HIGHWAY EFFECTS ON GRAY WOLVES WITHIN THE GOLDEN CANYON, BRITISH COLUMBIA AND WOLF SURVIVAL IN THE CENTRAL ROCKY MOUNTAINS

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began in France (Keller and Pfister 1995). These underpasses were constructed for game animals, and their narrow width limited their success. The planning of faunal passages evolved to include the needs of a broader array of wildlife, and led to the construction of overpasses.

Culverts originally designed for water drainage across roads are used as crossing structures by smaller species, including some reptiles, amphibians, small mammals, and forest carnivores (Jalkotzy *et al.* 1997). Some species may prefer to use smaller culverts to cross highways, and the highway planning process should consider the needs of a variety of species.

Underpasses have been used for many species with varying success. Underpasses constructed for cougar (*Felis concolor)* and black bear (*Ursus americanus)* in Florida have been used by the target species as well as white-tailed deer (*Odocoileus virginianus)*, alligator (*Alligator mississipiensis)* bobcat (*Lynx rufus)*, and racoon (*Procyon lotor)* (Land and Lotz 1996). Some species, including white-tailed deer, elk *(Cervus elphus)*, and coyotes (*Canis latrans)* have become accustomed to using underpasses in Banff National Park. These underpasses have been far less effective for large carnivores including wolves, grizzly bears *(Ursus arctos)*, cougar, lynx, and wolverine (*Gulo gulo)* (Waters 1988). Moose *(Alces alces)* and bighorn sheep (*Ovis canadensis)* have been more reluctant than elk and deer to use the underpasses (Leeson 1996). However, observations of individuals using a faunal structure do not demonstrate its effectiveness at the population level, because the structure may be differentially filtering movements (Keller and Pfister 1995). An adequate assessment of faunal passages requires long term data collection of wildlife movements in relation to habitat quality and wildlife movement corridors in proximity to the faunal structure.

Faunal underpass structures were reported to be unsuccessful for wolves in the Bow Valley of Banff National Park by Paquet and Callaghan (1996) for several reasons. First, the placement of some underpasses did not reflect natural crossings, forcing wolves to modify travel patterns. Second, the highway and highway fencing dramatically reduced the number of natural crossings, thus depriving wolves of crossing alternatives. Third, not all wolves were willing to use underpasses, which created a differential sieve that is selective for certain wolves.

Overpasses are used for wildlife in France, The Netherlands, Germany, Switzerland, the United States and Canada. Width is the variable most closely correlated with overpass effectiveness. Overpass structures 50 - 80 m wide have effectively maintained habitat connectivity across highways in Holland and Germany for deer-sized and smaller animals (Forman and Hersperger 1996). Two 50 m wide overpasses were constructed in Banff National Park to maintain habitat connectivity for large carnivores. The effectiveness of these overpasses is yet to be determined. Preliminary results of a study comparing effectiveness of underpasses and overpasses in 4 European countries suggest that overpasses are more effective than underpasses for wildlife crossings (Keller and Pfister 1995). In contrast, Jalkotzy *et al.* (1997) summarize 2 studies that report greater success for underpasses than overpasses for the target species. Factors

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ASSESSMENT OF POTENTIAL HIGHWAY EFFECTS ON GRAY WOLF HABITAT USE AND MOVEMENTS WITHIN THE GOLDEN CANYON, BRITISH COLUMBIA

Linear developments such as roads have many effects on wildlife. Among the primary effects are direct mortality and impeded movements. Indirect effects of roads include habitat alienation, where animals abandon habitat because of nearby disturbances or are isolated from using them because of impediments to movements. Roads can cause population changes directly through mortalities or alterations in habitat and indirectly because of disturbing activities.

Scale is an important consideration in assessing effects of roads. Species that have large home ranges or long distance dispersal requirements are more sensitive to linear development effects than species with smaller area requirements. The probability of encountering a road is much greater for species that range over a broad area (Jalkotzy *et al.* 1997).

Roads are a primary source of habitat fragmentation, which confines species into networks of small patches. This condition intensifies the threat to the survival of species that originally occupied more extensive and continuous habitats. The threat of habitat fragmentation is acute for species, such as the gray wolf, which exists in low densities and occupies large home ranges. These effects combine to have local and population-level influences by altering the composition of biological communities upon which wolves are dependent, reducing prey populations, restricting movements, and limiting access to prey. Obstructing movements also increases the vulnerability of wolves to other disturbances as they attempt to learn new travel routes. In the Rocky Mountains, natural landforms and the condensed arrangement of habitats make wolves highly susceptible to the adverse effects of roads. Because roads often occur in areas preferred by wolves, they elevate the risk of death and injury for wolves. Associated effects include decreased opportunities for wolves to move freely about, displacement or alienation from preferred ranges, and interruption of normal periods of activity. In less physiographically complex environments, multiple travel routes link patches of wolf habitat. Within these environments, destruction or degradation of 1 or 2 routes is not usually critical, because safe alternative routes are available. In contrast, wolves in the Rocky Mountains cannot avoid valley bottoms or use other travel routes without affecting their fitness. Therefore, tolerance of disturbance is probably lower than in other human-dominated environments where wolves can avoid disturbed sites without seriously jeopardizing survival.

Traffic and recreational development will continue to increase within the central Rockies, stimulating a demand for additional roads, highways, and railways. Plans exist for expanding the Trans Canada Highway through the Golden Canyon, British Columbia. Considering the potential effects of the expansion on wolf movements and survival, we require a better understanding of how linear infrastructures affect movements of wolves. Herein, we summarize effects of roads on wildlife including wolves. We assess the influence of the Trans Canada Highway on habitat use, travel patterns, and dispersal capabilities of gray wolves in the Golden Canyon, British Columbia. We use a Geographic Information System (GIS) to model the connectivity, spatial distribution, availability, and quality of key habitats, report on the results of a pathway analysis for wolves moving through the Golden Canyon, and provide recommendations for mitigating highway effects. We also summarize the survivability of wolves in the central Rockies.

Habitat Fragmentation

Assessing the ecological effects of habitat fragmentation requires an understanding of the spatial pattern of the landscape (Forman and Hersperger 1996). Linear developments may alter the spatial structure of a landscape and alter its ecological processes.

Landscape pattern pertains to the distribution of resources across a broad area (Harrison and Fahrig 1995). Forman (1995) describes the landscape as a mosaic of habitat patches and corridors within the surrounding matrix (the patch-corridor-matrix model). In this model, a landscape is a kilometers-wide matrix in which a habitat patch is a relatively homogeneous, nonlinear area within dissimilar surroundings; a corridor is a linear strip of relatively homogeneous habitat differing from its surroundings and a matrix is the background mosaic of land uses or ecosystems.

Many species require more than 1 kind of community and the spatial arrangement of communities can affect the viability of populations. The entire habitat complex of a species very often consists of several partial habitats, and each particular habitat contains only 1 resource required for long term survival. Therefore, conserving populations may require more than just protecting what we perceive to be important habitats and connective linkages. In other words, the entire landscape mosaic may be of greater value than its independent parts. Preserving only what we perceive to be important may only delay a long term decline in population viability.

A major concern in the conservation of species is the loss and modification of habitat, which often results in the fragmentation and isolation of populations into small island subpopulations (Wilcove *et al.* 1986, Lovejoy *et al.* 1986, Schonewald-Cox and Buechner 1992). Isolation, destruction, and degradation of habitat are likely the most important causes of species endangerment and extinction. Although isolation and degradation are less apparent than outright destruction, they may be a more serious conservation concern (Doak 1995). Isolation and degradation often result in a slow conversion from optimal to unsuitable conditions for species' survival.

Most ecologists believe that ensured connectivity of effective habitats is an essential element of biodiversity. Persistence of populations that inhabit fragmented landscapes is thought to be greater where connectivity (among habitats, e.g., via corridors) enhances the exchange of individuals (Gilpin 1987). All else being equal, continuous suitable habitat supports more individuals of a species than does fragmented (discontinuous) habitat. In unaltered environments large mammals move between valuable habitat in response to seasonal food availability and stages in their life cycle. As habitats shrink, insular patches are created with limited connections. These patches become further subdivided by the presence of human facilities (physical impediments) that displace wildlife from traditional paths, force them to adopt alternate routes, or lead to permanent abandonment of habitat that was once contiguous or connected by the route. Typically, inhospitable linkage corridors limit movement among the remaining habitat patches. Thus, patches of habitat that can potentially support wildlife are rendered unavailable.

Much research over the past 2 decades has shown the importance of spatially patchy environments in influencing population dynamics. Of contemporary interest has been the relationship between the dynamics of subpopulations at local and regional scales, considering especially the extent to which natural populations persist as a set of linked subpopulations, each of which is prone to be unstable (Harrison 1991, see Doak 1995). Such persisting metapopulations are sensitive to the number of subpopulations and ease of movements between them. Thus, any reduction of habitat size or fragmentation of habitat can disrupt the entire system, either by reducing the number of subpopulations below some critical level required for the metapopulation to persist, or by interfering with the movements required to link the locally unstable subpopulations.

Wildlife Movement Corridors

Many ecologists believe we can reduce the adverse effects of human disturbance with the maintenance or provision of landscape linkages among subpopulations. Much recent literature in conservation biology supports the idea of providing "corridors" of suitable habitat between population centres (Forman and Godron 1986, Harris and Gallagher 1989, Noss 1993). Corridors provide travel lanes to accommodate daily, seasonal, and dispersal movements from 1 large habitat block to another. In theory, corridors greatly reduce the possibilities of inbreeding and chance environmental catastrophes by providing opportunity for the introgression of new genetic materials and the exchange of individuals from source populations.

Wildlife movement corridors facilitate the biologically effective transport of animals between larger patches of habitat. Corridors are linear habitats whose primary wildlife function is to connect 2 or more significant habitat areas. Although corridors may have intrinsic wildlife value, their salient value is that they connect more substantive patches of habitat. Corridors generally are used to maintain connectivity among formerly contiguous habitat, not to connect naturally isolated units. Conservation theory suggests that by protecting landscape linkages between the remaining patches of habitat we can prevent or forestall the future loss of species, but at population levels lower than in pristine conditions. When human activities threaten to disrupt natural patterns of wildlife movement, we must take measures to avoid impacts or create a wildlife movement corridor out of another area.

We can categorize most species into 1 of 2 types of corridor users. "Passage species" need corridors to allow individuals to pass directly between 2 areas in discrete events of brief duration, e.g., dispersal of a juvenile, seasonal migration, or moving between parts of a large home range. For passage species, corridors may function as transitional habitats that provide only those ecological services and resources required when individuals move between patches. Large herbivores and medium to large carnivores are typically passage species, as are many migratory animals. These species do not have to meet all of their life requirements within the corridor, but the corridor must provide conditions that motivate the animal to enter and use the corridor. In other cases, corridors may comprise habitats that are critical for day to day survival. In contrast to passage species, "corridor dwellers" need several days to several generations to pass through the corridor (e.g., plants, insects, amphibians, small mammals).

In pristine conditions, wildlife movements are the product of the individual or group's search for life requisites. Species adaptations, population size, demographic structure, interspecific relations, the abundance and distribution of food, availability of habitat for security, physiography, climate, disturbance activities, and wildlife management actions affect movements. Moreover, some movements might be learned behaviours. In unaltered environments, large mammals move between preferred habitats in response to seasonal forage availability and stages in their life cycle. For example, strong evidence suggests that long-lived species such as wolves or bears (*Ursus sp.*), pass on knowledge of traditional travel routes from generation to generation (Mech 1970, Curatolo and Murphy 1986, Thurber *et al.* 1994, S. Herrero pers. commun., S. Minta pers. commun., P. Paquet unpublished data).

Ecological factors that determine the availability and quality of wildlife corridors are dynamic and we can expect these elements to change seasonally and among years. Corridors appear to follow "paths of least resistance" (e.g., topography and habitat) that have greatest visibility and fewest obstructions. Many species establish corridors along routes characterized by low disturbance and escape terrain. Observed travel routes for wolves include human trails, wildlife trails, ridges, open edges, riparian valley bottoms, shorelines, open forest, and roads.

Major river and creek valleys, and interconnecting passes, function as local and regional travel corridors (Paquet 1993).

Studies have shown that the width of a corridor is particularly important to allow for unimpeded movement of wildlife. Whereas narrow corridors may work well for small mammals and some bird species, corridors several kilometres in width may be necessary for use by large mammal species such as wolves (Harrison 1992, Merriam and Lanoue 1990). The width required for a corridor to be effective may depend upon its length. Effective corridors may be narrow if they are short enough that dispersers may pass through without foraging.

In human-dominated landscapes, the availability and quality of movement corridors are limited by competing land uses that may directly or indirectly conflict with species requirements. The presence of human facilities (physical impediments) along natural routes may displace wildlife from traditional paths, force them to adopt alternative routes, or lead to permanent abandonment of habitat that was once contiguous or connected by the route. Obstructions to movements may be physical or psychological, consisting of physical impediments, sensory impediments, and the loss of forest cover in travel corridors and in adjacent areas. For example, divided highways 90 m wide were considered the equivalent of bodies of water twice as wide in obstructing movements of small forest animals (Oxley *et al.* 1984). Concrete embankments, highway fences, urban communities, and motor vehicle traffic were barriers to cougar movement in Southern California (Beier in press, via K. Heuer pers. commun.). Many animals perceive darkness as a form of cover, travelling in open areas during the night. Wolves in Italy, for example, living in a densely populated and highly fragmented landscape shifted to nocturnal behaviour to avoid humans (Boitani 1982). Night lighting was identified as factor that compromised the potential effectiveness of a corridor for cougars in Southern California (Beier in press, via K. Heuer pers. commun.).

Effects of Roads on Wildlife

Jalkotzy *et al.* (1997) subdivide effects of linear developments such as roads into 6 categories: individual disruption, habitat avoidance, social disruption, habitat disruption or enhancement, direct and indirect mortality, and population effects. Typically, the road itself does not disturb most vagile species. Traffic volumes and associated human activities are the disturbance factors.

Individual disruption occurs when disturbance caused by the road results in animals altering their movement or use patterns next to the road. A more acute effect of roads is avoidance of adjacent habitat in response to the disturbance. Social disruption occurs when the road disturbance causes changes to the social structure of a population, such as differential mortality of population classes. Roads may cause habitat disruption by fragmenting contiguous habitat or may enhance habitats for species that prefer edges. They may act as mortality sinks, as with highway mortality or may be an indirect contributor to wildlife mortality by providing greater access for hunters, poachers or predators. Roads may cause direct mortality of wildlife through wildlife-vehicle collisions. Roads may ultimately contribute to population effects, primarily by causing a reduction in the population (Jalkotzy *et al.* 1997).

Highway traffic noise has potentially serious effects on wildlife (Alexandre *et al.* 1975, Larkin 1996). Such effects are rarely considered during the road development planning process, however. The effects of anthropogenic noise on wildlife are situational and species-dependent, and the effects vary from undetectable to serious (Larkin 1996). Risk of hearing damage from long-term exposure to continuous traffic noise is species-specific. Besides hearing damage, noise effects may be exhibited in behavioural changes. Shifts in behaviour that may result in decreased survival include avoidance of high quality habitat next to noise sources and reduced time spent feeding with coincident energy depletion. Automobile noise can also interfere with animal communication essential for reproduction. Much research has been conducted on habituation of wildlife to noise, and involves decreased responsiveness after exposure to repeated noises (Larkin 1996).

Effects of Roads on Wolves

Highway mortality is an important cause of wolf mortality in the central Rockies, and there is accumulating evidence of habitat loss, fragmentation, and degradation related to roads (Purves *et al.* 1992, Paquet 1993, Paquet and Callaghan 1996, Paquet *et al.* (1996), Paquet *et al.* in press, Callaghan in progress). Ensured connectivity of quality habitats is important for survival of large carnivores (Beier 1993, Paquet and Hackman 1995, Doak 1995, Noss *et al.* in press), especially for those that face a high risk of mortality from humans or vehicles when travelling across settled landscapes (Noss 1992, Beier 1993).

Besides functioning as a direct mortality source, roads may also be physical or psychological impediments to wolf movement. Studies in Wisconsin, Michigan, Ontario, and Minnesota have shown a strong relationship between road density and the absence of wolves (Thiel 1985, Jensen *et al.* 1986, Mech *et al.* 1988, Fuller 1989). Wolves generally are not present where the density of roads exceeds 0.58 km/km^2 (Thiel 1985 and Jensen *et al.* 1986, cf. Fuller 1989). Landscape level analysis in Wisconsin, Minnesota, and Michigan found mean road density was much lower in pack territories (0.23 km/km^2 in 80% use area) than in random non pack areas (0.74 km/km^2) or the region overall (0.71 km/km^2). Few areas of use exceeded a road density of >0.45 km/km^2 (Mladenoff *et al.* 1995). Road density was the strongest predictor of wolf habitat preference out of 5 habitat characteristics and 6 indices of landscape complexity. Notably, territories of radio-collared packs were not bisected by any major federal or state highway (Mladenoff *et al.* 1995).

In Minnesota, densities of roads for the primary range, peripheral range, and disjunct range of wolves were all below a threshold of 0.58 km/km². Along the Ontario-Michigan border, distribution of breeding packs occurred only in Ontario, where road densities are low. High human densities, represented by road densities of > 0.6 km/km², were believed to be a barrier to wolf dispersal into Michigan (Jensen *et al.* 1986). These results, however, probably do not apply to areas on which public access is restricted. Mech (1989), for example, reported wolves using an area with a road density of 0.76 km/km², but it was next to a large, roadless area. He speculated that individuals dispersing from the adjacent roadless area compensated for excessive mortality experienced by the wolf population in the roaded area.

The absence of wolves in densely roaded areas has several plausible explanations. Wolves may behaviorally avoid densely roaded areas depending on the type of use the road receives (Thurber *et al.* 1994). In other instances, their absence may be a direct result of mortality associated with roads (Van Ballenberghe *et al.* 1975, Mech 1977, Berg and Kuehn 1982). Besides fragmenting and consuming critical habitat, roads provide access to remote regions, which allows humans to deliberately, accidentally, or incidentally kill wolves (Van Ballenberghe *et al.* 1975, Mech 1977, Berg and Kuehn 1982).

The response of wolves to road type and human presence at the boundaries of Kenai National Wildlife Refuge, Alaska, was examined in a study of radio-collared wolves (Thurber *et al.* 1994). Wolves avoided oilfield access roads open to public use, yet were attracted to a gated pipeline access road and secondary gravel roads with limited human use. Thurber *et al.* (1994) speculated that roads with low human activity provide easy travel corridors for wolves. The response of wolves to a major public highway was equivocal. Wolf absence from settled areas and some roads was thought to have been caused by behavioral avoidance rather than direct attrition resulting from killing of animals. In Montana, Singleton (1995) found that wolves preferred areas 0.5-1 km from open roads for travel routes. He speculated that wolves selected areas within this margin because of the greater probability of finding wintering ungulates.

The effects of highway traffic noise on wolves have not been researched, but we should not overlook them. Wolves use sound in detecting prey, and use vocalizations for inter and intra-pack communication. In particular, vocalizations between pack members are an important means of coordinating a search for prey. In the central Rockies, we detected pack vocalizations regularly near den sites far from roads, whereas we rarely detected vocalizations near den sites close to the Trans Canada Highway (Paquet and Callaghan unpublished data).

Paquet and Callaghan (1996) assessed the barrier effect of the Trans Canada Highway (TCH), the 1A Highway, the Bow River and the Canadian Pacific Railway (CPR) on wolves during winter in the Bow River Valley of Banff National Park, Alberta between 1989 and 1992. Data was collected via snow tracking and radiotelemetry monitoring. Wolves avoided crossing the TCH 80% of the time that they attempted to cross. In contrast, wolves avoided the 1A

Highway 15% of the time, the Bow River 14% and the CPR 11% of the time that they attempted to cross. The unfenced portion of the TCH is a serious barrier that wolves seldom crossed; only 14 crossings of the TCH in 4 years were inferred from radiotelemetry. Several attempts to cross the TCH resulted in death or injury by collision with vehicles (n = 9). A habitat effect could not be attributed to the low incidence of TCH crossings.

Paquet and Callaghan (1996) also assessed the permeability of 2 wildlife underpasses in the Bow River Valley to wolves. The Healy underpass, which is an open span construction (13 m wide by 4 m high), was avoided by wolves 47% of the time they attempted to use the structure. The Five-Mile Bridge, a highway bridge (140 m wide by 20 m high), was avoided 12% of the time the wolves attempted to use it. Solitary wolves and groups of wolves appeared to respond differently to the underpasses, although the difference was not statistically significant. We recorded a significant decline in the proportion of approaches to complete passes through the Healy underpass for over a year following the death of a breeding female identified as a dominant pack member. This suggests that a learned component accompanies the success rate of underpasses, and that personalities of pack leaders influence the permeability of underpasses for wolves.

Mitigating Road Effects

Engineers and biologists have developed a wide array of mitigative techniques to reduce the potentially negative effects of roads. Mitigative techniques vary in their efficacy, and rarely compensate fully for road effects (Keller and Pfister 1995). The 2 primary effects of roads for which mitigations are attempted are habitat fragmentation and direct mortality. The most acute effects of roads occur at a landscape scale, and thus approaches should attempt to mitigate these effects. Knowledge of local and regional wildlife movement corridors is essential for mitigating effects at a landscape scale. Species that benefit the most from mitigative approaches are those that experience a high rate of mortality due to collisions with vehicles, have large home range requirements and display dispersal or migratory behaviour.

Fencing, underpasses, overpasses, elevated highways, and optical and auditory warning devices have been used to mitigate road effects. Researchers have not evaluated the effectiveness of most of these techniques (Jalkotzy *et al.* 1997). Fencing has been used extensively to reduce wildlife-vehicle collisions. Adequate fencing prevents wildlife from reaching habitat on the opposite side of the highway, thus effectively fragmenting the habitat. Faunal crossings are required to mitigate the barrier effect of fencing, and regular fence maintenance is imperative to prevent wildlife from using the highway corridor (Jalkotzy *et al.* 1997). Vegetation and topography can play an important role in reducing highway traffic noise (Alexandre, *et al.* 1975).

A variety of faunal passages, including culverts, underpasses, and overpasses have been used to mitigate the barrier effect of roads. The construction of passages specifically for wildlife began in France (Keller and Pfister 1995). These underpasses were constructed for game animals, and their narrow width limited their success. The planning of faunal passages evolved to include the needs of a broader array of wildlife, and led to the construction of overpasses.

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Landscape connectors are overpasses or underpasses wide enough to provide linkages for all natural movements across the landscape. These structures allow the passage of a broad spectrum of wildlife, natural fires, wind dispersing seeds, water, and nutrient flows (Forman and Hersperger 1996). Two such overpasses exist in Switzerland, and are 140 m and 200 m wide (Keller and Pfister 1995). Planning for future highway expansion projects in Holland and Switzerland include the consideration of tunneling the highway along extended sections to maintain landscape linkages (Forman and Hersperger 1996). In the Bow Valley of Banff National Park, the most effective faunal passage is a bridge structure that is 140 m wide and 20 m high. This Trans Canada Highway bridge spans the Bow River, the rail line and a secondary highway. Elevated sections of Interstate Highway 70 near Vail, Colorado have conferred beneficial effects to wildlife. Such highway designs may be feasible for other highway projects whose objective is to maintain habitat connectivity across the landscape.

An understanding of the spatial pattern of the landscape is critical for assessing and mitigating the ecological effects of linear developments such as roads. Maintaining landscape connectivity is a critical element of a highway project in a landscape that provides for wildlife movements. Successful faunal passages require careful consideration of the type and placement of the structure.

METHODS

Study Area

We developed wolf movement and highway crossing mitigation models for the Golden Canyon, which is situated west of Yoho National Park at 51°, 24' N and -116°, 65' W and east of Golden, British Columbia at 51°, 30' N and -116°,94' W (Figure 1). The study area is approximately 156 km^2, and includes the Golden Canyon and approximately 23 km of the Trans Canada Highway. The Golden Canyon forms part of the Kicking Horse River drainage and is part of the continental ranges of the central Rocky Mountains.

Topographic features of the study area include rugged mountainous terrain, narrow, steep-walled tributary valleys, and a broad, canyon-like main valley. The main tributary is oriented in an east-west trend. Elevations range from 800 m to 2700 m. Most vegetation occurs along the valley bottoms and lower mountain slopes and shoulders.

The climate is continental, characterized by cold, moist, and snowy conditions. The winters are typically cold and long, and summers short and cool. Mean annual temperature ranges

Five-Mile Bridge
Ten-Mile Bridge
N
W
E
S
0
1.25
2.5
Kilometers
en Canyon Wildlife Movement Study Area
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rea
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from -2 °C to +2°C (Meidinger and Pojar 1991). Elevation and topography throughout the study area influence the regional climate and vegetation communities and thus contribute to a highly variable climate. The complex climate regimen is evidenced by the distribution of plants and animals in the study area (Janz and Storr 1977).

Precipitation increases with increasing elevation. Mean annual precipitation for the area ranges from 491 mm at 1000 m above sea level in Golden (British Columbia Ministry of the Environment) to 687.7 mm at 4100 m above sea level at the Yoho National Park Warden Compound (Yoho National Park Warden Service). The snowfall regimen within the study area exerts a significant ecological influence on the study area. Many alpine areas remain snow-covered for 10 months a year; montane areas have snow cover for 6 or 7 months a year. Snowfall can vary dramatically from year to year. Mean annual winter snowfall varies from 184 cm in Golden (British Columbia Ministry of the Environment) to 230.5 cm at the Yoho National Park Warden Compound (Yoho National Park Warden Service). Maximum snow depths occur in November-December and maximum snow crusting occurs in March-April.

The Golden Canyon lies in the Engelmann spruce-subalpine fir ecological zone (Meidinger and Pojar 1991). Engelmann spruce (*Picea engelmannii)* and subalpine fir *(Abies lasiocarpa)* dominate the climax forest canopy. Engelmann spruce typically dominates the lower elevation canopies and subalpine fir typically dominates the moist and upper elevation canopies. Lodgepole pine(*Pinus contorta)*, limber pine *(Pinus flexilius)*, alpine larch (*Larix lyallii)*, Douglas fir (*Pseudotsuga menziesii),* western red cedar *(Thuga plicata*), and western hemlock *(Tsuga heterophylla)* also occur within the Egelmann spruce-subalpine fir ecological zone. Avalanche slide paths are common in the study area (Meidinger and Pojar 1991), where vegetation consists of a mosaic of shrub and herbaceous species, including slide alder (*Alnus crispa spp.)* and cow parsnip *(Herqcleum lanatum).*

A portion of the Trans Canada Highway occurs throughout the Golden Canyon. The highway consists of single lanes interspersed with passing lanes. Monthly traffic volumes range from 15, 298 to 139, 862. Annual traffic volume was 1, 438, 874 in 1997 (Parks Canada unpublished data).

The Friction Model

We constructed a probabilistic model of wolf habitat use and movements using biological information collected from studies of wolf ecology in the Rocky Mountains (Cowan 1947, Carbyn 1974, Huggard 1991, 1993a, 1993b, 1993c, Paquet 1993, Weaver 1994, Callaghan in progress). The model relates the movements and habitat use of wolves to availability of prey, physiography, and human activity. The model is spatially explicit and runs in a Geographical Information System. We euphemistically call the model the "friction model" because it quantifies the resistance of the landscape surface to movement of wolves. We emphasize that many extraneous factors contribute to a variance in behaviour of individual wolves. Because ecologists have developed no reasonable expression of those differences, we apply this model at the pack level.

The Central Rockies Wolf Project and Geomar developed the original friction model for the Bow Valley Study (Paquet *et al.* 1996). The model assessed the effects of human activity on wolf movements and persistence in the Bow Valley of Banff National Park. The model was developed using snow tracking and radiotelemetry data collected in Banff National Park between 1989 and 1993.

The friction model presented herein is an empirically-derived simulation, which quantitatively assesses the probability of a wolf pack using and moving through the Golden Canyon, British Columbia during winter. The model simulates how wolves may use the valley by assessing the probability and suitability for movements by wolves within a specific landscape window. The simulation is based on known relationships between wolf movements and factors such as elevation, slope, aspect, terrain ruggedness, vegetation cover, and prey habitat quality. Each simulation predicts the "pathway of least resistance" and estimates the "cost" of moving along the preferred route. Cost is an amalgamation of energetic expenditures, attraction to preferred habitats (e.g., slope, aspect, prey availability), and level of security (e.g., exposure to human activities and facilities).

We used biophysical coefficients to create a landscape surface that reflects the effectiveness of habitat to support wolves without the presence of humans. The probability that a wolf will use a certain habitat or travel a particular path is expressed as a function of behavioural characteristics, physical environment, and distribution of resources (water, cover, prey). Included are the effects of physiography on the distribution, size, geometry, and juxtaposition of habitat patches and behavioural responses of wolves to the natural physical environment. The model output displays graphically the probability of any given pixel being of high survival value to the wolves.

Habitat Model

To develop a wolf habitat suitability model for the study area, we used the methodology of Paquet *et al.* (in press), which we summarize in the following paragraphs. We developed a wolf habitat suitability model for the central Rocky Mountains based on 1, 350 radiotelemetry locations collected between 1989 and 1997, after removing data points associated with den sites. We tested the model using an independent set of 1, 000 radiotelemetry locations collected over the same period. We divided data into 2 seasons: the summer season occurred between April 1 and September 30 and the winter season occurred between October 1 and March 31. These seasons correspond with the summer and winter activity patterns of wolves.

We developed density maps for summer and winter wolf habitat use in the central Rockies. We assumed that density of radiotelemetry locations is positively correlated with wolf habitat quality. To test the telemetry data for optimal size of the experimental units (window), we built 15 summer and winter density location (DL) maps, using a variety of window sizes. We conducted an interpercentile analysis (SPSS) to determine the window size that provides the best spread of values. The best spread of area-weighted density values provides the greatest discriminating power among low, moderate, and high concentrations of wolf telemetry locations. To avoid potential bias in the analysis due to selection of the point of origin of the density maps, we repeated the interpercentile analysis after shifting the point of origin of the density maps by half a window size to the south, east, and southeast. We determined that the point of origin did not bias the testing for optimal window size. A window size of 0.5 km X 0.5 km for the winter model and 0.6 km X 0.6 km for the summer optimized the spread of the density of radiotelemetry fixes. We then classified the DL maps into the following discrete density classes: no locations; low DL; Moderate DL; high DL.

For each of the DL classes, the following biophysical parameters were extracted: terrain ruggedness, elevation, aspect, hiding cover, and prey habitat quality. We used a Digital Elevation Model (DEM) to derive information on elevation and aspect. We developed a Terrain Ruggedness (TR) index of the central Rockies using a moving window technique. TR is an index capturing complexity of terrain, and was derived using the following equation:

$$TR = (De\ Ac)/(De+Ac),$$

where De = density of contour lines within a given window and Ac = an index of aspect variability within a given window. We generated a prey habitat suitability layer and a hiding cover layer using an Ecological Land Classification System (Holroyd and Van Tighem 1983) and wolf prey preference data from kill sites and scat analyses (Paquet and Callaghan unpublished data).

We examined the distribution of wolf locations in relation to the biophysical parameters using polytomous logistic regression (North and Reynolds 1996, SAS, SPSS). We also used univariate statistics to determine pairwise comparisons of all biophysical parameters to determine the relative contribution of each parameter on the model. Parameters were ranked according to their contribution. The biophysical associations were tested for predictive reliability using independent data. Our analysis produced a strong, statistical model for summer and winter seasons. From this model, we generated a probability surface layer, which shows continuous probability values expressing the likelihood of each 30 m X 30 m pixel within the study area of being suitable wolf habitat.

The Golden Canyon Habitat Suitability Model was developed using the above methods for winter only (Figure 2). To apply the wolf habitat suitability model to the Golden Canyon study area, we developed a 1:20,000 Digital Elevation Model of the area based on the elevation points and break lines provided in the British Columbia TRIM digital land information data sets. From the DEM, we derived elevation and aspect information. We used the British Columbia Ministry of Forests forest cover data to derive information on hiding cover and prey habitat quality.

Given very limited information on the distribution of ungulates in the study area, we developed the map of elk (*Cervus elaphus)* distribution by using a set of decision rules solicited from wildlife experts (D. Pole and P. Paquet, pers. comm.), rather than from empirical data collected in the study area. Elk were chosen as the focal prey species because they are the primary food source for wolves in the central Rockies (Paquet 1993) and because wolf and elk habitat use overlaps by >90% (Paquet unpublished data). Table 1 summarizes the decision rules applied to the construction of the four-class elk habitat-suitability map. "Open areas" were defined as 100 meter wide "edge" zones around and into openings in the forest.

Table 1. Decision rules used to generate a four-class elk habitat suitability map. Expert advice on elk habitat use provided by D. Pole and P. Paquet.

	SUITABILITY			
ATTRIBUTE	None	Low	Moderate	High
Elevation (N-facing slopes)	>1400 m	<1400 m	<1400 m	<1400 m
Elevation (S-facing slopes)	>1200 m	<1200 m	<1200 m	<1200 m
Slope angle (%)	>30%	<30%	<30%	<30%
Vegetation	Any type	Conifer	Open areas	Deciduous

Movement Model

In modelling wolf movement, we made 2 fundamental assumptions inferred from previous research in the Bow Valley watershed (Paquet 1993, Paquet *et al.* 1996, Paquet *et al.* in press):

- Wolf habitat selection as defined by the Habitat Model equates with wolf habitat selection for movement (i.e., the spatial juxtaposition of habitat patches of various qualities strongly influences movement);
- Wolves are aware of the presence of all human land use developments.

We developed a deterministic movement stimulus to model potential wolf movement corridors in the Golden Canyon area. The deterministic mode of movement implies that wolf packs move through the landscape determined to go from point A to point B. Simulated wolves are placed into the rasterised landscape and moved to a target area.[1] A pathway analysis is used to simulate movements and calculate the cost of travel. Cost is the summation of resistance levied by individual pixels. Higher costs reflect increased environmental resistance to movement. Simulated wolves select travel routes that provide an optimal combination of security, habitat quality, and energetic efficiency. Conversely, wolves avoid human facilities and activities, terrain that is difficult to negotiate, and habitat of low quality. For example, wolves avoid deep snow, are attracted to concentrations of prey, and avoid the Trans Canada Highway.

For the "pristine" model run (Figure 3), we developed the wolf "friction" surface (a surface expressing, in relative terms, ease of movement through the landscape) as the reciprocal of the winter habitat probability values (e.g., we would assign areas of low habitat quality a relatively high friction value). We modified this surface to reflect the influence of the Kicking Horse River and the Trans Canada Highway on wolf movement. We used crossing coefficients developed for the Bow River and the portion of TCH that runs through Banff National Park as modifiers (Paquet *et al.* 1996).

Initially, we selected 2 movement entry points, at the east end of the study area, on either side of Trans Canada Highway and calculated a series of equivalent "cost" surfaces. Cost surfaces express cumulative cost of movement relative to the point of entry, calculated in 8 directions with the search radius equal to the extent of the study area. Diagonal directions increased a cell's friction value by 41%. For each of the cost surfaces, we assigned 2 exit points at the west end of the study area (on both sides of the TCH) and calculated the routes of least resistance (pathways) connecting the point of entry with exit points (Figure 3).

Preliminary evaluation of the computer simulated routes indicated minor differences between the routes generated from either of the entry points. Therefore, we focussed our attention on a single entry point that corresponded to the more likely entry position into the study area (i.e., the point within favourable winter habitat, at the valley bottom). We conducted multiple runs of the model, each time disabling the pathway generated in the previous simulation. This allowed us to generate the primary, secondary, and third order pathways that, while reflecting decreasing probability of route selection, allowed us to delineate a wolf "movement corridor" through the Golden Canyon area. Finally, we plotted the simulated least resistance pathways on the map to identify potential "conflict" areas where a crossing of the highway is more likely to occur (Figure 4 - 6).

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[1]In the simulation, we "force" wolves to complete a travel assignment. In reality, human activity often deters wolves from moving through an area. However, we have not identified how much disturbance wolves will tolerate. Forcing wolves through an area allows us to attach a cost to routes we know wolves will not use, thus proving insights into tolerance.

In modelling wolf lateral movement (across the valley), we assumed that the crossings are likely to occur in locations where high quality wolf or elk habitat spans either side of the highway (Figure 7 - 9). We tested the TCH crossing points against crossing location data collected for ungulates in the Golden Canyon between December 1997 and March 1998.

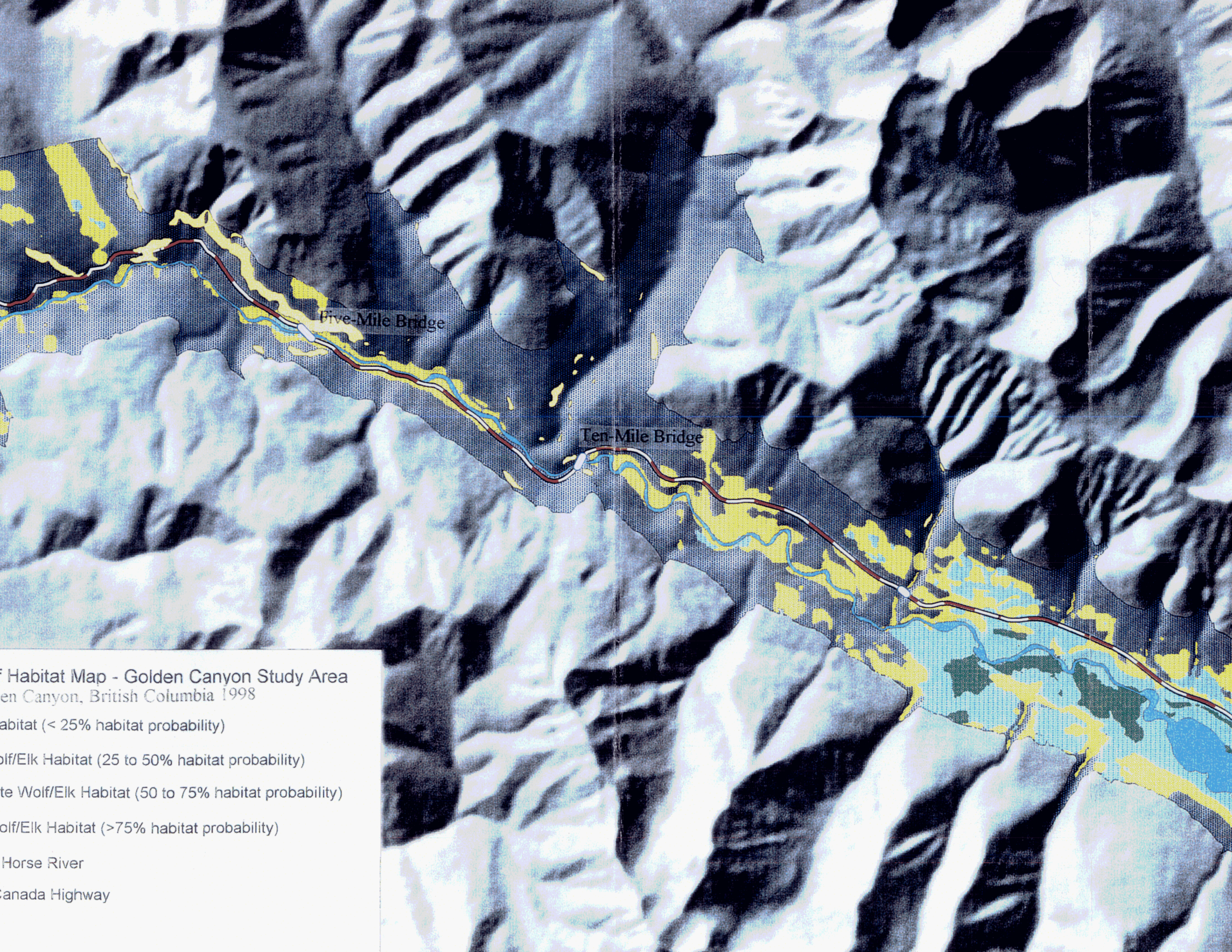
RESULTS

The Wolf Habitat Suitability Model shows that high quality wolf habitat is limited in the Golden Canyon (Figure 2). The canyon's steep terrain and narrow walls influence the availability of habitat for wolves and elk. Ninety-two per cent of wolf telemetry locations (n = 3, 350) in the Bow Valley were on slopes below 20° and 95% of locations occurred below 1,850 m (Paquet and Callaghan unpublished data). Steep rock, ice-covered slopes, and deep snow, which are associated with higher elevations, are avoided by wolves and their prey. The highest quality habitat within the study area occurs along the river flats next to Yoho National Park, and along the benches near the town of Golden.

Preliminary evaluation of the simulated routes through the study area, where wolves had an option of starting at the east end of the study area on either side of the TCH, indicated small differences between the routes generated from either of the entry points (Figure 3). The simulated pathway follows the best available habitat through the canyon. The pathways originated on either side of the TCH, where the valley bottom is broad, then pinched into 1 pathway where the valley bottom is narrow, and split into 2 pathways where the valley broadens on the west end of the study area. This suggests that the narrow valley bottom limits travel options for wolves travelling between Yoho National Park and the Columbia Valley.

The primary least resistance pathway shows 2 TCH crossings (Figure 4 – 6). Two of the crossings occur near bridges over the Kicking Horse River; the other crossing occurs at the west end of the study area, close to high quality elk habitat. The secondary and tertiary least resistance pathways show 3 and 4 TCH crossings (Figure 4 – 6). All pathways are near the TCH and Railway because these structures are situated close to the valley bottom. Moreover, the highway and railway likely follow topographically efficient routes and gradients.

In modeling wolf lateral movement (across the valley), we assumed that crossings are likely to occur in locations where high quality wolf or elk habitat spans the highway. Computer simulations of lateral movement showed a series of wide zones of increased crossing probabilities (Figures 7 - 9). Eight crossing zones for wolves and elk were established throughout the study area. We tested the crossing points against crossing location data collected for ungulates in the Golden Canyon between December 1997 and March 1998. Fifty-six per cent of ungulate crossings observed (n = 25) occurred within the zones predicted by the model.



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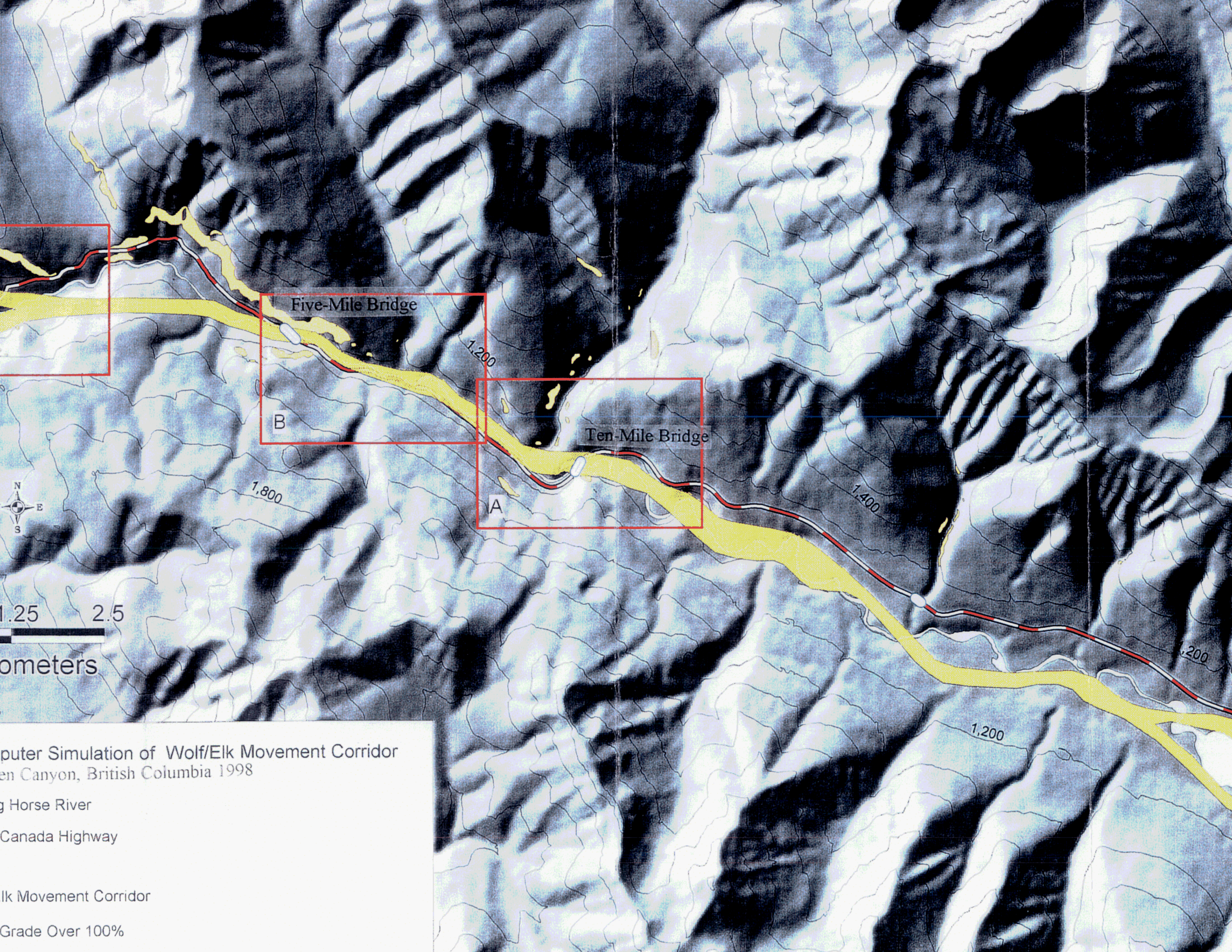

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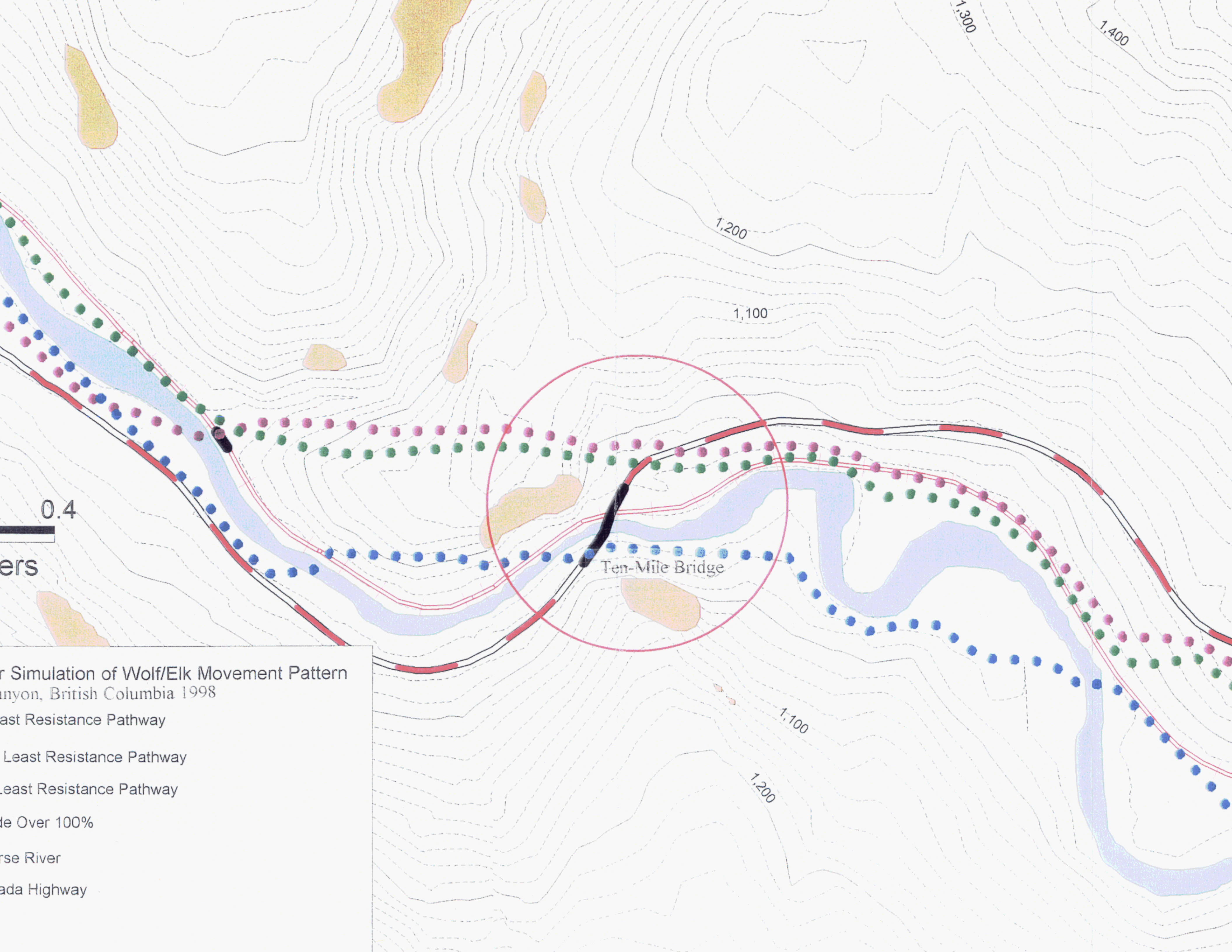

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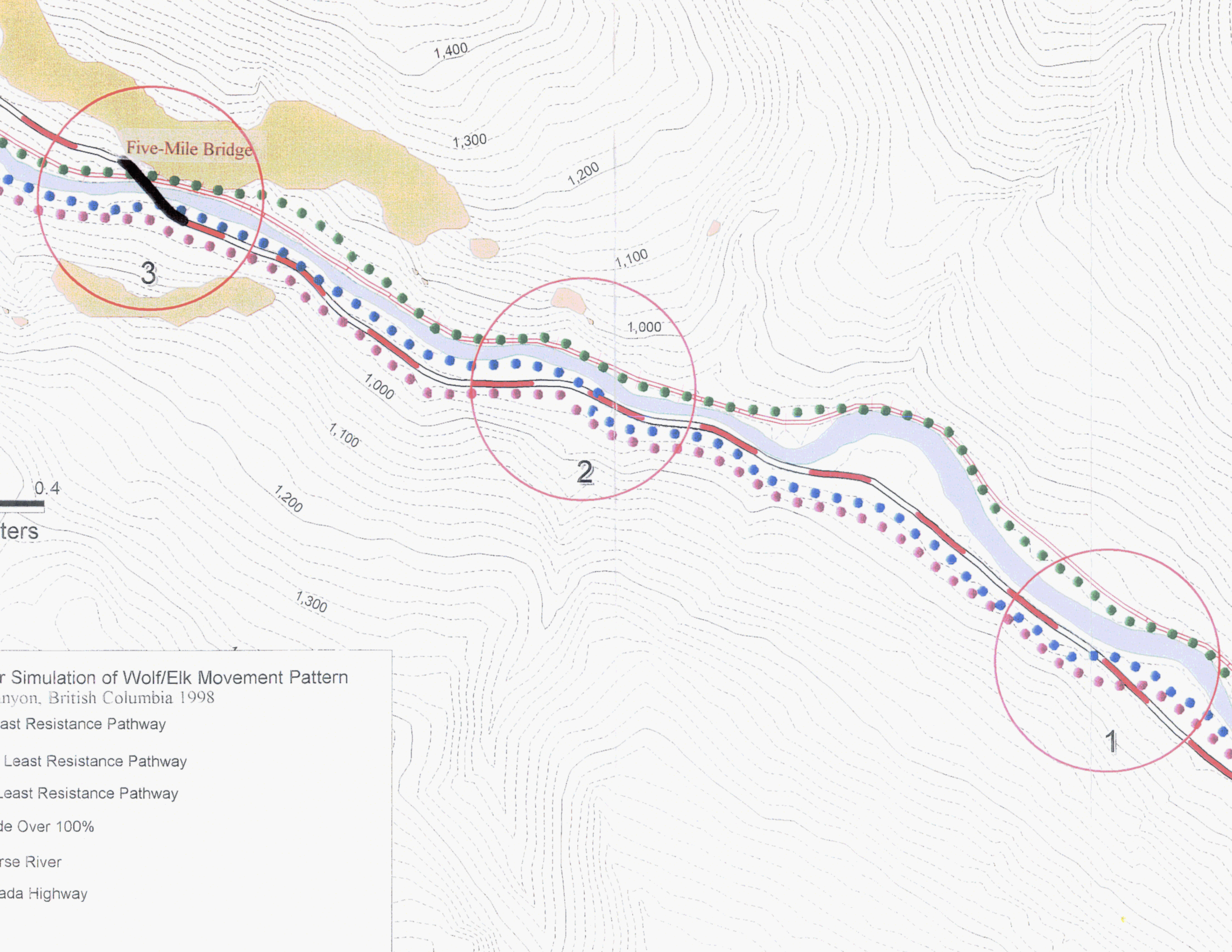

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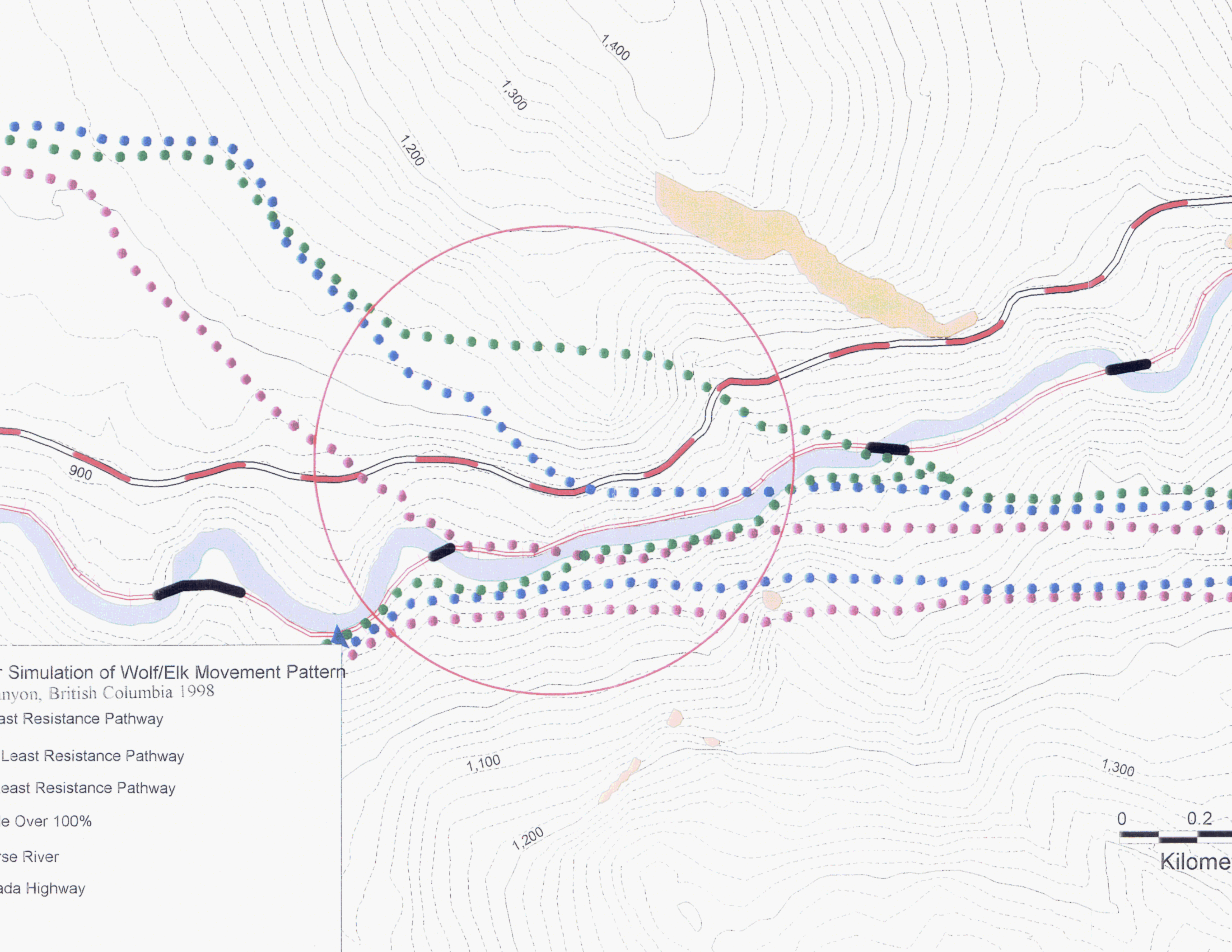

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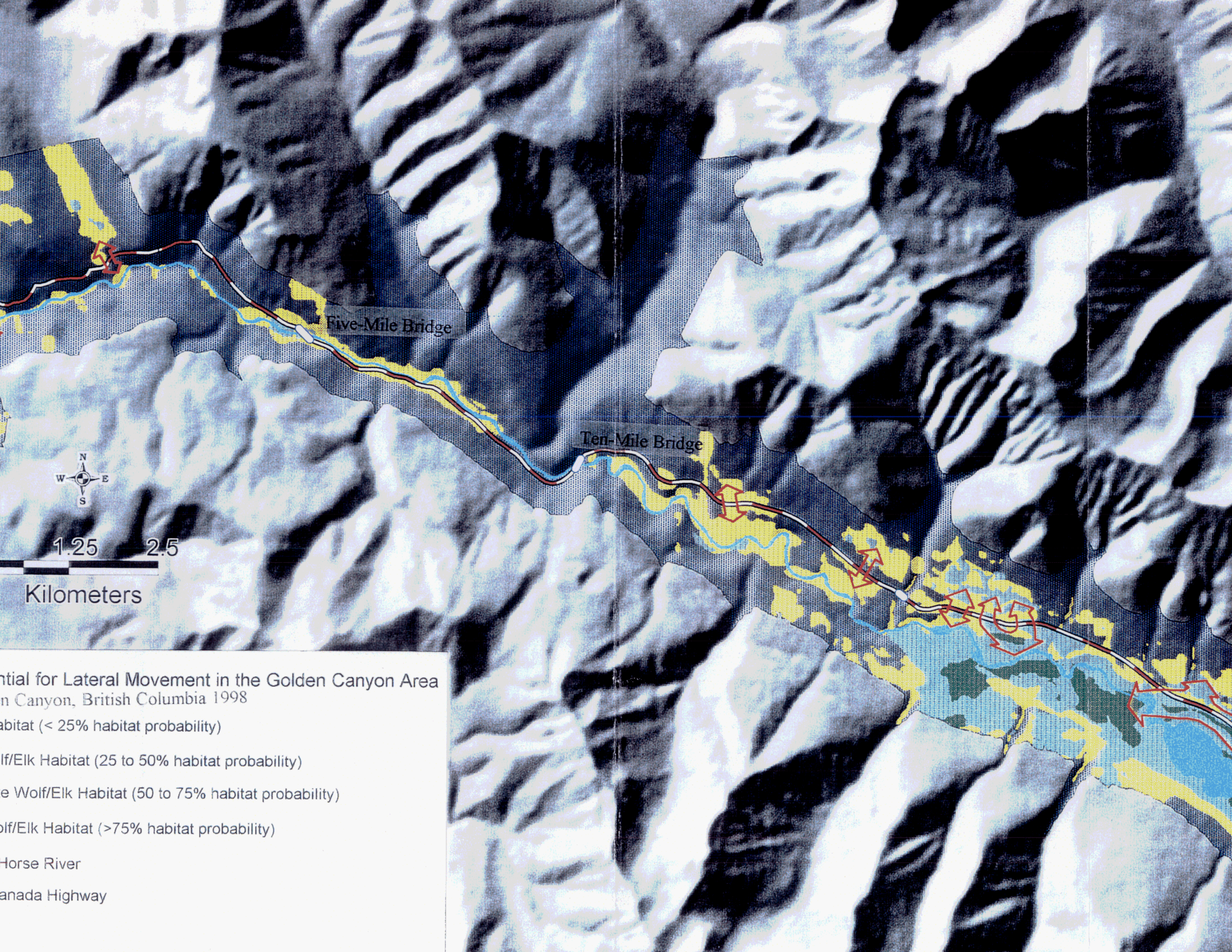

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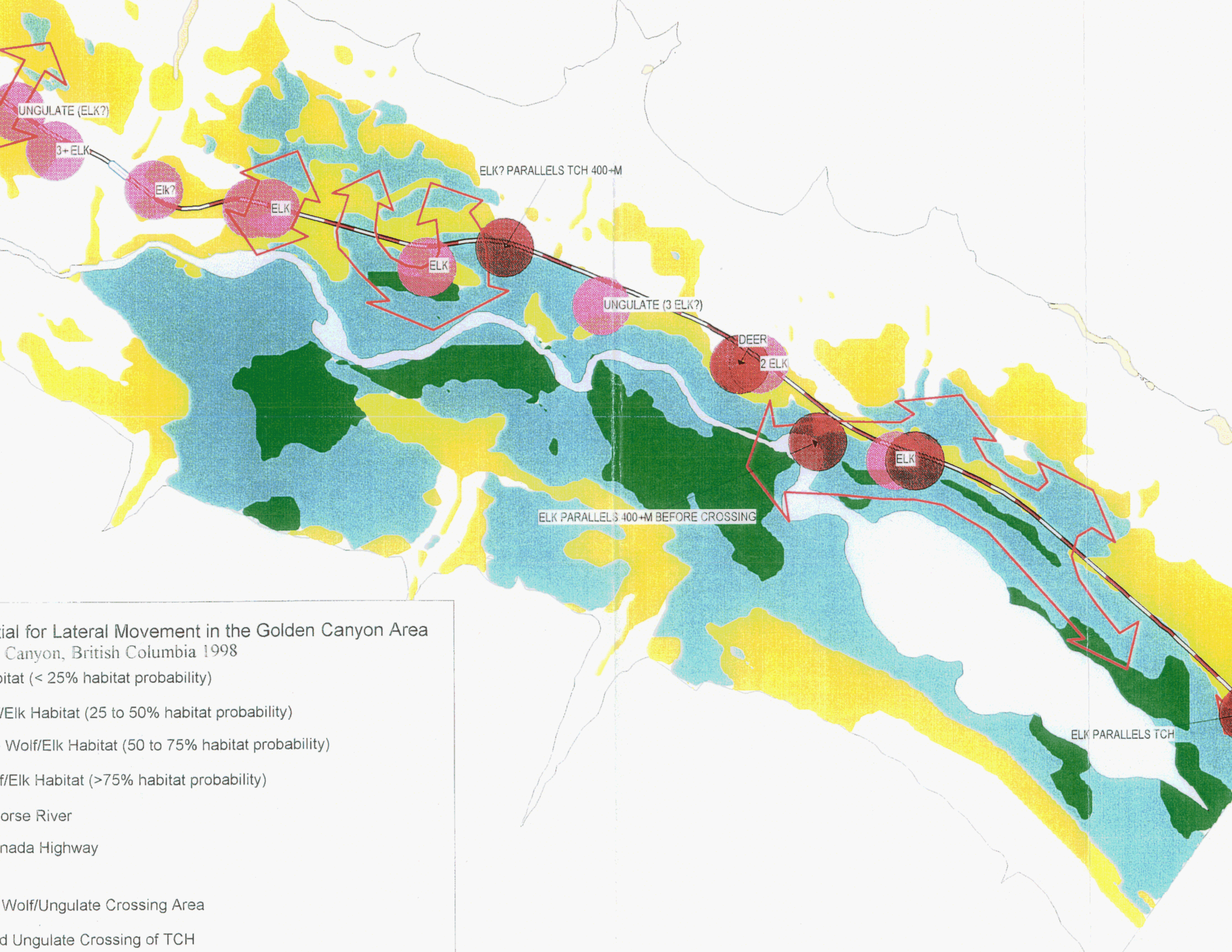
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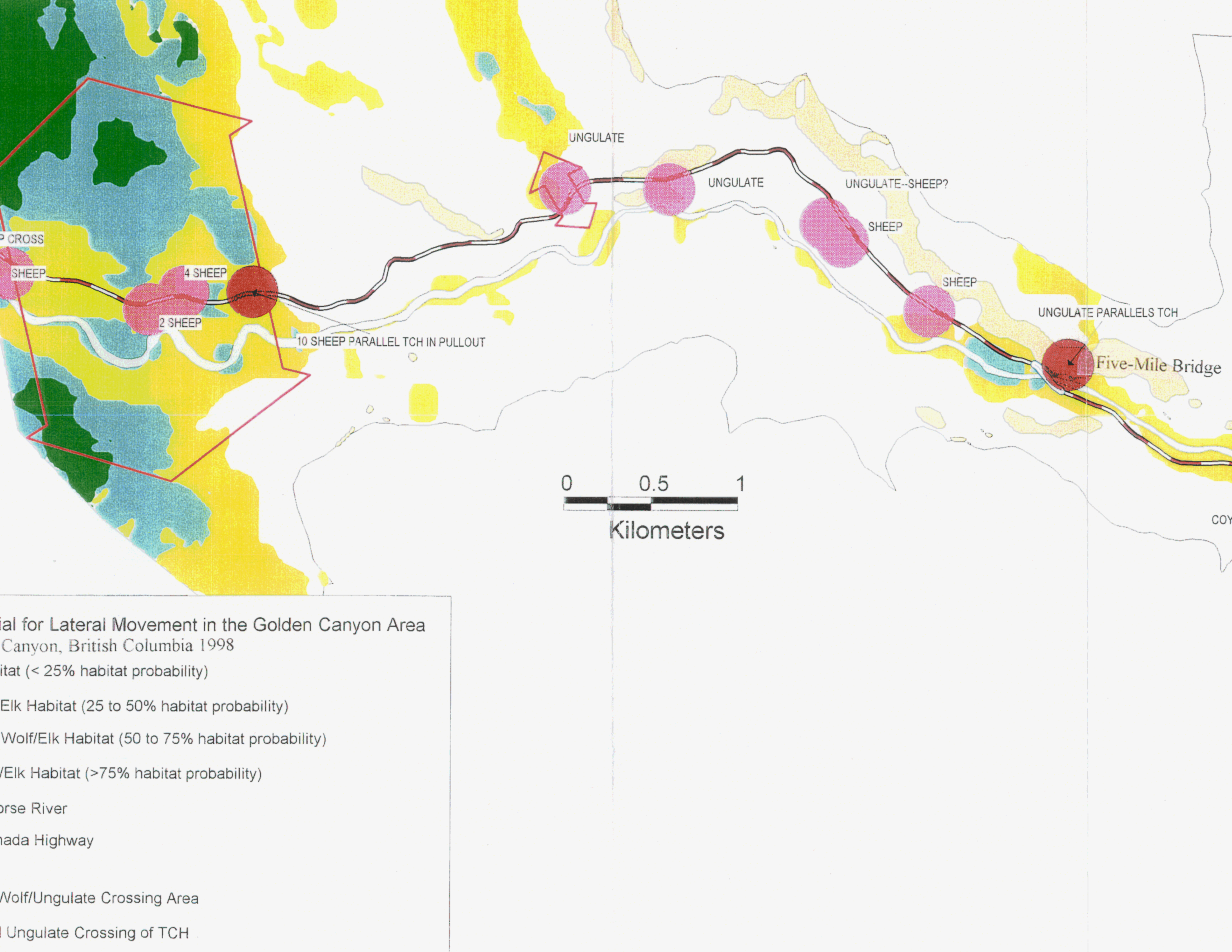

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DISCUSSION

Physiographic restrictions limit the availability of wolf habitat in the Golden Canyon. Consequently, the canyon area is not likely to support core habitat for a wolf pack. Telemetry and snow tracking data collected from the Yoho wolf pack, for example, suggest the pack travels through the canyon only occasionally. The canyon, however, likely functions as a regional corridor between the Columbia Valley and the Beaverfoot Valley and Yoho National Park. Wolves dispersing between the northwestern portion of Banff National Park or the southwestern portion of Jasper National Park and the Columbia Valley would also travel through the Golden Canyon. Thus the importance of the Golden Canyon as a linkage between subpopulations of wolves should not be understated.

The simulated pathways through the canyon show that the TCH and the Railway converge on the best available habitat for wolves in the study area. The crossing coefficients used to weight the probability of wolves crossing the railway did not incorporate the probability of wolves travelling on the railway. Consequently, the simulation of the primary least resistance pathway may not accurately predict the movement of wolves through the canyon. Train traffic may displace wolves to a sub-optimal movement corridor in more difficult terrain, with an associated cost of travelling with increased energy expenditure. Alternatively, if wolves choose to travel along the railway, the consequence may be reduced survivability.

The simulated pathways predict where wolf crossings are likely to occur through the canyon. The number of highway crossings is small due to the barrier effect of the TCH. Because the optimal pathway for wolves occurs along the valley bottom, 2 significant crossings of the TCH occur where the highway crosses the Kicking Horse River.

The simulations of wolf lateral movements connect patches of high quality wolf or elk habitat occurring on either side of the TCH. Stressing that the crossing zones are based on analysis of the habitat quality in the canyon, and not high resolution information on local movement impediments (e.g., small rock outcrops or scree slopes) is imperative. Thus the identified crossing zones should be used as focal points for further analysis of potential crossing sites, based on the interpretation of large-scale ortho-corrected aerial photographs and ground-truthed data. This would enhance the establishment of site-specific mitigative recommendations.

Because wolves are sensitive to human disturbance, exist in low densities, occupy large home ranges, and specialize in valley bottom habitats that often overlap with linear developments, they are adequate indicators of road effects. Wolf habitat is also highly correlated with elk habitat (Paquet *et al.* 1996). Thus, mitigative strategies for wolves will likely have positive effects for elk. We must be careful, however, to assure that land development is compatible with a broad range of wildlife. A selective focus on wolves might inadvertently alter the composition of established biological communities, reduce abundance of some species, and reduce species diversity. Wolf movements and habitat use are not strongly correlated with those of bighorn sheep (*Ovis canadensis)*, for example. Sheep habitat needs and highway crossings are therefore not captured by this model. Sheep are likely affected by the TCH in the Golden Canyon, and we recommend an independent assessment of these effects.

SECTION 2
SURVIVAL AND CAUSE-SPECIFIC MORTALITY OF WOLVES IN THE CENTRAL ROCKY MOUNTAINS OF CANADA

Survival is a critical population process and estimating survival rates is an important part of measuring viability of populations. Management of protected wolf populations requires quantitative survival measurements so causes of mortality can be identified and unnatural causes reduced. In mountainous areas estimates of survival rates are difficult to obtain for wolves, however, owing to low densities and wide-ranging movements. We used the Heisey-Fuller method (Heisey and Fuller 1985a) to calculate survival and cause-specific mortality rates for wolves in the Central Canadian Rockies.

METHODS

We collected information on wolf mortality in the Central Rocky Mountains of Canada for the period 1981-1998. Causes of mortality were categorized as highway, railway, shooting or trapping, natural accidents, and unknown. Natural accidents included deaths resulting from avalanche, drowning, and injuries sustained during depredation attempts. Mortality data were obtained from radiocollared wolves, the Cranbrook District Ministry of Lands and Parks, BC, Yoho Warden Service, Kootenay Warden Service, Banff Warden Service, Kananaskis Country Ranger Service, local hunting guides, and outfitters. For purposes of comparison, data were divided into East Slopes, centred on Banff National Park, and West Slopes, centred on Kootenay and Yoho National Parks. We further partitioned survival data of radio-marked wolves into sex, protected areas, unprotected areas, and general areas. Protected areas were assigned to collared wolves whose territory encompassed areas not exposed to roads, rail or harvesting pressure; unprotected areas were assigned to collared wolves whose territories were exposed to roads, rail or harvesting pressure. Radiocollared survival data was also partitioned into Banff National Park, Alberta; Kananaskis Country, Alberta; Kootenay National Park, British Columbia; and Yoho National Park, British Columbia.

We assessed the importance of single mortality agents as the number of deaths expressed as a percent of all deaths (Trainer *et al.* 1981, Trent and Rongstad 1974). Because of inherent problems in this approach, we also used data from 37 radio-marked wolves to determine unbiased estimates of survival and cause-specific-mortality rates (Heisey and Fuller 1985a). The latter method statistically evaluates competing risks and the relative importance of these risks over time

(Heisey and Fuller 1985b). Eleven-year and annual survival rates were extrapolated from daily rates using number of transmitter-days. Cause-specific mortalities and confidence limits (Heisey and Fuller 1985a) were also calculated by extrapolation from daily rates. We assumed all wolves whose radio-signals were lost (n = 9) were alive on the last day of contact, and died the following day. Consequently, our survival estimates are conservative. Our tests rejected the null hypothesis that survival rates did not differ between groups at an alpha level of 0.05.

RESULTS

We documented 229 mortalities for wolves in the Central Rockies between 1981 and 1998 (Figure 1). Few wolves (3.9%) died of natural accidents and no wolves were known to have died of old age or disease. Most deaths (86%) were caused by people. The most frequent cause of death was shooting, followed by collisions with vehicles and trains. An additional 4 radiocollared wolves were struck by vehicles but survived. Two of the 4 were killed in subsequent highway accidents, and another was killed by a train. In the East Slopes, death resulting from highway and rail collision occurred more frequently than in the West Slopes. Conversely, death by shooting predominated in the West Slopes (Figure 10).

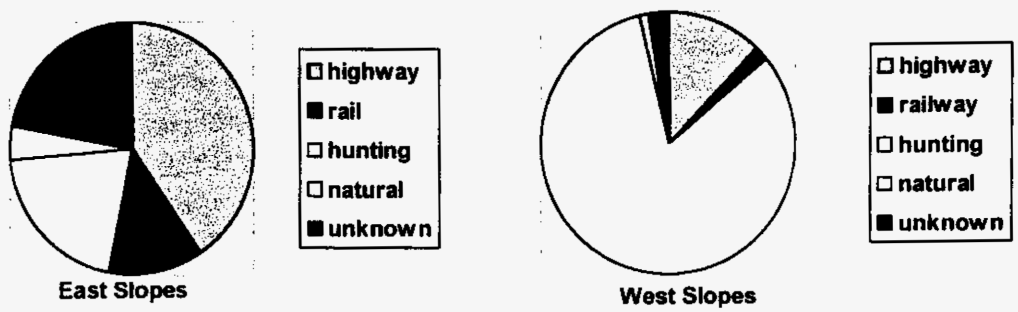

Figure 10. Cause-specific mortality rates of gray wolves in the Central Rockies (n = 229).

Survivorship and Cause Specific Mortality Rates

We derived survival and cause-specific mortality rates for 37 radiocollared wolves in the Central Canadian Rockies from 1987 to 1998. Eighty-five percent (85%) of the 20 known mortalities were attributed to shooting, road fatalities, and rail fatalities. Females had a higher annual survival rate than males, but the difference was not significant (P > 0.5) (Table 2). Among general areas, the mean annual survival rate was highest in Kananaskis Country (0.809) and lowest in Yoho National Park (0.688) (Table 4), although survival rates did not differ significantly among areas (P > 0.5). Collared wolves occupying protected areas (i.e., not exposed to highways, railways or harvesting pressure) had a significantly greater (P < 0.05) mean annual survival rate (0.890) than those occupying unprotected areas (0.710) (Table 6).

Overall, the 11-year survival rate (95% CI) of radiocollared wolves was 0.02846; shooting was the primary cause of death. For the 11-year interval, the survival rate for females (0.0132) was greater than the survival rate for males (0.0171), although the difference was not significant (Table 3). Rates of survival and mortality varied among the Central Rocky Mountain Parks with the highest 11-year rate of survival (0.1457) in Yoho National Park (Table 5) and the lowest 11-year rate of survival (0.008753) in Banff National Park. The high survival rate of wolves in Yoho National Park may be an artifact of a low sample size; the low survival rate of wolves in Banff National Park is primarily due to exposure of most (10 of 15) collared wolves to high automobile and train traffic volumes in the Bow Valley. Wolves occupying protected areas had a higher 11-year survival rate (0.3563) than wolves occupying unprotected areas (0.0187) (Table 7).

Table 2. Mean annual survival rate by sex for radiocollared wolves in the central Rockies of Alberta and British Columbia between 1987 - 1998.

SEX	SURVIVAL RATE
Females (n = 21)	0.7629
Males (n = 16)	0.7294

Table 3. Eleven-year span survival rate by sex for radiocollared wolves in the central Rockies of Alberta and British Columbia between 1987 - 1998.

SEX	SURVIVAL RATE
Females (n = 21)	0.0178
Males (n = 16)	0.0132

Table 4. Mean annual survival rates by Park for radiocollared wolves in the Central Rockies of Alberta and British Columbia between 1987-1998.

AREA	SURVIVAL RATE
Banff National Park	0.7361
Kananaskis Country	0.8099
Kootenay National Park	0.7122
Yoho National Park	0.6883

Table 5. Eleven-year survival rates by park or region for radiocollared wolves in the Central Rockies of Alberta and British Columbia between 1987-1998.

AREA	SURVIVAL RATE
Banff National Park	0.008753
Kananaskis Country	0.072053
Kootenay National Park	0.09608
Yoho National Park	0.145715
Central Rockies	0.02846

Table 6. Mean annual survival rate for radiocollared wolves in protected and unprotected areas in the central Rockies of Alberta and British Columbia between 1987 - 1998. Protected status was assigned to areas where wolves are minimally exposed to roads, rail lines or harvesting pressure.

STATUS	SURVIVAL RATE
Protected (n=5)	0.8909
Unprotected (n=32)	0.7101

Table 7. Eleven-year span survival rate for radiocollared wolves in protected and unprotected areas in the central Rockies of Alberta and British Columbia between 1987 - 1998.

PROTECTED STATUS	SURVIVAL RATE
Protected (n = 5)	0.3563
Unprotected (n =32)	0.0187

DISCUSSION

Shooting is the major cause of death for wolves in the Central Rockies, whereas in protected areas such as the Bow River Valley, indirect causes such as highway and railway mortality predominate. Rates of natural mortality of adult wolves are very low. The numbers and types of mortality probably depend on the extent of protection and overlap with human activities. The cause of death likely depends on frequency of exposure to a particular agent of mortality.

Wolf packs have been active in the study area for less than 20 years, so the effect of 229 known deaths may be consequential. Human-caused deaths represent ~11 - 44% of the mean fall population (approximately14 packs, 100 wolves) in the Central Canadian Rockies (Paquet and Callaghan unpublished data). Annual rates of increase of exploited populations vary directly with mortality rates, and harvests exceeding 28% of the winter population often result in declines (Fuller 1989).

Nevertheless, risk assessment accounts for changes in sample size that occur during the sampling period, adjusts for biases in daily survival rates, and survival estimates are corrected for small sample sizes (Heisey and Fuller 1985a). Overall, we interpret the results to mean that there is a very low probability that wolves born in the Central Rockies will live a normal life span or die of natural causes. Small sample sizes for collared wolves in Kootenay and Yoho National Parks limited an accurate comparison of survival rates between parks. A comparison of survival rates between wolves occupying protected versus unprotected areas suggests that survival is better in the back country areas of Banff National Park, likely because wolves are buffered from outside influences. In the Bow Valley of Banff National Park, however, the risk of dying from rail or highway collisions is high.

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