Modelling and Management of Bighorn Sheep Movement Corridors

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Abstract: Open forest and grassland habitats in the mountains of south-eastern British Columbia are being lost to forest encroachment and urban development. These habitats provide critical winter and transitional ranges for bighorn sheep (*Ovis canadensis*) and play a crucial role in maintaining migratory behaviour. We used GPS telemetry data collected from a sample of bighorn sheep at Kootenay National Park and Radium Hot Springs, British Columbia to test a previously developed theoretical model of potential linkages between seasonal habitats for bighorn sheep. The theoretical linkage model was a poor predictor of bighorn sheep movement routes because migration events were rapid movements through poor quality habitat. We used the map of observed migration routes to prioritize mid-elevation transitional habitats for re-introduction of fire, and to identify a low elevation corridor connecting patches of historic winter range as a priority area for forest thinning, prescribed fire, and other treatments. We plan to continue to use GPS telemetry to monitor bighorn sheep response to management actions.

Key Words: bighorn sheep, British Columbia, GPS, Kootenay National Park, *Ovis canadensis*, prescribed fire, radiotelemetry, restoration, seasonal migration, wildlife corridor.

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In south-eastern British Columbia, forest encroachment into grasslands and other open habitats is a serious issue for biodiversity conservation and, more specifically, for the integrity of bighorn sheep (*Ovis canadensis*) habitat and movement corridors (Davidson 1991; Demarchi et al. 2000; Gray 2001; Gayton 2004). Conifer in-growth due to fire suppression on sheep winter ranges has reduced forage availability (Davidson 1991) and increased the risk of spread of disease by concentrating sheep in small areas (Schwantje 1988). Mid-elevation "transitional" habitats also usually include open forest habitats (British Columbia Forest Service 1997) and may be susceptible to degradation through conifer encroachment.

In the Radium Hot Springs area, sheep movements through valley bottoms (characterized by extensive human development) expose sheep to several risks, including the need to cross high-volume highways and exposure to lethal disease through contact with domestic animals. In spite of these threats, sheep must undertake regular movements across the landscape to optimize seasonal nutritional and habitat requirements (Hebert 1973; Festa-Bianchet 1988; Risenhoover et al. 1988). Examples of critical habitat elements include lambing ranges and mineral licks, both of which may be long distances away from core seasonal habitats. Sheep also need to undertake occasional long-distance movements to promote the interchange of animals and genes between populations (Geist 1971; Epps et al. 2005). Given the highly mobile manner in which sheep use the landscape, the identification and restoration of movement corridors of bighorn sheep is an important conservation measure for this species (Risenhoover et al. 1988; Demarchi et al. 2000; Tremblay 2001; Dibb 2004; Tremblay and Dibb 2004).

Our first formal attempt at understanding bighorn sheep movements in the Radium Hot Springs area consisted of a theoretical geographic information system (GIS)-based modelling exercise aimed at identifying potential movement corridors for sheep (hereafter referred to as the "linkage model"). This modelling work and accompanying management recommendations served as a basis for a multi-year ecosystem management project initiated by Parks Canada for the south end of KNP and that included ecosystem restoration measures (Dibb and Quinn 2006).

In 2002 we began a global positioning system (GPS) telemetry study on the Radium Hot Springs bighorn sheep with the aim of adding an empirical basis to our growing understanding of sheep movements in the area (Dibb 2006). More specifically, we wanted to identify seasonal ranges and critical habitats as well as movement corridors linking them. We also sought to use empirical data to test the theoretical linkage model and its underlying assumptions.

In this paper, we report on selected components of this telemetry study, which included the following objectives for the Radium Hot Springs bighorn sheep herd: (1) determine seasonal home ranges and use of unique habitats (e.g., lambing areas, mineral licks), (2) locate seasonal movement corridors, (3) test the linkage model, (4) compare corridor maps generated by the linkage model and the telemetry data, and (5) identify priorities for future habitat restoration work.

Study Area

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

Climate was 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). Low elevation forests were dominated by Douglas fir (*Pseudotsuga menziesii*), white spruce (*Picea glauca*), and aspen (*Populus tremuloides*) and were interspersed with patches of grassland (Achuff et al. 1984). Upper elevation forests were dominated by white spruce, Engelmann spruce (*Picea engelmannii*) and hybrids of these two species, and by subalpine fir (*Abies lasiocarpa*). Seral forests of lodgepole pine (*Pinus contorta*) were present after fire, except near tree-line. Tree-line occurred at approximately 2,300 m.

Approximately 10,000 permanent human residents occupied the Columbia Valley along the western edge of the study area, including 805 permanent residents of the village of Radium Hot Springs (British Columbia Stats 2008). However, the Columbia Valley also had a "shadow" population of second home owners and seasonal residents, estimated at 20,000 to 30,000 persons (District of Invermere 2008), and a growing tourism industry. Provincial Highways 93 and 95 crossed the study area east-west and north-south respectively. While human settlement was centred on the Columbia Valley, recreational activities occurred throughout the study area.

Methods

Development of the Linkage Model

We used the ARC/INFO GIS software (ESRI 1999) to develop a raster-based (25 x 25 m cell size), spatially explicit model aimed at delineating probable movement corridors for bighorn sheep within the study area. This theoretical model was based on information from a variety of sources including the literature, key informant interviews, personal observations in the field, and existing digital biophysical data sets. The model contained three submodels or routines (habitat, human disturbance, and movement), each containing variables believed to influence sheep movements (Figure 2). Detailed descriptions of the model can be found in Tremblay (2001) and Tremblay and Dibb (2004).

The habitat routine was designed to account for the quality of the habitat, without consideration of human disturbance. Habitat suitability ratings from existing biophysical data sets (Poll et al. 1984; Delta Environmental Management Group 1992; Marcoux et al. 1997) were standardized and reclassified into "habitat coefficients" ranging from 0 to 1, representing minimal and optimal habitat, respectively. Separate habitat layers were created for the growing and winter seasons.

The purpose of the disturbance routine was to account for the alienation effect that human disturbance has on bighorn sheep habitat use. We first conducted a comprehensive inventory of all sources of human disturbance including linear developments such as roads, railways and trails, as well as point sources such as settlements, campgrounds and picnic areas. We then determined human use levels for each of these features, on a seasonal basis, using a combination of existing traffic data for major roads, a series of automatic counters installed at strategic locations on selected secondary roads and trails throughout the study area, and key informant interviews. Zones of influence (ZOIs) and disturbance coefficients (DCs) were then determined for each feature based on empirical studies of the effects of humans on sheep (MacArthur et al 1979,1983; Stemp 1983) in addition to area-specific information gleaned from personal observations and key informant interviews pertaining to the sensitivity of bighorn sheep to human disturbance. Both the nature and predictability of disturbance were important considerations in determining ZOIs and DCs. For example, roads were given less extensive ZOIs than trails because sheep are generally less sensitive to vehicles than they are to humans on foot due to the greater predictability of disturbances along roads. We rated disturbance coefficients on a scale of 0 to 1, representing maximum and minimum disturbance, respectively, and produced separate disturbance layers for summer and winter.

The primary consideration in building the movement routine was security. From previous empirical studies of bighorn sheep ecology (Wishart 1958; Geist 1971; Becker et al. 1978; Martin and Stewart 1980; Lawson and Johnson 1982; Boyd et al. 1986; MacCallum 1991), we determined that the two most important security factors affecting sheep movements were the presence of escape terrain and visibility. We defined escape terrain as slopes >80%. Escape terrain coefficients were applied to bands surrounding these areas reflecting the fact that bighorn sheep use generally decreases with increasing distance from escape terrain (Tilton and Willard 1982; Stemp 1983; MacCallum 1991). Consistent with the overall modelling scheme, these coefficients were rated from 0 to 1, representing minimal and optimal security, respectively. Areas of high visibility were defined as those areas corresponding to “open” habitats, such as grasslands, rocky ridges and open forests. We assigned an optimal rating of 1.0 to areas of high visibility while areas of lesser visibility were given a rating of 0.5. This rating scheme reflected the belief that visibility enhances corridor suitability but the lack thereof does not act as an absolute constraint on sheep movements. Overall coefficients for the movement routine were obtained by multiplying the visibility and escape terrain coefficients.

The final output of the model consisted of maps representing, on a seasonal basis, the spatial distribution of "corridor value" across the study area for bighorn sheep. Corridor value was defined as the suitability of an area to support the movement of bighorn sheep. Seasonal corridor value was determined by combining the outputs of the habitat, disturbance and movement routines, according to the following equation:

final corridor value = habitat value x disturbance coef. x movement coef.

Seasonal corridor value maps were generated and served as the primary basis for delineating potential movement corridors for sheep across the study area. The final corridor maps included site-specific knowledge of sheep movements and habitat use acquired through key informant interviews and personal observations.

Collection of Telemetry Data

We captured bighorn sheep by free-range darting while the sheep occupied their winter ranges, between January and March inclusive in each year from 2002 through 2005. We selected 10 adult animals annually, including both males and females, out of a total population size of 150 to 200, and selected different animals each year. Among rams, we selected one-half to three-quarter curl rams, but avoided selecting full-curl rams since those animals could experience increased mortality risk during the fall hunting season. All study animals were fitted with GPS radio collars programmed to log two or more GPS locations per day for up to 12 months, covering at least 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. Collars were removed in November or December and were unavailable for approximately 8 – 10 weeks during annual refurbishment. Refurbished collars then were re-deployed on a new sample of sheep for the subsequent year.

The Parks Canada Agency Animal Care Committee approved animal capture and handling methods under Research and Collection Permits LLYK02-01, LLYK02-35, LLYK03-15, LLYK04-02, and KOONP-2005-3518. More details on sheep capture and GPS data acquisition methods are provided in Dibb (2006, 2007).

Telemetry-based Corridor Delineation

We constructed an approximate, visual representation of movement routes by considering sequences of telemetry points of individual animals within a GIS. This product was intended to be directly comparable with the final corridor map derived from the linkage model. We converted point sequences into linear representations of movement for each study animal in years 2002 to 2004. We 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 frequently used by sheep, with an average of approximately 5 km separating consecutive nodes. We constructed separate networks for males and females.

We 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 individual movement 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. We chose the threshold of 1 km per hour because this appeared to be the approximate limit separating movements typical within core habitats from movements between core habitats.

We 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. We 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.

Testing the Linkage Model

Our general approach to testing the linkage model was to use GPS telemetry data from study animals to determine sheep preference or avoidance of the corridor value classes generated by the linkage model. We accomplished this by first determining, for each study animal, the number of telemetry points in each of the linkage model’s corridor value classes. We then determined the relative proportions of these classes within each animal’s individual home range and within the overall study area. Finally, we 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 the linkage model’s 5 summer (May through October) corridor value classes (very low, low, moderate, high and very high). Since the linkage model did not differentiate corridor use by sex, we pooled the telemetry data for both sexes. We 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.

We performed compositional analyses by using the BYCOMP program (Ott and Hovey 1997) within SAS statistical software. BYCOMP first employed a multivariate analysis of variance (MANOVA) and calculated 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 we considered $p < 0.05$ to represent significant differences.

We 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, we considered selection at the home range scale in which availability was determined within the minimum convex polygon (MCP) home range of each animal. Then, we considered selection at the scale of the entire study area.

We conducted the analyses using: 1) all GPS location points meeting certain criteria for positional accuracy, and 2) "movement points", a subset of location points for which the straight line rates of travel from the one point to the next point were > 100 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.

Our assumption in testing the linkage model was that good model performance would be indicated by sheep preference for corridor value classes in the order expected. In other words, sheep would significantly prefer the "high" class to "moderate", would significantly prefer the "moderate" class to "low", and so on.

Comparison of Corridor Maps

We conducted a visual comparison of the corridor map derived from the linkage model with the telemetry-based corridor map. We accomplished this by looking for differences in broad patterns of corridor delineation as well as for specific corridors that were present in one model but absent from the other.

Identification of Restoration Priorities

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

Finally, we considered the need to maintain sheep access to pockets of historic winter range located up to 15 km south of Radium Hot Springs. We 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.

Results

Linkage Model

The final output from the linkage model was a map representing, on a seasonal basis, the spatial distribution of "corridor values" across the study area (Fig. 3). Although separate maps were produced for summer and winter, we present only the former here since the latter was not subjected to the model testing exercise. Corridor values ranged from 0 to 1, representing no value and optimal value, respectively, and were assigned a rating as per Table 1. Based on this map and additional site-specific information, we identified 12 potential movement corridors for bighorn sheep within the study area (Fig. 4).

Delineation of Travel Routes from GPS Location Sequences

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. One study animal, a ram estimated at 7 years of age, was killed on highway 93/95 on 1 August 2002 having never moved to the high country. Five of 7 rams in 2002 and 2003 made brief winter excursions at least 6 km south of the Radium winter range; 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 travelled more than 2 km south of the Radium winter range.

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. 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. Most habitats selected by females in summer were in the northern half of the study area but relatively close to the Radium Hot Springs winter range. Males selected habitats in summer that were generally more distant from Radium Hot Springs. Consequently, the male network of migration corridors was longer and somewhat more complex than that of females.

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 lick sites (Figures 6 and 7). 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.

Testing the Linkage Model

The classification scheme used for the 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 2). Some individual animals were not recorded within the "very high" class, therefore we executed the compositional analysis after collapsing the high and very high classes into a single category.

At the scale of individual home ranges, bighorn sheep use of the linkage model's probability classes was significantly non-random ($\lambda = 0.14$, $F = 36.66$, $p < 0.001$, Table 3). 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 significant.

Similarly, at the scale of the entire study area, bighorn sheep exhibited selection for corridor value classes ($\lambda = 0.13$, $F = 41.85$, $p < 0.001$, Table 4), and class rankings were similar to the individual home range scale.

Overall, considering both scales of analysis, the moderate class was the most strongly selected for, followed in order by the combined high and very high class, the very low class, and the low class. Selection differences between the low and very low classes generally were not significant but differences in selection between other classes were significant.

We 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 5) and at the scale of the entire study area ($\lambda = 0.065$, $F = 57.40$, $p < 0.001$, Table 6). At the home range scale sheep preferred the moderate class to very low or low classes and preferred the combined high and very high class to low; all other differences among class preferences were not significant. At the study area scale sheep preferred the moderate class relative to all others, and preferred the combined high and very high class to very low. Other differences among class preferences were not significant.

Table 7 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.

Development of Restoration Priorities

We completed the selection and prioritization of candidate sites for restoration and show these in figures 7 and 8. Two high priority sites were identified on the north side of Sinclair Creek and would be expected to improve security and forage opportunity as sheep migrate between the Radium Hot Springs area and high elevation ridges in the Brisco Range. A third high priority site is intended to provide similar benefits to a linkage between the village and the upper slopes of Redstreak Mountain in the Stanford Ranges.

Discussion

Comparison of Linkage Model and GPS Telemetry Corridor Maps

At a scale encompassing the entire study area, some broad patterns of corridor delineation were similar in the two approaches. The most obvious similarity was that both maps showed a predominantly north-south movement axis following the natural orientation of major ridge systems. Additionally, the network of corridors in both maps converged on the winter range areas near Radium Hot Springs.

We also found a number of dissimilarities between the two maps. First, the telemetry-based approach mapped separate corridor networks for males and females, with striking differences between the two, as discussed above. In contrast, the linkage model-based map did not distinguish between male and female corridors. This represents an obvious limitation of the linkage model.

A second difference was that the telemetry-based map included a number of small corridors that provide east-west linkage at mid to high elevations between major ridge systems. In contrast, the linkage zone model depicted a single east-west corridor following highway 93 along Sinclair Creek up towards the height of land at Sinclair Summit. Although sheep frequently occurred along Sinclair Creek, telemetry data showed that sheep rarely used it as a travel route above the confluence with McKay Creek. Instead, sheep followed ridges down to Sinclair Creek where they accessed minerals at several locations along the side of highway 93. The presence of sheep along the highway has created the apparently mistaken impression among even long-time observers that the sheep use the highway corridor as a travel route.

A third discrepancy we observed was that the linkage model map predicted a higher elevation corridor linking the Radium area south to Stoddart Creek via Redstreak Mountain, in addition to the low elevation corridor that the telemetry-based map also depicted. The lack of sheep use of the high elevation corridor likely reflects the diminished status of the Stoddart Creek area as winter range, thereby reducing the need for sheep to travel there. The telemetry-based map depicted sheep use of a low elevation corridor north of Radium as well, running approximately parallel to highway 95 near the foot of the Brisco Range in the Columbia Valley. The linkage model map did not predict this corridor, likely due to its presence within zones of thick forest cover, flat terrain and, for some portions, far from escape terrain.

Fourth, the linkage model predicted corridors extending further north and south of the Radium Hot Springs area than was found in the telemetry-based analysis. These corridors are likely indicative of potential long distance travel routes linking the Radium herd to other sheep populations, but that were unused by our study animals.

Finally, at a finer scale, the linkage model predicted the occurrence of a set of corridors within the village of Radium Hot Springs and immediate surrounding areas. The telemetry-based analysis did not have the resolution to map corridors at this scale, although the data exists to conduct such a finer-scale analysis in future. However, use of the village by sheep is sufficiently heavy that it will likely prove difficult to separate fine-scale movements from foraging activity.

Linkage Model Performance

The generally poor performance of the linkage model can be attributed to a number of limitations, some of which are inherent to all models and some more specific to the linkage model itself.

One of the most significant limitations of any model is that it is usually based on several, often untested, assumptions. At the time of model development, very little information was found in the literature describing the factors driving the selection of movement habitat by bighorn sheep. Most of the existing research we reviewed to create the theoretical model focused on habitat selection, home range size, or behavioural and physiological responses to human-related disturbances. The selection of movement habitat by sheep had not received much attention and was generally poorly understood. This dearth of information on wildlife movements required us to make a number of tenuous assumptions. Three such assumptions that influenced the performance of the model are described below.

The first assumption, which formed the basis of the habitat routine, was that sheep choose to travel through areas of suitable, rather than unsuitable, habitat. This assumption, which has been applied to other corridor modelling efforts (e.g. Walker and Craighead 1997, Callaghan et al. 1998), is based on the belief that movement corridor habitat should be similar to core habitat in providing optimal cover and forage. However, this assumption did not hold true for our telemetry data, which showed that the Radium sheep often underwent rapid migrations through largely unsuitable, "risky" habitat.

The second assumption was that empirical data collected in other areas could be applied to the present study, i.e. that bighorn sheep located within the present study area select habitat and travel routes and react to humans in the same way as their counterparts living outside the Radium study area. However, it is possible that the literature failed to capture some of the particularities of the Radium herd, most notably its high level of habituation to human presence, particularly on its lower-elevation winter and transitional ranges.

A third important assumption of the linkage model was that male and female bighorn sheep have similar movement patterns and use the same criteria in the choice of travel routes. However, sexual segregation in bighorn sheep is well documented. Rams and ewes have different biological requirements, a situation that leads to differences in foraging strategies and the use of different ranges during much of the year (Main et al. 1996). Such differences result in distinct movement patterns for rams and ewes. In support of this, our telemetry results show that males and females exhibited sexual segregation in summer when their respective ranges were separated by, typically, 1 to several km.

Beyond its reliance on untested assumptions, another factor that might have contributed to the poor performance of the linkage model is its dependence on existing data sets. While such an approach was necessary for time and resource considerations, it also entailed a number of constraints, which were particularly evident in the case of the habitat suitability data. Due to the multijurisdictional nature of the study area, the habitat suitability ratings used in the model were derived from a combination of provincial and federal data sets. These data sets required a number of manipulations in order to meet the needs of the model, which inevitably led to a loss of accuracy. Moreover, the habitat suitability ratings in the existing data sets were not assigned on a seasonal basis but rather, on a carrying capacity basis. As a result, winter range habitats, which generally support higher densities of ungulates, were systematically assigned higher ratings than summer habitats. This system made it difficult to differentiate between high and low quality habitats for a given season.

Another possible reason explaining the poor performance of the linkage model may be its lack of focus on a specific scale of movement. In retrospect, we would recommend taking a multi-scale approach to modelling corridors which would distinguish between large-scale inter-range dispersal movements, medium scale movements between seasonal ranges, and, at the finest scale, movement routes linking key habitats within seasonal ranges.

Finally, perhaps one of the most important limitations of using a spatial modeling approach for identifying corridors stems from its inability to adequately account for non-spatial factors such as predator-prey relationships, learned behaviours passed on from generation to generation, behavioural differences amongst individuals, knowledge of the landscape, and motivation to reach a particular destination. It is easy to conceive how some or all of these factors could affect the choice of travel lanes and yet, such factors are not readily accounted for in a spatial model.

In spite of the many limitations discussed above, a theoretical modelling approach to corridor delineation can offer some important advantages over a more empirical approach. One such advantage is that a theoretical model tells the researcher something about where the animals should be moving rather than simply where they are moving. For example, wildlife may be avoiding optimal corridors because of human-related impediments, or may be forced to use sub-optimal corridors because no alternatives exist.

A case in point may be the bighorn sheep herd in our study, which essentially used only 3 seasonal ranges: winter, lambing, and summer. They made little use of mid-elevation habitats, instead making rapid migrations between valley floors and alpine regions – a situation which may have placed additional pressure on limited, crowded winter ranges. The traditional migration routes, now degraded through coniferous in-growth, provide risky travel for bighorn sheep since the routes do not provide for good visibility and predator detection. Risky migration routes may eventually be abandoned by sheep (Risenhoover et al. 1988), leading to a suite of problems associated with sedentary populations. Although we have not yet detected increases in sedentary behaviour by the Radium sheep, this problem may yet emerge if sheep corridors in our study area continue to deteriorate.

Long-distance Movements

On a broader scale, the spatial distribution of bighorn sheep in western Canada and western North America appears to be consistent with a classic metapopulation structure (Bleich et al. 1996; Demarchi et al. 2000). Interchange between herds is believed to be essential to maintaining a functioning metapopulation (Bleich et al. 1996) through mechanisms including demographic rescue or re-colonization of declining or extirpated herds and the exchange of genes among relatively isolated subpopulations (Epps et al. 2005). We did not detect any dispersal or interchange between the Radium herd and other herds, despite acquiring daily location data for 9 to 10 animals of both sexes per year for a total of 4 years. However, the lack of evidence of interchange between herds in our study does not necessarily mean that none occurs, especially given that dispersal appears to be rare among bighorn sheep (Geist 1971; Singer et al. 2001). Our sample size may have been too small relative to the rarity of such events, particularly in the age-sex classes (3 year old males [Geist 1971]) most likely to move long distances. Moreover, there exists reliable historical evidence of occasional sheep movements between our study area and other sheep ranges, such as the Kicking Horse canyon located over 100 km to the north (Stelfox et al. 1985; Tremblay 2001).

A second, more worrisome, explanation for our failure to document inter-range movements may be that such movements are increasingly impeded by the degradation, through conifer encroachment and various urban and recreational developments, of the low elevation and valley bottom corridors that likely provide the linkage between neighbouring herds. This situation may prove difficult to address as human developments can severely constrain landscape managers in the application of prescribed fire to mitigate the coniferous in-growth problem. Ever-increasing demand for permanent homes and recreational properties in the region will likely exacerbate the problem in the future.

Bighorn sheep in our study area sometimes chose valley floor travel routes, even where it appeared that more secure, higher elevation ridge routes were available. These valley floor routes carried increased risk of contact with domestic livestock, highway crossings with risk of collisions with motor vehicles, and, presumably, predation. The reasons why sheep chose these high-risk routes are not clear although we speculate that habitat degradation due to forest ingrowth on the adjacent mountain slopes may be a factor.

Management Implications

The results of our study point to a number of recommendations aimed at improving functional landscape connectivity for bighorn sheep in the present study area as well as other areas where wild sheep persist in heavily human-impacted landscapes. We begin by providing specific recommendations for habitat restoration in the Radium area. We then discuss other important management issues pertaining to sheep movements. Finally, we present recommendations on the continued use of models to inform future restoration efforts.

Our recommendation for priority habitat restoration in the Radium area is burning and thinning of coniferous ingrowth within the currently utilized seasonal migration corridors. Of particular concern are mid-elevation slopes located immediately adjacent to current winter range areas (Figure 7). Secondary priorities are mid-elevation slopes that connect summer ranges to current or historic winter ranges, but are not currently being utilized by the Radium herd to the extent expected. We also recommend restoration of the narrow, low elevation corridor connecting winter habitat at Radium with historic winter ranges at Stoddart, Shuswap, and Windermere Creeks (Figure 8). A longer term project is recommended to extend restoration of this corridor further south to provide linkage to the Columbia Lake bighorn sheep herd near Fairmont Hot Springs, British Columbia. Both sections of this low elevation corridor would likely require emphasis on low-risk mechanical thinning techniques due to proximity to built facilities.

Our results illustrate that wild sheep in our study area are at considerable risk of coming into close contact with domestic sheep ranches in the Columbia Valley. While we recognize that progress has been made recently at identifying high-risk areas (e.g., working with local ranchers, and, in one instance, replacing a local domestic sheep herd with cattle), risk levels remain high. Lowering the risk for disease transmission will require continued and coordinated interagency effort across all jurisdictions that contain land considered important for sheep movements. Restoration work, as described above, will also be an important part of the solution if it enables bighorn sheep to choose travel routes that are further removed from the valley floor.

In our view, the frequent occurrence of bighorn sheep in proximity to humans is a significant conservation challenge for the Radium herd. The concentration of sheep on very small areas of artificial habitats for 7 to 8 months each year exacerbates problems of animal-vehicle collisions, spread of disease, habituation of sheep to humans, and may also serve as a disincentive to migratory behaviour. Strategies to improve the separation of humans and bighorns could include limited sections of highway fencing and land use planning to minimize human encroachment into areas important to sheep. Habitat restoration work in areas outside local communities could also provide sheep with opportunities to forage in areas with less human activity and that can be reached without having to cross major highways.

Finally, we recommend the development of improved models of bighorn sheep habitat and movement corridors as important planning tools for future restoration work. Although we have identified a series of priority areas for restoration that are likely to occupy forest managers for several years, improved modelling tools could enable refinement of secondary priorities for restoration such as highway mitigation, human use management, and land use planning. Moreover, although an empirical resource selection function (RSF) habitat model for the Radium study area was developed by Dibb (2007), improved empirical models could incorporate some or all of the following: (1) separate models for males and females, (2) model biologically relevant seasons, (3) model corridors by collecting GPS location data more frequently during migratory periods, and (4) focus corridor modelling on a particular scale of movement, such as seasonal migration.

Acknowledgments

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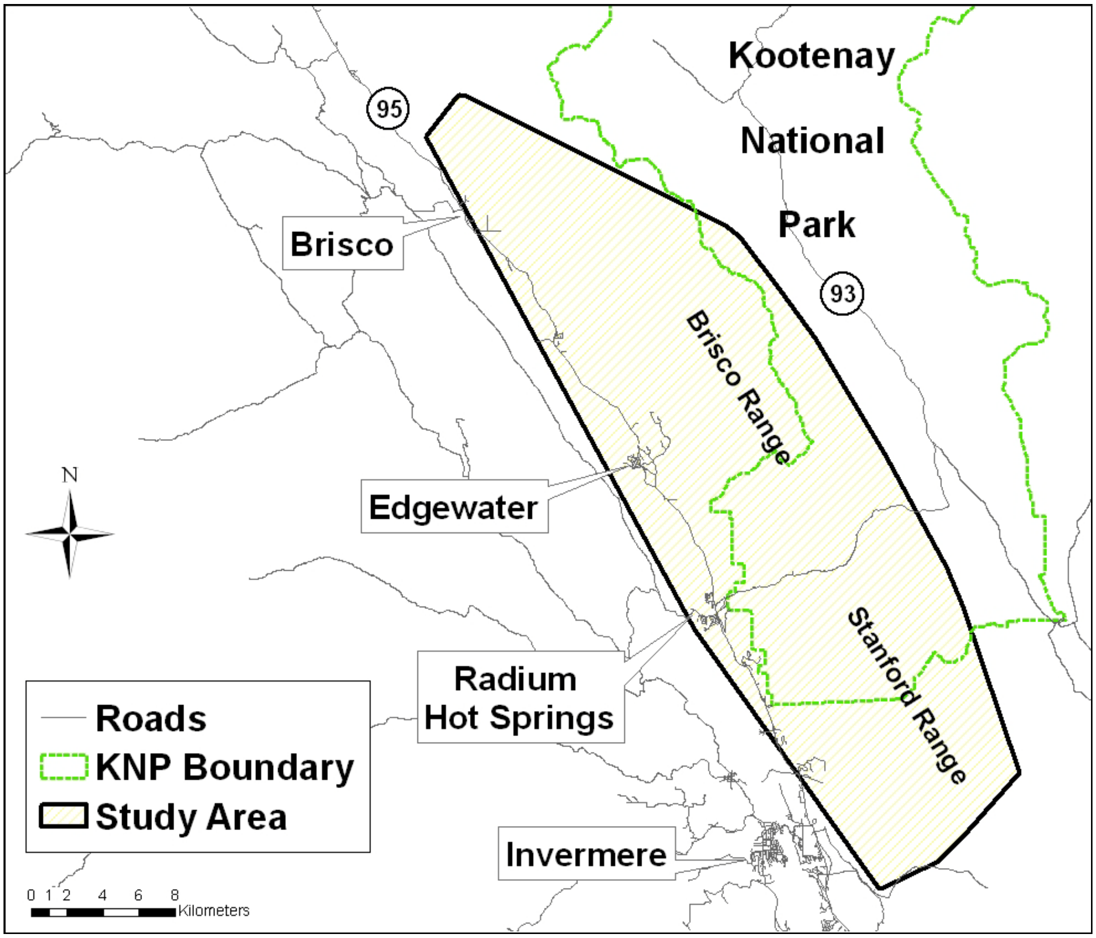

Figure 1. Study Area.

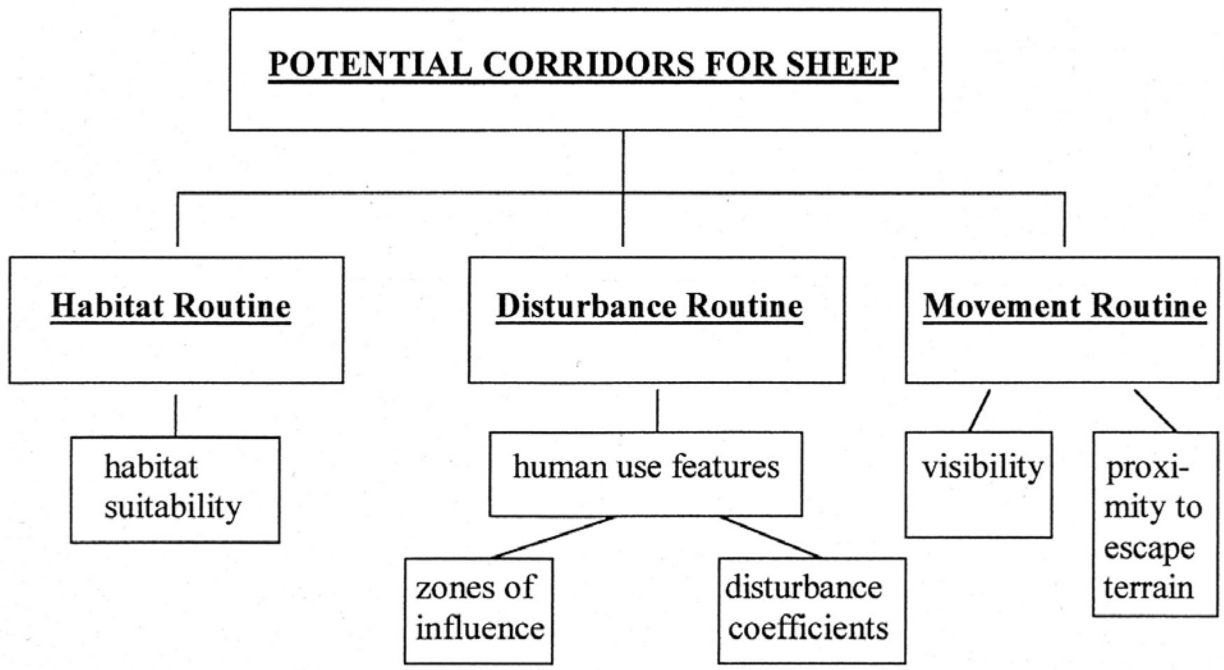

Figure 2. Conceptual diagram of the bighorn sheep linkage model.

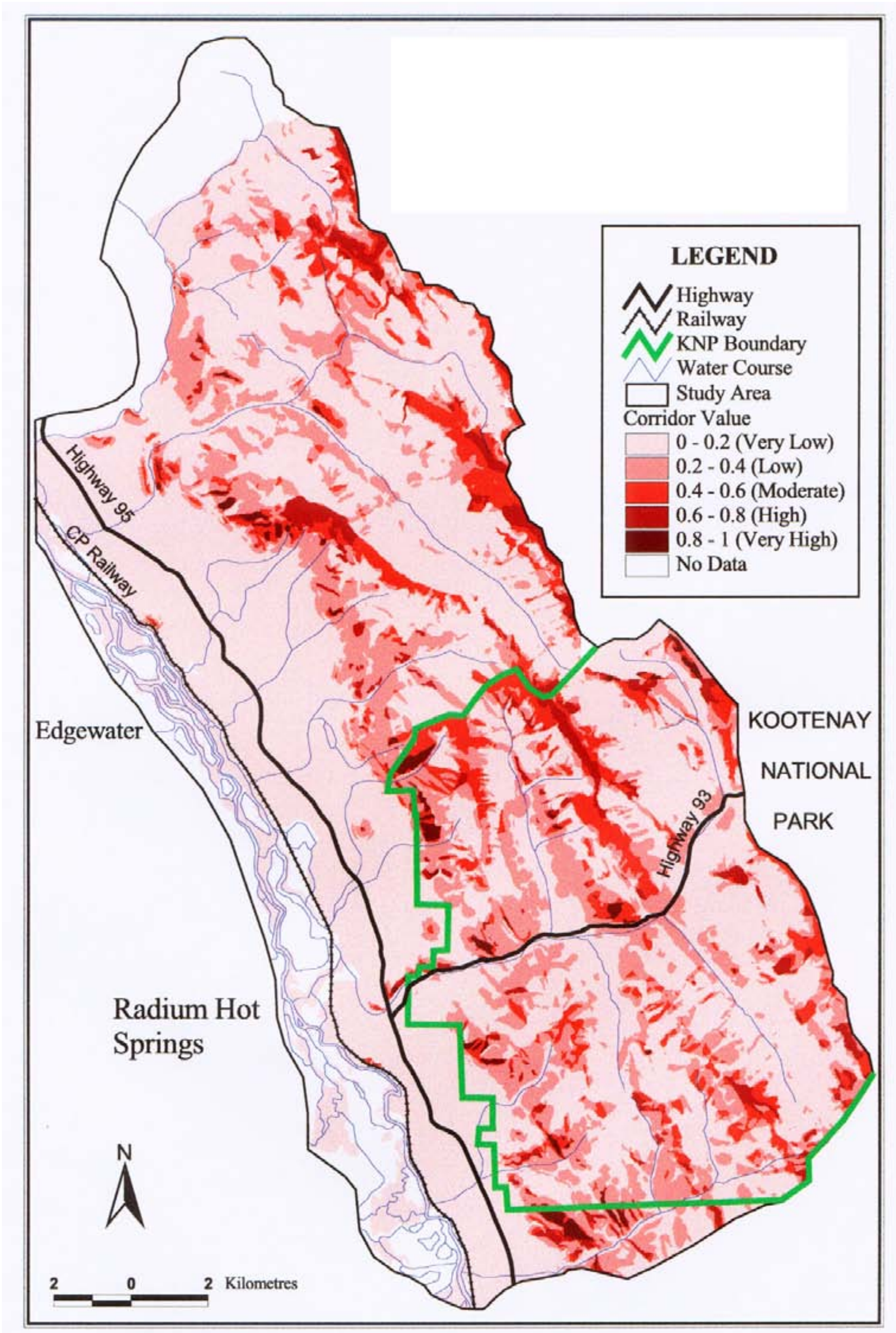

Figure 3. Map of corridor values generated from the theoretical bighorn sheep linkage model**.**

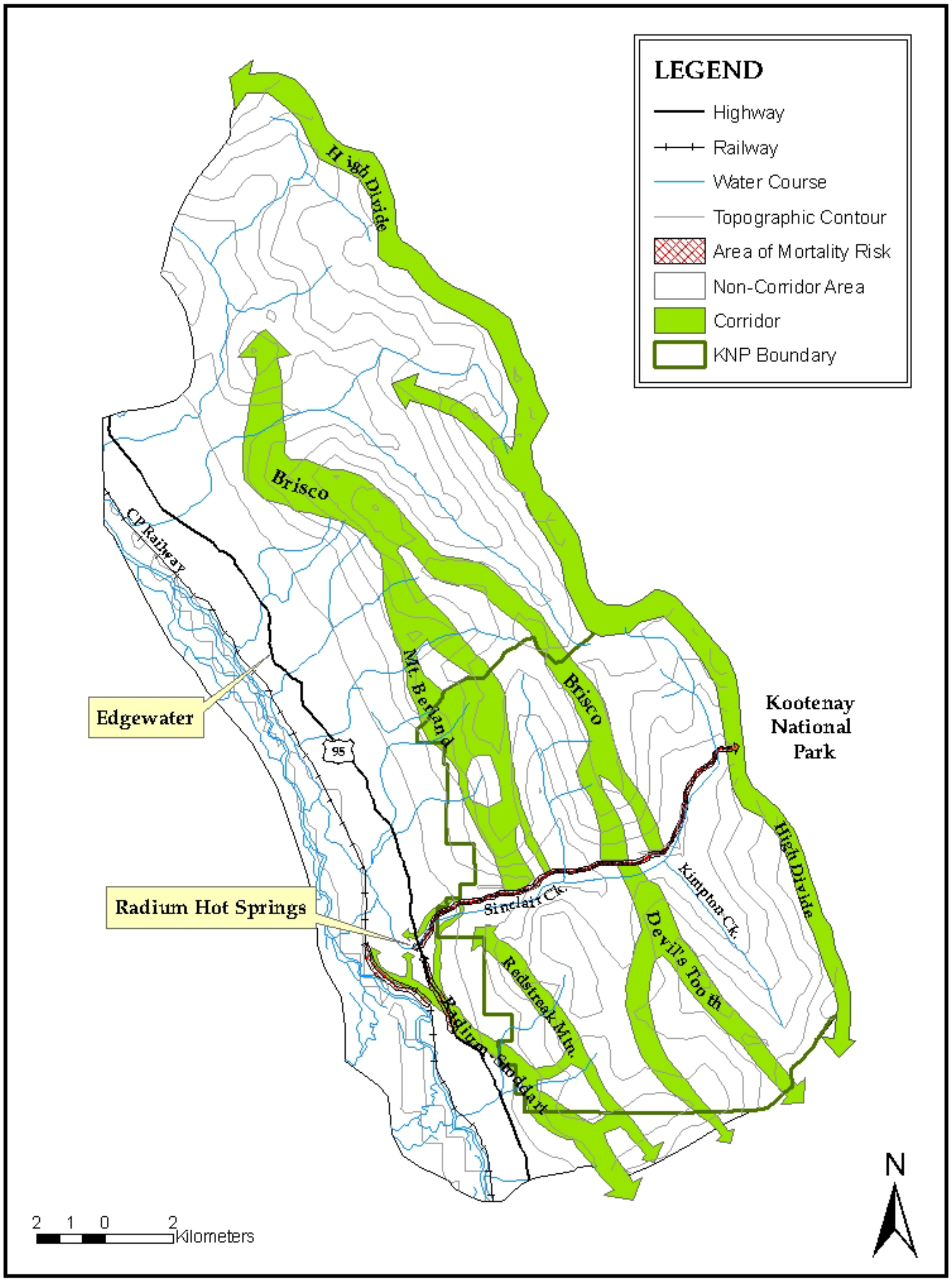

Figure 4. Potential corridors for bighorn sheep based on the linkage model corridor values, site-specific information, and personal observations.

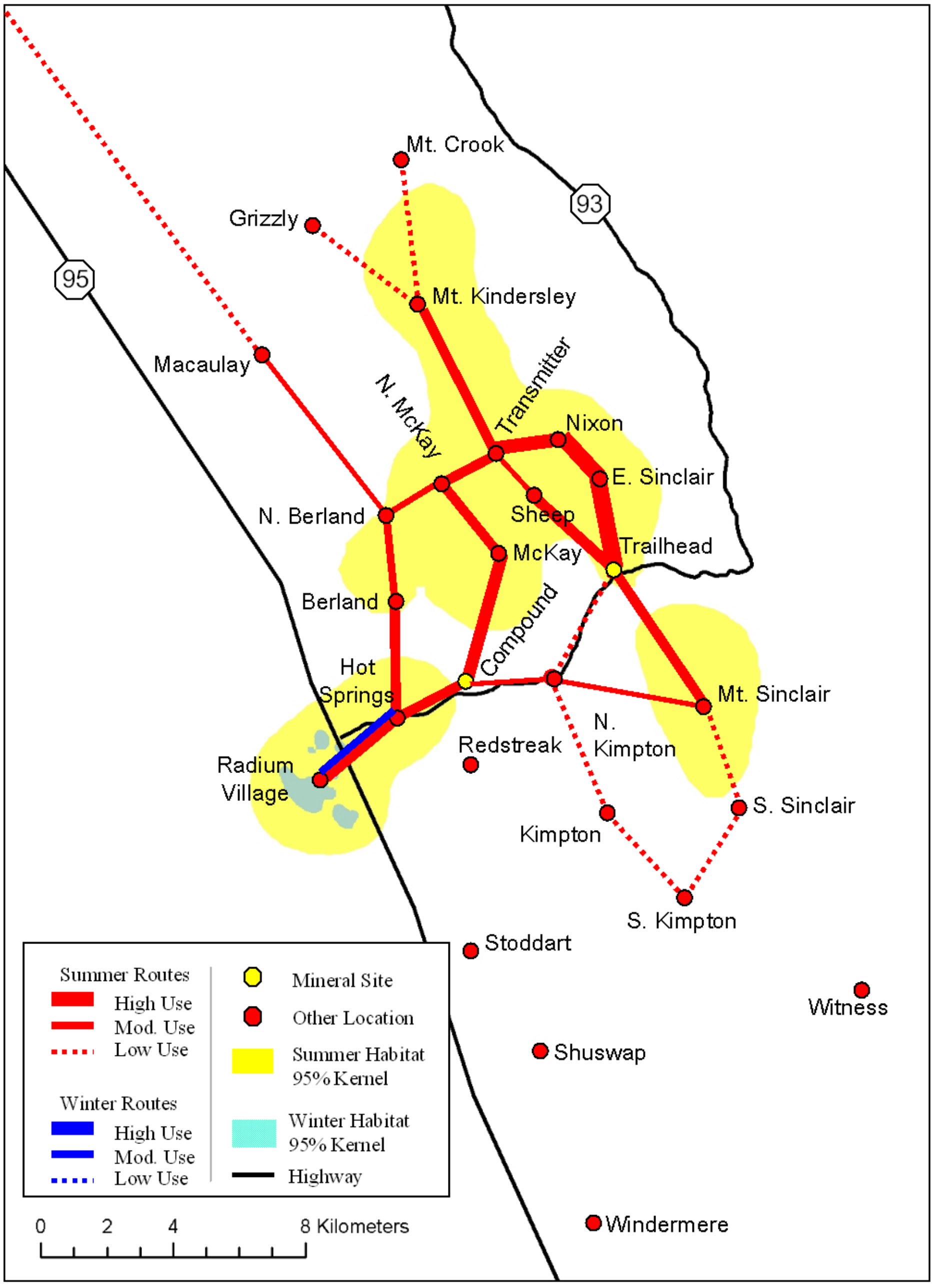

Figure 5. Female movement routes and core ranges from GPS location sequences.

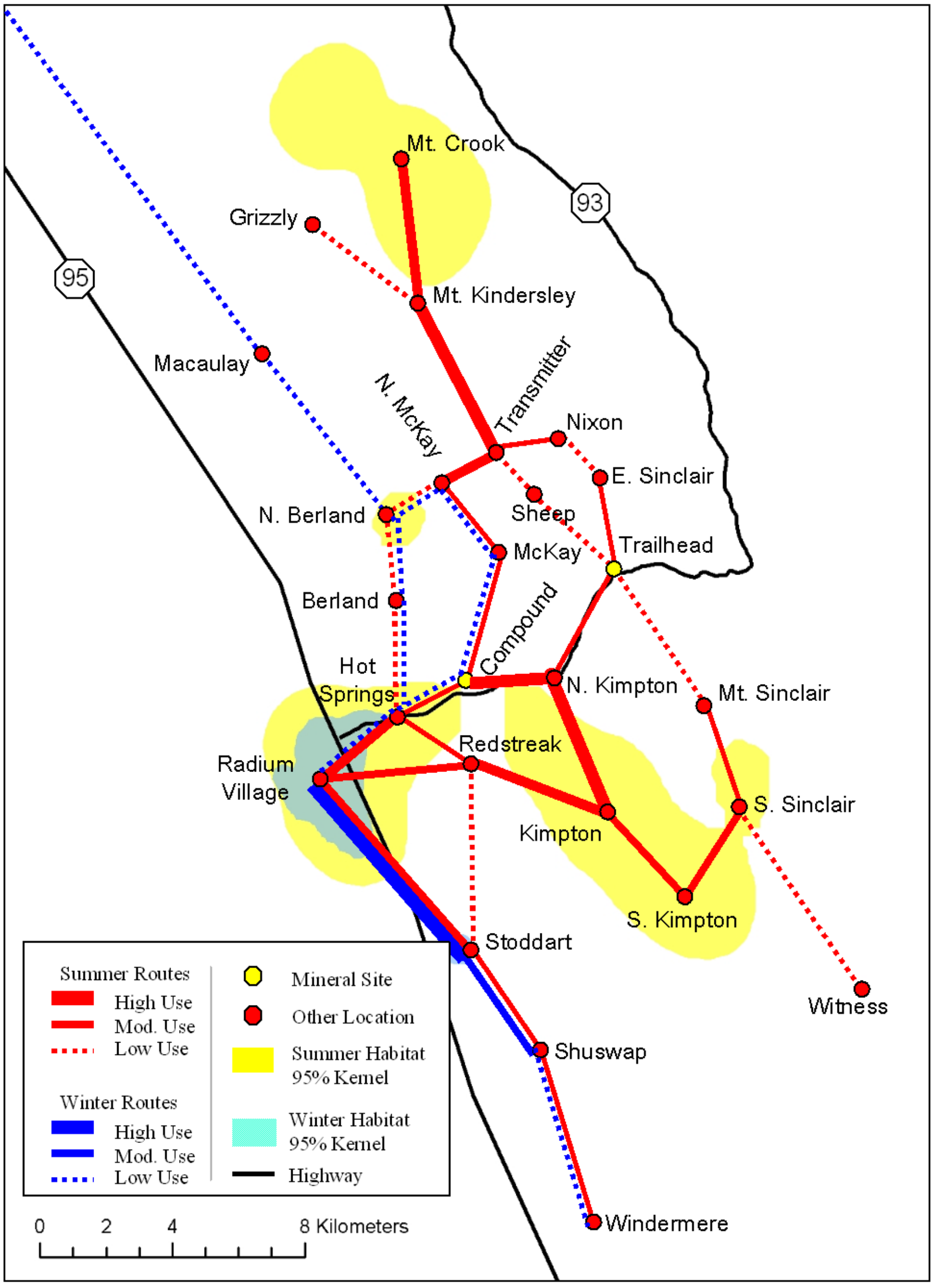

Figure 6. Male movement routes and core ranges from GPS location sequences.

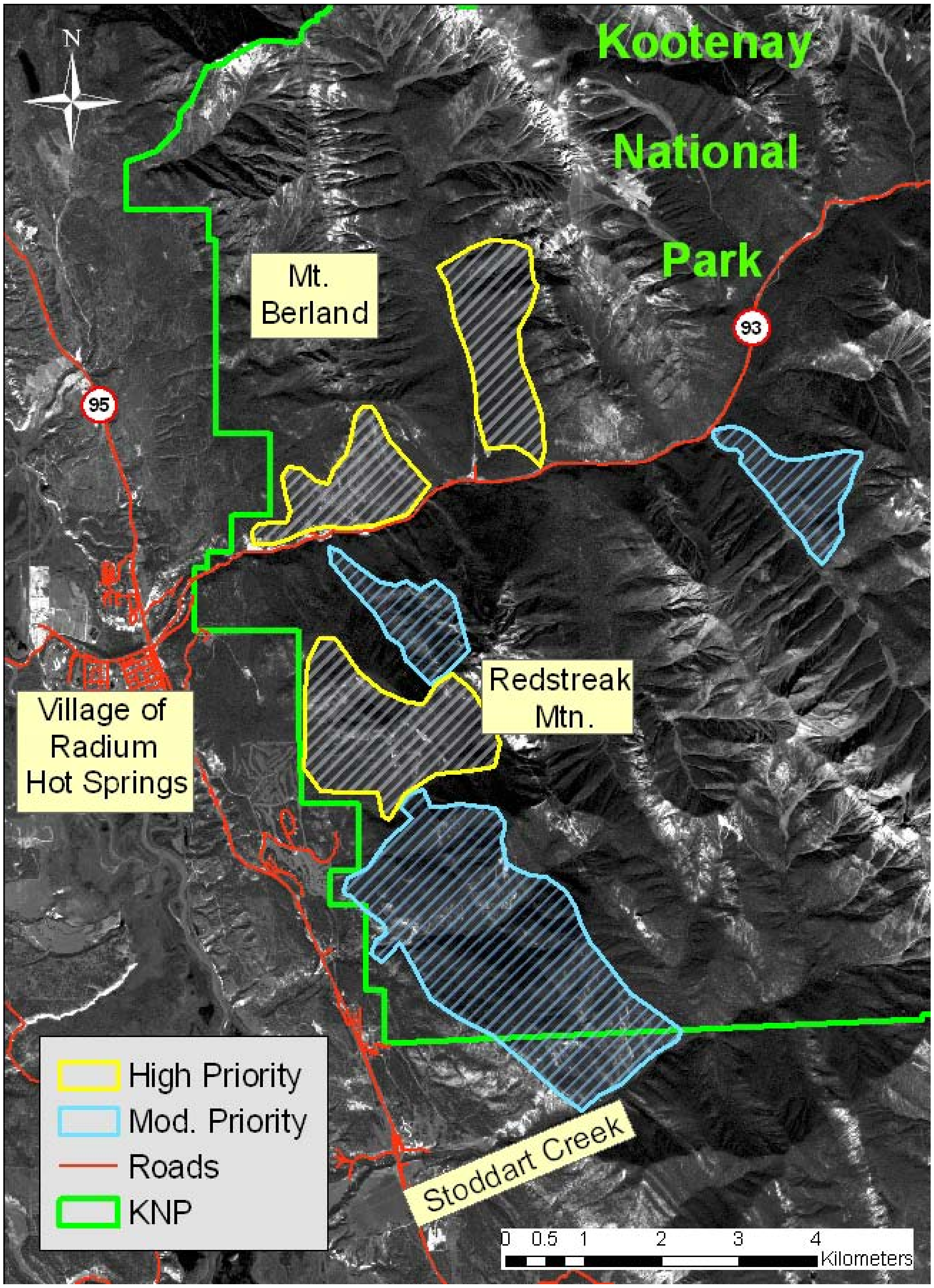

Figure 7. Map of recommended mid-elevation sites for restoration treatments.

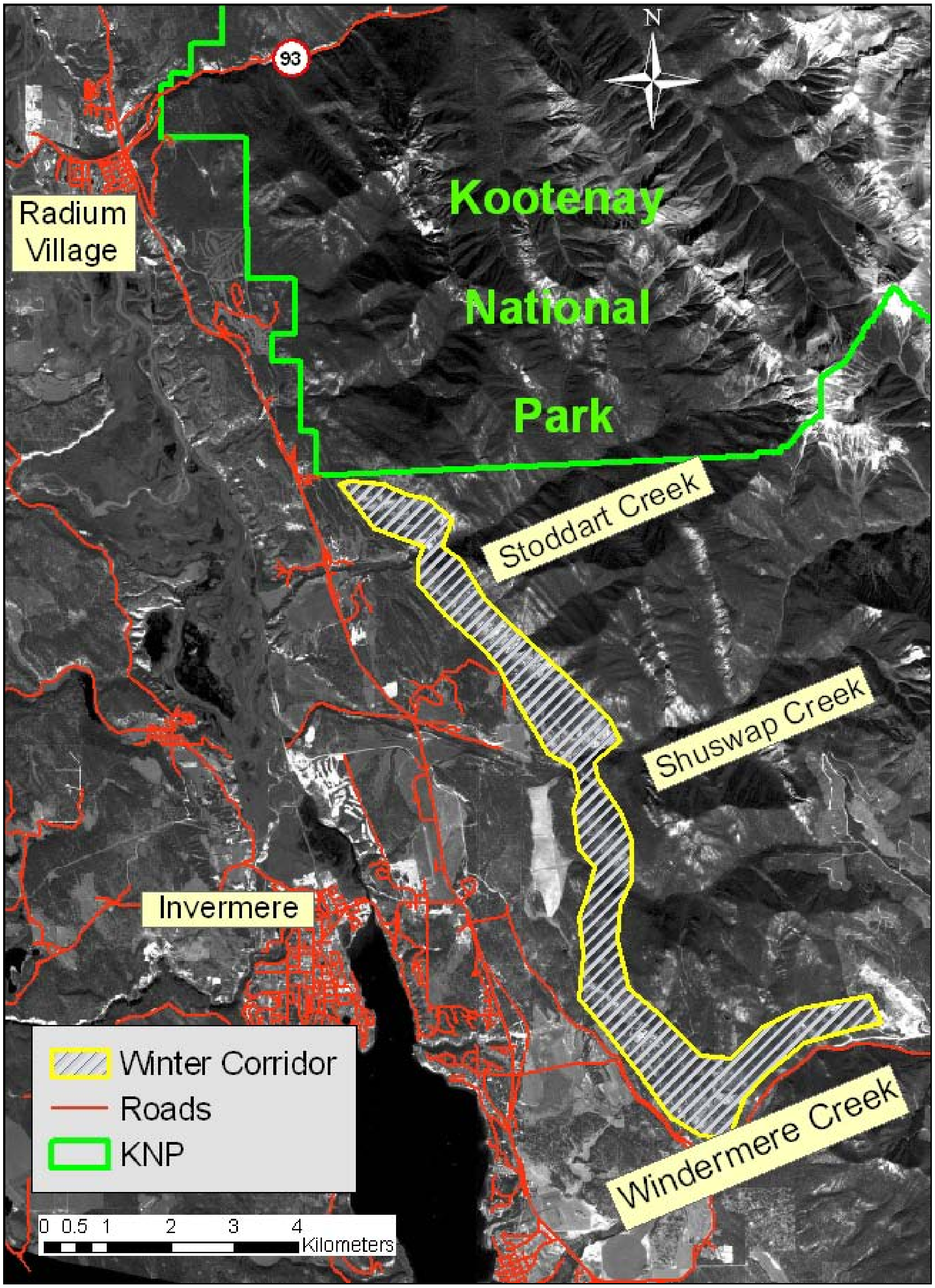

Figure 8. Map of corridor connecting historic winter ranges.

Table 1. Rating scheme for corridor values of the bighorn sheep linkage model presented in Fig. 3.

Corridor Value	Rating
0.0 - 0.2	Very Low
0.2 - 0.4	Low
0.4 - 0.6	Moderate
0.6 - 0.8	High
0.8 - 1.0	Very High

Table 2. Proportions of summer telemetry points in each class of the bighorn sheep linkage model, all study animals, 2002-2004.

	Availability	Use					
		All Telemetry Points			Movement Points		
Tremblay Model Class	Proportion of Study Area Per Class	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 3. Simplified ranking matrices for bighorn sheep proportional use of linkage model corridor value classes to available proportions of corridor value classes within individual MCP home ranges. Linkage model "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 4. Simplified ranking matrices for bighorn sheep proportional use of linkage model corridor value classes to available proportions of corridor value classes within entire study area. Linkage model “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 5. Simplified ranking matrices for bighorn sheep proportional use of linkage model 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. Linkage model “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 6. Simplified ranking matrices for bighorn sheep proportional use of linkage model corridor value classes to available proportions of corridor value classes within entire study area. Utilization was quantified based on movement points only, 2002-2004. Linkage model “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 7. Summary of compositional analysis class rankings from tables 2 through 5. “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)	Movement Points	Least Preferred Class --> Most Preferred Class						
2	MCP	.	L	<	VL	<<	H	<<	M
3	SA	.	VL	<	L	<<	H	<<	M
4	MCP	Y	L	<	VL	<	H	<	M
5	SA	Y	VL	<	L	<	H	<<	M