

**Wolverine Winter Travel Routes and Response to Transportation Corridors
in Kicking Horse Pass Between Yoho and Banff National Parks**

A Master's Degree Project
Prepared in Partial Fulfillment of the Requirements of the
Master of Environmental Design Degree
in the Faculty of Environmental Design, The University of Calgary

By
Matt Austin, B.Sc.

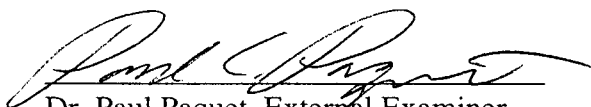
March, 1998

THE UNIVERSITY OF CALGARY
FACULTY OF ENVIRONMENTAL DESIGN

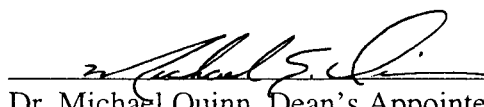
The undersigned certify that they have read, and recommend to the Faculty of Environmental Design for acceptance, a Master's Degree Project entitled "Wolverine Winter Travel Routes and Response to Transportation Corridors in Kicking Horse Pass Between Yoho and Banff National Parks," submitted by Matt Austin in partial fulfillment of the requirements for the degree of Master of Environmental Design (Environmental Science).



Dr. Stephen Herrero, Supervisor
Faculty of Environmental Design



Dr. Paul Paquet, External Examiner
Faculty of Biology



Dr. Michael Quinn, Dean's Appointee
Faculty of Environmental Design

Date: March 25, 1998

ABSTRACT

Wolverine Winter Travel Routes and Response to Transportation Corridors
in Kicking Horse Pass Between Yoho and Banff National Parks

by Matt Austin

Prepared in Partial Fulfillment of the Requirements of the M.E.Des. Degree
in the Faculty of Environmental Design, The University of Calgary

Supervisor: Dr. Stephen Herrero

March, 1998

During two winters I investigated the influence of transportation corridors on wolverine (*Gulo gulo*) movements through snow-tracking. Analysis of movements within the study area showed avoidance of areas within 100 m of the Trans Canada Highway and preference for areas >1100 m from the highway. Analysis of movements on the ski trail that formed the boundary of the study area showed a similar trend with avoidance of sections of the trail within 200 m of the highway and preference for sections >1100 m away. Mean width of the right-of-way for highway crossings by wolverines (68 m) was significantly shorter than that of approaches without crossing (165 m). Wolverines approaching the highway made repeated approaches and retreats and only crossed three out of six times. Wolverines did not hesitate to cross the Canadian Pacific Railway in areas where it does not share a common right-of-way with the highway. Total wolverine activity, behaviour and the fact that I observed almost twice (1.93 times) as much movement on the east-west axis across the study area compared to the north-south axis, strongly indicate that Kicking Horse Pass is an important east-west movement corridor for wolverines. The Trans Canada Highway currently appears to be having a significant impact on wolverine movements. I believe that roads with narrow rights-of-way (<50 m) have less impact on wolverine movements than roads with wide rights-of-way (>100 m). I expect the impact of the highway on wolverines is greater during the summer when traffic volume is higher.

Key Words: Canadian Pacific Railway, corridor, *Gulo gulo*, Kicking Horse Pass, movements, snow-tracking, Trans Canada Highway, winter, wolverine, Yoho National Park

TABLE OF CONTENTS

| | |
|---|-----|
| List of Figures | iii |
| List of Tables | iii |
| Acknowledgments | iv |
| Introduction | 1 |
| Movements and Home Range | 2 |
| Habitat Use | 4 |
| Sensitivity to Human Disturbance | 5 |
| The Influence of Roads on Large and Medium-Sized Carnivores | 6 |
| Project Outline | 7 |
| Hypotheses | 8 |
| Study Area | 9 |
| Location | 9 |
| Physical Geography | 9 |
| Climate | 9 |
| Vegetation | 9 |
| Wildlife | 12 |
| Human Development and Activity | 12 |
| Methods | 16 |
| The "Loop" Method of Snow-tracking | 16 |
| Data Analysis | 16 |
| Results | 19 |
| The Influence of the Trans Canada Highway | 19 |
| Axes of Movements | 19 |
| Highway Crossing | 25 |
| Railway Crossing | 25 |
| Movements on Ski Trails | 29 |
| Wolverine Feeding | 29 |
| Discussion | 30 |
| The Influence of the Trans Canada Highway | 30 |
| Axes of Movements | 31 |
| Highway Crossing | 31 |
| Railway Crossing | 33 |
| Movements on Ski Trails | 33 |
| Wolverine Feeding | 33 |
| Management Implications | 34 |
| Literature Cited | 36 |

LIST OF FIGURES

| | | | |
|-----------|---|-------|----|
| Figure 1. | Location of study area | | 10 |
| Figure 2. | Shaded relief map of the study area | | 11 |
| Figure 3. | Study area map | | 13 |
| Figure 4. | Average traffic volume by hour in January and July for the Trans Canada Highway through Kicking Horse Pass from 1993-1997 | | 15 |
| Figure 5. | Buffers used for data analysis | | 17 |
| Figure 6. | Wolverine movements observed | | 20 |
| Figure 7. | Relative use based on distance from the Trans Canada Highway for wolverine movements within the study area | | 22 |
| Figure 8. | Relative use based on distance from the Trans Canada Highway for wolverine movements along the study area boundary | | 24 |
| Figure 9. | Locations where wolverines crossed, and approached without crossing, the Trans Canada Highway | | 27 |

LIST OF TABLES

| | | | |
|----------|---|-------|----|
| Table 1. | Relative use based on distance from the Trans Canada Highway (TCH) for wolverine movements within the study area | | 21 |
| Table 2. | Relative use based on distance from the Trans Canada Highway (TCH) for wolverine movements along the study area boundary | | 23 |
| Table 3. | Distance travelled along the east-west and north-south axes for wolverine movements and the Trans Canada Highway (TCH) | | 26 |
| Table 4. | Width of the right-of-way for locations where wolverines crossed, and approached without crossing, the Trans Canada Highway | | 28 |

ACKNOWLEDGMENTS

Funding for this study was provided by Yoho National Park. I would like to thank Derek Petersen for his help in securing this funding, for his interest in the project and for his patience in awaiting the final product.

I would like to thank my supervisor Dr. Stephen Herrero for finding the time both to take me on as a student and to join me in the field, for his enthusiasm for the project, for always being positive and flexible and for his support while I strived to complete this project while working full-time. My thanks to the other half of my committee as well, Dr. Paul Paquet, for his interest and helpful advice.

I would like to thank Linda Wiggins and Ken Schroeder for volunteering to come out into the field with me; their assistance and energy were most welcome on what was usually a solitary task. I would particularly like to express my gratitude to my field assistant, Lyle Walton for his dedication and hard work and for being such a good sport about learning to ski! Eric Lofroth reviewed an early draft of the manuscript and provided me with valuable advice on the use of electivity indices. This project could not have been completed without the aid of Kristin Karr who skillfully performed the GIS analysis required and prepared the maps; her help is much appreciated.

Finally, I would like to thank my wife, Elizabeth Austin, for her support and encouragement, for her assistance in editing this manuscript and for always wishing me luck in my pursuit of the next wolverine trail.

INTRODUCTION

The wolverine is the largest terrestrial mustelid and is a powerful animal with a circumpolar distribution. Wolverines are one of the most poorly understood large carnivores in North America with only five field studies having been completed (Hornocker & Hash 1981; Magoun 1985; Gardner 1985; Banci 1987; Copeland 1996).

The Committee on the Status of Endangered Wildlife in Canada recognizes two populations of wolverines, both of which are felt to be at risk. They list the population east of Hudson's Bay as endangered and the population west of Hudson's Bay as vulnerable (COSEWIC 1994). In British Columbia, the Vancouver Island wolverine (*Gulo gulo vancouverensis*), a sub-species found only on Vancouver Island, is listed as endangered and the remaining population is listed as vulnerable (Harper et al. 1994).

All of the North American studies of wolverines to date have relied primarily on radio-telemetry. This method, while useful for determining gross movements and home range size, does not provide fine scale information on movements and habitat use that may be important in explaining the larger scale patterns observed.

One method that provides fine scale information on wolverine movements and habitat use is snow-tracking. This technique has played a minor role in North American wolverine research (Cockerton & Herrero 1973; Hornocker & Hash 1981; Gardner 1985; Magoun 1985; Becker 1991; Copeland 1996) but has been the primary method used in several studies of wolverines in Scandinavia (Krott 1960; Haglund 1966; Myhre 1968; Myrberget et al. 1969). In addition to being limited seasonally, snow-tracking data have traditionally been used to describe wolverine activity subjectively but have not been collected so as to allow for hypothesis testing. Another limitation is that researchers are unable to consistently identify individuals or determine their residency status (Haglund 1966; Magoun 1985).

Although North American studies of wolverine have focused on measuring home range size, differences in the methods used complicate any attempt to compare their results. Whitman et al. (1986) used logarithmic projection to estimate home range size, Hornocker & Hash (1981)

combined data from different years for individuals and Magoun (1985) used all locations for individuals in a year but had little winter data.

All of the studies to date have involved small sample sizes, particularly after individuals were divided into reproductive classes for analysis. Usually there were less than five individuals within any given reproductive class in these studies and commonly only one. Even those individuals that were represented were usually relocated infrequently and may have only been followed for a short period.

Movements and Home Range

It appears that food availability is the primary factor determining the movements and range of wolverines (Krott 1960; Hornocker & Hash 1981; Banci 1994). Large herbivores, probably obtained as carrion, are the most important food item in the diet, particularly during the winter (Krott 1960; Haglund 1966; Myhre 1968; Rausch & Pearson 1972; Myhre & Myrberget 1975; Hornocker & Hash 1981; Magoun 1985; Banci 1987). Wolverines alter their home ranges during the winter, possibly due to food availability. Copeland (1996) found that adult wolverines had smaller home ranges during winter. Hornocker & Hash (1981), Magoun (1985), Whitman et al. (1986) and Banci (1987) found no difference in home range size between seasons, however, different areas were used.

Wolverine home ranges are based on the daily movements of individuals. These movements may exceed 30 km (Krott 1960; Haglund 1966; Pulliainen 1968). Geographic features, such as mountain ranges and large rivers, that limit the movements of many species do not constrain wolverines (Hornocker & Hash 1981; Banci 1987). Males make longer, more direct daily movements than females who tend to be more meandering (Hornocker & Hash 1981; Magoun 1985). Individuals tend to travel similar routes through their home ranges from year to year (Krott 1960; Haglund 1966; Koehler et al. 1980).

Wolverines have intra-sexual territories, which is typical of mustelids (Powell 1979). Individuals will defend territories from members of the same sex, although there may be some overlap. Home ranges overlap substantially with those of the opposite sex (Krott 1960; Magoun

1985; Banci & Harestad 1990; Copeland 1996). Females with overlapping home ranges may be mother-daughter (Magoun 1985; Banci 1987). Hornocker & Hash (1981) found extensive overlap of home ranges both within and between sexes, which they suggest may have been due to harvest pressure causing behavioural instability. Individuals of the same sex may also tolerate each other when resources are abundant, predictable and not easily defensible (Banci 1987).

All of the studies that have examined wolverine home ranges have found that adult male wolverines had the largest home ranges of all reproductive classes. The size of adult male home ranges, however, has varied dramatically from 382-1522 km² (Hornocker & Hash 1981; Magoun 1985; Gardner 1985; Whitman et al. 1986; Banci 1987; Copeland 1996). The findings of these studies were probably biased toward smaller home range estimates because males can not always be located due to their wide-ranging movements (Magoun 1985).

One male's home range may overlap those of two to six females (Magoun 1985; Banci 1987; Copeland 1996). Magoun (1985) suggested that adult males may monitor the breeding condition of four to six females between May and August and therefore spend more time travelling and take more direct routes than females.

Adult females with kits have consistently been found to have the smallest home ranges among wolverine cohorts, ranging from 73-416 km² (Hornocker & Hash 1981; Magoun 1985; Gardner 1985; Whitman et al. 1986; Banci 1987; Copeland 1996). Radio-telemetry may bias this estimate downward because females with young spend a great deal of time at or near den or rendezvous sites (Magoun 1985). Female wolverines without kits have slightly larger home ranges than those with kits, ranging from 126-432 km² (Hornocker & Hash 1981; Magoun 1985; Banci 1987; Copeland 1996).

Wolverines undergo particularly extensive movements when searching for a home range. Magoun (1985) and Banci (1987) found that sub-adults normally disperse during their first winter. However, Copeland (1996) found that dispersal did not occur until sub-adults were at least two years old. Males disperse farther than females who often establish home ranges next to their mother's (Hornocker & Hash 1981; Magoun 1985; Copeland 1996). The longest recorded

dispersal distance for a subadult male is 378 km (Gardner et al. 1986). The size of a subadult male's home range varies from 435-1104 km² (Banci 1987; Copeland 1996). The home range of a subadult male may overlap that of its mother and of an adult male prior to dispersal (Magoun 1985; Banci & Harestad 1990; Copeland 1996).

Habitat Use

Hornocker & Hash (1981) found that wolverines preferred intermediate and mature forest types while avoiding dense young stands. However, Banci & Harestad (1990) found no significant difference in use compared with availability for riparian habitat, forest cover type, aspect or elevation.

Some studies have observed seasonal shifts in habitat use among wolverines with higher elevations receiving preferred use during the summer (Hornocker & Hash 1981; Gardner 1985; Whitman et al. 1986; Copeland 1996). Hornocker & Hash (1981) found increased use of sub-alpine fir habitats during summer. Banci (1987) found avoidance of alpine talus by males whereas Whitman et al. (1986) and Copeland (1996) found that males avoided forest types and preferred alpine habitats. The elevational shift observed may be due to wolverines avoiding high temperatures, humans or both (Hornocker & Hash 1981). Whitman et al. (1986) suggested that this change may be due to the increased availability of small mammals and ground-nesting birds in these areas.

During the winter, wolverines move to lower elevations (Hornocker & Hash 1981; Gardner 1985; Whitman et al. 1986; Copeland 1996) and avoid alpine tundra habitats (Whitman et al. 1986). Banci (1987) observed this shift in elevation among males only. Increased use of sub-alpine coniferous habitats during the winter may be due to the higher densities of ungulate kills available for scavenging (Gardner 1985; Whitman et al. 1986; Banci 1987).

Wolverine natal dens in Idaho have been found predominantly in sub-alpine cirques, on north or northeast facing slopes in large boulder talus (Copeland 1996). Proximity to cover appears to have been important as natal dens were located in small talus sites, less than 100 m wide, surrounded by trees. In Finland, den sites had a northerly aspect as well and were strongly

associated with subalpine and alpine slopes, with approximately half of the dens located at or above treeline (Pulliainen 1968). In Norway, approximately one third of den sites were found at or above the treeline and most were on south to southwest facing slopes (Myrberget 1968). Haglund (1966) found that dens in Sweden were associated with large boulder talus usually above treeline. Natal den sites may be re-used in subsequent years by the same female (Copeland 1996).

Seclusion appears to be the most important factor in the selection of natal den sites (Copeland 1996). Females with kits are extremely sensitive to human disturbance and will abandon den sites if disturbed (Krott 1960; Pulliainen 1968; Copeland 1996). In contrast, Magoun (1985) found that females did not abandon dens even when approached by observers although females did move young from rendezvous sites if disturbed.

Sensitivity to Human Disturbance

Wolverines are thought to be negatively affected by human activity and habitat alteration and are generally found in remote areas of undisturbed wilderness (Krott 1960; van Zyll de Jong 1975; Hornocker & Hash 1981; Whitman et al. 1986; Banci 1994). Interactions with humans and human developments result in lower wolverine populations. Direct anthropogenic mortality was considered by van Zyll de Jong (1975) as the most likely factor to have affected wolverine populations. This is based on the indirect evidence of the species disappearing from areas with dense human populations. Others have suggested that habitat loss and fragmentation are the primary causes of reduced or extirpated wolverine populations (Hornocker & Hash 1981; Magoun 1985; Banci 1994).

Hornocker & Hash (1981) found that cover is important to wolverines. Individuals were reluctant to cross openings such as clearcuts and ran straight across when they did instead of their normal meandering pattern when travelling in forests. Banci (1987) and Copeland (1996) did not find a reluctance of wolverines to cross natural openings. Hornocker & Hash (1981) and Banci (1987) also found that reservoirs and highways did not affect movements. However, they felt habitat alteration by humans may influence use. Differences in the level of human activity

between these study areas may partially explain the divergent findings on the importance of cover and the varying reaction of wolverines to habitat alterations such as clearcuts or highways.

Some differences may exist between the sexes in their level of sensitivity to human disturbance. Males have been found to use areas further from active roads, clearcuts and burns than females (Hornocker & Hash 1981). Wolverines may be disturbed by human access on snowmobiles and all-terrain vehicles during the winter and early spring (Hornocker & Hash 1981). However, wolverines will readily use trails made by snowmobiles or snowshoes in deep powdery snow (Haglund 1966).

In areas with moderate to high human use wolverines are usually found in the most inaccessible places available (van Zyll de Jong 1975; Banci 1994). Remote areas where human activity is limited appear essential to maintaining viable wolverine populations as wolverines appear not to tolerate land-use activities such as agriculture, forestry, oil and gas exploration and urban development that permanently alter habitats (Hornocker & Hash 1981; Banci 1994). Magoun (1985), however, found no evidence that oil and gas exploration was affecting wolverines in northwestern Alaska.

The Influence of Roads on Large and Medium-Sized Carnivores

Substantial evidence suggests that roads and associated human development and activity negatively influence the movements of large and medium-sized carnivores. Coulter (1966) found that fishers (*Martes pennanti*) avoided crossing highway right-of-ways, fields and frozen lakes and Powell (1977) found that fishers avoided open areas 25 m across and less. Lovallo and Anderson (1996) found that bobcats (*Lynx rufus*) avoided areas ≤ 100 m from paved roads and crossed them less than expected based on their occurrence within established home ranges. Wolves (*Canis lupus*) have exhibited some avoidance of areas ≤ 1 km from open roads (Thurber et al. 1994). It has been suggested that road densities of ≤ 0.58 km/km² are required to maintain viable wolf populations (Mech et al. 1988). Cougars (*Felis concolor*) have been observed to select home ranges with lower road densities than are found in the surrounding area (Van Dyke et al. 1986). Grizzly bears (*Ursus arctos*) avoid areas within 100-900 m of open

roads (Mattson et al. 1987; McLellan & Shackleton 1988; Aune & Kasworm 1989; Kasworm & Manley 1990; Mace et al. 1996). Mace et al. (1996) also found that the road density in areas used by adult female grizzly bears (0.6 km/km^2) was much lower than in the remainder of their study area (1.1 km/km^2). Similarly, black bears (*Ursus americanus*) appear to shift their home ranges to avoid heavily roaded areas (Brody & Pelton 1989).

Project Outline

I conducted the fieldwork for this project in Kicking Horse Pass between Yoho National Park and Banff National Park during two winter field seasons. The first was from December 1994 to March 1995, and the second from January 1996 to March 1996. I designed the project to determine the impacts of transportation corridors, particularly the Trans Canada Highway, on wolverine movements in this area. This information is important because the federal government plans to re-develop the Trans Canada Highway, which crosses the Continental Divide through Kicking Horse Pass, from the current two lanes into a divided four lane highway. This proposed development has implications for wolverines as previous research has suggested the pass is a possible wolverine movement corridor (McCrorry & Blood 1978). The closest forested pass across the Continental Divide is Vermilion Pass, which is approximately 30 km to the south and is also traversed by a highway (British Columbia Highway 93). Low elevation, forested passes may be significant because trees provide security cover and a means of escape for wolverines when threatened (Grinnell 1921; Burkholder 1962; Boles 1977; Banci 1994).

Winter movements of wolverines were documented using a novel snow-tracking technique. A loop ski trail formed the boundary of the study area, which allowed any movements within the study area to be analyzed objectively by comparing use versus availability.

Hypotheses

I investigated the following hypotheses:

1. H_O : Wolverines in the study area do not avoid areas close to the Trans Canada Highway.
 H_A : Wolverines in the study area avoid areas close to the Trans Canada Highway.
2. H_O : Wolverine movements through the study area are not directionally biased.
 H_A : Wolverine movements through the study area are predominantly along the east-west axis.
3. H_O : Wolverine crossings of the Trans Canada Highway are not biased by the width of the right-of-way.
 H_A : Wolverine crossings of the Trans Canada Highway are biased toward locations where the right-of-way is relatively narrow.

STUDY AREA

Location

The study area is 5.4 km² and is located in Kicking Horse Pass within Yoho National Park in the Rocky Mountains of southeastern British Columbia (Figure 1). The eastern boundary of the study area is approximately 1 km west of the Continental Divide, which forms the provincial border between British Columbia and Alberta and the boundary between Yoho and Banff National Parks. Yoho also shares a boundary with Kootenay National Park.

Physical Geography

Kicking Horse Pass runs east-west and crosses the Continental Divide at an elevation of 1627 m (5339 ft). The pass is wide and flat with approximately 2.5 km between the 1829 m (6000 ft) contours on the north and south sides of the pass (Figure 2). The study area itself ranges between 1585 m (5200 ft) and 1829 m (6000 ft).

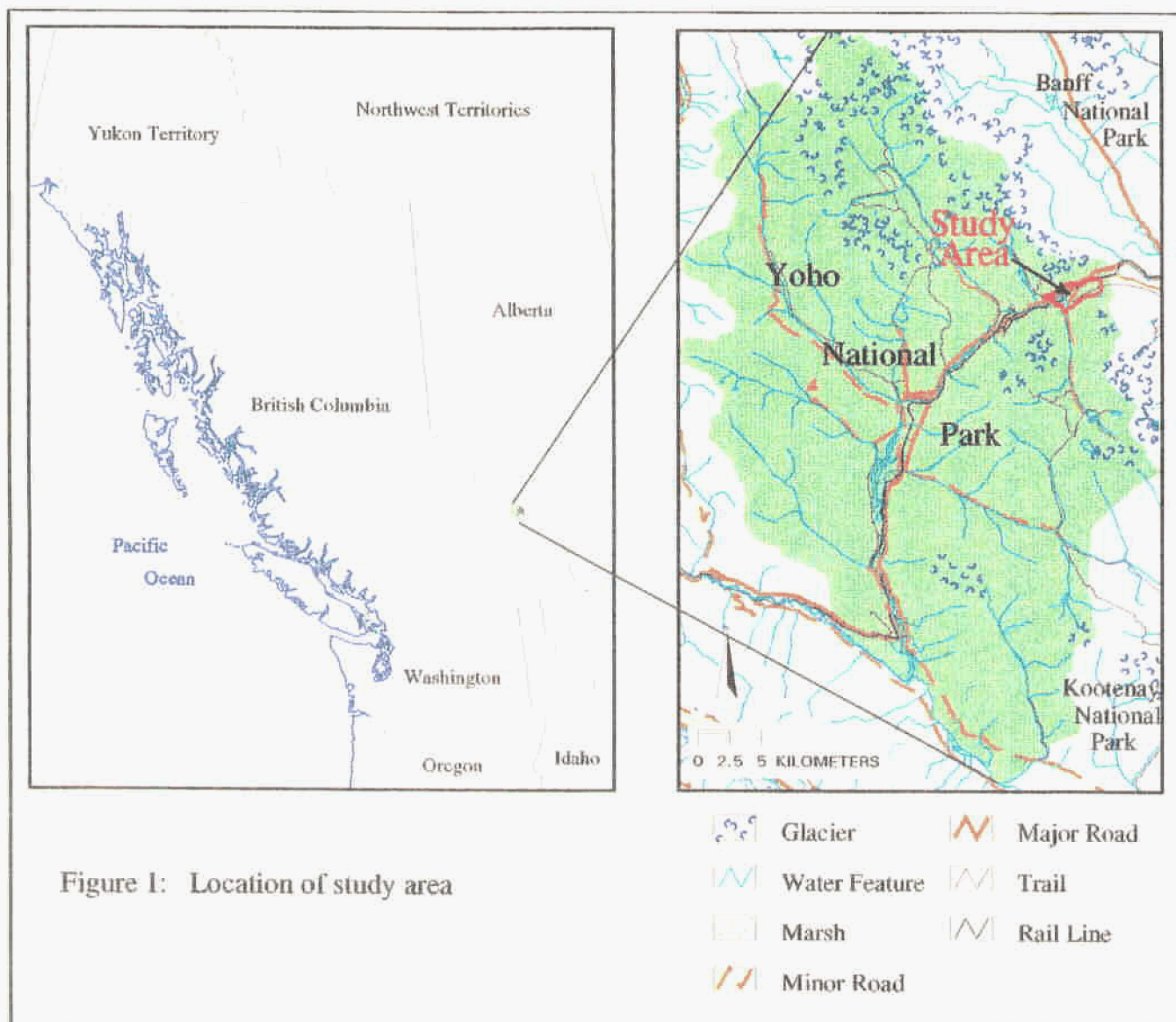
Within the study area is Wapta Lake, which is approximately 25 ha. Wapta Lake is the headwater of the Kicking Horse River, which flows west through Yoho National Park.

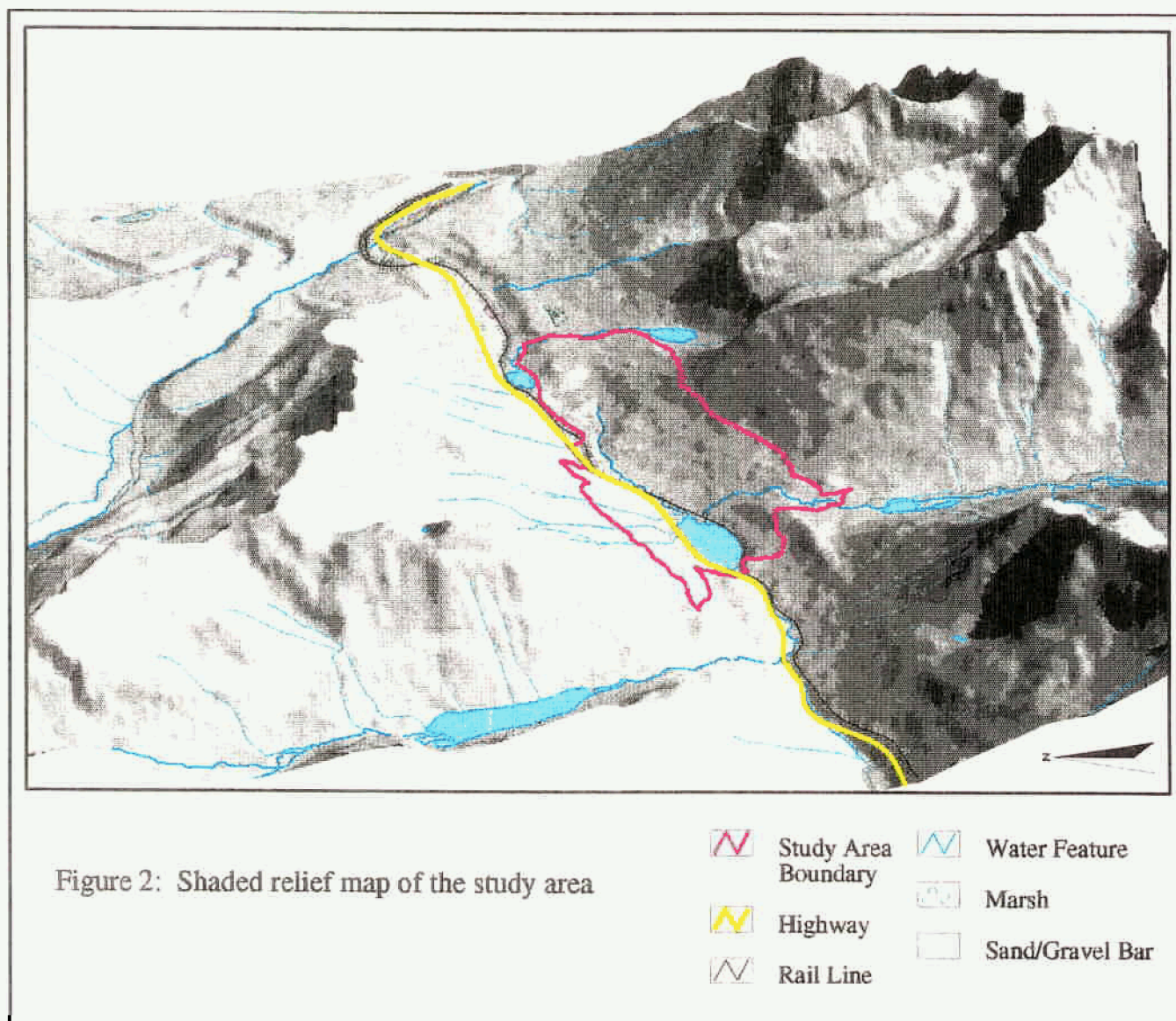
Climate

Yoho National Park has a continental macroclimate and is characterized by short, cool summers and long winters with high snowfall. This is even more pronounced at higher elevations and along the Continental Divide such as in Kicking Horse Pass (Achuff et al. 1993).

Vegetation

The vegetation of the study area is dominated by mature to old (approximately 200-400 years) stands of Engelmann spruce (*Picea engelmannii*) and sub-alpine fir (*Abies lasiocarpa*) with some successional intermediate (approximately 50-200 years) stands of lodgepole pine (*Pinus contorta*). The shrub layer is dominated by buffaloberry (*Shepherdia canadensis*), green alder (*Alnus crispa*), Labrador tea (*Ledum groenlandicum*), common juniper (*Juniperus communis*), false azalea (*Menziesia ferruginea*) and regenerating sub-alpine fir and Engelmann spruce. The herb layer is dominated by bunchberry (*Cornus canadensis*), five-leaved bramble





(*Rubus pedatus*), prickly rose (*Rosa acicularis*), twinflower (*Linnaea borealis*), kinnikinnick (*Arctostaphylos uva-ursi*) and *Vaccinium* spp. (Achuff et al. 1993)

Except for Wapta Lake, there are few natural openings within the study area. Those that do exist are small (<1 ha). Outside of the study area but nearby, however, there are avalanche paths that measure up to approximately 500 m wide. There are also four small lakes (<10 ha) within a kilometer of the study area. Stand-replacing fires are rare in the Kicking Horse Pass area due to the cool, moist climate.

Wildlife

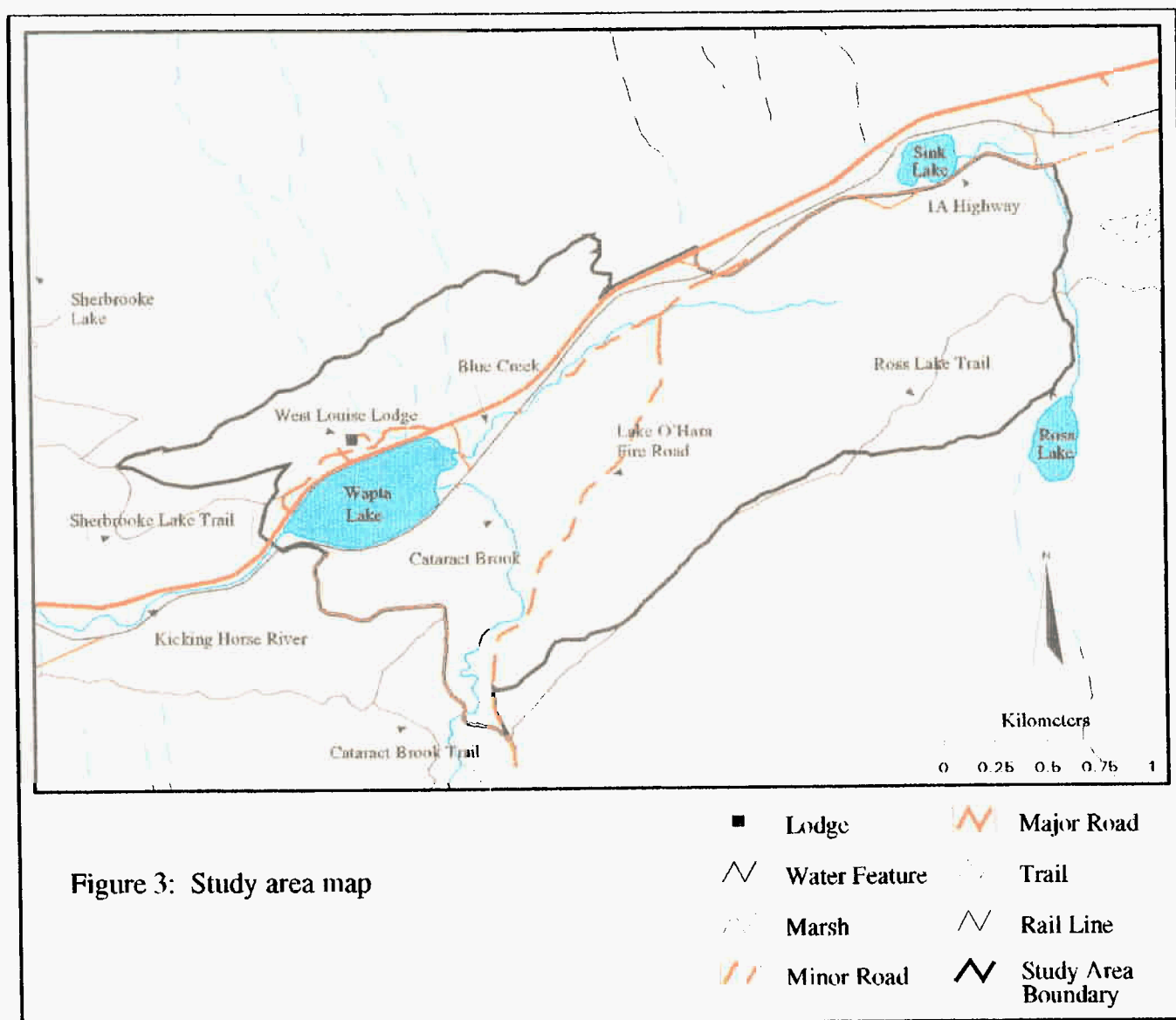
During the winter active wildlife in the study area includes red squirrel (*Tamiasciurus hudsonicus*), snowshoe hare (*Lepus americanus*), marten (*Martes americana*) and coyote (*Canis latrans*). Elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) are infrequent visitors in early and late winter.

The wolverine is "about as common in Yoho National Park as it ever gets anywhere" (Cowan 1944). The population was estimated in 1978 to be approximately 30 wolverines in the 1313 km² park with the highest numbers along the Continental Divide including the Lake O'Hara and Lake Louise areas. Sub-alpine spruce-fir forests were thought to be the preferred habitat in Yoho (McCrary & Blood 1978). Salt et al. (1995) also found that sub-alpine habitats were most important for wolverines in Yoho.

There is one record of a wolverine being killed on the highway in Yoho. This occurred in April, 1974, approximately 5 km west of the study area (McCrary & Blood 1978). A wolverine was also killed on the highway in Banff National Park, approximately 5 km east of the study area in March 1997 (K. Schroeder personal communication).

Human Development and Activity

Substantial human development and activity occur within the study area. Most of this activity is directly associated with the Trans Canada Highway and the Canadian Pacific Railway, which run parallel to each other through Kicking Horse Pass (Figure 3). The Trans Canada Highway is a two lane highway and it receives heavy passenger vehicle and commercial truck



use year round as Canada's primary east-west transportation corridor (Figure 4). The Canadian Pacific Railway is single track for the portion passing through the study area. The railway receives substantial use as one of Canada's two national rail corridors with approximately 25-30 trains/day (K. Schroeder personal communication).

Within the study area and along the Trans Canada Highway is a motel development with a gas station and cabins. Other developments include the two lane 1A Highway, which is used by passenger vehicles during the summer. The 1A is closed during the winter, becoming a cross country ski trail. Similarly, the Lake O'Hara Fire Road is closed to passenger vehicles during the winter and becomes a cross country ski trail.

There are two hiking trails in the study area and both are used for cross country skiing during the winter. The Ross Lake trail begins along the 1A Highway and continues south to Ross Lake and then west to the Lake O'Hara Fire Road. The Sherbrooke Lake trail begins at the Trans Canada Highway and continues north to Sherbrooke Lake. Except for the Lake O'Hara Fire Road, which is used by 10-50 parties each week on average and also has some snowmobile traffic - approximately 5-10 round trips each week - the remainder of the ski trails in the study area are normally used by fewer than 10 parties each week (K. Schroeder personal communication). Approximately 80% of all ski traffic in the study area occurs on Saturday or Sunday (D. Petersen personal communication).

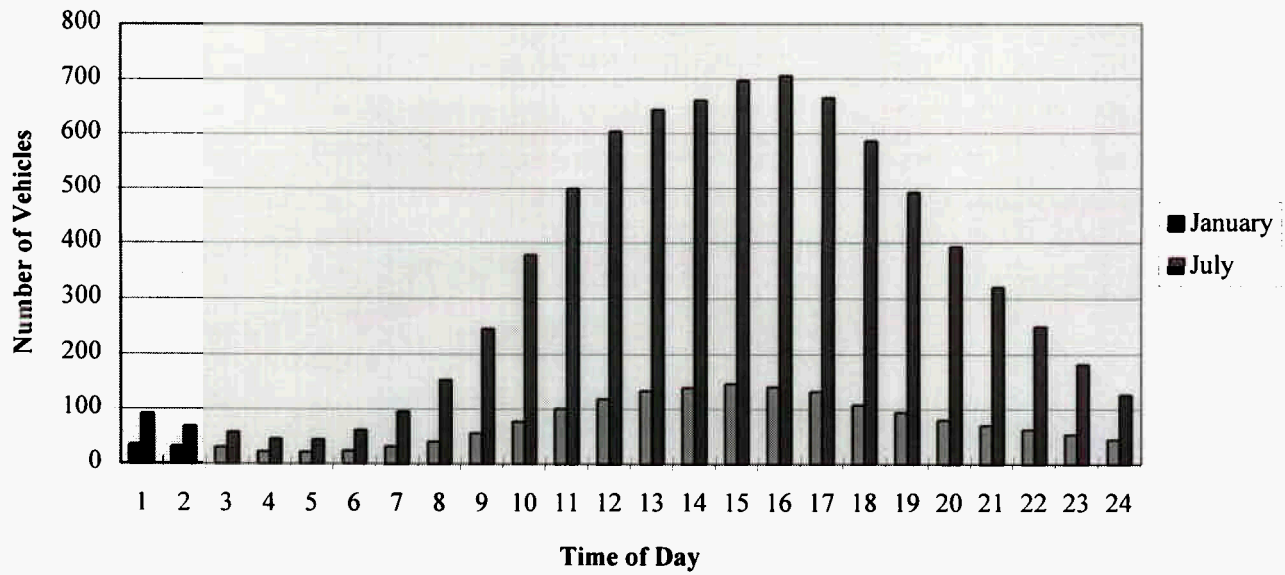


Figure 4: Average traffic volume by hour in January and July for the Trans Canada Highway through Kicking Horse Pass from 1993-1997 (B. Persello unpublished data)

METHODS

The "Loop" Method of Snow-tracking

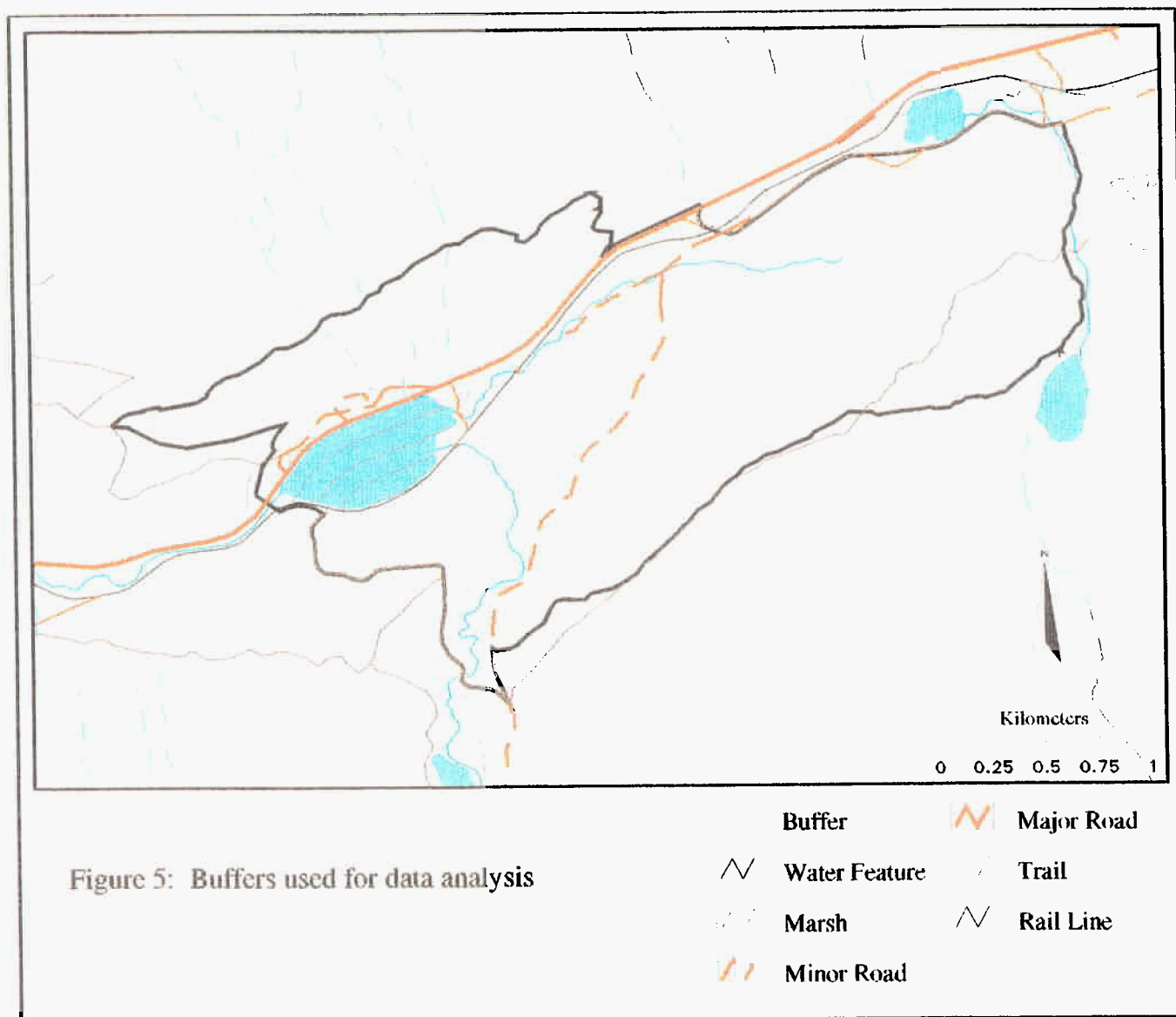
To compare habitat use versus availability for wolverines, the study area was bounded by a loop ski trail (Figure 3). The loop trail was usually skied in one day by myself or my field assistant. Occasionally we would need part of the next day to complete the route. On average the boundary trail was skied twice each week during the first field season and five times each week during the second. All wolverine trails travelling on the loop trail or crossing into the study area were located and recorded using a Global Positioning System (Garmin GPS 45). The accuracy of uncorrected GPS locations is about 40 m 50% of the time and 100 m 95% of the time (Hurn 1989).

After we had skied the entire loop we tracked wolverine trails that entered the study area in random order using the GPS to record waypoints every 100-300 m. A few trails were not completed due to weather or lack of time. Only trails that we followed completely from entrance to exit were included for data analysis. We also periodically followed trails beyond the study area to provide information on where wolverines were travelling to and from.

Data Analysis

All geographic data analysis was done using a Geographic Information System (ARC/INFO). The influence of the Trans Canada Highway on wolverine movements was investigated by determining the proportion of the total wolverine movements documented in the study area that occurred within each of a series of 100 m buffers based on horizontal distance from the highway (e.g. 0-<100 m, 100-<200 m etc.) (Figure 5). I amalgamated buffers on either side of the highway for analysis. The result of this was a measure of use as a percentage of total movements within each buffer. I also conducted the same analysis on wolverine movements on the loop ski trail that formed the study area boundary.

Availability for movements within the study area was measured by determining the areal proportion of each buffer within the study area. A comparison of two dimensional and three dimensional area measurements resulted in a consistent and negligible (2-4%) increase in the



area of each buffer for three dimensional measurements, therefore two dimensional measurements were used for simplicity. Availability for movements on the boundary ski trail was defined as the proportion of the boundary ski trail within each buffer. Relative use was calculated using Vanderploeg and Scavia's relativized electivity index, E^* (1979). An index of $E^*=0$ indicates that use and availability are equal (no avoidance or preference). The maximum levels of avoidance and preference possible with this index are $E^*=-1.0$ and $E^*=1.0$, respectively. Vanderploeg and Scavia's relativized electivity index (1979) is considered the best of the available electivity indices (Lechowicz 1982).

To determine if there was a directional bias to wolverine movements through the study area, the straight line east-west and north-south distances travelled between the entrance and exit points of the study area were determined for each trail. As the axis of travel was of interest, not the direction, I measured movements in the same manner regardless of the direction of travel. The distance travelled along each axis was then compared by dividing the total movement on the east-west axis by the total travelled on the north-south axis.

To test the assumption that the shape of the study area has no influence on this measure, a 100 m grid consisting of north-south and east-west lines was placed on the study area. The total length of the east-west lines was then divided by the total length of the north-south lines.

To determine the influence of the width of the right-of-way on highway crossing by wolverines, the distance between cover at all of the points where wolverines were observed crossing the Trans Canada Highway was measured using a GPS (Trimble Prolite) with differential correction. The width of the right-of-way at crossing locations was compared with the width at points where wolverines approached to the edge of cover but did not cross. Differentially corrected GPS locations are usually accurate within 1-2 m, although location error may be as large as 5 m at times (J. Buchanan-Mappin personal communication). I used a *t*-test to determine if the width of the right-of-way at crossing points was significantly smaller than points where wolverines approached without crossing.

RESULTS

The Influence of the Trans Canada Highway

I documented 22.6 km of complete wolverine movements through the study area and these were used to examine the influence of the Trans Canada Highway (Figure 6, Table 1). I amalgamated buffers where necessary for analysis to ensure that no buffer represented less than 5% of the study area. Relative use of the 0-<100 m buffer was quite low, with $E^* = -0.84$. Relative use of the remainder of the study area showed little deviation from the expected ($E^* = 0$) except for the 900-<1000 m buffer, which had low relative use ($E^* = -0.36$) and the 1100-<1500 m buffer, the furthest from the highway, which had the highest relative use with $E^* = 0.34$ (Figure 7).

I also recorded 20.0 km of wolverine movements on the ski trails that formed the boundary of the study area (Table 2, Figure 8). As with the analysis of movements within the study area, I amalgamated buffers where necessary to ensure that no buffer represented less than 5% of the boundary ski trail. Of the total wolverine movements documented on the boundary ski trail, 72% (14.5 km) were on trails greater than 1100 m from the highway. Although 20% of the boundary ski trail was within 200 m of the Trans Canada Highway, I observed no wolverine movements this close to the highway on the boundary ski trail. As a result, relative use of the ski trails within the 0-<100 and 100-<200 m buffers was as low as possible, with $E^* = -1.0$. The 200-<300 m buffer also had very low relative use ($E^* = -0.64$) while the 300-<400, 400-<500 and 500-<600 m buffers showed little deviation from the expected. Relative use of the 600-<700 m buffer was lower than expected ($E^* = -0.36$) and very low for the 700-<1100 m buffer ($E^* = -0.97$). The 1100-<1200 m buffer contained 44% of the movements documented on the boundary ski trail and had the highest relative use with $E^* = 0.54$. The 1200-<1300 and 1300-<1500 m buffers both had higher than expected use as well ($E^* = 0.32$ and 0.34 respectively).

Axes of Movements

The 18 movements within the study area with defined entrance and exit locations were

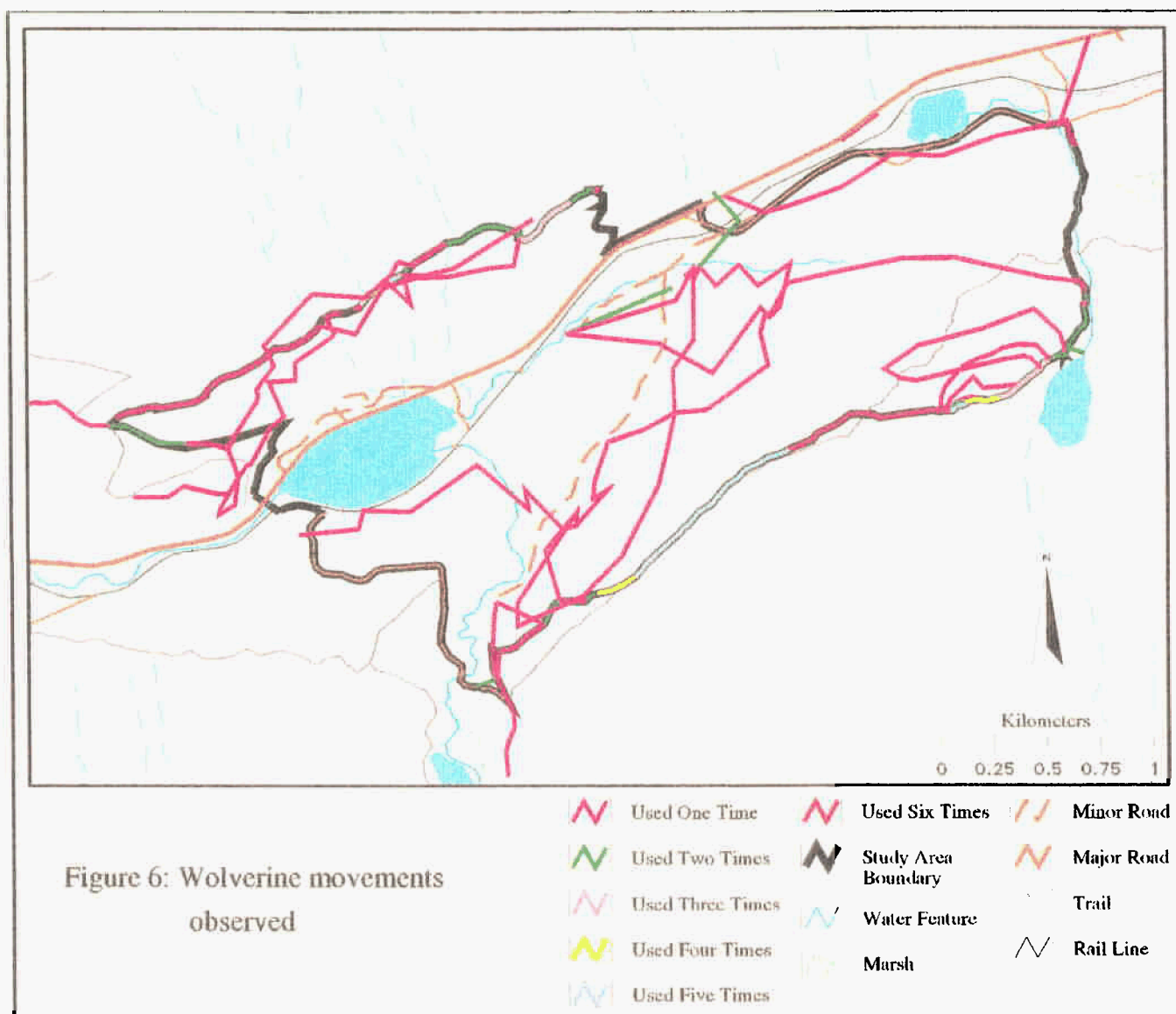


Table 1: Relative use based on distance from the Trans Canada Highway (TCH) for wolverine movements within the study area

| Distance from the TCH (m) | Area Within Buffer (m²) | (Availability) | Wolverine Movements (m) | (Use) | E* |
|--------------------------------------|---|-----------------------|------------------------------------|--------------|-----------|
| 0-<100 | 468949 | 8.66% | 168 | 0.74% | -0.84 |
| 100-<200 | 489809 | 9.04% | 2038 | 8.99% | 0.01 |
| 200-<300 | 552414 | 10.20% | 2660 | 11.73% | 0.09 |
| 300-<400 | 589613 | 10.88% | 2716 | 11.98% | 0.06 |
| 400-<500 | 569637 | 10.51% | 2902 | 12.80% | 0.11 |
| 500-<600 | 472533 | 8.72% | 2054 | 9.06% | 0.03 |
| 600-<700 | 396079 | 7.31% | 1550 | 6.83% | -0.02 |
| 700-<800 | 358505 | 6.62% | 1122 | 4.95% | -0.13 |
| 800-<900 | 342939 | 6.33% | 1330 | 5.86% | -0.02 |
| 900-<1000 | 341455 | 6.30% | 648 | 2.86% | -0.36 |
| 1000-<1100 | 348564 | 6.43% | 1472 | 6.49% | 0.02 |
| 1100-<1500 | 486953 | 8.99% | 4019 | 17.72% | 0.34 |
| Total | 5417448 | 100.00% | 22679 | 100.00% | |

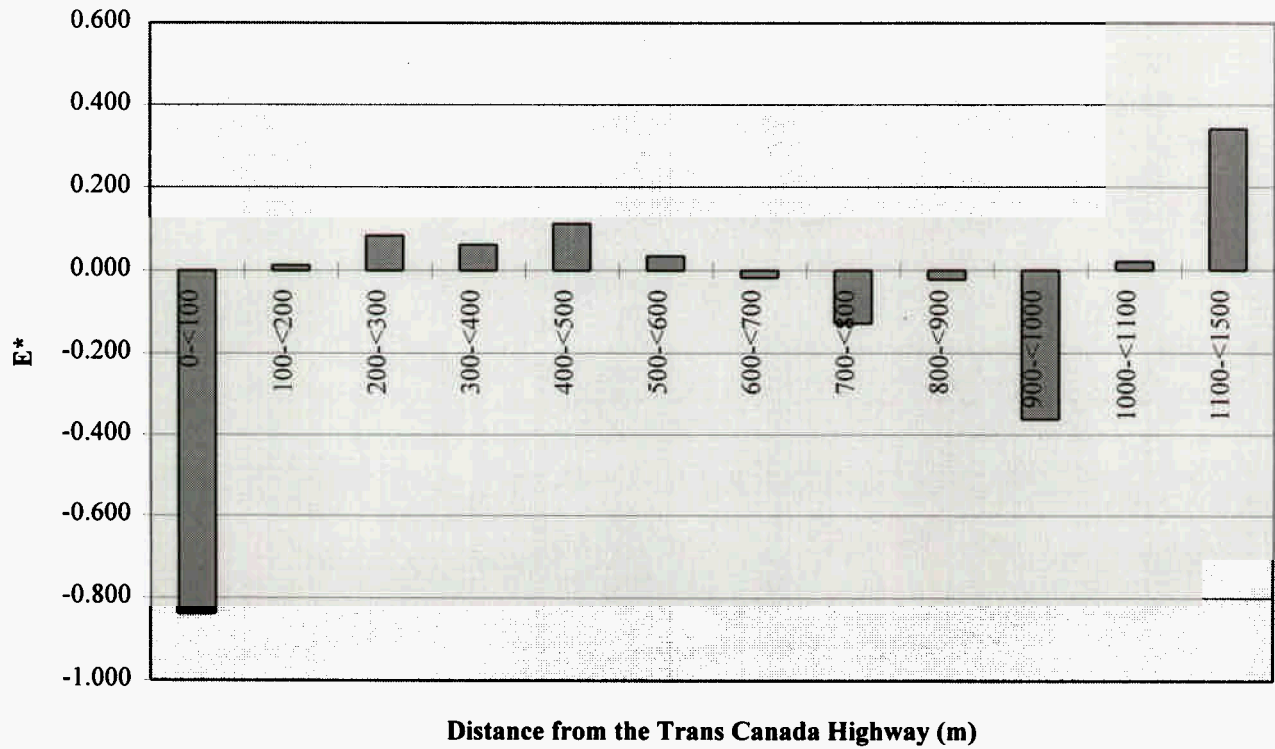


Figure 7: Relative use based on distance from the Trans Canada Highway for wolverine movements within the study area

Table 2: Relative use based on distance from the Trans Canada Highway (TCH) for wolverine movements along the study area boundary

| Distance from the TCH (m) | Length of Boundary Trail (m) | (Availability) | Wolverine Movements (m) | (Use) | E* |
|--------------------------------------|---|-----------------------|------------------------------------|----------------|-----------|
| 0-<100 | 1411 | 10.22% | 0 | 0.00% | -1.00 |
| 100-<200 | 1381 | 10.00% | 0 | 0.00% | -1.00 |
| 200-<300 | 1184 | 8.58% | 335 | 2.34% | -0.63 |
| 300-<400 | 1031 | 7.47% | 1114 | 7.77% | -0.08 |
| 400-<500 | 1349 | 9.77% | 1439 | 10.04% | -0.09 |
| 500-<600 | 1368 | 9.91% | 2203 | 15.36% | 0.12 |
| 600-<700 | 710 | 5.14% | 422 | 2.94% | -0.36 |
| 700-<1100 | 1048 | 7.59% | 22 | 0.15% | -0.97 |
| 1100-<1200 | 2079 | 15.06% | 8804 | 44.00% | 0.54 |
| 1200-<1300 | 887 | 6.42% | 2184 | 10.91% | 0.32 |
| 1300-<1500 | 1359 | 9.84% | 3488 | 17.43% | 0.34 |
| Total | 13808 | 100.00% | 20011 | 100.00% | |

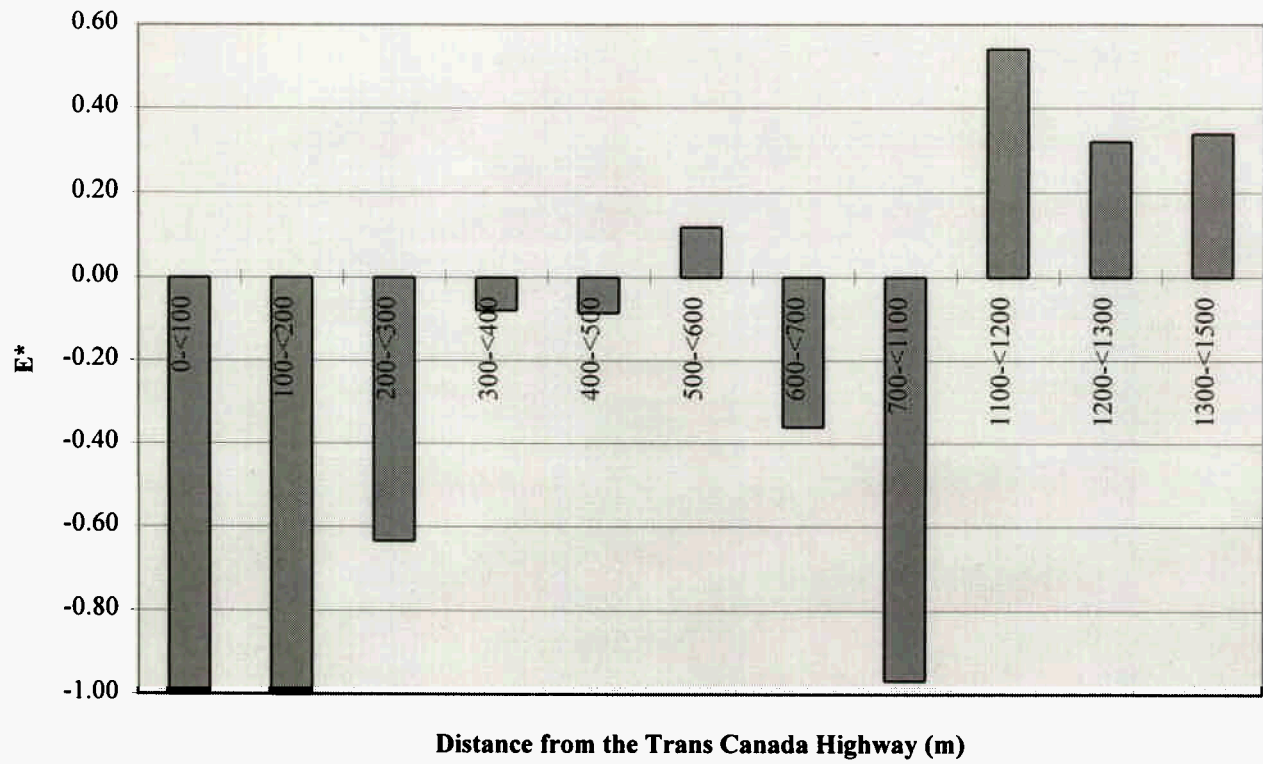


Figure 8: Relative use based on distance from the Trans Canada Highway for wolverine movements along the study area boundary

used to examine the directional bias of wolverine movements (Table 3). The total distance travelled on the east-west axis by these movements was 8817 m, almost twice (1.93 times) the distance, 4562 m, travelled on the north-south axis. Of the 18 movements, only 4 involved a greater distance travelled on the north-south axis than the east-west axis. When the same calculation was done for the Trans Canada Highway based upon its entrance and exit from the study area, the result was quite similar to that of the total wolverine movements. The highway traverses over twice (2.03) the distance on the east-west axis as on the north-south axis as it passes through the study area (Table 3).

The results from the test of the effect of study area shape on this measure were as predicted. The length of the east-west lines was 55.3 km compared with 52.9 km for the north-south lines. These results are very similar (1.05 times greater distance along the east-west axis than the north-south axis) and support the assumption that study area shape has no influence on the measurement of directional bias. For any study area the expected result of random movements with respect to two perpendicular axes would be equal movements along each axis.

Highway Crossing

I observed three instances of wolverines crossing the Trans Canada Highway and three instances where wolverines approached the highway to the edge of the right-of-way and then did not cross (Figure 9, Table 4). I documented all crossings and approaches during the first field season of the study (1994-95). A one tailed *t*-test was used to test the hypothesis that the crossings had shorter distances across the right-of-way and was significant ($p < 0.017$). For both crossings and non-crossings I observed a similar behaviour pattern. Wolverines tended to approach the edge of the right-of-way and retreat back into cover several times before either crossing or abandoning the attempt.

Railway Crossing

The Canadian Pacific Railway and the Trans Canada Highway share a combined right-of-way in many locations within the study area and the surrounding area. Wolverines that crossed the highway at these locations also crossed the railway. This occurred once. In areas where the

Table 3: Distance travelled along the east-west and north-south axes for wolverine movements and the Trans Canada Highway (TCH)

| Movement | East-West Axis (m) | North-South Axis (m) | East-West/North-South |
|-----------------|---------------------------|-----------------------------|------------------------------|
| 1 | 221 | 371 | 0.60 |
| 2 | 324 | 469 | 0.69 |
| 3 | 1068 | 499 | 2.14 |
| 4 | 988 | 278 | 3.56 |
| 5 | 30 | 30 | 1.02 |
| 6 | 12 | 16 | 0.77 |
| 7 | 98 | 25 | 3.93 |
| 8 | 80 | 23 | 3.47 |
| 9 | 543 | 130 | 4.18 |
| 10 | 260 | 93 | 2.80 |
| 11 | 1007 | 1600 | 0.63 |
| 12 | 1589 | 427 | 3.72 |
| 13 | 1366 | 234 | 5.84 |
| 14 | 82 | 24 | 3.37 |
| 15 | 136 | 35 | 3.89 |
| 16 | 126 | 62 | 2.02 |
| 17 | 346 | 77 | 4.48 |
| 18 | 543 | 172 | 3.16 |
| Total | 8817 | 4562 | 1.93 |
| TCH | 2231 | 1099 | 2.03 |

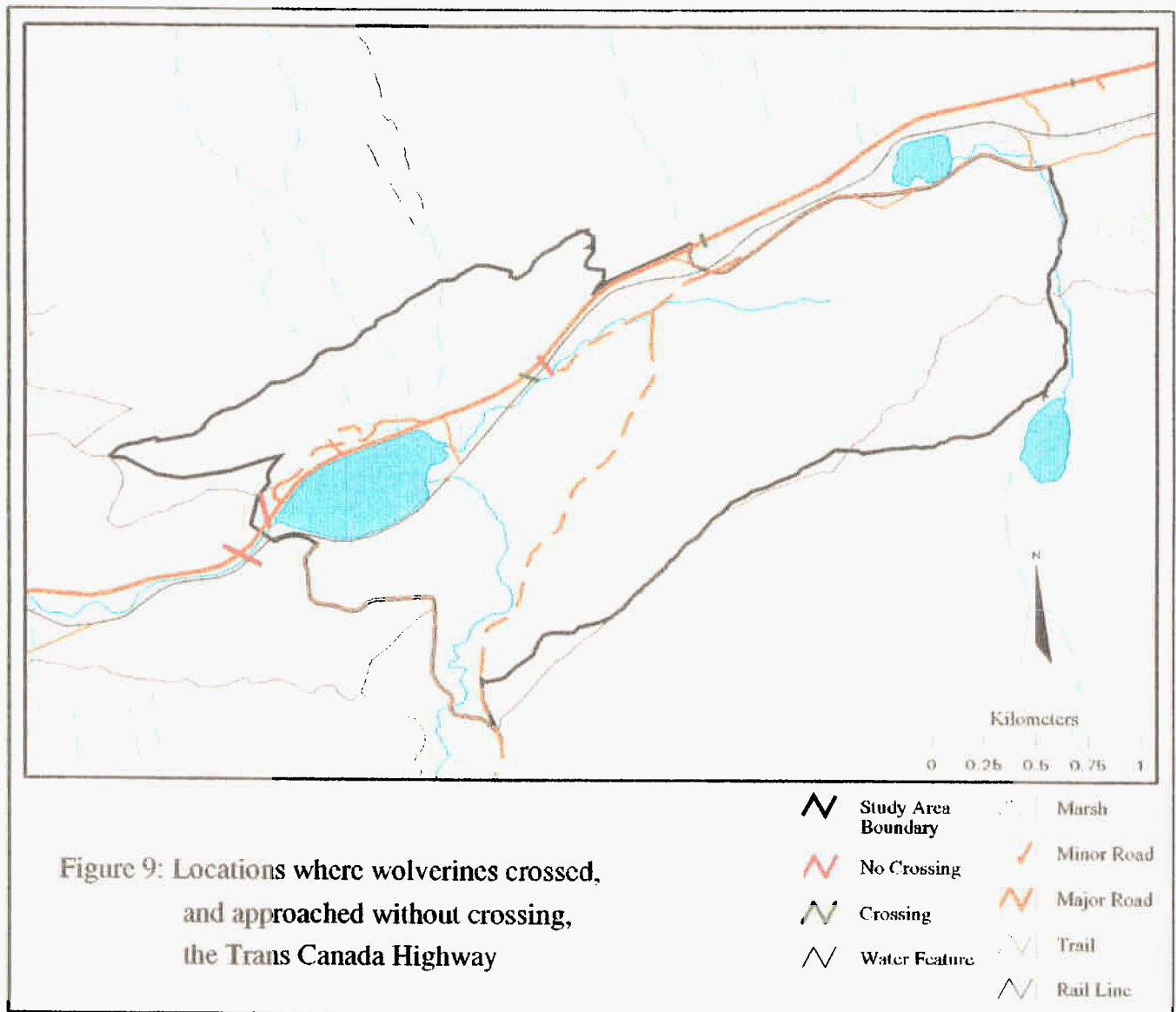


Figure 9: Locations where wolverines crossed, and approached without crossing, the Trans Canada Highway

Table 4: Width of the right-of-way for locations where wolverines crossed, and approached without crossing, the Trans Canada Highway

| Crossing | Width of the Right-of-Way (m) |
|-----------------|--------------------------------------|
| 1 | 39 |
| 2 | 66 |
| 3 | 100 |
| Mean | 68 |
| Approach | |
| 1 | 117 |
| 2 | 177 |
| 3 | 202 |
| Mean | 165 |

rights-of-way for the highway and railway are separated, wolverines showed no reluctance to cross the railway. I documented wolverines crossing the railway where it is separated from the highway on three occasions. I did not observe wolverines retreating after approaching the edge of the railway right-of-way where it is separated from the highway. In comparison, wolverines retreated twice without crossing after approaching the combined right-of-way for the highway and railway and once after approaching the highway right-of-way where it is separated from the railway.

Movements on Ski Trails

I documented a considerable amount (20.0 km) of wolverine movement on the boundary ski trail. The portions of the boundary ski trail that were furthest from, and oriented approximately parallel to, the highway were used most frequently. Portions of the boundary trail were used repeatedly. The greatest use was a section of the Ross Lake trail that wolverines travelled on six times (Figure 6).

Wolverine Feeding

The only definitive sign of wolverine feeding observed during the study was in early January 1994. The trails of what appeared to be three wolverines travelling together, led to a well used bedding site underneath a large conifer. The bed was well protected by the lower branches of the tree and snow. Some bone splinters and a small piece of hide (approximately 5 cm diameter) of a mule deer were found under the tree along with numerous wolverine scats.

DISCUSSION

The Influence of the Trans Canada Highway

I have presented results from two separate measures of the influence of the Trans Canada Highway on wolverine movements. The first was the relative use of the study area. The second was the relative use of the ski trails that formed the study area boundary. The results of the analysis of wolverine movements within the study area are discussed first.

I observed the strongest avoidance of the buffer closest to the highway (0-<100 m) and strongest preference for the buffer furthest from the highway (1100-<1500 m), which supports the hypothesis that wolverines avoid areas near the highway. Moderate avoidance of areas 900-<1000 m from the highway may reflect the small sample size and the small area of this buffer.

The results of the analysis of wolverine movements on the ski trails that formed the study area boundary show the same general trend. There was complete avoidance of ski trails within 200 m of the highway, strong avoidance of ski trails 200-<300 m from the highway, no evidence of selection or avoidance of portions of the boundary ski trail that were 300-<600 m from the highway and strong preference for ski trails 1100-<1500 m from the highway. Avoidance of the portions of the ski trail within the 600-<700 m buffer and very strong avoidance of the 700-<1100 m buffer may be due to the orientation of the boundary ski trail within those buffers, which was predominantly north-south. Correlations between distance from the highway and attributes of ski trails such as human use levels, right-of-way width, orientation and other factors that potentially influence wolverine use may have biased these results. This may also explain why the trend observed in this analysis is more pronounced than was observed for the movements within the study area. Despite these complicating factors, the results of this analysis closely match the results of the first analysis and further support the hypothesis that wolverines avoid areas close to the Trans Canada Highway.

I obtained these results during the winter. I expect the influence on wolverines to be greater during the summer when both the traffic volume on the Trans Canada Highway (Figure 4) and other human activity in the study area increase dramatically. Combined with the tendency

of wolverines to use higher elevations during the summer, possibly in part to avoid humans (Hornocker & Hash 1981), I predict that wolverine use of the lower elevations in Kicking Horse Pass is much lower during the summer months.

Axes of Movements

Wolverine movements in the study area showed a strong bias toward the east-west axis and this trend was relatively consistent across movements. This supports the hypothesis that Kicking Horse Pass is predominantly used as an east-west movement corridor by wolverines as suggested by McCrory & Blood (1978). The sheer number of wolverine trails detected in such a small study area, the extensive movements observed on ski trails, as well as the evidence from tracking of little foraging activity also support this conclusion.

Avoidance of the Trans Canada Highway does not appear to be restricting wolverine use of this movement corridor along the east-west axis. It may, however, have seriously compromised a previous north-south movement corridor to the west of the study area between the Sherbrooke Creek drainage and the Cataract Brook drainage (Figure 2, Figure 3). Wolverines moving through the pass appear to avoid crossing or coming close to the highway and therefore the highway is probably limiting movement along the north-south axis of individuals travelling through Kicking Horse Pass.

The relative distance travelled by wolverines along the two axes is similar to that of the Trans Canada Highway, which suggests that the highway is causing wolverines to travel along routes that are parallel to the highway (Figure 6). The high level of use by wolverines of trail segments on both sides of the highway that generally parallel the highway further supports this interpretation.

Highway Crossing

The width of the right-of-way affects crossing of the Trans Canada Highway by wolverines. Individuals were more likely to cross the highway where the right-of-way is short; the longest distance crossed by a wolverine was 100 m. Based upon the behaviour of wolverines when approaching the right-of-way, it appeared that they were quite agitated. I speculate that

due to their sensitivity to human disturbance, wolverines often do not attempt to cross the highway if they detect a vehicle approaching. This may mean that traffic volume is critical.

Crossings may be more likely to occur at night when traffic volume is at its lowest level (Figure 4). Wolverines tend to use areas in proximity to human activity and development at night (Hash 1987). Stevens et al. (1996) observed a wolverine trail that repeatedly approached two different roads in Banff National Park and retreated each time without crossing. This movement occurred during the morning when traffic volume on these roads is relatively high.

While wolverines appear to select areas where the distance across the right-of-way is short, given that a wolverine attempts to cross a road, the likelihood of it being killed by a vehicle may increase with increasing distance across the right-of-way. This may be due to an increased chance that a wolverine does not detect an approaching vehicle, which may be more likely where sight lines are shorter such as along winding roads. The ideal design of a road with high traffic volume for wolverines may be one that is straight with a narrow right-of-way of less than 50 m.

The incident previously mentioned of a wolverine being killed on the Trans Canada Highway in March 1997 illustrates how wolverines may select for short right-of-way distances when crossing roads. The wolverine was killed at a location where the width of the right-of-way is approximately 90 m. This is the narrowest section of the right-of-way for over one kilometer in either direction (K. Shroeder personal communication).

Highway underpasses or overpasses for wildlife may also prove effective for wolverines especially if adequate cover is provided. Wolverines have not been documented using the wildlife underpasses under the divided portion of the Trans Canada Highway in Banff National Park (Gibeau & Heuer 1996). However, these structures were primarily designed for ungulates with minimal cover provided (V. Geist personal communication) and wolverine activity in the surrounding area is quite low.

Railway Crossing

Where the right-of-way of the railway is separate from that of the highway, it appears to have little if any influence on wolverine movements. This is likely because, for the most part, little human activity occurs along the railway. If a wolverine approached the railway when there was traffic, I expect that this would deter crossing at least in the short-term.

Although not observed during this study, the greatest concern regarding the railway is the potential mortality of wolverines that are struck by rail traffic. An ongoing wolverine study in the Columbia Mountains of British Columbia has documented one wolverine mortality on the Canadian Pacific Railway associated with feeding on a rail killed moose (*Alces alces*) (J. Krebs personal communication).

Movements on Ski Trails

I frequently documented wolverine movements on ski trails with wolverines appearing to favour travelling on the packed snow for ease of movement. At the current low level of human use, wolverines appear to actively seek out these transportation corridors in the winter. It is not known what levels of human activity on these trails would preclude or reduce their use by wolverines or whether they receive similar use during the summer.

While there was wolverine activity detected throughout the study area, the area to the north and west of Ross Lake was particularly heavily used by wolverines. The boundary ski trail in this area was frequently used with some movements following it for a kilometer or more.

Although most of the movements documented in this area were of wolverines travelling on the ski trail, this is one of the only areas where I observed signs of foraging behaviour (erratic trails with periodic investigation of tree wells). The area to the south of the ski trail and west of Ross Lake on Narao Peak has the general habitat characteristics described by Copeland (1996) as those of wolverine denning sites. Given this, and the wolverine activity and behaviour I observed, I consider this area a potential denning site.

Wolverine Feeding

I do not know whether a wolverine(s) killed or scavenged the deer whose remains were

found. No road killed deer had been reported recently in that area and no activity by any other large carnivores, except coyotes, was observed at any time during the study. Snow depth exceeded 30 cm in the study area at that time. Deer tracks observed suggested that deer would have had difficulty escaping predators if pursued. Wolverine tracks observed showed that wolverines were not sinking into the snow and could move easily. Wolverines have been known to prey upon ungulates when snow depths hamper their movements (Grinnell 1920, 1926; Burkholder 1962; Haglund 1974; E. Lofroth personal communication, personal observation).

Management Implications

I have provided strong evidence that the Trans Canada Highway has a negative impact on wolverine winter movements through Kicking Horse Pass. The pass appears to be an important movement corridor across the Continental Divide for this vulnerable species and almost certainly provided greater opportunities for wolverines to move along the north-south axis across the pass before the construction of the highway. Wolverines avoided areas within 100 m of the highway, preferred areas >1100 m and selected for areas where the distance across the right-of-way is relatively short when they did cross it.

Despite this impact, Kicking Horse Pass area may still offer some of the best remaining opportunities for north-south movement across the Trans Canada Highway within the Rocky Mountains. This is due to the amount of wolverine activity along the Continental Divide and the narrow sections in the right-of-way found along this two lane section of the highway.

Roads have the potential to seriously affect wolverines both directly and indirectly and must be planned carefully to ensure that these impacts are properly mitigated. Based on my results, I suggest that roads should be avoided where possible in wolverine habitat, especially in important movement corridors such as low elevation passes. Where a road is necessary, designers should seek to maintain as narrow a right-of-way as is practical (<50 m) in order to reduce the impact on wolverines. For a divided highway one way to accomplish this would be to maintain separate rights-of-way for both sides with as much distance and cover as possible

provided in between. The use of wildlife crossing structures should be further investigated to determine their effectiveness for wolverines.

Given these findings it may also be desirable to avoid having a combined right-of-way for parallel transportation corridors such as a highway and a railway. As with a divided highway, I would expect two narrower rights-of-way separated by 50+ m of cover to allow greater wolverine movement than one wider, combined right-of-way.

Managers should be aware that ski and snow machine trails may attract wolverines during the winter as travel routes. However, above a certain low level of human use these activities, particularly the use of snow machines, may disturb and displace wolverines from areas. Of greatest concern is the potential for displacement from natal and maternal denning sites (Copeland 1996). In areas of known wolverine activity such as Kicking Horse Pass and particularly in potential or known denning habitat, human use and wolverine activity should be carefully monitored. Where increasing human use may be affecting wolverines, actions such as trail or area closures, limits on use levels or types of use and other options to mitigate this impact should be considered.

LITERATURE CITED

- Achuff, P. L., W. S. Taylor, and L. J. Knapik. 1993. Ecological land classification of Yoho National Park, British Columbia. Unpublished manuscript. 283pp.
- Aune, K. W., and W. F. Kasworm. 1989. Final report on East Front grizzly bear study. Montana Department of Fish, Wildlife, and Parks, Helena, Montana. 332pp.
- Banci, V. 1987. Ecology and behaviour of wolverine in Yukon. M.Sc. Thesis, Simon Fraser University, Burnaby, British Columbia. 178pp.
- Banci, V., and A. S. Harestad. 1990. Home range and habitat use of wolverines *Gulo gulo* in Yukon, Canada. *Holarctic Ecology* **13**:195-200.
- Banci, V. 1994. Wolverine. pgs 99-127 In: **The Scientific Basis for Conserving Forest Carnivores in the Western United States: American Marten, Fisher, Lynx and Wolverine**. L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski (eds). USDA Forest Service General Technical Report RM-254.
- Becker, E. F. 1991. A terrestrial furbearer estimator based on probability sampling. *Journal of Wildlife Management* **55**:730-737.
- Boles, B. K. 1977. Predation by wolves on wolverines. *Canadian Field-Naturalist* **91**:68-69.
- Brody, A. J., and M. P. Pelton. 1989. Effects of roads on black bear movements in western North Carolina. *Wildlife Society Bulletin* **17**:5-10.
- Burkholder, B. L. 1962. Observations concerning wolverine. *Journal of Mammalogy* **43**:263-264.
- COSEWIC. 1994. Canadian species at risk: April 1994. Ottawa, Ontario. 12pp.
- Cockerton, D., and S. Herrero. 1973. A study of wolverine home range and behaviour by tracking. Unpublished manuscript. 23pp.
- Copeland, J. P. 1996. Biology of wolverine in central Idaho. M.Sc. Thesis, University of Idaho, Moscow, Idaho. 178pp.
- Coulter, M. W. 1966. Ecology and management of fishers in Maine. Ph.D. Thesis, Syracuse University, Syracuse, New York. 196pp.

- Cowan, I. McT. 1944. Report on game conditions in Banff, Jasper and Kootenay National Parks. Unpublished manuscript. (cited by McCrory & Blood 1978)
- Gardner, C. L. 1985. The ecology of wolverines in southcentral Alaska. M.Sc. Thesis, University of Alaska, Fairbanks, Alaska. 82pp.
- Gardner, C. L., W. B. Ballard, and R. H. Jessup. 1986. Long distance movement by an adult wolverine. *Journal of Mammalogy* **67**:603.
- Gibeau, M. L., and K. Heuer. 1996. Effects of transportation corridors on large carnivores in the Bow River Valley, Alberta. pgs 67-79 In: **Transportation and wildlife: reducing wildlife mortality and improving wildlife passageways across transportation corridors**. G. Evink, D. Ziegler, P. Garrett, and J. Berry (eds). Florida Department of Transportation, Tallahassee, Florida.
- Grinnell, G. B. 1920. As to the wolverine. *Journal of Mammalogy* **1**:182-184.
- Grinnell, G. B. 1921. The tree-climbing wolverine. *Journal of Mammalogy* **2**:36-37.
- Grinnell, G. B. 1926. Some habits of the wolverine. *Journal of Mammalogy* **7**:30-34.
- Haglund, B. 1966. Winter habits of the lynx (*Lynx lynx* L.) and wolverine (*Gulo gulo* L.) as revealed by tracking in snow. *Viltrevy* **4**:81-309.
- Haglund, B. 1974. Moose relations with predators in Sweden, with special reference to bear and wolverine. *Le Naturaliste Canadien* **101**:457-466.
- Harper, B., S. Cannings, D. Fraser, and W. T. Munro. 1994. Provincial lists of species at risk. pgs 16-23. In: **Biodiversity in British Columbia - Our Changing Environment**. L. Harding, and E. McCullum (eds). UBC Press, Vancouver, British Columbia.
- Hash, H.S. 1987. Wolverine. pgs 575-585. In: **Wild furbearer management and conservation in North America**. M. Novak, J.A. Baker, and M.E. Obbard (eds). Ontario Ministry of Natural Resources, Toronto, Ontario.
- Hornocker, M. G., and H. S. Hash. 1981. Ecology of the wolverine in northwestern Montana. *Canadian Journal of Zoology* **59**:1286-1301.
- Hurn, J. 1989. GPS: a guide to the next utility. Trimble Navigation, Ltd. Sunnyvale, Calif. 76pp.

- Kasworm, W. F., and T. M. Manley. 1990. Road and trail influences on grizzly bears and black bears in northwest Montana. *International Conference on Bear Research and Management* **8**:79-85.
- Koehler, G. M., M. G. Hornocker, and H. S. Hash. 1980. Wolverine marking behavior. *Canadian Field-Naturalist* **94**:339-341.
- Krott, P. 1960. Ways of the wolverine. *Natural History* **69**:16-29.
- Lechowicz, M. J. 1982. The sampling characteristics of electivity indices. *Oecologia* **52**:22-30.
- Lovallo, M. J. and E. M. Anderson. 1996. Bobcat movements and home ranges relative to roads in Wisconsin. *Wildlife Society Bulletin* **24**:71-76.
- Mace, R. D., J. S. Waller, T. L. Manley, L. J. Lyon, and H. Zuuring. 1996. Relationships among grizzly bears, roads, and habitat in the Swan Mountains, Montana. *Journal of Applied Ecology* **33**:1395-1404.
- Magoun, A. J. 1985. Population characteristics, ecology, and management of wolverines in northwestern Alaska. Ph.D. Thesis, University of Alaska, Fairbanks, Alaska. 197pp.
- Mattson, D. J., R. R. Knight, and B. M. Blanchard. 1987. The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. *International Conference on Bear Research and Management* **7**:259-273.
- McCrory, W. P., and D. A. Blood. 1978. An inventory of mammals in Yoho National Park. Unpublished manuscript.
- Mech, L. D., S. H. Fritts, G. L. Radde, and W. J. Paul. 1988. Wolf distribution and road density in Minnesota. *Wildlife Society Bulletin* **16**:85-87.
- McLellan, B. N., and D. M. Shackleton. 1988. Grizzly bears and resource extraction industries: effects of roads on behavior, habitat use and demography. *Journal of Applied Ecology* **25**:451-460.
- Myhre, R. 1968. Jerven i Norge. (The wolverine in Norway). M.Sc. Thesis, University of Oslo, Norway. 73pp. (Translated from Norwegian to English)

- Myhre, R., and S. Myrberget. 1975. Diet of wolverines (*Gulo gulo*) in Norway. *Journal of Mammalogy* **56**:752-757.
- Myrberget, S. 1968. Jervens ynglehi. *Fauna* **21**:108-115. (cited in Pulliainen 1968)
- Myrberget, S., B. Groven, and R. Myhre. 1969. Jervesporinger i Jotunheimen. (Tracking wolverines, *Gulo gulo*, in the Jotunheim mountains, South Norway, 1965-68). *Fauna* **22**:237-252. (Norwegian with summary in English)
- Pulliainen, E. 1968. Breeding biology of the wolverine (*Gulo gulo* L.) in Finland. *Annales Zoologici Fennici* **5**:338-344.
- Pulliainen, E. 1988. Ecology, status, and management of the Finnish wolverine *Gulo gulo* populations. *Lutra* **31**:21-28.
- Powell, R. A. 1977. Hunting behavior, ecological energetics and predator-prey community stability of the fisher (*Martes pennanti*). Ph.D. Thesis, University of Chicago, Chicago, Illinois. 132pp.
- Powell, R. A. 1979. Mustelid spacing patterns: variations on a theme by *Mustela*. *Zhurnal Tierpsychologie* **50**:153-165.
- Rausch, R. A., and A. M. Pearson. 1972. Notes on the wolverine in Alaska and the Yukon Territory. *Journal of Wildlife Management* **36**:249-268.
- Salt, J., C. Wallis, and C. Wershler. 1995. Yoho National Park ecological land classification (wildlife component): interim report, 1993-95. Unpublished manuscript. 168pp.
- Stevens, S., C. Callaghan, and R. Owchar. 1996. A survey of wildlife corridors in the Bow Valley of Banff National Park - Winter 1994/95. Unpublished manuscript. 41pp.
- Thurber, J. M., R. O. Peterson, T. D. Drummer, and S. A. Thomasma. 1994. Gray wolf response to refuge boundaries and roads in Alaska. *Wildlife Society Bulletin* **22**:61-68.
- Vanderploeg, H. A., and D. Scavia. 1979. Calculation and use of selectivity coefficients of feeding: zooplankton grazing. *Ecological Modelling* **7**:135-149.

- Van Dyke, F. G., R. H. Brocke, H. G. Shaw, B. B. Ackerman, T. P. Hemker, and F. G. Lindzey. 1986. Reactions of mountain lions to logging and human activity. *Journal of Wildlife Management*: **50**:95-102
- van Zyll de Jong, C. G. 1975. The distribution and abundance of wolverine (*Gulo gulo*) in Canada. *Canadian Field-Naturalist* **89**:431-437.
- Whitman, J. S., W. B. Ballard, and C. L. Gardner. 1986. Home range and habitat use by wolverines in southcentral Alaska. *Journal of Wildlife Management* **50**:460-463.