 1 class of flat. All 9 classes treated as separate variables in SAS statistical software	** ArcGIS Spatial Analyst calculation from DEM
Slope angle in degrees	* ArcGIS Spatial Analyst calculation from DEM
Pseudo-habitat map from Landsat satellite imagery	* Stevens (2002)
Sun insolation values - January	Derived from DEM
Sun insolation values - March	Derived from DEM
Sun insolation values - May	* Derived from DEM
Sun insolation values - July	Derived from DEM
Sun insolation values - September	Derived from DEM
Forest canopy closure	* British Columbia Forest Service 1988 Forest Cover Mapping and British Columbia Forest Service 2005 Vegetation Resource Inventory
Terrain Ruggedness Index - 300 m circular window	Saher (2005), derived from DEM
Terrain Ruggedness Index - 300 m circular window	Nellemann and Fry (1995), derived from DEM
Standard deviation of cell elevations within 300 m circular window	* Derived from DEM
Standard deviation of cell elevations within 600 m circular window	Derived from DEM
Proportion of all aspect classes represented in 300 m circular window	Derived from DEM
Proportion of all aspect classes represented in 600 m circular window	Derived from DEM

* Variables used in selected RSF model

** Aspect variable for "East" class used in RSF model; other aspect variables not used

Table 4. Predictive ability of models based on criteria of Howlin et al. (2003)

Slope (β)	95% Confidence Interval on β	Predictive Abilities of Model
+ or -	CI includes 0	Unacceptable
$0 < \beta < 1$	CI excludes 0 and 1	Acceptable
$\beta > 0$	CI excludes 0 and includes 1	Good
$\beta > 1$	CI excludes 0 and 1	Acceptable

Table 5. Percent association of study animals in summer, 2002 - 2004

	Animal ID	001	004	005	006	007	009	010	002
2002	001		0	1.4	4	0	4.4	9.2	0
	004	0		0	2.4	1.1	1.7	3.7	0
	005	1.2	0		0	0	0	0	16.3
	006	6.4	0	0		4.6	30.9	9.2	1
	007	0	0	0	3.2		0.8	0.9	6.5
	009	6.4	0	0	28.6	1.1		9.2	1
	010	12.8	0	0	8.1	1.1	8.8		0
	002	0	0	21.4	0.8	6.9	0.8	0	

	Animal ID	007	101	103	104	105	106	107	108	002
2003	007		2.4	24.8	26.9	0	0	16.5	18.5	2.7
	101	2.2		0.5	2.7	13.9	20.1	0	2.1	5.4
	103	25.1	0.6		40.6	0	0.7	30.1	18	3.2
	104	27.3	3	40.8		0	2.3	23.6	14.2	2.7
	105	0	13.4	0	0		24	0	1	4.3
	106	0	15.8	0.5	1.6	19.6		0	0.5	4.9
	107	15.6	0	28.1	21.9	0	0		12.5	1
	108	18.9	2.4	18.2	14.2	1.2	0.7	13.6		2.1
	002	2.7	6	3.3	2.7	5	6.9	1.1	2.1	

	Animal ID	202	203	204	205	206	207	208	209	002
2004	202		14.7	7	6	1.5	6.1	2.3	0	1.3
	203	12		2.8	0.6	1.5	5	4.1	0	1.9
	204	3	1.4		13.5	1.5	2.2	0	0	0
	205	5.4	0.7	28.1		0	4.4	1.7	0	1.3
	206	1.2	1.4	2.8	0		4.4	19.1	0	1.3
	207	6.6	6.6	5.6	5.4	6.2		17.9	0	74.3
	208	2.4	5.1	0	2	25.1	16.7		0	13.1
	209	1.8	2.2	7	0	0.7	1.1	0.5		0
	002	1.2	2.2	0	1.3	1.5	63.1	11.9	0	

Table 6. Proportions of summer telemetry points in each class of Tremblay corridor model, all study animals, 2002 - 2004

Tremblay Model Class	Availability		Use					
	Proportion of Study Area Per Class		All Telemetry Points			Movement Points		
			Proportion of Points Per Class (N = 22311)	Use / Availability Ratio	Rank (0 - 4)	Proportion of Points Per Class (N = 1957)	Use / Availability Ratio	Rank (0 - 4)
1 (very low)	0.670		0.408	0.609	0	0.586	0.874	2
2 (low)	0.211		0.178	0.843	1	0.159	0.753	1
3 (moderate)	0.076		0.271	3.563	3	0.170	2.232	3
4 (high)	0.033		0.128	3.867	4	0.082	2.494	4
5 (very high)	0.008		0.016	1.950	2	0.004	0.450	0

Table 7. Simplified ranking matrices for bighorn sheep proportional use of corridor value classes to available proportions of corridor value classes within individual MCP home ranges. A small non-zero number replaced animal utilization values of zero. Classes are ranked from least preferred (1) to most preferred (5). Classes that differ significantly in preference from random at $p = 0.05$ are indicated by either “+++” or “---”. Classes that differ in preference from random at $p > 0.05$ are indicated by either “+” or “-”. GPS telemetry data is from 2002-2004.

HSI Model Class	1 (very low)	2 (low)	3 (moderate)	4 (high)	5 (very high)	Rank
1 (very low)	.	+	---	---	+	3
2 (low)	-	.	---	---	+	2
3 (moderate)	+++	+++	.	+	+++	5
4 (high)	+++	+++	-	.	+++	4
5 (very high)	-	-	---	---	.	1

Table 8. Simplified ranking matrices for bighorn sheep proportional use of corridor value classes to available proportions of corridor value classes within individual MCP home ranges. Tremblay’s (2001) “high” and “very high” classes were collapsed into a single class. Classes are ranked from least preferred (1) to most preferred (4). Classes that differ significantly in preference from random at $p = 0.05$ are indicated by either “+++” or “---”. Classes that differ in preference from random at $p > 0.05$ are indicated by either “+” or “-”. GPS telemetry data is from 2002-2004.

HSI Model Class	1 (very low)	2 (low)	3 (moderate)	4 (high, v. high)	Rank
1 (very low)	.	+	---	---	2
2 (low)	-	.	---	---	1
3 (moderate)	+++	+++	.	+++	4
4 (high, v. high)	+++	+++	---	.	3

Table 9. Simplified ranking matrices for bighorn sheep proportional use of corridor value classes to available proportions of corridor value classes within entire study area. A small non-zero number replaced animal utilization values of zero. Classes are ranked from least preferred (1) to most preferred (5). Classes that differ significantly in preference from random at $p = 0.05$ are indicated by either “+++” or “---”. Classes that differ in preference from random at $p > 0.05$ are indicated by either “+” or “-”. GPS telemetry data is from 2002-2004.

HSI Model Class	1 (very low)	2 (low)	3 (moderate)	4 (high)	5 (very high)	Rank
1 (very low)	.	-	---	---	+	2
2 (low)	+	.	---	---	+	3
3 (moderate)	+++	+++	.	+++	+++	5
4 (high)	+++	+++	---	.	+++	4
5 (very high)	-	-	---	---	.	1

Table 10. Simplified ranking matrices for bighorn sheep proportional use of corridor value classes to available proportions of corridor value classes within entire study area. Tremblay’s (2001) “high” and “very high” classes were collapsed into a single class. Classes are ranked from least preferred (1) to most preferred (4). Classes that differ significantly in preference from random at $p = 0.05$ are indicated by either “+++” or “---”. Classes that differ in preference from random at $p > 0.05$ are indicated by either “+” or “-”. GPS telemetry data is from 2002-2004.

HSI Model Class	1 (very low)	2 (low)	3 (moderate)	4 (high, v. high)	Rank
1 (very low)	.	-	---	---	1
2 (low)	+	.	---	---	2
3 (moderate)	+++	+++	.	+++	4
4 (high, v. high)	+++	+++	---	.	3

Table 11. Simplified ranking matrices for bighorn sheep proportional use of corridor value classes to available proportions of corridor value classes within individual MCP home ranges. Utilization was quantified based on movement points only, 2002-2004. Tremblay's (2001) "high" and "very high" classes were collapsed into a single class. Classes are ranked from least preferred (1) to most preferred (4). Classes that differ significantly in preference from random at $p = 0.05$ are indicated by either "+++" or "---". Classes that differ in preference from random at $p > 0.05$ are indicated by either "+" or "-".

Tremblay Model Class	1 (very low)	2 (low)	3 (moderate)	4 (high, v. high)	Rank
1 (very low)	.	+	---	-	2
2 (low)	-	.	---	---	1
3 (moderate)	+++	+++	.	+	4
4 (high, v. high)	+	+++	-	.	3

Table 12. Simplified ranking matrices for bighorn sheep proportional use of corridor value classes to available proportions of corridor value classes within entire study area. Utilization was quantified based on movement points only, 2002-2004. Tremblay's (2001) "high" and "very high" classes were collapsed into a single class. Classes are ranked from least preferred (1) to most preferred (4). Classes that differ significantly in preference from random at $p = 0.05$ are indicated by either "+++" or "---". Classes that differ in preference from random at $p > 0.05$ are indicated by either "+" or "-".

HSI Model Class	1 (very low)	2 (low)	3 (moderate)	4 (high)	Rank
1 (very low)	.	-	---	---	1
2 (low)	+	.	---	-	2
3 (moderate)	+++	+++	.	+++	4
4 (high)	+++	+	---	.	3

Table 13. Summary of compositional analysis class rankings from tables 2 through 7. “MCP” = Minimum Convex Polygon; “SA” = Study Area; “<” indicates that the difference in preference between two consecutive classes is not significant to $p < 0.05$; “<<” indicates that the difference in preference between two consecutive classes is significant to $p < 0.05$.

Table Number	Scale (MCP vs. SA)	Number of Classes	Movement Points	Least Preferred Class --> Most Preferred Class								
7	MCP	5	.	VH	<	L	<	VL	<<	H	<<	M
8	MCP	4	.	L	<	VL	<<	H	<<	M		
9	SA	5	.	VH	<	VL	<	L	<<	H	<<	M
10	SA	4	.	VL	<	L	<<	H	<<	M		
11	MCP	4	Y	L	<	VL	<	H	<	M		
12	SA	4	Y	VL	<	L	<	H	<<	M		

Table 14. AIC rankings of candidate RSF models

Model Number	Title	Variables	# Ind. Vars	K	-2LL	AIC	n	AICc	Rank	Δi	$\exp(-0.5 * \Delta i)$	w_i
2	Terrain Model 2	Slope, DEM, DEM300SD	3	4	10838.4	10846.4	8019	10846.4	7	982.3	0.000	0.0000
1	Terrain Model 1	DEM, Slope, TRI, DEM300SD, AspVar300, Aspect	6	7	10572.9	10586.9	8019	10586.9	6	722.7	0.000	0.0000
3	Vegetation Model	CrownClosu, Greenness, Rad_May	3	4	9953.5	9961.5	8019	9961.5	5	97.3	0.000	0.0000
7	Terrain + Vegetation Model 4	Slope, DEM, Greenness, Crownclosu, RAD_May	5	6	9896.2	9908.2	8019	9908.2	4	44.1	0.000	0.0000
4	Terrain + Vegetation Model 1	Slope, DEM, DEM300SD, Greenness, CrownClosu, Rad_May	6	7	9893.0	9907.0	8019	9907.0	3	42.8	0.000	0.0000
6	Terrain + Vegetation Model 3	Slope, DEM, Greenness, CrownClosu, Rad_May, aspect3	6	7	9854.0	9868.0	8019	9868.0	2	3.8	0.151	0.1310
5	Terrain + Vegetation Model 2	Slope, DEM, DEM300SD, Greenness, CrownClosu, Rad_May, aspect3	7	8	9848.2	9864.2	8019	9864.2	1	0.0	1.000	0.8690
								$\frac{9864.2}{\min AICc}$				
									$\frac{1.151}{\sum(\exp(-0.5 * \Delta i))}$			

Table 15. RSF model simplified ranking matrices for bighorn sheep proportional use of habitat value classes to available proportions of habitat value classes within individual MCP home ranges. Classes are ranked from least preferred (1) to most preferred (4). Classes that differ significantly in preference from random at $p = 0.05$ are indicated by either “+++” or “---”. Classes that differ in preference from random at $p > 0.05$ are indicated by either “+” or “-”. GPS telemetry data is from 2005.

RSF Model Class	1 (very low)	2 (low)	3 (moderate)	4 (high)	5 (very high)	Rank
1 (very low)	.	---	---	---	---	1
2 (low)	+++	.	---	---	---	2
3 (moderate)	+++	+++	.	---	-	3
4 (high)	+++	+++	+++	.	+++	5
5 (very high)	+++	+++	+	---	.	4

Table 16. RSF model simplified ranking matrices for bighorn sheep proportional use of habitat value classes to available proportions of habitat value classes within individual MCP home ranges. “High” and “very high” classes were collapsed into a single class. Classes are ranked from least preferred (1) to most preferred (4). Classes that differ significantly in preference from random at $p = 0.05$ are indicated by either “+++” or “---”. Classes that differ in preference from random at $p > 0.05$ are indicated by either “+” or “-”. GPS telemetry data is from 2005.

RSF Model Class	1 (very low)	2 (low)	3 (moderate)	4 (high, v. high)	Rank
1 (very low)	.	---	---	---	1
2 (low)	+++	.	---	---	2
3 (moderate)	+++	+++	.	---	3
4 (high, v. high)	+++	+++	+++	.	4

Table 17. RSF model simplified ranking matrices for bighorn sheep proportional use of habitat value classes to available proportions of habitat value classes within study area. Classes are ranked from least preferred (1) to most preferred (5). Classes that differ significantly in preference from random at $p = 0.05$ are indicated by either “+++” or “---”. Classes that differ in preference from random at $p > 0.05$ are indicated by either “+” or “-”. GPS telemetry data is from 2005.

RSF Model Class	1 (very low)	2 (low)	3 (moderate)	4 (high)	5 (very high)	Rank
1 (very low)	.	---	---	---	---	1
2 (low)	+++	.	---	---	---	2
3 (moderate)	+++	+++	.	---	-	3
4 (high)	+++	+++	+++	.	+	5
5 (very high)	+++	+++	+	-	.	4

Table 18. RSF model simplified ranking matrices for bighorn sheep proportional use of habitat value classes to available proportions of habitat value classes within study area. “High” and “very high” classes were collapsed into a single class. Classes are ranked from least preferred (1) to most preferred (4). Classes that differ significantly in preference from random at $p = 0.05$ are indicated by either “+++” or “---”. Classes that differ in preference from random at $p > 0.05$ are indicated by either “+” or “-”. GPS telemetry data is from 2005.

RSF Model Class	1 (very low)	2 (low)	3 (moderate)	4 (high, v. high)	Rank
1 (very low)	.	---	---	---	1
2 (low)	+++	.	---	---	2
3 (moderate)	+++	+++	.	---	3
4 (high, v. high)	+++	+++	+++	.	4

Table 19. HSI model simplified ranking matrices for bighorn sheep proportional use of habitat value classes to available proportions of habitat value classes within individual MCP home ranges. Classes are ranked from least preferred (1) to most preferred (5). Classes that differ significantly in preference from random at $p = 0.05$ are indicated by either “+++” or “---”. Classes that differ in preference from random at $p > 0.05$ are indicated by either “+” or “-”. GPS telemetry data is from 2005.

HSI Model Class	1 (very low)	2 (low)	3 (moderate)	4 (high)	5 (very high)	Rank
1 (very low)	.	+	---	---	-	2
2 (low)	-	.	---	---	-	1
3 (moderate)	+++	+++	.	-	+++	4
4 (high)	+++	+++	+	.	+++	5
5 (very high)	+	+	---	---	.	3

Table 20. HSI model simplified ranking matrices for bighorn sheep proportional use of habitat value classes to available proportions of habitat value classes within individual MCP home ranges. “High” and “very high” classes were collapsed into a single class. Classes are ranked from least preferred (1) to most preferred (4). Classes that differ significantly in preference from random at $p = 0.05$ are indicated by either “+++” or “---”. Classes that differ in preference from random at $p > 0.05$ are indicated by either “+” or “-”. GPS telemetry data is from 2005.

HSI Model Class	1 (very low)	2 (low)	3 (moderate)	4 (high, v. high)	Rank
1 (very low)	.	+	---	---	2
2 (low)	-	.	---	---	1
3 (moderate)	+++	+++	.	-	3
4 (high, v. high)	+++	+++	+	.	4

Table 21. HSI model simplified ranking matrices for bighorn sheep proportional use of habitat value classes to available proportions of habitat value classes within study area. Classes are ranked from least preferred (1) to most preferred (5). Classes that differ significantly in preference from random at $p = 0.05$ are indicated by either “+++” or “---”. Classes that differ in preference from random at $p > 0.05$ are indicated by either “+” or “-”. GPS telemetry data is from 2005.

HSI Model Class	1 (very low)	2 (low)	3 (moderate)	4 (high)	5 (very high)	Rank
1 (very low)	.	+	---	---	-	2
2 (low)	-	.	---	---	---	1
3 (moderate)	+++	+++	.	-	+++	4
4 (high)	+++	+++	+	.	+++	5
5 (very high)	+	+++	---	---	.	3

Table 22. HSI model simplified ranking matrices for bighorn sheep proportional use of habitat value classes to available proportions of habitat value classes within study area. “High” and “very high” classes were collapsed into a single class. Classes are ranked from least preferred (1) to most preferred (4). Classes that differ significantly in preference from random at $p = 0.05$ are indicated by either “+++” or “---”. Classes that differ in preference from random at $p > 0.05$ are indicated by either “+” or “-”. GPS telemetry data is from 2005.

HSI Model Class	1 (very low)	2 (low)	3 (moderate)	4 (high, v. high)	Rank
1 (very low)	.	+	---	---	2
2 (low)	-	.	---	---	1
3 (moderate)	+++	+++	.	+	4
4 (high, v. high)	+++	+++	-	.	3

Table 23. Summary of compositional analysis class rankings from tables 8 through 15. “MCP” = Minimum Convex Polygon; “SA” = Study Area; “<” indicates that the difference in preference between two consecutive classes is not significant to $p < 0.05$; “<<” indicates that the difference in preference between two consecutive classes is significant to $p < 0.05$.

Model (HSI vs. RSF)	Scale (MCP vs. SA)	Number of Classes	Least Preferred Class --> Most Preferred Class									Wilk's	
												λ	p
RSF	MCP	5	VL	<<	L	<<	M	<	VH	<<	H	0.083	0.0193
RSF	SA	5	VL	<<	L	<<	M	<	VH	<	H	0.063	0.0114
RSF	MCP	4	VL	<<	L	<<	M	<<	H			0.084	0.0041
RSF	SA	4	VL	<<	L	<<	M	<<	H			0.061	0.0018
HSI	MCP	5	L	<	VL	<	VH	<<	M	<	H	0.026	0.0020
HSI	SA	5	L	<	VL	<	VH	<<	M	<	H	0.021	0.0013
HSI	MCP	4	L	<	VL	<<	M	<	H			0.033	0.0004
HSI	SA	4	L	<	VL	<<	H	<	M			0.023	0.0002

Table 24. Expected and used counts of points per percentile bin, using sample validation method of Howlin et al. (2003) for both the HSI and RSF models.

Bin #	Percentile	# Points	HSI Model				RSF Model			
			Percentile Cutoff Value	Sum of Unscaled Model Values	Sum of Scaled Model Values (Expected count per bin)	Used Sample Count per Bin	Percentile Cutoff Value	Sum of Unscaled Model Values	Sum of Scaled Model Values (Expected count per bin)	Used Sample Count per Bin
1	5	498	0.00938	2.00	1.06	217	0.16105	66.27	17.00	3
2	10	497	0.01875	7.04	3.73	82	0.19868	90.12	23.12	4
3	15	498	0.02500	9.79	5.19	20	0.22775	105.90	27.17	8
4	20	497	0.37500	14.77	7.82	23	0.25289	119.26	30.60	16
5	25	498	0.06250	25.15	13.33	15	0.27568	131.62	33.77	32
6	30	497	0.09375	36.63	19.41	20	0.29943	143.19	36.74	37
7	35	498	0.09375	46.69	24.74	7	0.31996	154.29	39.58	25
8	40	498	0.12500	52.72	27.94	14	0.34244	164.82	42.29	21
9	45	497	0.12500	62.13	32.92	6	0.36444	175.59	45.05	26
10	50	497	0.12500	62.13	32.92	7	0.39019	187.30	48.05	47
11	55	497	0.12500	62.13	32.92	7	0.41938	201.21	51.62	26
12	60	498	0.18750	80.84	42.84	23	0.45177	216.63	55.58	29
13	65	498	0.25000	99.70	52.83	46	0.48336	232.89	59.75	33
14	70	497	0.25000	124.25	65.84	27	0.51286	247.96	63.62	25
15	75	497	0.25000	124.25	65.84	27	0.54296	261.93	67.20	36
16	80	498	0.28125	133.69	70.84	9	0.57347	278.15	71.36	46
17	85	497	0.37500	184.88	97.97	35	0.61040	293.78	75.37	66
18	90	498	0.50000	224.17	118.79	165	0.66116	315.76	81.01	100
19	95	497	0.56250	250.81	132.91	163	0.72938	343.34	88.09	190
20	100	497	1.00000	390.88	207.14	144	1.00000	389.56	99.95	287
		9949			1057	1057			1057	1057

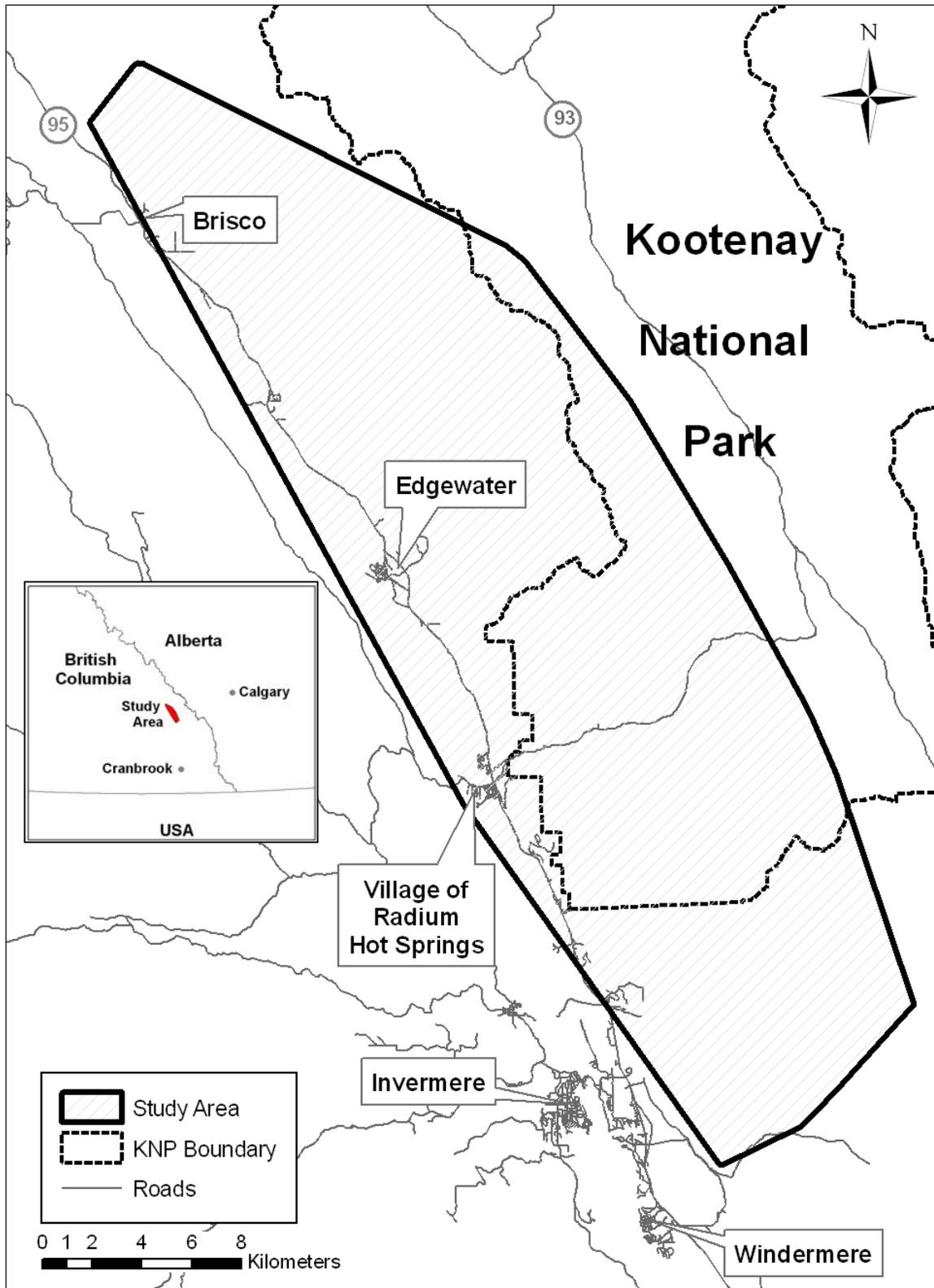


Figure 1. Radium Hot Springs, B.C. Bighorn Sheep Study Area

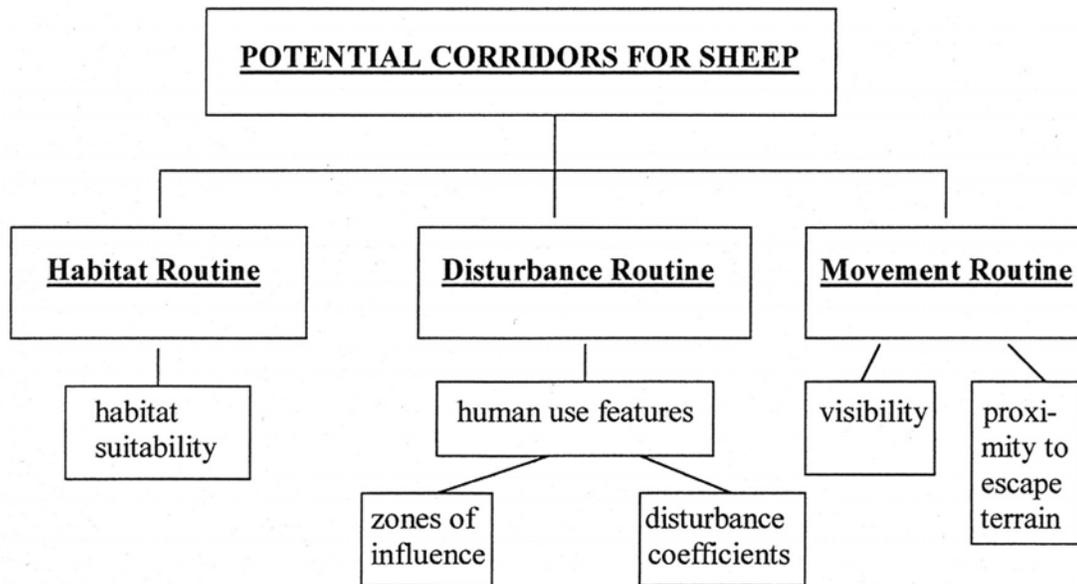


Figure 2 Conceptual Diagram of the Tremblay Bighorn Sheep Model (Tremblay 2001, figure 3-3, page 137).

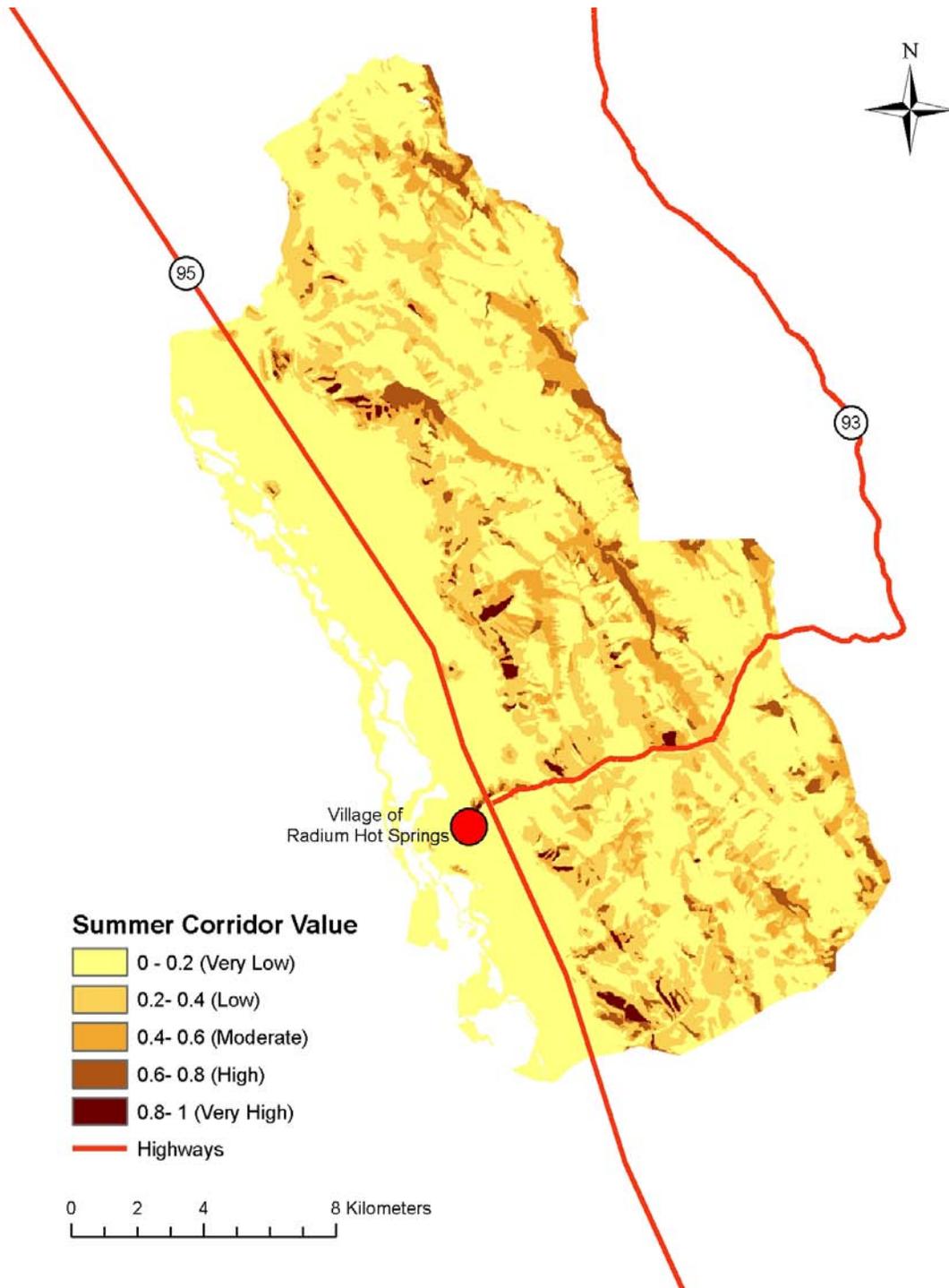


Figure 3. HSI Map of Summer Corridor Values in the Radium Hot Springs Area, from Tremblay (2001)

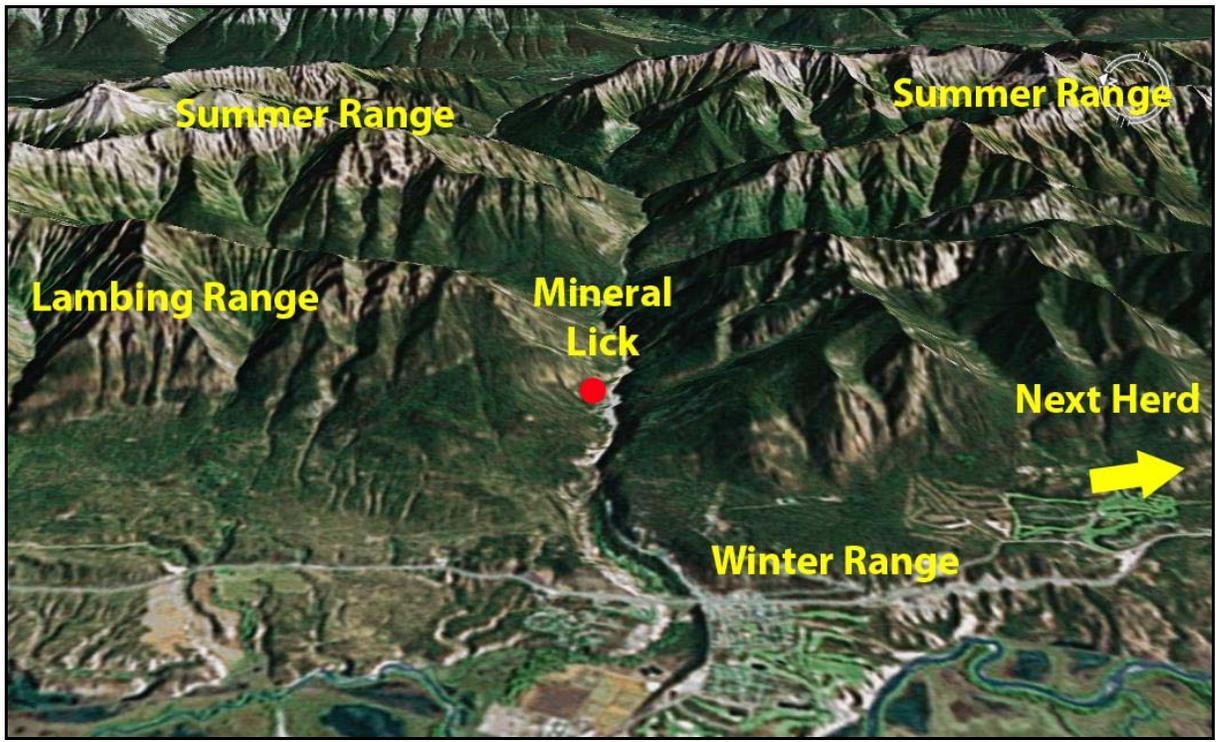


Figure 4. 3D Perspective View of Approximate Locations of Bighorn Sheep Seasonal Ranges, Radium Hot Springs, BC. Base Image from Google Earth.

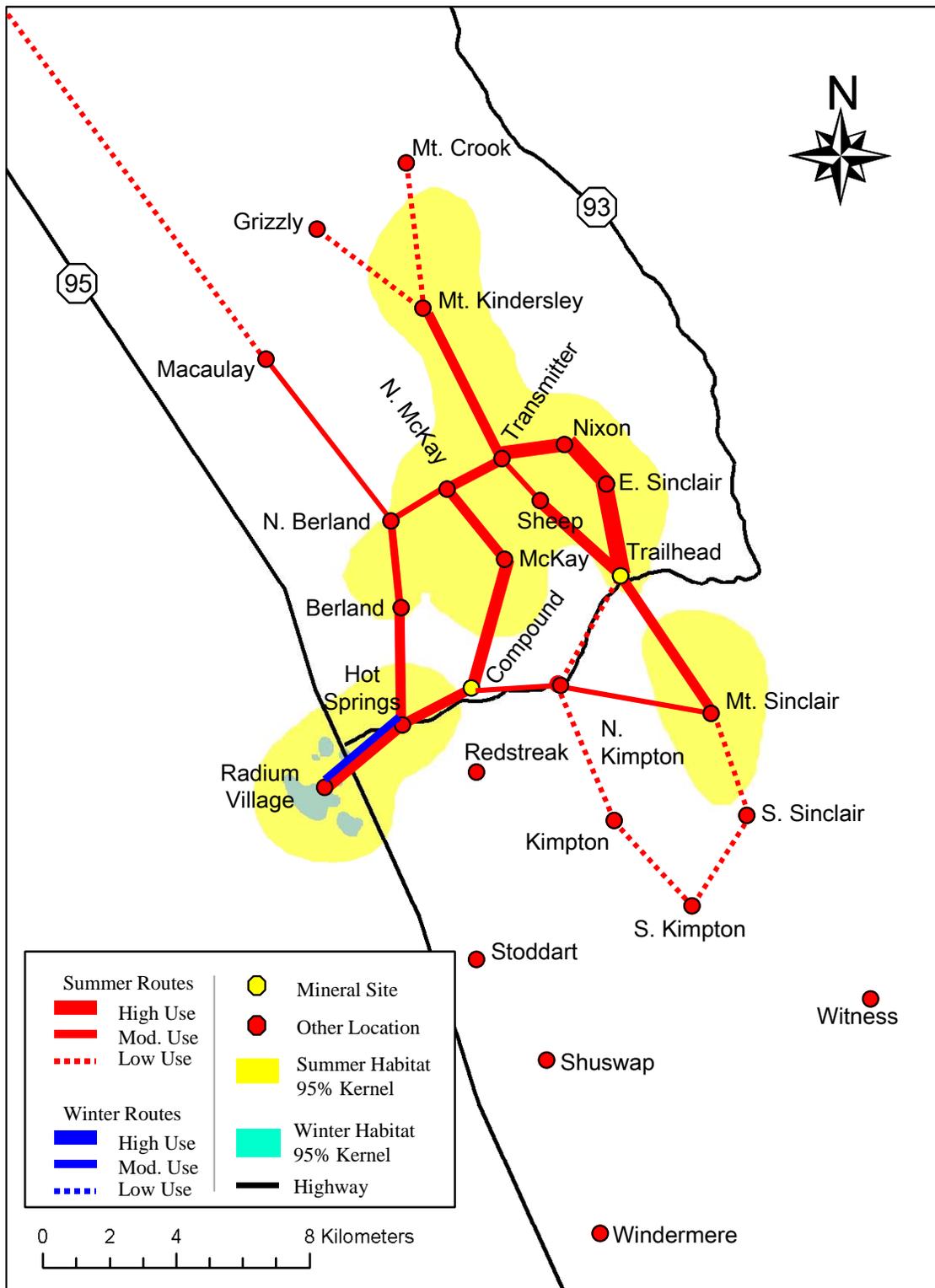


Figure 5. Female Movement Routes and Core Ranges: 2002-2004.

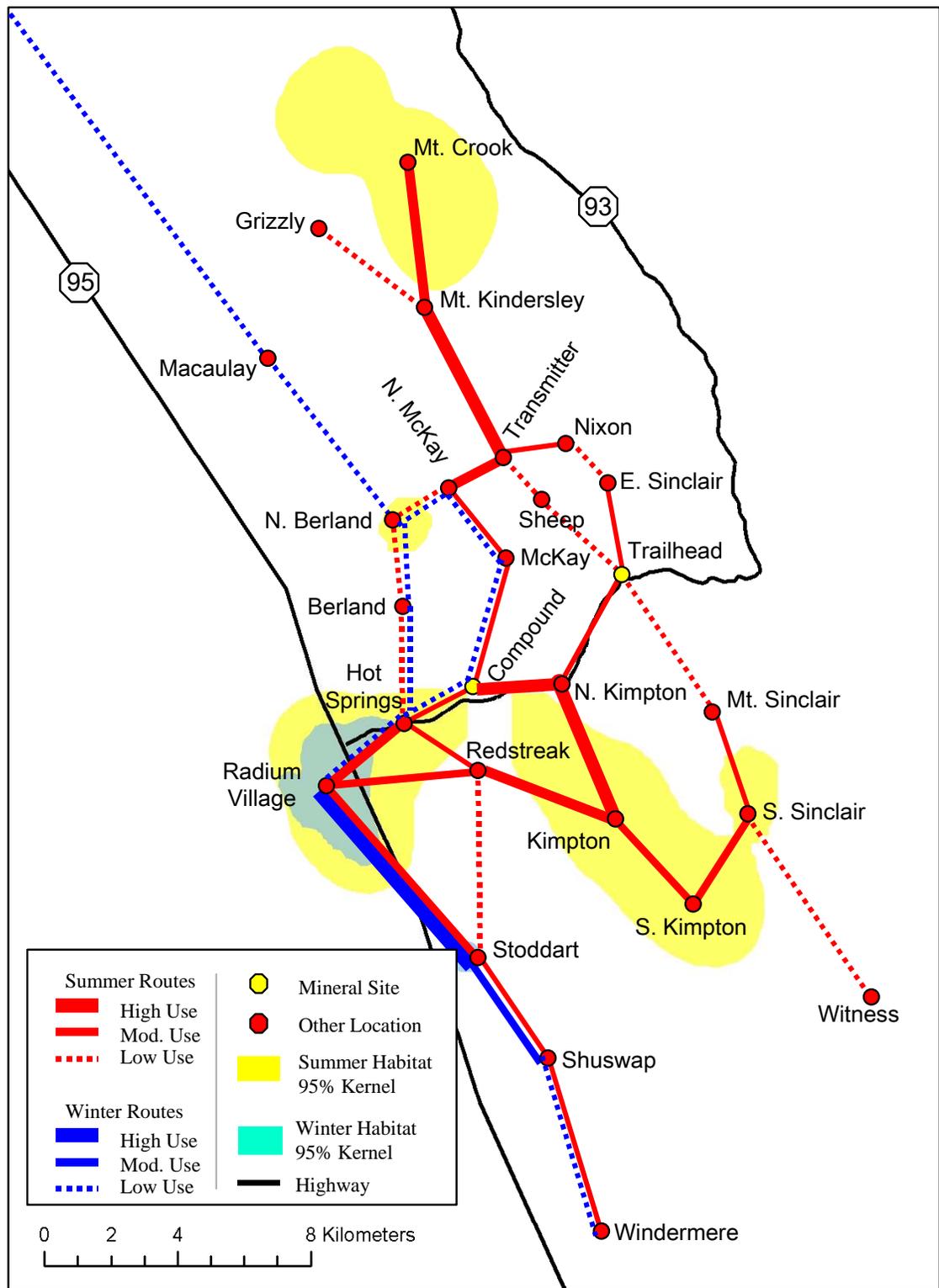


Figure 6. Male Movement Routes and Core Ranges: 2002-2004.

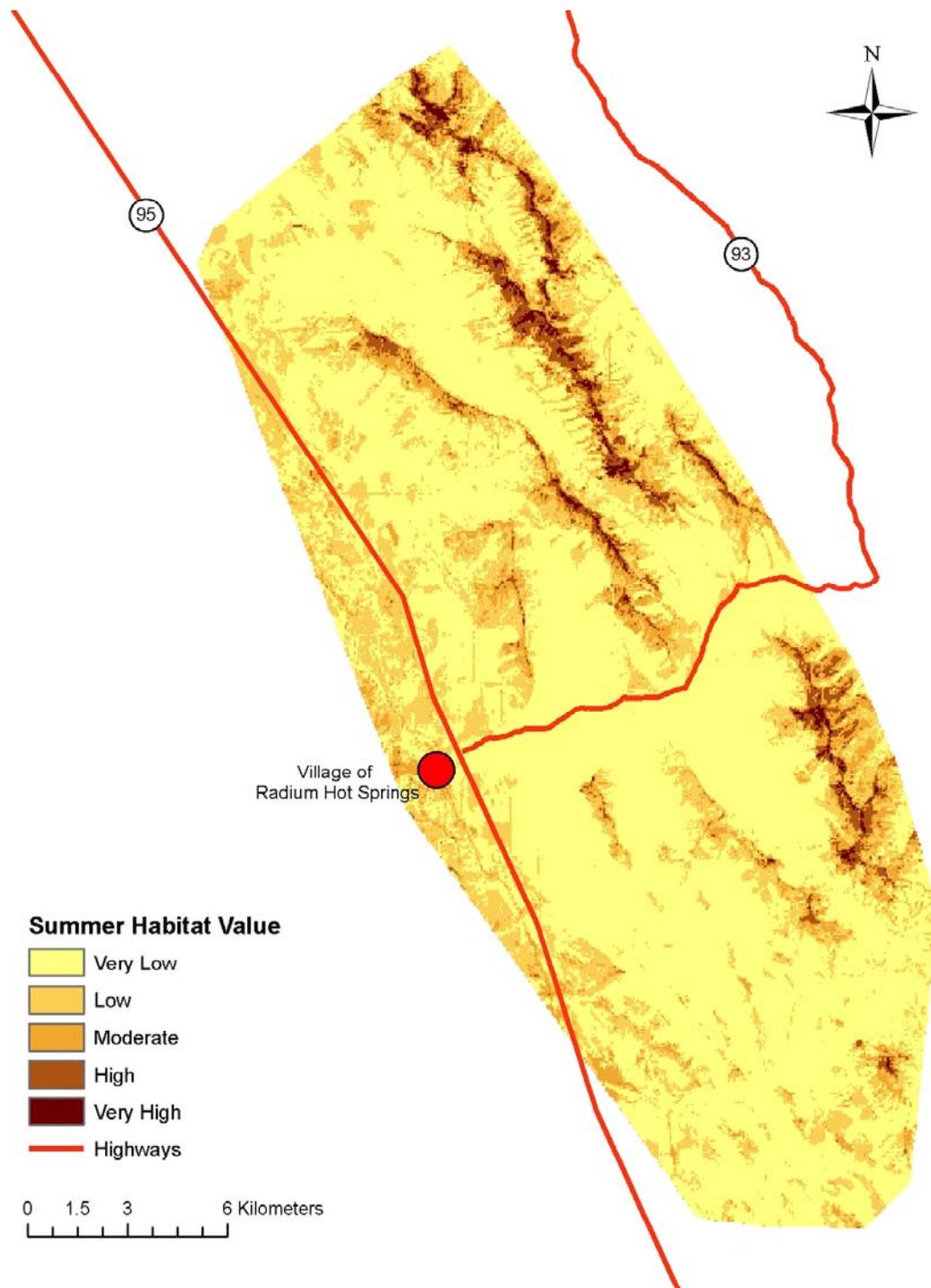


Figure 7. RSF Map of Summer Habitat Values in the Radium Hot Springs Area, this study.

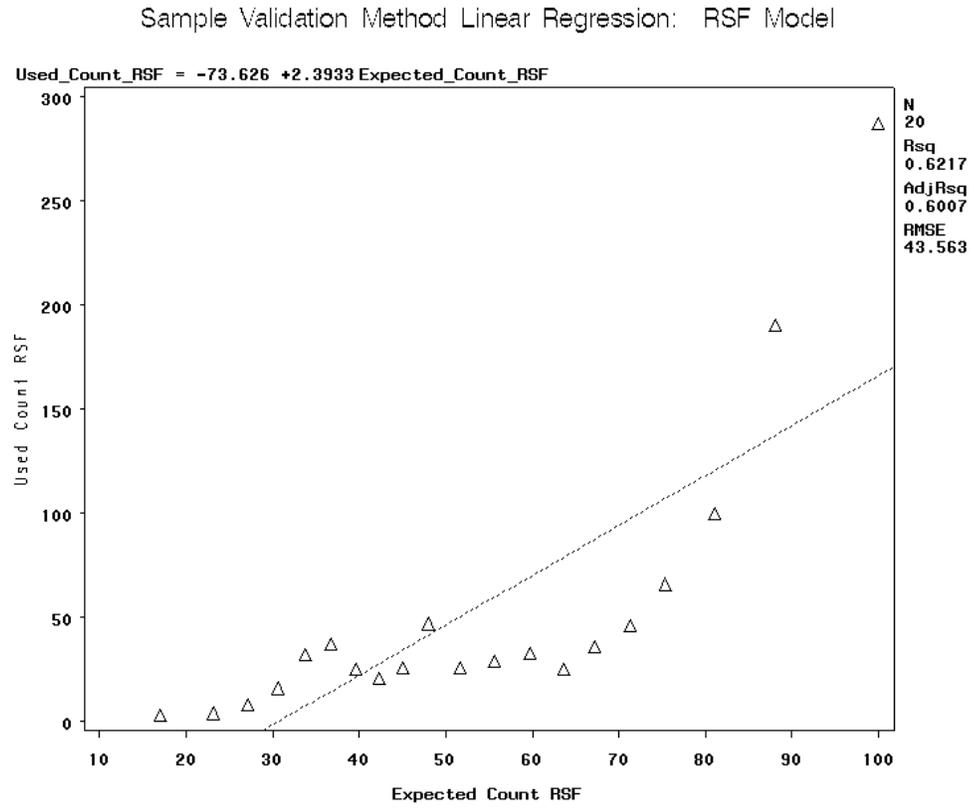


Figure 8. Sample Validation Method Linear Regression: RSF Model.

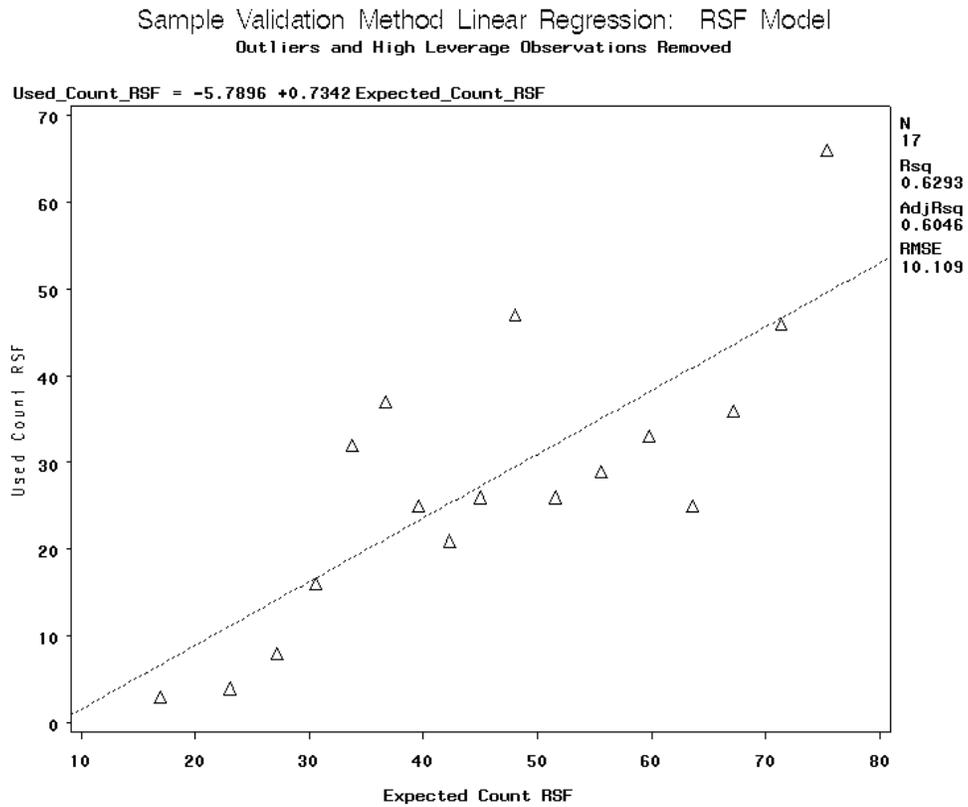


Figure 9. Sample Validation Method Linear Regression: RSF Model, Outliers Removed.

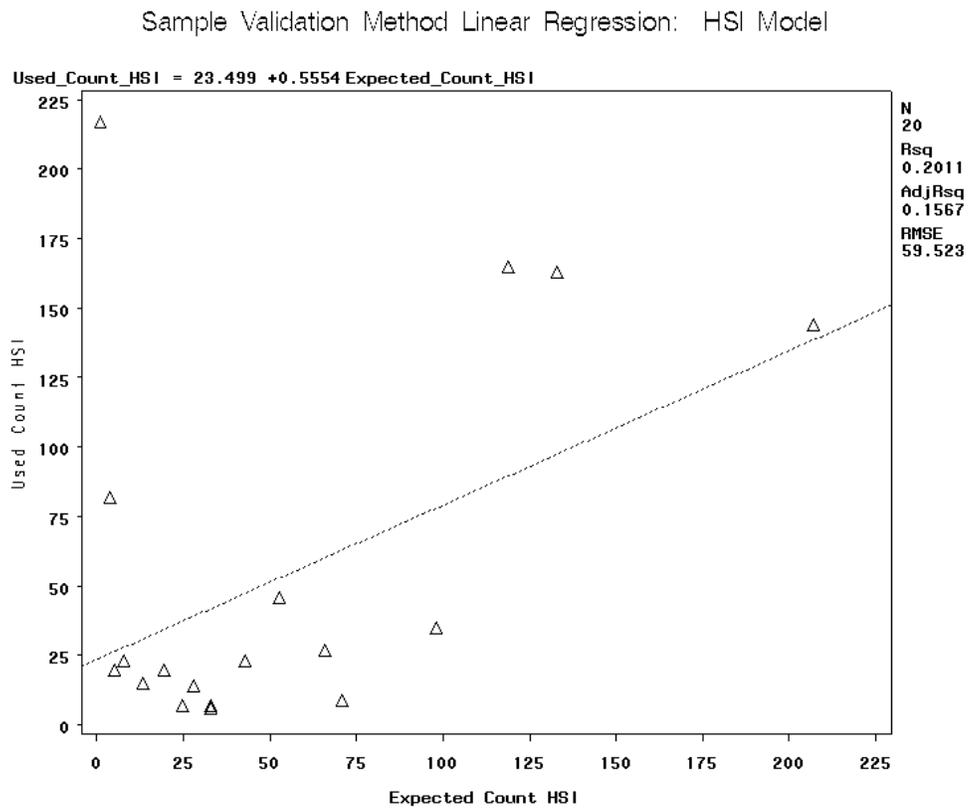


Figure 10. Sample Validation Method Linear Regression: HSI Model.

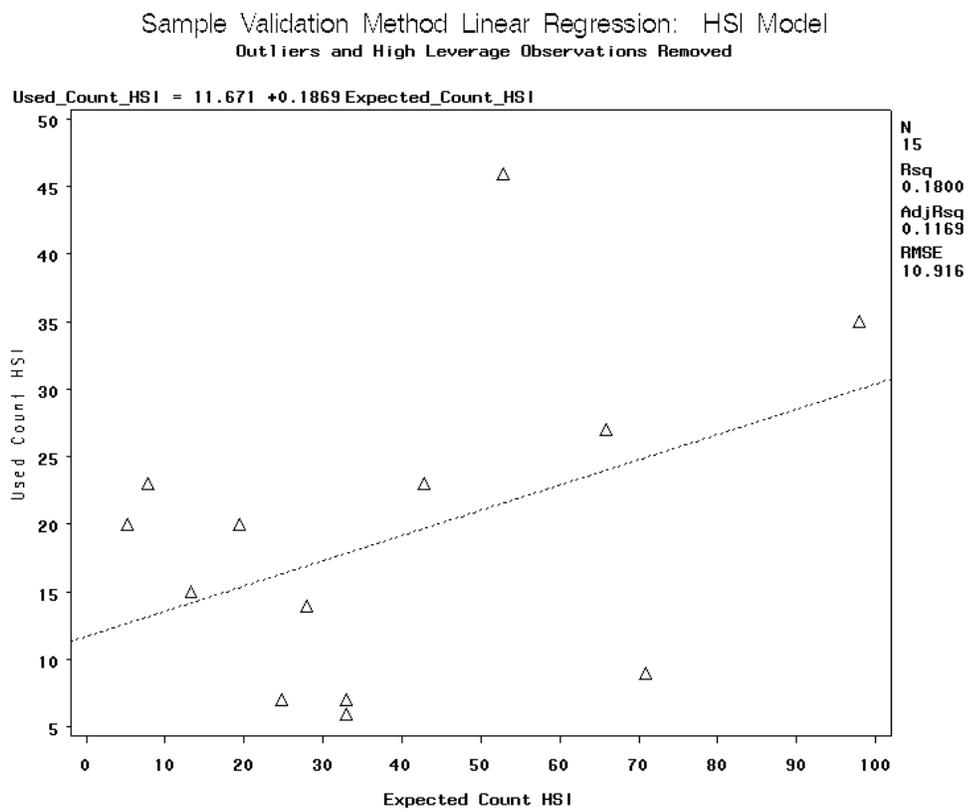


Figure 11. Sample Validation Method Linear Regression: HSI Model, Outliers Removed

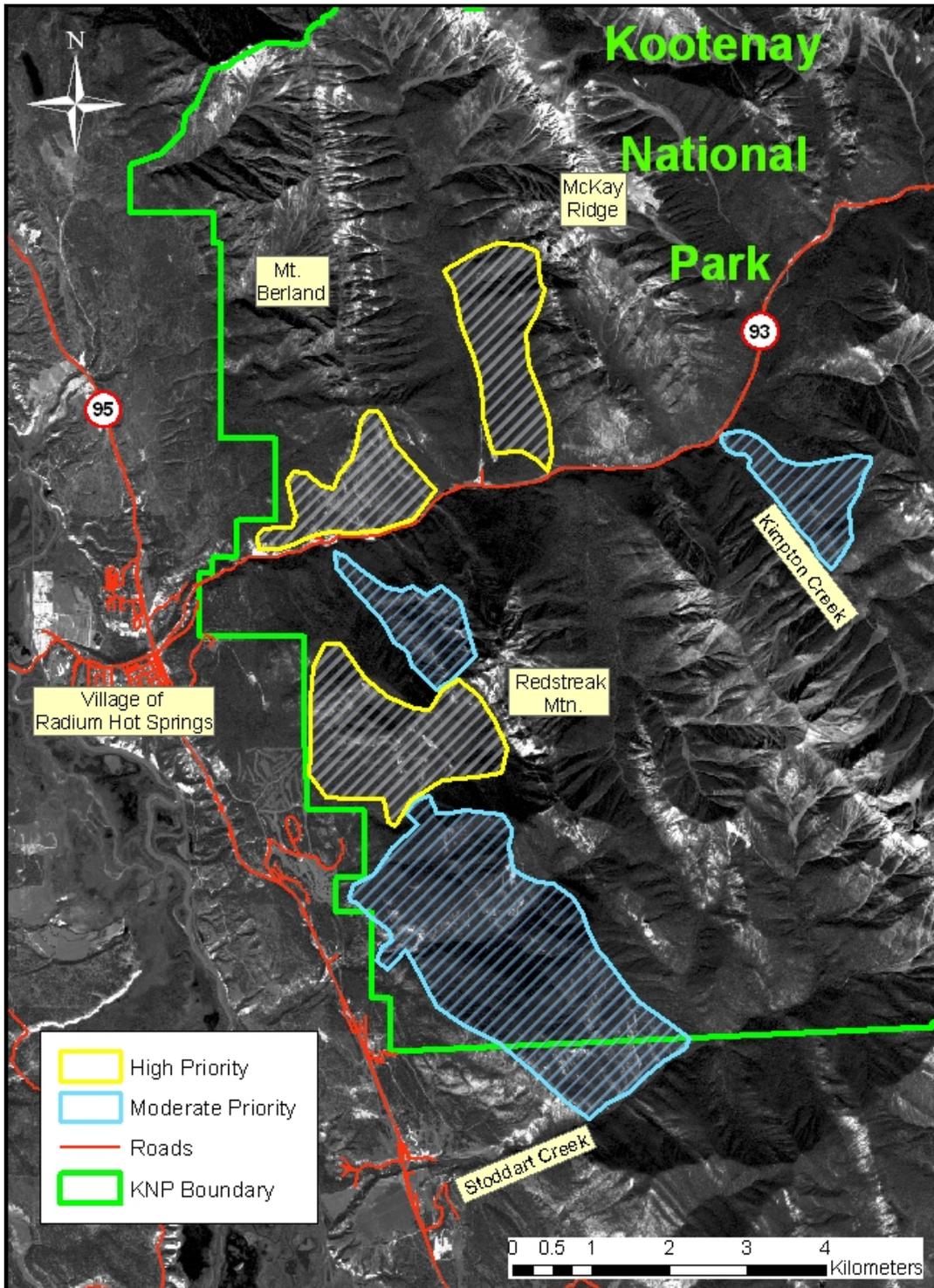


Figure 12. Map of Recommended Mid-Elevation Sites for Future Restoration Treatments.

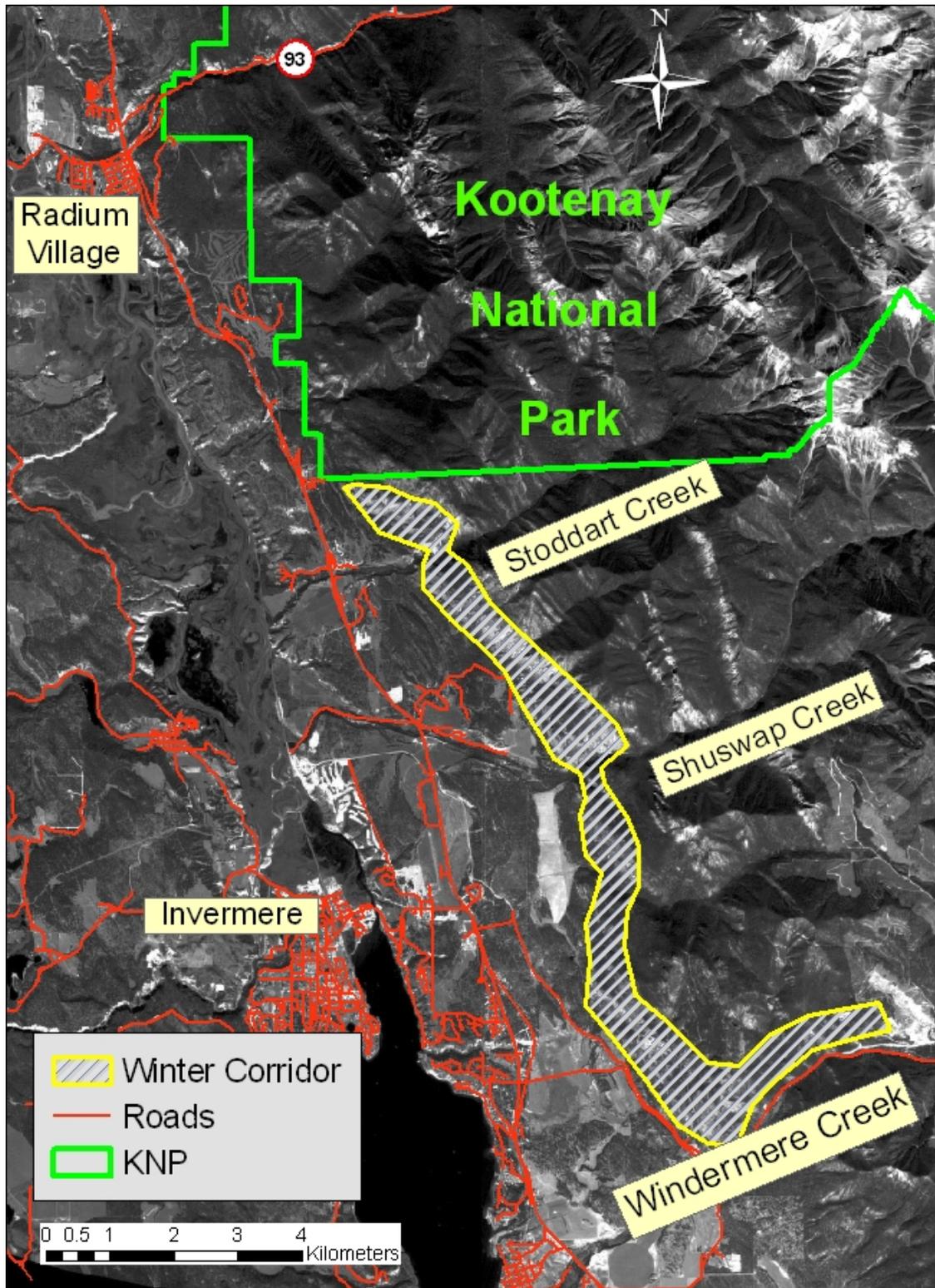


Figure 13. Map of Corridor Connecting Historic Winter Ranges.

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