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Winter habitat selection by wolves in the North Fork of the Flathead River Basin Montana and British Columbia

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Winter Habitat Selection by Wolves in the North Fork of the Flathead River Basin, Montana and British Columbia.

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Animals select habitat at multiple scales. Many choose to use certain areas based on a continuum of characteristics ranging from broad landscape features to fine habitat structure conditions. Within areas that animals choose to use, they move along a continuous trajectory through space and time. By documenting habitat use by continuous snow tracking of grey wolves (*Canis lupus*), and analyzing this data at 3 spatial scales, I investigated habitat characteristics along travel routes and within home ranges.

I analyzed 11 winters of snow tracking data collected in the North Fork of the Flathead River drainage in northwestern Montana and southeastern British Columbia. I tested the following three hypotheses: 1) Home ranges differ from available area within the North Fork drainage in regard to landscape characteristics. 2) Intra-territorial travel routes differ from areas within home ranges in regard to landscape characteristics. 3) Travel routes differ from areas nearby in regard to structural habitat features.

I used a geographic information system (GIS) for the analysis of the landscape characteristics of home ranges and travel routes. Home ranges were delineated using a combination of radio telemetry and snow tracking. Travel routes were identified from ground snow tracking. Habitat characteristics of home ranges and travel routes were determined using GIS overlays on digital maps of slope, vegetation type, topographic position, distance to water, distance to open roads, and total road density. A total of 2748 km of tracking routes and 14 winter home ranges were analyzed. Comparison of home ranges to available habitat within the basin found significant differences between use and availability of topographic position, slope, aspect, distance to water, vegetation, and road density classes. Comparison of travel routes to home ranges found significant differences between use and availability of topographic position, slope, aspect, distance to roads, distance to water, and road density.

During the winter of 1993-94 we collected data on the structural habitat and snowpack characteristics of wolf travel routes and areas adjacent to travel routes. Substantial differences between travel routes and adjacent areas were not detected.

Acknowledgments

Scientific investigation is a process of building on the work of one's predecessors. The research presented in this thesis is certainly an example of this axiom. To thank all those who laid the groundwork for and helped me in this process would take too much space. I wholeheartedly thank all of you, you know who you are. But, there are a few names I would like to mention.

Diane Boyd and Mike Jimenez were my mentors in wolf research and became good friends in the process, thank you! Kyran Kunkle provided essential input and support during my field work in the winter of 1993-94. He and the North Fork field technicians, Wendy Clark, Sarah Cooper, Gordon Dicus, Blair French, Winsor Lowe, and Mark Rohweder, made my field season a success. The logistical support provided by the National Park Service, particularly Scott Emerich, Polebridge District Ranger, was very much appreciated. Thanks also to Mike Fairchild and all the previous North Fork researchers and field technicians that contributed to documenting the nearly 3000 km of snow tracking that I analyzed.

Special thanks go to the GIS and computer support staff at the School of Forestry, Rohn Wood, Scott Perl, Ken Wall, Mike Sweet, and Joe Grigsby. Thanks for getting me through system crashes, data translations, and unintelligible syntaxes! Essential statistics advice came from Hans Zurring, Dave Patterson, and Rich Harris.

My committee members, Erick Green and Dan Pletscher, were indispensable throughout the process. Dan Pletscher, in addition to being one of the best teachers I have ever encountered, provided invariably good advice and always made time for questions. My advisor, Bob Ream, contributed consistent support, encouragement, and friendship. Bob's smile and good humor were always a treat!

Thanks is also due to the graduate student community in Wildlife Biology and the School of Forestry. It takes someone else going through the grad school experience to know when to say you are taking things too seriously. You guys were right up there with sunny days in the North Fork in terms of making sure that this experience had an element of fun and laughter.

Finally, I would like to thank everyone who takes the time to sit down and page through my work. Thanks for being interested, and thanks for thinking about the ideas and results that I present here.

Dedication

To the wolves of the North Fork,

who have carried the burden of this project (and many others) in radio collars and

bruised paws. I hope it's been worth it guys!

To Anne and John Singleton,

whose constant support provided an anchor to weather the ups and downs of a long and

sometimes difficult journey.

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Chapter 1: INTRODUCTION

Although the gray wolf (*Canis lupus*) was once common throughout the western United States, the species had become extremely rare by the mid-1930s. The primary causes of its decline were human persecution and concerted predator control efforts (Day 1981). Sightings of wolves in western Montana were sporadic through the 1970s. In 1979 a lone female wolf was radio-collared in the North Fork of the Flathead River basin (Ream et al. 1985). The first denning of wolves in the North Fork basin was documented in 1982, approximately 6 km north of the Canadian border. In 1986 the first known denning of wolves in the western United States in approximately 50 years occurred in the western portion of Glacier National Park (Ream et al. 1989). By the completion of my field work, in the spring of 1994, the wolf population in the North Fork basin had grown to approximately 35-45 individuals in 3 packs, and dispersers were regularly leaving the area to establish territories in other parts of Montana, Alberta, British Columbia, and Idaho (Diane Boyd pers. commun.).

In 1979 the Wolf Ecology Project of the University of Montana was established (Ream et al. 1991, Pletscher et al. 1991). Research on population dynamics, food habits, predation rates, and movement patterns of wolves in the North Fork has continued since that time. More than a decade's worth of wolf movement information has been gathered. These spatially explicit data were the central focus for this study.

Research Objectives

My objectives were to quantitatively describe habitat characteristics of winter home ranges and travel routes used by wolves in the North Fork drainage, and to identify characteristics that influence the selection of these areas. To meet my objectives, I tested the following three hypotheses; 1) that home ranges differed from available area within the North Fork drainage in regards to landscape characteristics such as forest cover type, distance to water, road density and other features, 2) that travel routes differed from areas within the home ranges in regards to the same landscape characteristics identified for the first hypothesis, and 3) that travel routes differed from areas nearby in regards to structural habitat features such as canopy closure, hiding cover, and other characteristics.

Habitat use by wolves

Wolves are not associated with any specific ecosystems. Wolves were distributed throughout the northern hemisphere prior to extensive predator control efforts (Mech 1970). Today, wolves occupy a variety of different habitats in many regions of the globe (Harrington and Paquet 1982). The present distribution of wolves is primarily limited by human caused mortality, intraspecific strife, disease, and prey abundance (Mech 1970, Mech 1977, Fuller 1989, Fuller 1995).

Most studies of wolf ecology have focused on population dynamics and predator-prey relationships (Fritts & Mech 1981, Nelson & Mech 1981, Messier 1985, Ream et al. 1986, Ballard et al. 1987, Ballard 1991, Pletscher et al. 1991, Ream et al. 1991, Carbyn et al. 1993, Huggard 1993a&b, Boyd et al. 1994, Weaver 1994, and others). Some of these authors have mentioned interesting patterns of habitat use by wolves. Bergerud (1985) suggested that territories of wolf packs in an area along the north shore of Lake Superior appeared to be oriented along rivers which the wolves used as travel routes when frozen. Fritts and Mech (1981) mentioned that wolves avoided treeless marshes and homogenous conifer forests, and that these areas sometimes functioned as buffers between territories. Snow depth (Nelson and Mech 1986, Fuller 1991), road density (Theil 1985, Mech and Fritts 1988), broad scale habitat suitability (Mladenoff 1995) and habitat characteristics of den sites (Ballard and Dau 1983, Ream et al. 1989, Ciucci and Mech 1992, Heard and Williams 1992, Matteson 1993) have been investigated in relation to wolf habitat use. Passing treatment of wolf habitat requirements has also been given in more general wildlife habitat works (Herman and Willard 1979, Cooperider et al. 1986, Frederick 1991).

While many authors have mentioned the existence of obvious intra-territorial movement routes (Mech 1970:153-159, Peters 1974, Bergerud 1985), none has provided a quantitative assessment of the characteristics of those travel routes.

Scale and the analysis of habitat use

The decisions that an animal makes in the habitat selection process are influenced by landscape and habitat structure at a variety of scales (Johnson 1980, Morse and Fritz 1982, Arditi and Dacorogna 1988, Dunning et al. 1992, Johnson et al. 1992). Hutto (1985) proposed that habitat selection for neotropical migrant birds involved a hierarchical series of choices. These choices range from the very broad scale (what part of the continent is good winter habitat) to the very fine scale (what part of a leaf holds the best foraging potential). Other authors have suggested that this paradigm of habitat selection is appropriate for non-avian species as well (Johnson 1980, Senft et al. 1987, Morrison et al. 1992:33-36, Aebischer et al. 1993).

Addressing research questions to multiple scales of habitat selection is critical to conservation of wildlife habitat. Many authors have noted the importance of determining appropriate spatial scales for ecological investigation (Wiens 1976, Johnson 1980, Morris 1987, Russell et al. 1992), but few have employed techniques and addressed hypotheses that investigate habitat selection at multiple scales (Aebischer et al. 1993, Ward and Saltz 1994). This issue is directly related to problems in identifying and comparing used and available habitat for habitat preference studies (Thomas and Taylor 1990, Porter and Church 1987, Johnson 1980, Aebischer et al. 1993).

Analysis of home range characteristics has been a focus of much research (e.g. Harestad and Bunnell 1979, Mace et al. 1984, Grant et al. 1992, Basset 1995). Home range has been defined as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young" (Burt 1943). Clearly, information on the area and habitat characteristics needed by an animal to meet its requirements for survival and reproduction are important for wildlife conservation.

The way an animal uses its home range is largely determined by the dispersion of resources within that area and the costs associated with moving between resource patches. Charnov's marginal value theorem (Charnov 1986) suggests that an animal will maximize its over-all rate of energy gain if it remains in a resource patch until its net rate of energy gain in that patch has decreased to the over-all rate in the habitat. The over-all rate of energy gain in the habitat is determined by patch quality, spatial distribution of patches, and travel time (or travel cost) between patches. Therefore, the characteristics of travel routes within home ranges can be of critical importance in determining the quality of the home range.

Patch utilization and residence time have been common research topics (see Stephens and Krebs 1986 for a review). Inter-patch travel and prey search patterns have also attracted attention (Crist et al. 1992, Dukas and Clark 1995, Dukas and Ellner 1993), but little has been done on characteristics of inter-patch travel for large free roaming mammals (Johnson et al. 1992).

Collection of spatial habitat use data

Most studies of habitat use have employed data from radio-telemetry or point observations to identify used habitat (e.g. Aebischer et al. 1993, Clark et al. 1993, Pauley et al. 1993, Pereira and Itami 1991, Stoms et al 1993). These can be excellent techniques for approximating habitat utilization patterns. However, habitat use is a trajectory through 4 dimensional space (3 geographic coordinates, and a time dimension) (White and Garrot 1990). Radio-telemetry provides a sample of discrete points in that 4 dimensional space and results in a "connect the dots" representation of movement patterns.

Full documentation of an animal's habitat utilization trajectory is desirable when studying habitat use patterns, particularly for research addressing the characteristics of inter-patch travel routes. Standard radio-telemetry or point observation techniques typically do not provide for continuous monitoring of movements over long periods of time. Automated telemetry systems (Mech 1983) and new GPS technology (Rempel et al. 1995) can provide essentially continuous information on animal movements, however these techniques are not widely used.

Simply following animal tracks on the ground provides a continuous sample of a habitat utilization trajectory. Mapping routes along which animals have been followed produces a very different image of spatial use than is provided by radio-telemetry and other point count methods. Intensive ground tracking can highlight areas of concentrated movement, connecting travel routes, and areas of dispersed exploration or foraging. Ground tracking is particularly well suited for large terrestrial mammals in snowy climates where individuals or groups of individuals can be easily identified. Snow tracking has been used to document presence (e.g. Litvaitis et al. 1985, Jenkins and Wright 1988, Thompson et al. 1989), but tracking has rarely been used to determine continuous habitat utilization (Snyder and Bissonette 1987).

One drawback to using ground tracking for documenting the habitat utilization trajectory is that ground tracking serves to document the 3 geographic coordinates of the trajectory but does not provide information on the time coordinate. While radio-telemetry provides discrete points in the 4 dimensional space, ground tracking provides continuous information in the 3 geographic coordinates but does not provide information on the time coordinate except in the broadest sense (e.g. these tracks were made since the last snowfall). Because of this limitation, ground tracking is useful for identifying the location of travel routes but does not provide information on how long the animal spends along the route (see Appendix D). Ground tracking and radio-telemetry provide different, yet complementary, documentations of spatial use patterns.

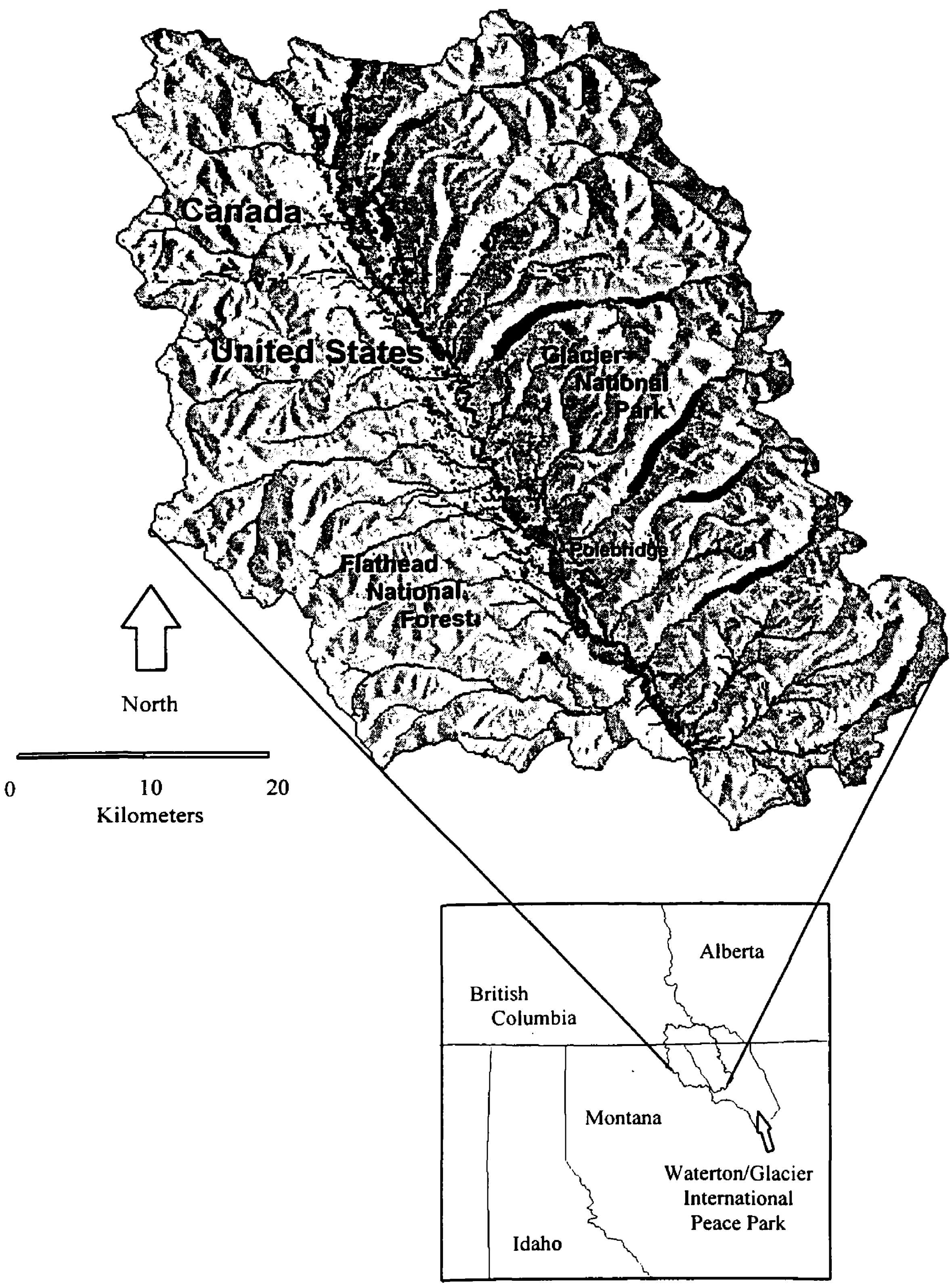
Analysis of spatial habitat use data

Computerized geographic information systems (GIS) have become a common tool in wildlife habitat assessment. Many investigators have employed GIS in wildlife research (e.g. Donovan et al. 1987, Pereira and Itami 1991, and Schultz and Joyce 1992, Scott et al. 1993, Clark et al. 1993). GIS provides an excellent tool for analysis of continuous spatial use data. The combination of medium to broad scale digital habitat datasets and continuous spatial habitat use data from winter ground tracking and radio-telemetry can provide a powerful combination for the analysis of habitat use at home range and inter-patch scales.

Study Area

My study was conducted in the North Fork of the Flathead River basin, located along the Canadian - U. S. border in and adjacent to Glacier National Park, Montana (Fig. 1-1). I focused on the portion of the basin most frequently used by wolves. This section of broad valley extends from Commerce Creek, 21 km north of the international border, to Huckleberry Mountain, 47 km south of the border. This area encompasses approximately 3000 km^2. Elevation of the valley bottom ranges from 3300 ft at the south end of the study area to 4400 ft at the north. Rugged peaks that bound the basin reach elevations of 9000 to 10,000 ft on the east side and 6500 to 7500 ft on the west. Narrow side drainages radiate east and west from the valley bottom.

Figure 1-1: North Fork of the Flathead River study area.



The North Fork basin was formed in the early Tertiary period when the Precambrian rocks that form the spectacular peaks of Glacier National Park slid east on the Lewis overthrust fault (Alt and Hyndman 1973). In the Pleistocene era, glacial action and erosion filled much of the valley with sediment and created the broad valley bottom with rolling topography that characterizes the basin today (Alt and Hyndman 1973).

Average temperatures in the basin range from 16.1°C in July to -9.3°C in January. On average, 59 cm of precipitation falls in the basin annually, mostly during the winter (Singer 1979). Finklin (1986) reported average snow depths at Polebridge to be 46 cm for December, 71 cm for January, 76 cm for February, and 68 cm for March, though snow depths vary considerably at a local scale. Vegetative characteristics of the North Fork basin have been well documented (Habeck 1970, Koterba & Habeck 1971, Singer 1979, and Allen 1980, Jenkins & Wright 1985, White et al. 1994). Habeck (1970) noted that floodplain forests in the area were characterized by *Populus trichocarpa, Pinus ponderosa, Picea engelmanni x glauca, Pseudotsuga menziesii,* and *Populus tremuloides*. Upland forests are dominated by *Pseudotsuga menziesii, Abies lasiocarpa,* and *Pinus contorta* (Habeck 1970, Singer 1979). Scattered patches of open grassland form a unique characteristic of the North Fork basin (Koterba and Habeck 1971).

Fire has been acknowledged as an important force in the generation of vegetative conditions in the North Fork basin (Habeck 1970, Koterba and Habeck 1971, Singer

1979). This was reinforced during September of 1988 when the Red Bench Fire burned over 15,400 ha in the vicinity of Polebridge (White et al. 1994).

Ungulate populations in the North Fork basin have been well studied (Singer 1979, Jenkins & Wright 1985, Rachel 1992, Bureau 1992, Langley 1993, Tucker 1991). White-tailed deer (*Odecoileus virginianus*) are the most common ungulate in the North Fork, followed by elk (*Cervus elaphus*) and moose (*Alces alces*). This population of ungulates supports a diverse community of large predators. Along with wolves, the basin is home to coyotes (*Canis latrans*), grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), cougar (*Felis concolor*) and humans.

The North Fork basin is characterized by a mosaic of land ownerships. Within the U. S. portion of the basin, the area to the east of the North Fork river is all within Glacier National Park. On the west side of the river, much of the land in the valley bottom is in private ownership while the Flathead National Forest holds most of the land farther from the river. Most of the land in the Canadian portion of the study area is held by the British Columbia Ministry of Environment.

Chapter 2: LANDSCAPE SCALE HABITAT CHARACTERISTICS OF WINTER WOLF HOME RANGES AND TRAVEL ROUTES

Methods

Data collection

Winter ground tracking has been an important part of wolf research in the North Fork. I defined winter as the period between November 15 and March 31 of each year. We found wolf tracks by skiing or snowshoeing into areas where wolves had recently been located using radio telemetry. Wolf tracks were regularly followed both forward and backward, though sufficient distance was maintained so that the wolves were not disturbed. Tracks were followed until changes in snow conditions (usually fresh snowfall or melting) made continuing to follow that set of tracks impossible. These continuous periods of following an unbroken stretch of tracks will be called tracking "bouts". Tracking bouts often lasted several days. The primary purposes for tracking the wolves were to determine spatial use patterns and to locate kill sites to determine prey selection and predation rates.

For each tracking bout, location of the route followed, kill sites, bed sites, and ungulate track transects were permanently recorded by tracing locations onto 8.5x11 in transparent plastic sheets overlaid on 1:24,000 USGS or 1:50,000 Canadian Dept. of Energy and Mines topographic maps (Blakesley 1989). The 8.5x11 in plastic sheets were marked with map registration tics and labeled with observers name(s), date of tracking, number of wolves that created the tracks, the pack that the wolves belonged to, and the name of the map sheet that the overlay was traced from.

I compared the accuracy of mapping wolf movement routes using traditional map and compass techniques to GPS (see Appendix C). Mapping errors of up to 200 m may be common for this data set.

<u>GIS data entry</u>

I digitized all the winter wolf tracking information documented from November 1983 to March 1994, for use with geographic information system (GIS) software. PAMAP version 4.1 (Essential Planning Systems 1993), run on 486-66 and pentium-90 personal computers, was used for all digitizing, most data processing, and most analysis. A unique number was assigned to each tracking bout so non-spatial data, such as the wolf pack responsible for creating the tracks, number of wolves, date, etc., could be associated with each bout. Non-spatial data relating to tracking bouts were not entered into the GIS. See Appendix A for a summary of the North Fork Wolf Ecology Project data entered into the GIS.

During digitizing, I placed the plastic sheets with the tracking routes over mylar copies of the topographic maps they were traced from. I checked the locations of the wolf travel routes against geographic features to ensure accuracy. All data were converted into NAD 1927 map datum and UTM (zone 11) map projection after entry.

I then generated analysis corridors around the travel routes using 100 m buffers on both sides of the travel route. I selected the 100 m buffer distance because I judged this to be a general approximation of the sensory distance of wolves, and it corresponded well with the 50 m pixel size of my raster data. These corridors were then converted into a polygon map layer.

I also entered all winter radio telemetry data that had been collected from 1983 to 1994. Radio telemetry locations for each winter were merged into the maps with the tracking information. Minimum convex polygon (MCP) home ranges were generated for each winter by digitizing the polygon connecting the outermost telemetry points and the outermost locations on tracking routes. Only telemetry locations recorded between November 15 and March 31 were included in the winter MCP home range delineation.

Total available habitat for wolves within the study area was delineated by identifying those areas that were within 500 m elevation of the North Fork of the Flathead River. This elevation range was chosen because preliminary review of the wolf tracking data showed that all tracking (with 1 minor exception) had occurred within 500 m elevation of the North Fork. The available area had maximum elevations of approximately 6040 ft at the north end of the study area to 4940 ft at the south. Areas above these elevations tended to be rugged peaks and ridges subject to extreme weather conditions and were not considered to be available habitat for wolves. Regions outside of the available area were excluded from analysis even if they were within winter MCP home ranges.

Habitat map layer generation

GIS map layers representing pre and post-fire vegetation type, topographic position, slope, aspect, distance to open roads, distance to water, and road density were generated from a variety of available data sources (Table 2-1). I selected these landscape habitat characteristics based on relevance to wolf ecology and data availability.

I included vegetation type to identify the gross vegetation and cover characteristics of areas used by wolves. Vegetation type was derived from landsat TM imagery (White et al. 1994) and B. C. Ministry of Environment forest stand inventory maps. I used pre-fire and post-fire vegetation type maps to account for the changes in forest cover caused by the 1988 Red Bench Fire. Other information on forest stand structural characteristics (e.g. canopy closure, age class, size class) was not available for the entire study area. I considered slope, aspect, topographic position and distance to water because of their potential influence on ungulate distribution and ease of travel.

Table 2-1: Landscape habitat characteristics and classes used in analysis of MCP home ranges and travel routes.

Slope
- very steep (>60%)
- steep (36-60%)
- moderate (16-35%)
- slight (5-15%)
- flat (<5%)

Aspect
- flat
- north
- northwest
- west
- southwest
- south
- southeast
- east
- northeast

Distance to water
- <200 m
- 200 - 500 m
- .5 - 1 km
- > 1 km

Distance to open roads
- <200 m
- 200 - 500 m
- .5 - 1 km
- > 1 km

Road density
- no roads
- 0.01 - 2 mi/mi^2
- 2 - 4 mi/mi^2
- >4 mi/mi^2

Vegetation type (pre and post fire)
- water
- bare ground
- shrub/meadow
- mix
- deciduous
- *Pinus contorta* forest
- *Pseudotsuga menziesii/Larix occidentalis* forest
- *Pinus albicalus* forest
- *Abies lasiocarpa/Picea engelmanni* forest
- burned

Topographic position
- ridge (RDG)
- side valley lower slope (SVL)
- bench (BEN)
- side valley upper slope (SVU)
- side valley bottom (SVB)
- main valley upper slope (MVU)
- main valley lower slope (MVL)
- main valley bottom (MVB)

Distance to open roads and road density are indicators of potential human disturbance. The leading causes of mortality for wolves in the North Fork are human related (Boyd unpublished data). Theil (1985) and Mech and Fritts (1988) have suggested that wolves may be excluded from areas of high road density. I included both distance to open roads and total road density because most roads in the North Fork are not passable in winter (excepting by snowmobile). In calculating distance from open roads, I calculated the distance to the main North Fork Road, major access roads that were known to be regularly plowed, and all roads that were within 2 km road distance of the open roads. I included the roads within 2 km road distance of open roads because these areas often contained residences and these portions of road were more likely to be used by cross-country skiers and snowmobilers. I generated 2 distance to open road map layers; one for the period prior to 1990 and another for the period after 1990. The layer after 1990 included access roads that were regularly plowed starting around 1990.

Because the study area encompassed the international border, two data sets were generally required to generate each layer. All habitat map layers were converted into NAD 27 map datum in UTM (zone 11) map projection, with a 50 m pixel size. For a more detailed discussion of data sources and processing procedures, please refer to Appendix B.

GIS overlay procedures

I combined the yearly wolf travel route analysis corridor polygon layers, the yearly minimum convex polygon home range layers, and the basin-wide available habitat layer into a single polygon layer for each pack-year. I then overlaid these composite use-availability layers onto the habitat map layers. I derived the area within each habitat class for tracking analysis corridors, MCP home ranges, and the basin-wide available habitat in this manner.

Statistical analysis

I compared landscape characteristics of used to available areas at 2 scales. For testing the hypothesis that home ranges differed from available areas within the North Fork drainage, MCP home ranges were considered to be the used areas and the area less than 500 m in elevation above the North Fork River was considered to be available. For testing the hypothesis that travel routes differed from available areas within the home range, the tracking route analysis corridors were considered to be the used areas and the areas that were within the MCP home range of that pack for that year were considered to be available.

Univariate comparisons of used and available areas at these scales were conducted using compositional analysis (Aebischer et al. 1993). Compositional analysis focuses on the log-ratio analysis of proportion data (Aitchison 1986). Aebischer et al. (1993) recommend this technique for habitat utilization analysis based on radio-telemetry data points, but the technique is also well suited to the analysis of proportion data generated during GIS spatial analysis. This technique evaluates habitat use based on the probability of overall random use (i.e. no preference shown for any of the considered habitat types) and provides for the generation of preference ranking matrices (Aebischer et al. 1993). Within the preference ranking matrices, the probability of differences in use between habitat classes can be identified based on t values (Aebischer et al. 1993). Compositional analysis was conducted using Systat, version 5 for windows (Systat Inc. 1992). Ranking matrices were generated in Excel, version 5 (Microsoft Corp. 1993). Refer to Appendix E for a more complete discussion of compositional analysis.

Each pack-year was used as the sample unit for the compositional analysis. In other words, the MCP home range for each year was compared to the available habitat within the basin, and the entire set of tracking for each pack each year was compared to that pack's home range for that winter. There were two reasons to use the pack-year as the sampling unit. First, there was questionable independence between subsequent tracking bouts. When one set of tracks were lost, another group of more recent tracks were commonly found in the vicinity of where the first set was lost. These consecutive tracking bouts often followed tracks left by the same group of wolves, but due to constraints imposed by snow conditions and time, a portion of the travel route could not be followed. Second, different tracking bouts were of different lengths. The longer the tracking bout, the better the representation of the wolves' habitat utilization trajectory. Rather than weighting the individual tracking bouts by length, it is more intuitive to group all the bouts attributed to a pack in a year into one composition. In this manner the longer bouts contribute more to the composition than the shorter bouts. Pack-years with less than 30 km of tracking were excluded from the analysis of travel routes for all habitat characteristics excepting vegetation. For vegetation type, periods before and after the Red Bench fire were analyzed separately. All years were included in these analyses because of the small sample size caused by this division.

The pack-year was also used as the sample unit for analyzing home range areas compared to available habitat within the basin. Independence of home ranges for the same pack across years may be disputable to some degree. Home ranges were traditionally used areas for each pack, and therefore very similar across the years that the pack existed. However, I used the pack-year as the sample unit at this scale because it provided the most independent unit that still allowed a large enough sample size for statistical analysis.

Stepwise multiple logistic regression was used to identify which combinations of habitat factors provided the strongest predictors of habitat use (Press and Wilson 1978, Trexler and Travis 1993, Manley et al. 1993). Multiple logistic regression was conducted for each pack-year separately and the resulting models were compared across years to identify which factors were consistent predictors of wolf habitat use. Habitat characteristics were reclassified to reduce the number of classes for categorical habitat characteristics. The new classes reflected the prefrence rankings generated during compositional analysis. For the analysis of MCP home ranges compared to basin-wide available habitat from 1991 to 1994, one regression was conducted for each year. Areas within any one of the three home ranges were considered used and areas outside of the home ranges were considered unused.

I generated 2 systematic grids of points to represent the GIS data for the stepwise logistic regression (see Appendix F for the GIS steps used in generating these point grids). A 400 m grid of points (sampling 1 out of every 64 pixels) was generated to represent the MCP home range and basin-wide available habitat areas. A grid of points every 150 m (sampling 1 out of every 9 pixels) was generated to represent the wolf travel route analysis corridors. I overlaid the point grids on the habitat map layers, MCP home range layers, and the wolf travel route layers so that each point was updated with wolf use and habitat data. The databases that resulted from the point overlays were exported from PAMAP and brought into SPSS for multiple logistic regression analysis.

The sample size of points used to estimate the characteristics of the GIS habitat and wolf use layers was very large (approximately 10,500 points for each scale). Because these sample sizes are determined by arbitrary subsampling of the GIS layers, the statistical significance levels reported during the stepwise regression analyses were not practically important except for comparison with other variables. The best models were subjectively identified from the stepwise logistic regression based on accuracy of identification of used and unused points and chi-square scores. Models that provided a balance between the minimum number of variables and the maximum predictive value were selected as the best. These best models were compared across years to identify which habitat characteristics were consistently predictive of wolf use.

Results

Routes of 374 tracking bouts totaling 2893 km of tracking were entered into the GIS. Tracking and home range data for 19 pack-years were compiled (see Appendix A). Amounts of tracking conducted during a pack-year ranged from none, for the Spruce Creek Pack during the winter of 1992-93, to 502.8 km, for the Magic Pack during the

Table 2-2: Tracking data and minimum convex polygon home range size for each pack-year.

Pack - Year	Home Range Area (Km^2)	Tracking Route Length (Km)	Analysis Corridor Area (Km^2)	Number of Tracking Bouts
Magic 1983-84**	122.6	100.9	10.2	19
Magic 1984-85	1064.5	201.6	37.9	24
Magic 1985-86	1157.9	246.7	43.9	33
Magic 1986-87	1310.5	502.8	89.5	87
Camas 1987-88	1403.3	292.0	63.2	44
Camas 1988-89	1015.7	404.7	82.1	23
Camas 1989-90	883.0	207.1	43.2	16
North Camas 1990-91	728.5	196.6	38.8	16
South Camas 1990-91	395.3	85.7	18.1	11
Spruce Creek 1990-91	300.6	98.3	22.6	8
North Camas 1991-92	242.8	139.1	35.5	17
South Camas 1991-92*	157.7	19.0	4.1	3
Spruce Creek 1991-92	76.1	35.2	6.7	4
North Camas 1992-93*	133.0	19.5	4.9	4
South Camas 1992-93	373.8	34.9	8.6	11
Spruce Creek 1992-93*	186.6	0.0	0.0	0
North Camas 1993-94	125.3	97.7	21.5	23
South Camas 1993-94	141.9	205.5	42.4	30
Spruce Creek 1993-94*	180.1	5.5	1.3	1
Total	9219.2	2747.9	554.2	347
Average	658.5	196.3	39.6	24.8

* These pack-years were excluded from most analysis (as well as totals and averages shown here) because less than 30km of tracking was conducted.

** Magic 1984 was excluded from analysis because no radio-telemetry data was available.

winter of 1986-87 ($\bar{x}$ = 152.2 km/pack-year). Total winter MCP home range sizes (including areas over 500 m in elevation above the North Fork River) ranged from 1403 km^2, for the Camas Pack during 1988, to 76 km^2 for the Spruce Creek Pack during the winter of 1991-92 ($\bar{x}$ = 526 km^2). Prior to the fall of 1990, when the wolf population in the North Fork basin split into 3 packs, average winter home range size was 994 km^2. After the spring of 1990 the average winter home range size was 260 km^2.

Insufficient data was a problem for a few pack-years. During the winter of 1983-84, no radio telemetry data was gathered within the study area. All tracking during this winter was conducted on tracks that had been opportunistically located along roads or trails. This winter was excluded from all analysis because of the potential bias due to tracking only on tracks opportunistically located along roads or trails, and the lack of radio telemetry data for adequate home range estimation. Four pack-years had less than 30 km of tracking (South Camas 1991-92, North Camas 1992-93, Spruce Creek 1992-93, and Spruce Creek 1993-94). These pack years were excluded from analysis comparing tracking routes to home ranges for all habitat characteristics excepting vegetation. Radio telemetry data was available for these years, so they were included in analysis comparing home range to total available habitat within the basin.

After excluding those years with insufficient data, 18 home ranges were analyzed in comparison to the total available habitat within the basin. Minimum convex polygon home ranges varied from 76 to 1403 km^2 ($\bar{x}$ = 659 km^2) for the years analyzed. A total of 2748 km of tracking, representing 14 pack-years, were analyzed in comparison to home ranges. Analyzed years ranged from 34.9 to 502.8 km of tracking ($\bar{x}$ = 196.3 km) collected in 4 to 87 tracking bouts ($\bar{x}$ = 24.8 km).

Habitat characteristics of home ranges within the North Fork drainage

Home ranges were not randomly located ($P < 0.10$) for any habitat characteristics excepting distance to open roads (Table 2-3, Fig. 2-1, complete compositional analysis ranking matrices are included in Appendix E). Aspects within home ranges differed substantially from the basin wide available habitat ($P < 0.001$). West, southwest, and flat aspect classes made up an average of 47.0% of the home ranges and only 32.0% of the basin-wide available habitat. Southern, northwestern, and southeastern exposures were included in home ranges about in proportion to their availability ($\bar{x}$ = 35.7% of home ranges and 36.7% of basin-wide available habitat area). Eastern, northern, and northeastern exposures were found within home ranges in substantially smaller proportions than they were available within the entire basin ($\bar{x}$ = 17.3% of home ranges and 31.0% of basin-wide habitat).

Topographic position classes in home ranges differed significantly from random ($P < 0.001$). Main valley bottoms and main valley lower slopes were the most common

Table 2-3: Compositional analysis results comparing home ranges to available habitat within the basin (see Appendix E for complete ranking matrices and computational forumlas). Relative use ranking, with the probability of no difference between the adjacent ranks, is shown. Differences between adjacent ranks are shown as follows: = indicates that classes are tied in rank, > no significant difference in rank between classes (P > 0.10), >> difference in rank significant at 0.10 level, >>> difference in rank significant at 0.05 level. N = 18 unless otherwise indicated

---

Topographic Position

MVB > MVL >>> MVU > BEN >>> SVL > SVB > RDG > SVU

0.729 0.001 0.996 0.011 0.123 0.188 0.381

Probability of overall random use: < 0.001

Slope

FLAT > SLIGHT >>> MOD >>> STEEP >>> V STEEP

0.342 <0.001 <0.001 0.002

Probability of overall random use: < 0.001

Aspect

W > SW > FLAT >> S > NW > SE >>> E >>> N > NE

0.716 0.386 0.082 0.645 0.305 0.023 <0.001 0.472

Probability of overall random use: < 0.001

Distance to open roads

gt1km > .5-1km >> 200-500m >> lt200m

0.302 0.106 0.087

Probability of overall random use: 0.277

Distance to water

gt1km >.5-1km >>> 200-500m >>> lt200m

0.534 <0.001 0.017

Probability of overall random use: < 0.001

Vegetation

Pre-fire (1984 - 1988 & Spruce Creek Pack, N = 9)

DECID >>> PICO >>> SHRUB/MEAD > PSME/LAOC > WATER > ABLA/PIEN > BARE GROUND > MIX

0.004 0.035 0.248 0.861 0.254 0.639 0.333

Probability of overall random use: 0.077

Post-fire (1989 - 1994, Spruce Creek pack not included, N = 10)

BURN>PSME/LAOC>>>MIX>PICO>ABLA/PIEN>WATER>BARE GROUND>>>SHRUB/MEAD>>DECID

0.162 0.012 0.663 0.187 0.541 0.773 0.022 0.062

Probability of overall random use: 0.043

Road Density

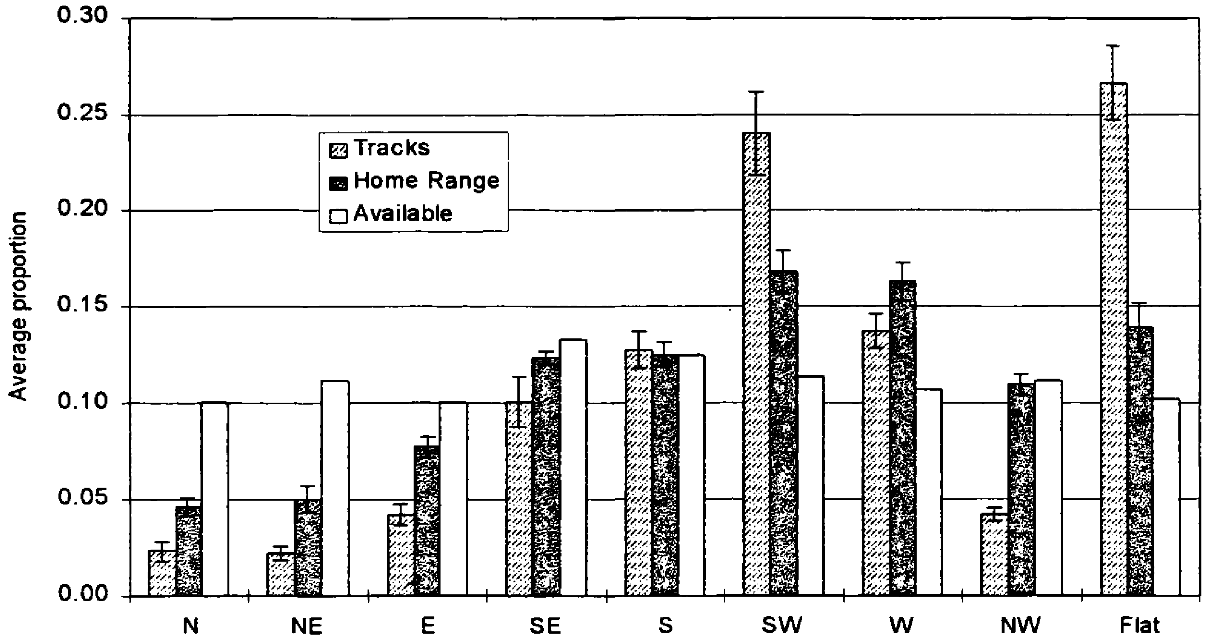
lt2mi/mi^2 > No Roads > 2-4mi/mi^2 >> gt4mi/mi^2

0.751 0.185 0.077

Probability of overall random use: 0.064

Figure 2-1: Average proportions of tracking analysis corridors, MCP home ranges, and total avaialble habitat area for each habitat characteristic class. Error bars indicate plus or minus one standard error. n = 14 for tracking routes and n = 18 for home ranges unless otherwise noted.

Aspect



Topographic Position

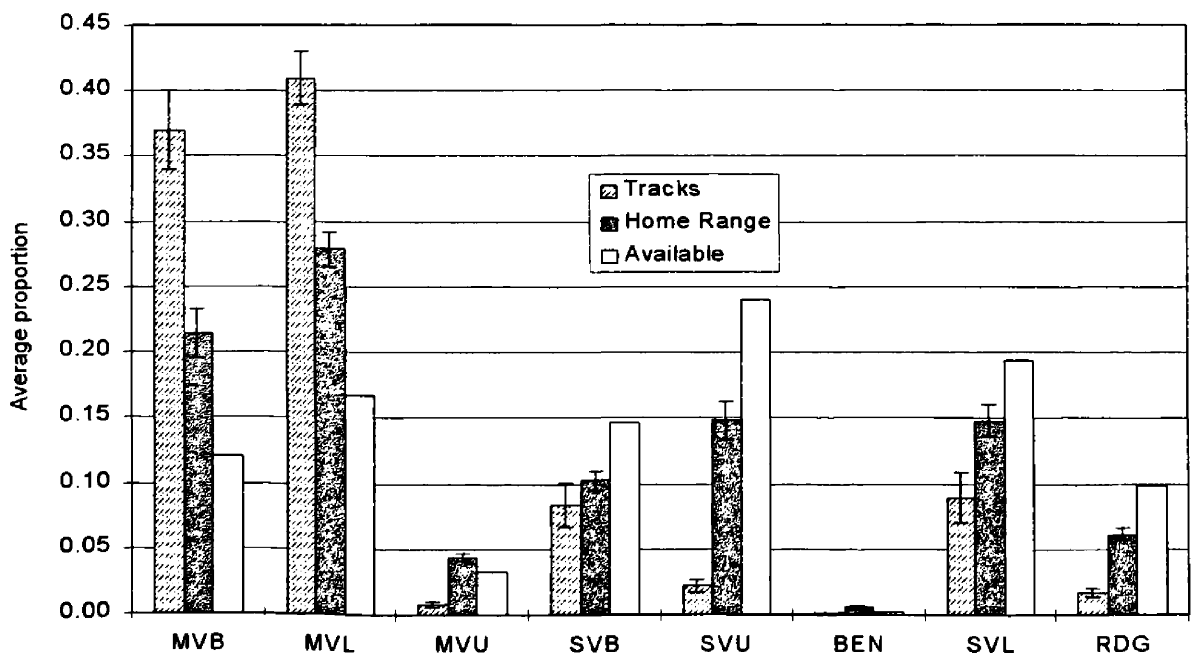
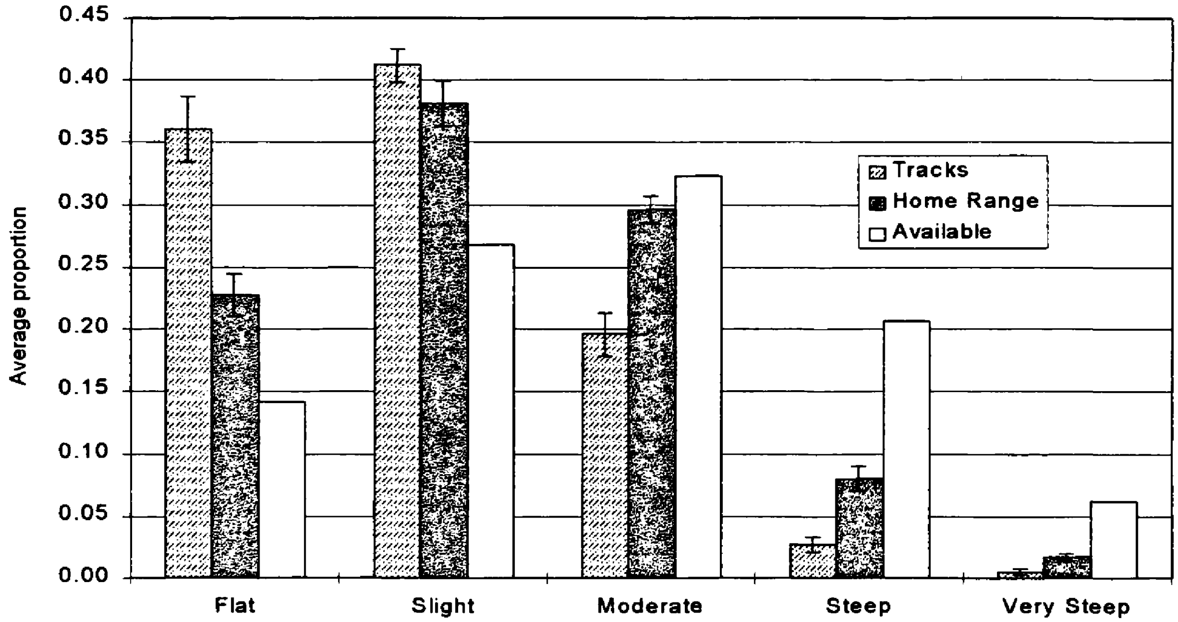


Figure 2-1 (continued): Average proportions of tracking analysis corridors, MCP home ranges, and total avaialble habitat area for each habitat characteristic class. Error bars indicate plus or minus one standard error. n = 14 for tracking routes and n = 18 for home ranges unless otherwise noted.

Slope



Distance to open roads

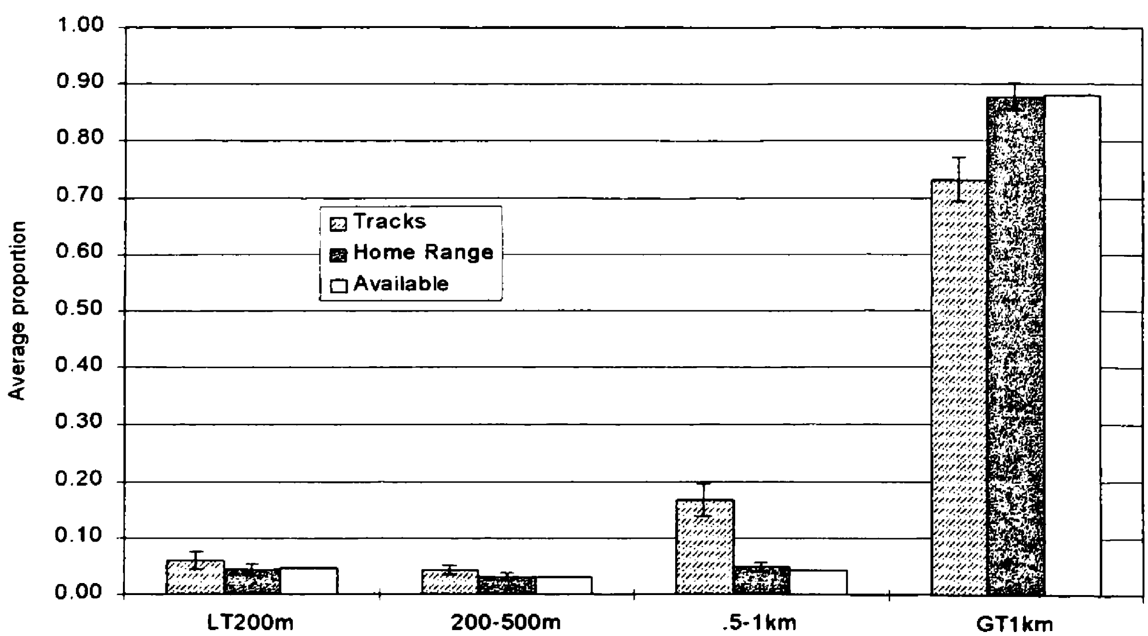
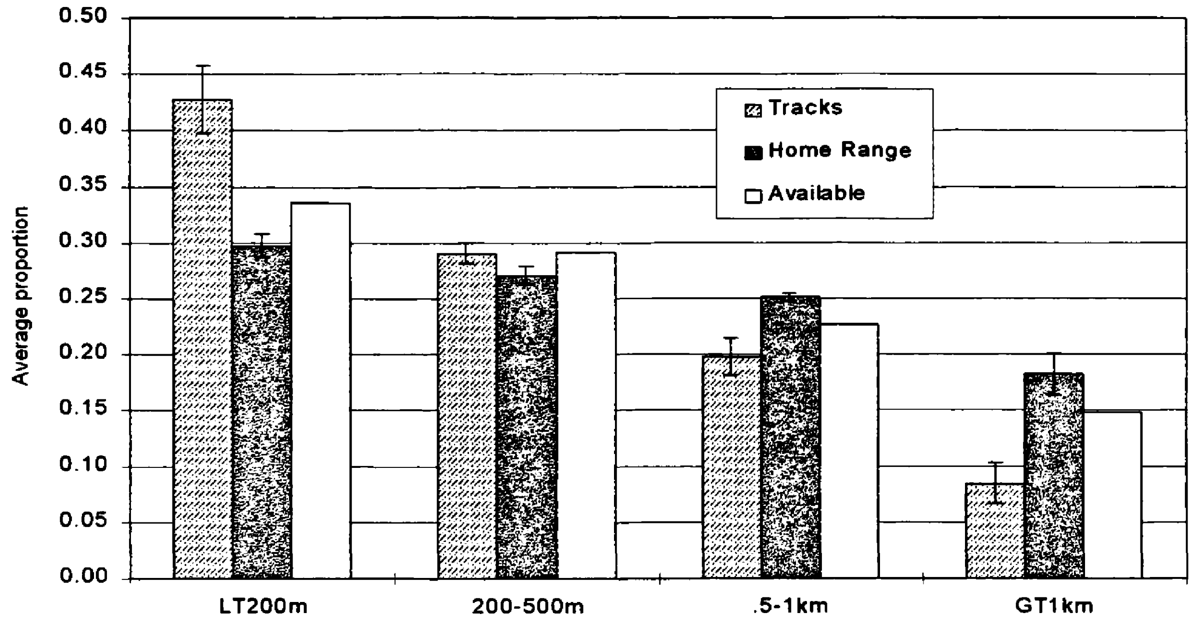


Figure 2-1 (continued): Average proportions of tracking analysis corridors, MCP home ranges, and total avaialble habitat area for each habitat characteristic class. Error bars indicate plus or minus one standard error. n = 14 for tracking routes and n = 18 for home ranges unless otherwise noted.

Distance to water



Road density

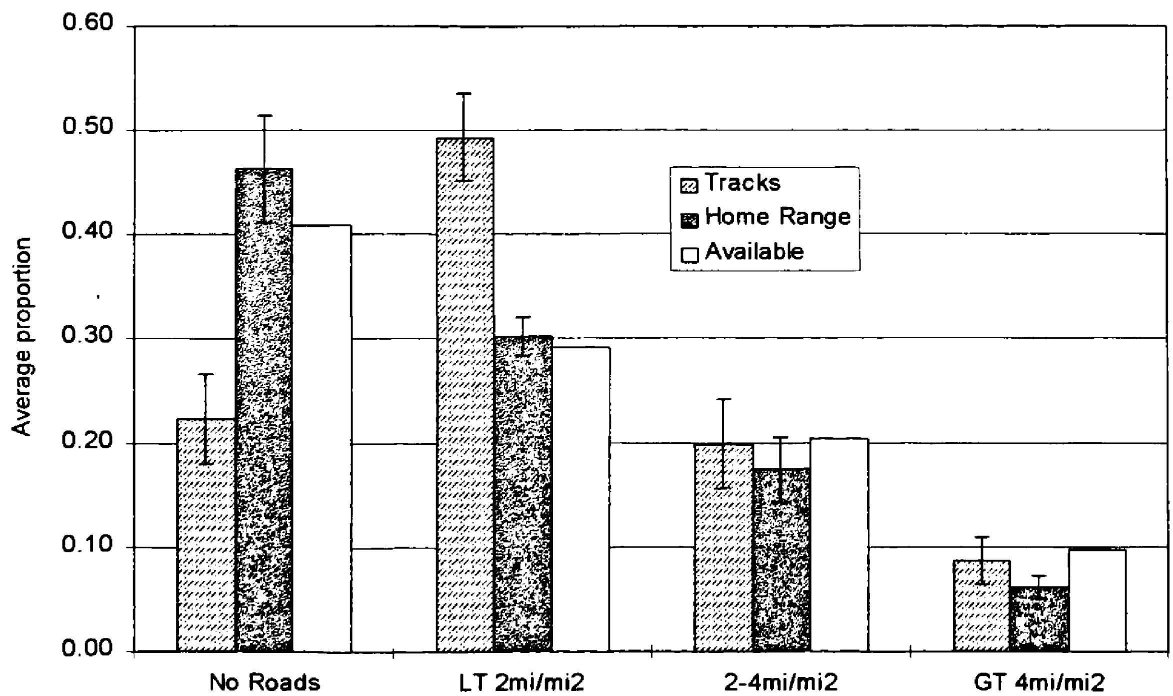
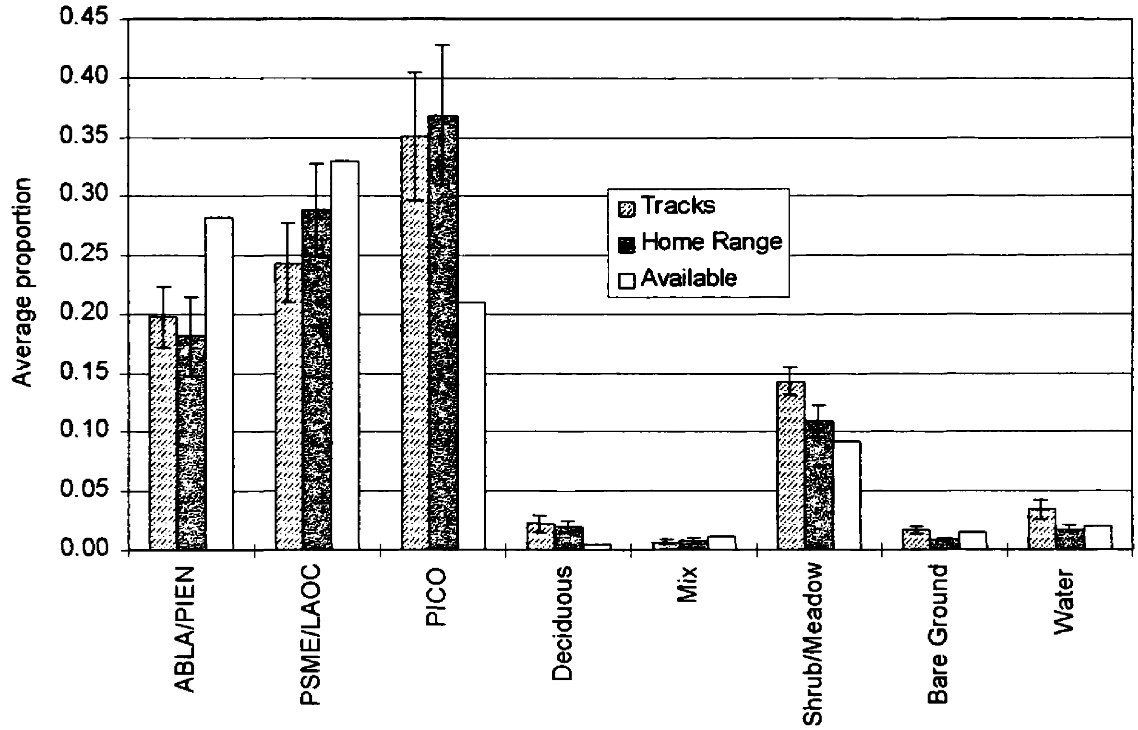
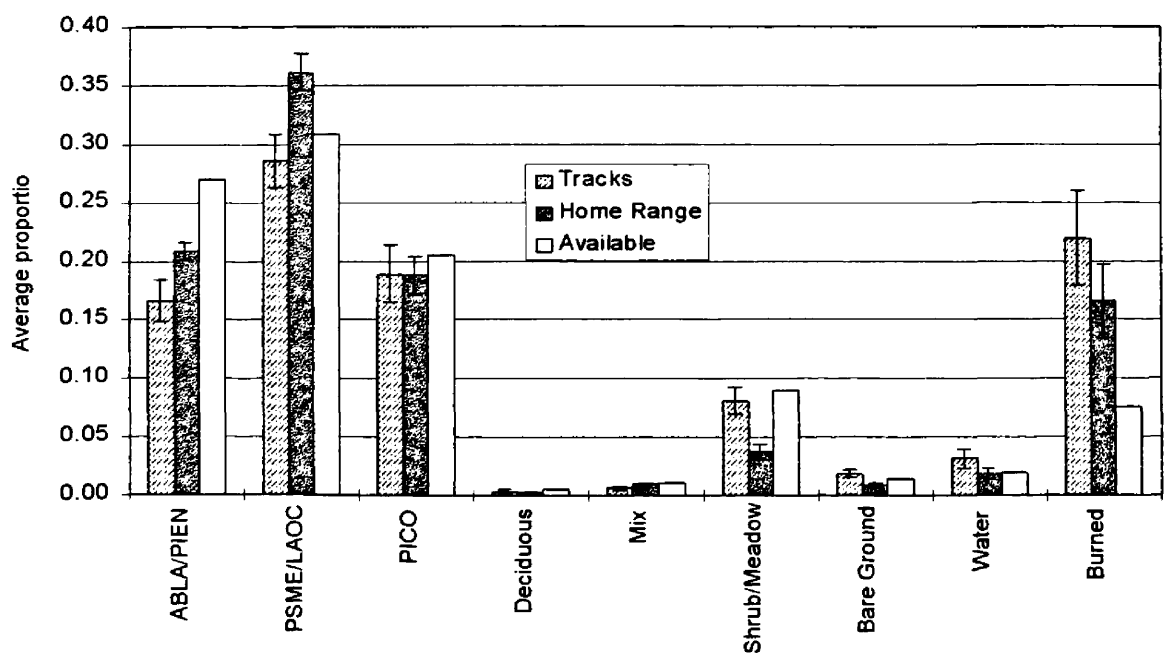


Figure 2-1(continued): Average proportions of tracking analysis corridors, MCP home ranges, and total avaialble habitat area for each habitat characteristic class. Error bars indicate plus or minus one standard error. n = 14 for tracking routes and n = 18 for home ranges unless otherwise noted.

Pre Fire vegetation



Post Fire vegetation



classes within home ranges ($\bar{x}$ = 49.2%) while they were much less common within the basin-wide available habitat (28.7%). Main valley upper slopes and benches were found within home ranges nearly in proportion to their availability ($\bar{x}$ = 4.9% of home ranges and 3.4% of basin-wide available habitat). Side valley lower slopes, side valley upper slopes, side valley bottoms and ridges were included in home ranges less than they were available within the basin ($\bar{x}$ = 45.8% of home ranges and 67.7% of basin wide available habitat).

Slope classes within home ranges differed significantly from random ($P < 0.001$). Flat areas and slight slopes were the most common classes within home ranges ($\bar{x}$ = 60.8% of a home ranges and 40.8% of the available habitat area). Moderate slopes were included in home ranges nearly in proportion to their availability ($\bar{x}$ = 29.6% of home ranges and 32.3% of available). Steep and very steep slopes were included in home ranges less than they were available within the basin ($\bar{x}$ = 9.7% home ranges and 26.8% of basin wide available habitat).

Distance to water differed between home ranges and basin-wide available habitat ($P < 0.001$). Home ranges most commonly encompassed areas greater than 0.5 km from water ($\bar{x}$ = 43.3% of home ranges and 37.4% of available habitat). Areas 200-500 m from water were included in home ranges nearly in proportion to their availability ($\bar{x}$ = 27.0% of home ranges and 29.0% of available). Areas less than 200 m from water were less likely to be included in home ranges ($\bar{x}$ = 29.7% of home ranges and 33.5% of available habitat).

Vegetation within wolf home ranges prior to the Red Bench fire was somewhat different from vegetation within the basin-wide available habitat area (P = 0.077). Deciduous forest ranked highest in the compositional analysis ranking ($\bar{x}$ = 1.9% of home ranges and 0.5% of basin-wide available). *Pinus contorta* forest ranked as the second most preferred vegetation class ($\bar{x}$ = 36.8% of home ranges and 20.9% of the available habitat). No significant differences in ranking for the other vegetation classes were detected.

Vegetation within wolf home ranges was also different from the basin-wide available habitat area after the Red Bench fire (P = 0.043). Burned areas and *Psudotsuga menziesii/Larix occidentalis* received the highest use rankings from the compositional analysis ranking matrix ($\bar{x}$ = 52.7% of home ranges and 38.5% of basin-wide available area), but no significant difference in use between these classes was detected (P = 0.162). Mixed forest, *Pinus contorta* forest, *Abies lasiocarpa/Picea englemanni* forest, water, and bare ground were not significantly different in the ranking ($\bar{x}$ = 43.3% of home ranges and 50.3% of the available habitat). Shrub/meadow and deciduous forest were the lowest ranked classes ($\bar{x}$ = 3.9% of home ranges and 9.5% of the basin-wide available).

Road densities within wolf home ranges differed from the basin-wide available habitat area ($P = 0.064$). Differences in use rank between the no roads, 0.01-2 mi roads/mi^2, and 2-4 mi roads/mi^2 classes were not significant ($P > 0.18$). However, these classes were all used more than the >4 mi roads/mi^2 class ($P = 0.077$). Areas with greater than 4 mi road/mi^2 composed 6.1% of wolf home ranges on average, and 9.7% of the basin-wide available area. Distance to open roads and roads within 2 km of open roads was not shown to be different between wolf home ranges and the basin-wide available area ($P = 0.277$).

As expected, nearly all variables were selected as significant in each of the stepwise multiple logistic regression analyses due to the large sample size used to represent the GIS data. Review of the models that best accounted for most of the variation between points showed that approximately 75% of the used and unused points could be accurately identified based on 3 or 4 habitat characteristics (Table 2-4). Gentle slopes or flat areas increased the probability of use in all of the best models. Presence of the no roads class increased the probability of use in the 9 models that road density was included in. Presence of the >2 mi/mi^2 class consistently decreased the probability of use in those models, and presence of the 0.01-2 mi/mi^2 class decreased the probability of use in 5 of the 9 models. Presence of the main valley and lower slope class increased the probability of use in the 9 models that topographic position was included in. Presence of the side valley bottoms and lower slopes class and the ridges and upper slopes class

Table 2-4: Multiple logistic regression results comparing home ranges to available habitat within the basin. Multiple logistic regression models take the form of $p = 1 / (e^{logit(p)})$ and $logit(p) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_i X_i$, where p = the probability that the point is used, β_0 = constant, β_i = the coefficient for habitat characteristic i, and X_i = the data value for habitat characteristic i.

Year	Road Density			Topographic Position			Slope	Distance to water	Constant	% Used correct	% Available correct	% Total correct
	No Roads	0.01-2mi/mi²	>2mi/mi²	MVB&L[a]	SVB&L[b]	Rdg&U[c]						
1985	1.294	0.150	-1.444	1.918	-1.283	-0.635	-0.043	*	0.988	82.8	69.7	76.8
1986	1.927	-0.262	-1.665	1.197	-0.757	-0.440	-0.042	*	1.053	88.4	63.8	78.6
1987	1.872	-0.281	-1.591	1.203	-0.578	-0.624	-0.041	*	0.921	86.8	63.0	76.9
1988	0.715	-0.458	-0.256	1.975	-1.406	-0.569	-0.041	*	2.556	91.4	43.5	78.8
1989	1.430	-0.231	-1.199	1.499	-1.041	-0.458	-0.036	*	0.094	69.7	74.2	72.3
1990	0.970	-0.203	-0.766	1.981	-1.201	-0.780	-0.037	0.001	0.201	72.9	81.7	77.4
1991	1.649	0.200	-1.849	0.747	-0.561	-0.186	-0.051	*	0.168	73.4	75.1	74.4
1992	*	*	*	0.798	-0.605	-0.193	-0.062	0.001	0.215	60.2	84.4	75.2
1993	1.412	0.300	-1.712	0.999	-0.607	-0.392	-0.035	0.001	-1.253	39.5	92.0	77.3
1994	1.530	0.044	-1.574	*	*	*	-0.002	*	0.513	79.8	74.1	76.6

a = main valley bottoms and lower slopes
b = side valley bottoms and lower slopes
c = ridges and upper slopes

decreased probability of use in all 9 models. Increasing distance from water increased probability of use in the 3 models distance to water was included in. Aspect and vegetation were not included in any of the best models.

Habitat characteristics of winter travel routes within home ranges

Areas within wolf tracking analysis corridors differed significantly ($P < 0.10$) from areas within MCP home ranges in regard to all habitat characteristics except vegetation (Table 2-5, Fig. 2-1).

Travel routes were not randomly located within home ranges in regard to topographic position ($P = 0.001$). Main valley bottom was the highest ranked class according to the compositional analysis ranking matrix ($\bar{x} = 37.0\%$ for tracking analysis corridor areas and $x = 21.4\%$ for yearly home ranges). Main valley lower slopes were ranked second ($x = 41.0\%$ for tracking and $\bar{x} = 27.8\%$ for home ranges). Side valley bottoms and lower slopes were not significantly different in ranking ($P = 0.165$) and were used in slightly smaller proportions than they were available ($\bar{x} = 17.2\%$ for tracking and 24.9% for home ranges). Ridges, main valley upper slopes, side valley upper slopes, and benches were the lowest ranked classes and were used substantially less than they were available ($\bar{x} = 4.8\%$ for tracking and $\bar{x} = 25.8\%$ for home ranges).

Table 2-5: Compositional analysis results comparing winter travel routes to home ranges (see Appendix E for complete ranking matrices and computational forumlas). Relative use ranking, with the probability of no difference between the adjacent ranks, is shown. Differences between adjacent ranks are shown as follows: = indicates that classes are tied in rank, > no significant difference in rank between classes (P > 0.10), >> difference in rank significant at 0.10 level, >>> difference in rank significant at 0.05 level. N = 14 unless otherwise indicated

Topographic Position

MVB>>>MVL>>>SVB>SVL>>>RDG>MVU>SVU>>BEN

0.020 0.011 0.165 0.020 0.105 0.985 0.090

Probability of overall random use: 0.001

Slope

FLAT>>>SLIGHT>>>MOD>>>STEEP>>V STEEP

<0.001 <0.001 0.013 0.089

Probability of overall random use: < 0.001

Aspect

FLAT >>> SW >>> S > W > SE >>> E > N > NE > NW

0.001 0.022 0.736 0.320 <0.001 0.589 0.580 0.902

Probability of overall random use: < 0.001

Distance to roads

.5-1km >>> 200-500m > lt200m > gt1km

< 0.001 0.424 0.582

Probability of overall random use: 0.001

Distance to water

lt200m >>> 200-500m >>> .5-1km >>> gt1km

0.036 0.038 0.001

Probability of overall random use: 0.006

Vegetation

Pre-fire (1984 - 1988 & Spruce Creek Pack, N = 8)

BARE GROUND > WATER > SHRUB/MEAD = ABLA/PIEN > PICO = PSME/LAOC > DECID > MIX

0.202 0.388 0.382 0.888 0.235 0.797 0.846

Probability of overall random use: 0.430

Post-fire (1989 - 1994, Spruce Creek Pack not included, N = 10)

BARE GROUND=SHRUB/MEAD>WATER>BURN>PICO>DECID=PSME/LAOC>ABLA/PIEN>MIX

0.786 0.660 0.368 0.196 0.447 0.969 0.808 0.148

Probability of overall random use: 0.133

Road Density

lt2mi/mi^2 >>> 2-4mi/mi^2 > gt4mi/mi^2 > No Roads

0.020 0.553 0.287

Probability of overall random use: < 0.001

Slope classes within areas where wolves were tracked differed from areas available within home ranges ($P < 0.001$). Differences in use rank between all classes of slope were significant ($P < 0.10$). Use decreased substantially as slope increased. Areas less than 15% slope gradient averaged 77.2% of yearly tracking route area compared to an average of 60.8% of yearly home range area.

Travel routes were not randomly located within home ranges in regard to aspect ($P < 0.001$). Flat areas received the highest use rank ($\bar{x}$ = 26.6% of tracking and $\bar{x}$ = 13.9% of home ranges). Southwestern exposures were the second highest ranked ($\bar{x}$ = 24.0% of tracking and $\bar{x}$ = 16.8% of home ranges). Southern, western, and southeastern exposures were not significantly different in rank ($\bar{x}$ = 36.5% of tracking and $\bar{x}$ = 41.1% of home ranges). Eastern, northern, northeastern, and northwestern exposures were not significantly different and received the lowest use rank ($\bar{x}$ = 12.9% of tracking and $\bar{x}$ = 28.3% of home ranges).

Distance to water in areas where wolves were tracked differed significantly from areas available within home ranges ($P = 0.006$). Significant differences in use rank ($P < 0.05$) existed between all four distance to water classes. As distance from water increased, use decreased. Areas less than 200m from water were ranked highest ($\bar{x}$ = 42.7% of tracking and $\bar{x}$ = 29.7% of home ranges). Areas that were greater than 1 km from water were ranked lowest ($\bar{x}$ = 8.4% of tracking analysis corridor area and $\bar{x}$ = 18.2% of yearly home range area).

Travel routes were not randomly located within home ranges in regard to distance to open roads (P = 0.001). Areas .5 to 1 km from open roads were used significantly more than all other classes ($P < 0.001$, $\bar{x}$ = 16.6% of tracking and 4.8% of home ranges). Other classes were not significantly different in use rank ($P > 0.40$) and were used nearly in proportion to their availability.

Travel routes were not randomly located within home ranges in regard to total road density ($P > 0.001$). Areas with 0.01 to 2 mi road/mi^2 were ranked highest for wolf use (x = 49.2% of tracking and $\bar{x}$ = 30.2% of home ranges). Other road density classes were not significantly different in use rank ($P > 0.25$). Areas with more than 2 mi road/mi^2 were used approximately in proportion to their availability ($\bar{x}$ = 28.5% of tracking and $\bar{x}$ = 23.5% of home ranges). Areas with no roads were used less than available ($\bar{x}$ = 22.3% of tracking and $\bar{x}$ = 46.3% of home ranges).

Travel route locations within yearly home ranges did not differ significantly from random in regard to vegetation either before the Red Bench fire (P = 0.430) or after it (P = 0.133).

Evaluation of the best models identified in the stepwise multiple logistic regression analysis showed that tracking corridor areas could be accurately distinguished from home range areas between 63.4 to 81.6% of the time based on 1 to 3 habitat characteristics (Table 2-6). Road density was included in 13 yearly best models. Presence of the 0.01-2 mi/mi^2 class increased probability that a point was within a travel route analysis corridor in 12 of the 13 models. Presence of the no roads within 1 mi^2 class decreased the probability that a point was within a travel route analysis corridor. Presence of the >2 mi/mi^2 class increased probability that a point was within a travel route analysis corridor in 9 years and decreased probability in 4 years.

Topographic position class was included in 7 of 14 yearly models. Presence of the main valley bottoms and lower slopes class increased the probability that a point was within a travel route analysis corridor in 6 out of 7 years. The side valley bottom and lower slope class increased the probability that a point was within a travel route analysis corridor in 4 out of 7 years. The ridges and upper slopes class decreased the probability that a point was within a travel route analysis corridor in all 7 years.

Vegetation was included in 5 of the 14 models. The deciduous and non-forest class increased probability that a point was within a travel route analysis corridor in 4 years. The coniferous forest and the *Pinus contorta* forest classes decreased the

Table 2-6: Multiple logistic regression results comparing winter travel routes to home ranges. Multiple logistic regression models take the form of $p = 1 / (e^{logit(p)})$ and $logit(p) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_i X_i$, where p = the probability that the point is used, β_0 = constant, β_i = the coefficient for habitat characteristic i, and X_i = the data value for habitat characteristic i.

Year	Aspect		Road Density			Topographic Position			Vegetation					Constant	% Used	%Avail.	%Total
	SW	Other	No Roads	0.01-2mi/mi²	>2mi /mi²	MVB&L[a]	SVB&L[b]	RDG&U[c]	Deciduous & Non-Forest	Conifer Forest	Pinus contorta Forest	Burn	Distance to Water		Correct	Correct	Correct
MAGC85	0.346	-0.346	-2.416	0.619	1.798	*	*	*	0.411	-0.754	0.343	N/A	*	1.141	72.0	85.6	81.6
MAGC86	0.629	-0.629	-2.042	1.233	0.809	*	*	*	*	*	*	N/A	*	1.068	72.1	84.1	80.6
MAGC87	*	*	-1.079	0.467	0.612	1.074	-0.189	-0.885	0.538	-0.536	-0.002	N/A	*	0.088	76.2	76.5	76.4
CAMA88	0.464	-0.464	-1.172	0.734	0.439	1.100	0.114	-1.214	*	*	*	N/A	*	1.368	69.9	82.0	77.9
CAMA89	*	*	-0.561	0.274	0.286	0.537	0.511	-1.047	*	*	*	*	*	0.319	67.2	60.8	63.8
CAMA90	0.481	-0.481	-1.046	0.577	0.470	*	*	*	*	*	*	*	*	0.944	59.1	73.4	68.9
NCAM91	*	*	-0.906	0.267	0.639	0.967	-0.446	-0.521	*	*	*	*	*	0.896	55.7	78.2	70.9
NCAM92	0.338	-0.338	-0.893	1.145	-0.252	*	*	*	*	*	*	*	*	0.517	62.5	78.4	71.8
NCAM94	*	*	-0.147	1.392	-1.245	-0.171	1.163	-0.992	*	*	*	*	*	0.512	79.4	66.0	72.3
SCAM91	*	*	-0.362	1.201	-0.839	*	*	*	1.584	-0.194	-0.014	-1.376	*	0.289	72.3	76.6	74.6
SCAM93	*	*	*	*	*	*	*	*	0.411	-0.585	-0.461	0.634	-0.002	-0.140	31.7	88.8	70.3
SCAM94	*	*	-0.345	1.539	-1.195	1.139	-0.542	-0.597	-0.054	0.085	-0.252	0.221	*	1.139	63.0	86.2	75.7
SPCR91	*	*	-0.575	-0.203	0.778	*	*	*	*	*	*	*	*	0.172	73.5	51.3	63.4
SPCR92	*	*	-1.287	1.112	0.175	0.635	0.797	-1.431	*	*	*	*	*	1.685	53.2	78.6	70.6

a = main valley bottoms and lower slopes
b = side valley bottoms and lower slopes
c = ridges and upper slopes

probability that a point was within a travel route analysis corridor in 4 years. The burn class increased the probability that a point was located within a travel route analysis corridor in 2 of the 3 years it was applicable to.

Southwestern aspects increased the probability that a point was within a tracking route analysis corridor in the 5 models that aspect was included in. The presence of aspects other than southwestern decreased the probability that a point was within a travel route analysis corridor in all 5 years.

Distance to water was included in 1 model. Probability that a point was within a travel route analysis corridor declined as distance to water increased.

Discussion

Locations of wolf home ranges and travel routes are influenced by habitat characteristics even though wolves are generalist carnivores and occupy a wide variety of habitats. Wolves locate their home ranges in areas where adequate prey are available and human interference minimized (Mladenoff et al. 1995) and wolves use areas within those home ranges in ways that maximize encounters with prey (Huggard 1993a&b). My analysis of landscape habitat characteristics of home ranges and travel routes in the North Fork basin support these ideas.

Topographic position influenced selection of home ranges and travel routes. Wolf use of valley bottoms and lower slopes corresponds to the presence of wintering ungulate prey in these areas (Singer 1979, Jenkins and Wright 1988, Rachel 1992, Bureau 1992, Langley 1993). Many authors have noted strong relationships between winter telemetry locations of wolves and wintering areas of prey (Frits and Mech 1981, Peterson et al. 1984, Ballard et al. 1987). If wolves are locating home ranges and travel routes to maximize encounter rates with ungulate prey (Huggard 1993a&b, Weaver 1994), home ranges and travel routes should be centered on these areas.

Distance to open roads should have been the best indicator of vulnerability to human interference during the winter. My findings indicated that wolf use did not differ from random based on distance to open roads for home ranges, and wolves preferred areas 0.5-1.0 km from open roads for travel routes. One factor confounding this analysis is the location of the North Fork river. The main North Fork road follows the west side of the river while the wolves typically restrict their movements to the east side. The river forms a barrier to human movement, thus protecting the wolves from most human interference even when they are in relatively close proximity to the road. Additionally, the primary open road is located in the main North Fork valley bottom, the same topographic region where winter ranges of ungulates tend to be concentrated (Singer 1979, Jenkins and Wright 1988, Rachel 1992, Bureau, 1992). That wolves did not select locations more distant from open roads for home ranges and travel routes is not surprising because of the distribution patterns of wintering ungulates and the barrier provided by the river.

Thiel (1985) suggested that road density should not exceed 0.93 mi/mi^2 (0.6 km/km^2) in areas managed for wolves. The results of Mech et al. (1988) and Jenson et al. (1986) supported these findings. Mladenoff et al. (1995) found that road density was the strongest predictor of wolf habitat favorability out of 5 habitat characteristics and 6 indices of landscape complexity in a regional analysis of wolf home ranges and potential habitat in Minnesota, Wisconsin, and Michigan. Mladenoff et al. (1995) found that mean road density in 80% harmonic mean home ranges of wolves in Wisconsin was 0.23 km/km^2 (0.37 mi/mi^2) and that no portion of 80% harmonic mean home ranges contained road densities >1.0 km/km^2 (1.61 mi/mi^2). My findings that wolves preferred areas with <4 mi/mi^2 for home ranges and areas with 0.01-2 mi/mi^2 for travel routes indicates a similar pattern of response to road density as reported by these authors. My definition of what constituted a road, and my technique for determining road density, differed from these authors, so the comparison of the effects of specific road density measures is inappropriate (see appendix B).

Total road density influenced both the location of home ranges within the North Fork drainage and the location of travel routes within home ranges. Wolves apparently choose to place their home ranges in areas with few or no roads (presence of road density of 0.01-2 mi/mi^2 decreases probability of home ranges being located in those areas), but choose to use those few roads or areas close to those few roads as travel routes (presence of road density 0.01-2 mi/mi^2 increases probability of travel routes being located in those areas). Roads as structural components of the landscape probably enhance wolf use by providing ready travel routes (Fritts and Mech 1981). However, the increased human use of roaded areas is potentially detrimental to wolves. The primary causes of mortality for radio-collared wolves in the North Fork basin have been human related (Diane Boyd unpublished data). Undoubtedly, wolves in the North Fork commonly use closed roads as travel routes. Even when the wolves are not traveling directly on the roads, wolves and humans probably key in on similar features in identifying the best way to get from one place to another. The reversal of the effect of the 0.01-2 mi/mi^2 road density class between the two analysis scales indicates that wolf use of areas with different road densities is a scale dependent phenomenon (sensu Gardner et al. 1989) and highlights the importance of evaluating habitat use at multiple scales.

My analysis did not provide strong evidence that wolves select for vegetation cover characteristics, though other authors have reported that they do. In reporting the results of a survey of wolf sign in northern Italy, Meriggi et al. (1991) suggested that wolves prefer pastures, conifer plantations, and shrub communities for winter habitat. Seip (1992) reported that wolves in 2 areas of British Columbia primarily used low elevation shrublands and adjacent forests. Neither of these authors conducted any statistical comparison of used versus available areas. Mladinoff et al. (1995) did not find vegetative cover type to be a significant predictor of wolf habitat favorability at a regional scale.

A number of factors potentially confounded my analysis of preference for vegetation classes. The Red Bench fire dramatically altered the composition of the vegetation in the area midway through the study period. Separate analysis of the periods before and after the fire substantially reduced the sample size for these periods compared to the entire study period, increasing the probability of a type I error. Additionally, the combination of the landsat TM image and the B. C. Ministry of Environment forest stand inventory maps may not have provided the resolution to detect vegetation characteristics influencing wolf habitat selection.

Another factor that appeared to influence landscape scale patterns of habitat use was the burned area that resulted from the Red Bench Fire. The home range of the South Camas Pack contained most of the area affected by the burn. Vegetation was an important predictor of travel route location for the South Camas Pack during the winters of 1990-91, 1992-93, and 1993-94 (I did not analyze travel routes for the winter of 1991-

92 due to inadequate sample size). For South Camas 1990-91, 1992-93, and 1993-94, burned areas made up 34.7%, 21.8%, and 24.8% respectively of the winter home ranges and 10.5%, 36.9% and 27.4% respectively of the documented tracking routes.

Chapter 3: SNOWPACK AND VEGETATION STRUCTURE CHARACTERISTICS OF WINTER WOLF TRAVEL ROUTES.

Methods

Data collection

From December 5, 1993 to March 31, 1994 we collected data on structural habitat characteristics of travel routes and adjacent areas to test the hypothesis that travel routes differed from areas nearby. Data were recorded for sample points at 1 km intervals on travel routes and for control points at 3 km intervals (Fig. 3-1). Control points were located 250 m perpendicular from travel routes, with each control point located on the opposite side of the travel route from the previous control point. I used GPS for mapping the wolf travel routes and locating sample and control points for later entry into the GIS.

Three classes of habitat variables were sampled on and near wolf travel routes: habitat structural and landform characteristics, wolf activity patterns, and snowpack characteristics. Structural and landform characteristics sampled were canopy closure, forest cover type, forest structural class, slope, aspect, hiding cover value, and landscape position class (Table 3-1). Wolf activity pattern data recorded were direction of travel, wolf activity at the site, minimum number of wolves, and wolf track depth. Snowpack characteristics recorded were depth of simulated wolf tracks, snow metamorphosis, surface snow character, and snow deposition patterns. These factors were chosen based

Figure 3-1: Habitat sampling protocol for habitat, landform, and snowpack characteristics measured along wolf travel routes during the winter of 1993-94. Data on structural characteristics, snowpack characteristics, and wolf use were recorded for sample points at 1 km intervals along wolf travel routes. Similar data were recorded for control points at 3 km intervals. Control points were located 250 m away from wolf travel routes, with each control point being located on the opposite side of the tracking route from the previous control point.

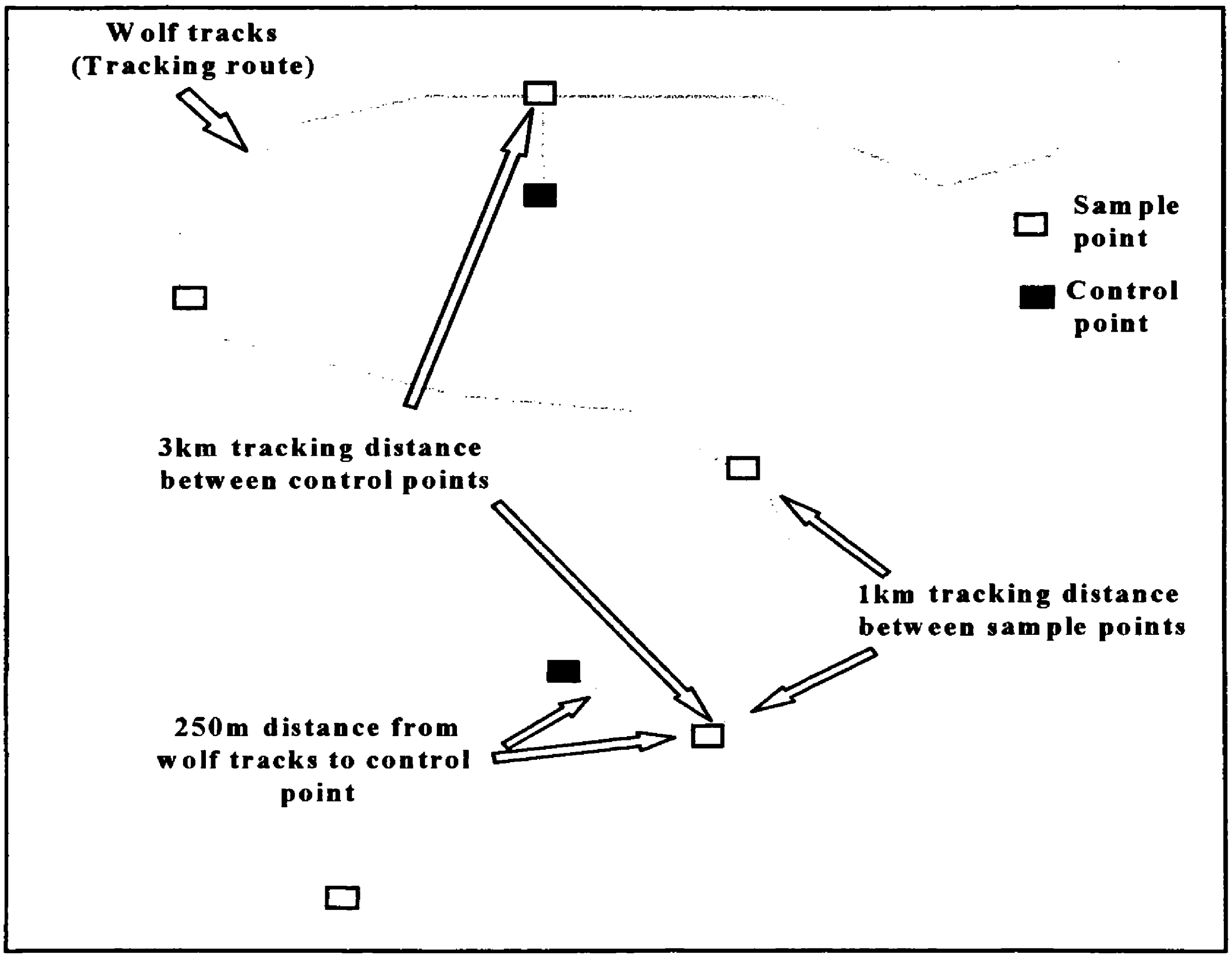


Table 3-1: Habitat, landform, and snowpack characteristics measured along wolf travel routes during the winter of 1993-94.

Variable	Description and Classes
Structural and Landscape Characteristics	
Canopy Closure	The presence or absence of canopy cover directly above the observer was determined at 2 m intervals while walking two 20 m transects (one north - south, the other east - west), centered on the sample point. Cover or no cover was counted for 20 points. Five times the number of points with cover yielded the estimate of percent canopy cover recorded for the sample point.
Forest Cover Type	Dominant forest type class was recorded based on Jenkins & Wright's (1988) forest type classes. Classes were; herbaceous wash, shrub wash, hydric wash, *Populus, Populus-Picea, Picea-Populus*, lowland *Picea*, upland *Picea*, *Pseudotsuga, Pinus contorta*, burned *Picea*, burned *Pinus contorta*, unknown burn, *Pinus contorta* savanna, grassland, lake/river ice, or other. These forest classes were used for consistency with data being collected by Kyran Kunkle.
Forest Structural Class	Forest structure was recorded based on classifications from USFS ecodata procedures (Keane et.al. 1990). Classes were; non-vegetated or moss, herbaceous or herbaceous/tree seedling, sapling (trees <3 in dbh), pole/sapling (trees 3-6 in dbh), young trees (trees 6-10 in dbh), mature trees (trees 10-14 in dbh), or old growth trees (trees >14 in dbh). These classes were used for consistency with data being collected by Kyran Kunkle.
Slope	Percent gradient was recorded using an inclinometer or visual estimate.
Aspect	Aspect was determined using a hand-held compass.
Hiding Cover Value	Visual estimates of the percent of a deer-sized animal obstructed from view at a distance of 30 m were recorded for the 4 cardinal directions from the sample point. Hiding cover classes were; class 1 (0-10% of a deer sized animal obscured at 30 m), class 2 (11-30% of a deer sized animal obscured at 30 m), class 3 (31-50% of a deer sized animal obscured at 30 m), class 4 (51-75% of a deer sized animal obscured at 30 m), or class 5 (75-100% of a deer sized animal obscured at 30 m).
Landscape Position Class	Position of the sample point within the landscape was recorded using standard landscape position classes based on USFS ecodata procedures (Keane et.al. 1990). These classes were used for consistency with data being collected by Kyran Kunkle. Landscape cover classes were; valley bottom, ravine, lower slope in narrow valley bottom, mid or lower slope in narrow valley bottom, slope in wide valley bottom, ridgetop or knoll, creek bottom, and bench, terrace or saddle.

Table 3-1 (continued): Habitat, landform, and snowpack characteristics measured along wolf travel routes during the winter of 1993-94.

Variable	Description and Classes
Wolf activity patterns	
Direction of Travel	General direction that the wolves were travelling was determined using a hand held compass.
Wolf Activity at the site	Wolf activity was determined by track patterns. Classes were; dispersed travel (wolves moving through the area in a spread out pattern), concentrated travel (wolves moving in single file), pursuit (tracks indicate a chase taking place), kill site, bedding site, or other.
Minimum Number of Wolves	The minimum number of wolves that had passed by the sample point was estimated from track patterns.
Depth of Wolf Tracks	The depth of five randomly selected wolf tracks were measured (at sample points only).
Snowpack characteristics	
Depth of Simulated Wolf Tracks	the depth of five randomly located simulated wolf tracks were recorded at control points (and at some sample points). Simulated wolf tracks were created by placing a 4 in diameter ski pole basket on the end of a ski pole. Twenty-five pounds of vertical pressure (measured by a pocket spring scale) was applied to the ski pole to create the simulated track.
Snow Metamorphosis	This was a categorical (yes, no) answer to the question "has the hardness of the snow changed since the wolves moved through the area?"
Surface Snow Character	The snow surface was classified as either loose (individual snow crystals clearly discernible and not bonded together), consolidated (individual snow crystals bonded together and not clearly discernible), ice (snow surface not easily penetrated with the tip of a ski pole), or breakable crust (the surface of the snow supports 20 pounds of vertical pressure on a ski pole with a 4 in diameter basket, but the basket portion of the ski pole penetrates through to a less dense underlying snow layer when more pressure is applied).
Snow Deposition	The pattern of snow deposition at the sample point was classified as either heavy snow deposition and drifting, wind scoured, snow deposition mitigated by dense forest canopy, average snow accumulation, or other.

on their presumed potential to effect energetic costs of travel, as well as prey distribution and detectability along travel routes.

Statistical Analysis

I compared sample points to control points to test the hypothesis that travel routes differed from areas nearby. I used Paired t-tests, Mann-Whitney U statistics, and Kolmogorov-Smirnov statistics for comparing continuous variables. I used Chi-square tests for categorical variables. I used 90% Bonferroni simultaneous confidence intervals to identify classes that were different for the sample and control points if a significant difference ($P \leq 0.10$) was found while using the chi-square statistic (Manly et al. 1993). SPSS for windows (version 6.1) was used for most analysis of field habitat data. Bonferroni simultaneous confidence intervals were calculated using Excel.

Due to the small sample size for control points, and the lack of clear habitat selection patterns from the univariate statistical analysis, I did not conduct multiple logistic regression with this data set.

Results

Fifty-four separate tracking bouts, totaling 308.7 km of winter tracking, were documented from December 5, 1993 to March 31, 1994. Habitat characteristics were measured at 337 points (264 sample points and 73 control points).

Wolf activity at the 264 sample points was mostly concentrated travel (119 points) or dispersed travel (140 points). Very few sample points fell at bed sites (2 points), kill sites (1 point), or along pursuit routes (2 points). Two hundred and twenty-six of the sample points (85.6%) fell along travel routes recently followed by 5 or more wolves. Only 24 sample points (9.1%) fell along travel routes recently followed by 2 or fewer wolves.

None of the continuous habitat variables (canopy closure, slope, aspect, or simulated track depth) was significant at the $P = 0.10$ level for paired t-tests, Mann-Whitney U statistics, or Kolomogorov-Smirnov statistics in comparing sample points to control points (Table 3-2).

Slope was nearly significant ($P = 0.103$) based on a paired t-test, with the wolves

Table 3-2: Analysis results for continuous variables at sample and control points along wolf travel routes.

Variable	N		Mean		Min.		Max.		Std. Dev.		Mann - Whitney U	Kolmogorov -Smirnov	Paired t-test
	Sample	Control	Sample	Control	Sample	Control	Sample	Control	Sample	Control			
Canopy Closure	264	73	30.97	29.86	0	0	95	80	28.83	27.55	P = 0.817	P = 0.999	P = 0.351
Slope	262	72	12.86	14.87	0	0	84	75	7.39	19.36	P = 0.321	P = 0.317	P = 0.103
Aspect	187	59	207.11	193.78	4	2	350	340	75.59	80.59	P = 0.415	P = 0.642	P = 0.654
Average Simulated Track Depth	37	51	6.32	7.45	1	1	35	53	7.39	9.58	P = 0.807	P = 0.995	P = 0.257

using areas that were less steep than the control points. However, Mann-Whitney U and Kolomogorov-Smirnov statistics were not significant for slope ($P=0.32$ for both). It is very likely that wolves select less steep areas as travel routes compared to adjacent areas. However, the null hypothesis that wolves use less steep areas only in proportion to their availability cannot be rejected based on my data.

Sample points differed significantly ($P \leq 0.10$) from control points in respect to maximum hiding cover, landscape position class, and snow deposition (Table 3-3). Simultaneous 90% confidence intervals showed that only one class differed significantly between sample and control points for each of these variables.

Control points fell on slopes in wide valley bottoms significantly more often than sample points. Differences in use of other landscape position classes were not significant, though the valley bottom, creek bottom, ridgetop or knoll, and bench, terrace, or saddle classes were all used in greater proportions than they were available. It is possible that the wolves avoided moving across the slopes in the wide valley in preference for more distinct landscape features such as valley bottoms, and small ridges. The ravine class was eliminated from the analysis and the 4 points (1 sample and 3 control) in this class were reclassified as lower slopes in narrow valley bottoms to facilitate chi-square analysis.

Table 3-3: Frequency of observations for categorical variables at sample and control points along wolf travel routes. Pearson significance levels from chi-square analyses are shown in parentheses after the variable name. † denotes classes showing significant differences between control and sample points based on 90% bonferroni simultaneous confidence intervals.

Variable	Class	Sample (n=264)	Control (n=73)
Forest Cover Type (P=0.231)			
	Burn	19.7%	27.4%
	Ice	1.9%	0.0%
	Meadow	11.7%	6.8%
	Riparian forest types	9.8%	5.5%
	Upland forest types	56.8%	60.3%
Forest Structural Class (P=0.608)			
	Non-vegetated or herbaceous	11.4%	8.2%
	Tree seedling / sapling (<3 in dbh)	7.6%	4.1%
	Young trees (3 - 10 in dbh)	44.3%	53.4%
	Mature trees (10-14 in dbh)	27.3%	24.7%
	Old growth trees (>14 in dbh)	9.5%	9.6%
Minimum Hiding Cover Value (P=0.956)			
	1	56.4%	58.9%
	2	25.8%	23.3%
	3	10.6%	12.3%
	4/5	7.2%	5.5%
Maximum Hiding Cover Value (P=0.097)			
	1	15.9%	11.0%
	2	16.3%	17.8%
	† 3	13.3%	26.0%
	4	20.1%	17.8%
	5	34.5%	27.4%
Landscape Position Class (P=0.001)			
	Valley Bottom	19.3%	8.2%
	Lower slope in narrow valley bottom	12.9%	16.4%
	Mid slope in narrow valley bottom	9.8%	11.0%
	† Slope in wide valley bottom	29.5%	53.4%
	Ridgetop or knoll	7.2%	1.4%
	Bench, terrace, or saddle	14.4%	6.8%
	Creek bottom	6.8%	2.7%

Table 3-3 (cont.): Frequency of observations for categorical variables at sample and control points along wolf travel routes. Pearson significance levels from chi-square analyses are shown in parentheses after the variable name. † denotes classes showing significant differences between control and sample points based on 90% bonferroni simultaneous confidence intervals.

Variable Class	Sample (n=264)	Control (n=73)
Snow Deopsition (P=0.089)		
Average	64.8%	75.3%
Mitigated	35.2%	24.7%
Surface Snow Character (P=0.970)		
Breakable crust	17.0%	16.4%
Consolodatedsnow	48.9%	47.9%
Loose snow	34.1%	35.6%

Occurrence of hiding cover class 3 (30-50% of a deer-sized animal obscured at 30 m) as the maximum hiding cover class was more common for control points than for sample points. Chi-square analysis for maximum hiding cover indicates that wolves may be using the maximum hiding cover class 1 (0-10 % of a deer-sized animal obscured at 30 m) and class 5 (75-100 % of a deer-sized animal obscured at 30 m) categories more than available. Chi-square analysis did not show a significant difference between sample and control points for minimum hiding cover class (P=0.896) or range of hiding cover classes (P=0.436). Classes 4 and 5 were grouped together to facilitate chi-square analysis for minimum hiding cover class, because only 7 points (6 sample and 1 control) had class 5 for minimum hiding cover.

Due to the large number of forest cover type classes that had few occurrences on sample or control points, individual forest types recorded in the field were grouped for chi-square analysis. Analysis groups were riparian herb/shrub types (including the field classes herbaceous wash, shrub wash, and hydric wash), riparian forest types (including *Populus, Populus-Picea, Picea-Populus,* and lowland *Picea* field classes), upland forest types (including upland *Picea, Pseudotsuga,* and *Pinus contorta* field classes), burn types (including burned *Picea*, burned *Pinus contorta*, and unknown burn field classes), meadow types (including *Pinus contorta* savanna, and grassland field classes), and ice (corresponding to the lake/river ice field class). Forest cover types did not differ significantly between sample and control points. Even though differences were not significant, larger proportions of sample points than control points fell on lake or river ice (1.9% of sample, 0.0% of control), in riparian forests (9.8% of sample, 5.5% of control), and in meadows (11.7% of sample, 6.8% of control).

Sample points did not differ significantly from control points in respect to forest structure (P=0.608). Adjacent forest structure classes were grouped together for the chi-square analysis due to the large number of classes. The analysis classes were non-vegetated or herbaceous, tree seedling/sapling (trees <3 in dbh), young trees (trees 3-10 in dbh), mature trees (trees 10-14 in dbh), and old growth trees (trees >14 in dbh). Slightly larger proportions of sample points than control points fell in the non-vegetated or herbaceous (11.4% of sample, 8.2% of control), tree seedling/sampling (7.6% of sample, 4.1% of control), and mature tree (27.3% of sample, 24.7% of control) classes.

Sample points were more often located in areas where snow deposition was mitigated by the forest canopy (35.2% of sample points) compared to control points (24.7% of control points). Despite the Chi-square analysis for these classes showing a significant difference in use compared to control (P=0.089), neither the mitigated or the average snow deposition classes showed a significant difference between sample and control points in the 90% simultaneous confidence intervals. The 2 points that were classified as drifted were grouped with the average snow deposition class, and the 1 point classified as wind swept was grouped with the mitigated snow deposition class to facilitate chi-square analysis.

Surface snow character did not differ between sample and control points (P=0.970). The proportions of sample compared to control points occurring in each surface snow character class was nearly identical. To facilitate chi-square analysis, the ice class was eliminated and the one point that was classified as ice was reclassified as consolidated.

Discussion

Wolves make decisions based on habitat characteristics at some scale. While ungulate prey are distributed on a landscape scale, prey vulnerability and detectability are determined at a finer spatial scale. I was able to detect only a few differences in vegetation structure, landform, and snowpack characteristics between wolf travel routes and adjacent areas.

Snowpack characteristics should influence winter habitat use by wolves. Wolves kill more prey during winters with deep snow (Nelson and Mech 1986, Fuller 1991), and snow depth influences deer vulnerability by acting as a physical impedance to escape and by reducing deer fat reserves due to restricted mobility and increased energy costs

(Nelson and Mech 1986). While I was unable to detect differences in simulated track depth and surface snow characteristics between travel route sample and control points, wolves did use areas with mitigated snow deposition greater than they occurred at control points.

Topographic position influenced travel route location in comparison to areas adjacent to travel routes. Wolves probably select travel routes to maximize prey encounter rate (Weaver 1994, Huggard 1993a&b). I found that control points fell on slopes in wide valley bottoms significantly more often than sample points. Perhaps the wolves avoided moving across the slopes in the wide valley in preference for more distinct landscape features such as valley bottoms, and small ridges. Use of topographic features (e.g. ridges and draws) may enhance the chances of ambushing prey opportunistically encountered while travelling.

My findings indicate that wolves do not select travel routes based on most vegetation structural characteristics. However, travel route selection appeared to be affected by visibility distance (a function of vegetation structure). Occurrence of hiding cover class 3 (30-50% of a deer-sized animal obscured at 30 m) as the maximum hiding cover class was more common for control than for sample points. Perhaps wolves are choosing to move through areas where they are either out in the open (maximum hiding cover class 1) or are close to dense hiding cover (maximum hiding cover class 5), but tend to avoid intermediate areas (like maximum hiding cover class 3). Preference for vegetation cover types or other structural characteristics may have been taking place.

A number of factors potentially confounded my analysis. I may not have detected habitat structure characteristics that were prefered due to the small number of control points that I collected. In addition, the control points were possibly located too close to travel routes to detect any difference. Perhaps with more field work and a better habitat sampling protocol, more structural habitat characteristics that influence selection of travel routes could be identified.

Chapter 4: WINTER HABITAT SELECTION BY WOLVES.

Conducting habitat preference studies at multiple scales can highlight scale dependent habitat selection phenomena that would otherwise remain undetected (Gardner et al. 1989). Consideration of the ecological significance of the scales being investigated is also important (Wiens 1976). For wolves, landscape scale analyses of home ranges and travel routes appear to be appropriate. These scales make sense ecologically because ungulate prey are distributed at a landscape scale while prey vulnerability and detectability are determined at a finer scale. My analyses of home range locations within the North Fork drainage and travel route locations within home ranges indicate that wolves are making decisions about what habitat features to use at landscape scales. Though my analysis of habitat structure along and adjacent to travel routes failed to identify substantial differences, wolves may make decisions based on habitat structural characteristics as well as landscape characteristics.

Winter movement and habitat selection patterns of wolves in the North Fork are probably determined by 2 primary factors; 1) prey patch distribution and quality, and 2) location and connectivity of optimal inter-patch travel routes. Charnov's marginal value theorem (Charnov 1976) suggests that an animal will maximize its over-all net rate of energy gain if it remains in a resource patch until its net rate of energy gain in that patch has decreased to the over-all rate in the habitat. The overall rate of energy gain in the habitat is largely determined by travel time (or travel cost) between patches. Selection of optimal travel routes is therefore important in the effective use of resources within a home range. Optimal travel routes should be those routes which minimize energy expenditure and maximize chance of random prey encounter. Identification of the characteristics of those inter-patch travel routes will be critical in understanding how wolves and other animals utilize the landscapes they occupy.

If wolves are selecting ungulate prey based on encounter rate, as Weaver (1994) and Huggard (1993a&b) suggested, they should modify their movement patterns to maximize encounters with prey during movement. Huggard (1993a) classified wolf kills as intentional or random based on whether they occurred in areas where ungulates regularly congregated (nodes of prey concentration) or whether they occurred when wolves randomly encountered prey during movements between areas where ungulates concentrated (wolves randomly encountering prey along connecting routes).

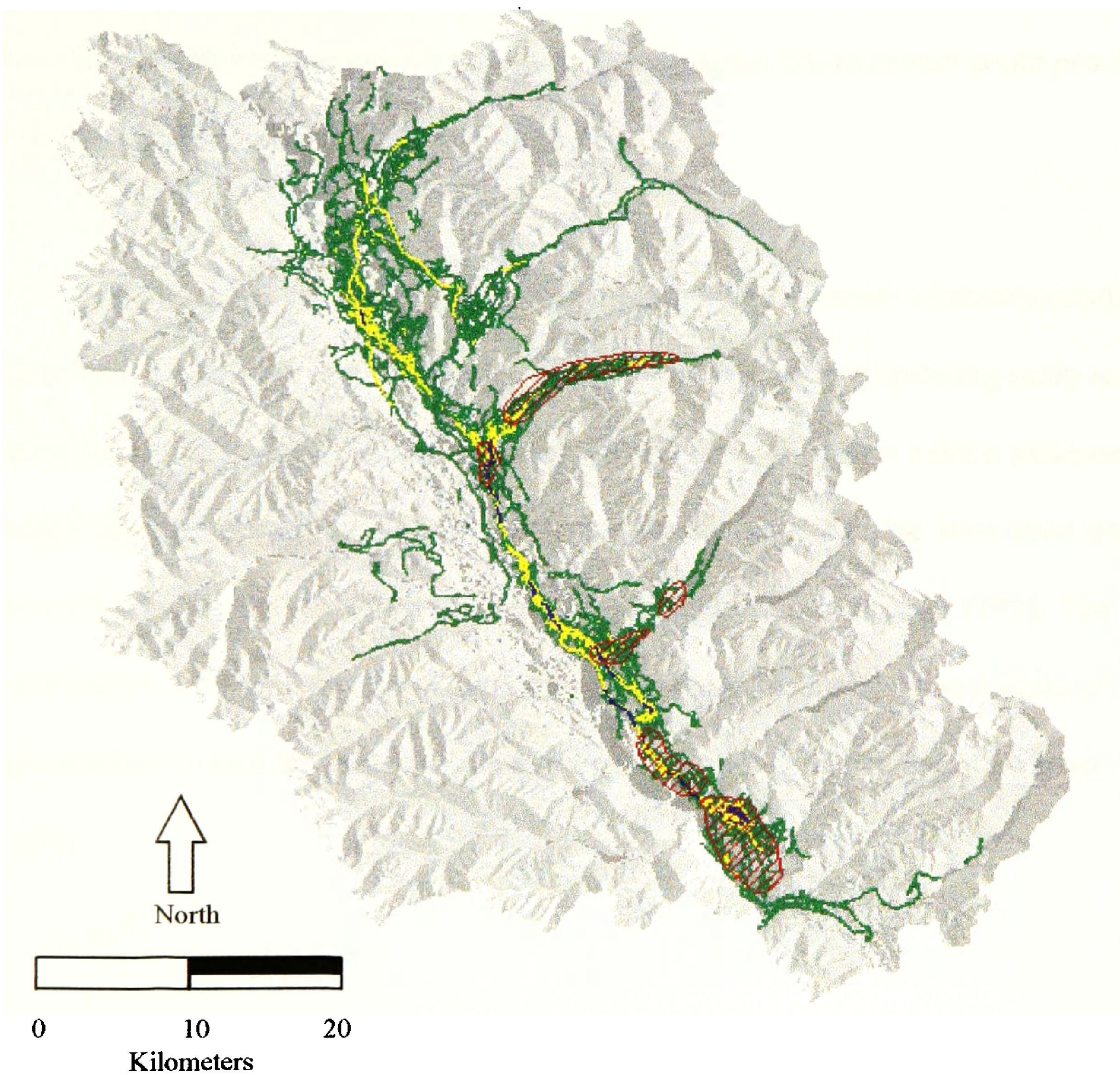
The primary prey of wolves in the North Fork are white-tailed deer and elk. Rachel (1992) identified 5 areas as primary winter ranges of white tailed deer in the North Fork. During his study of elk in the North Fork, Bureau (1992) noted that "most elk winter along the river from Sage Creek to Camas Creek". These areas correspond to areas where wolves have been frequently tracked during the 11 years analyzed here.

Wolves appear to have used these deer winter ranges intensively based on the frequency with which they were tracked there (Fig. 4-1). This is particularly true of those winter ranges located in the main North Fork valley bottom (the Kintla Creek, Polebridge, and Sullivan Meadow areas).

These patterns of spatial use support the concept that winter habitat use by wolves in the North Fork can be conceived of as a pattern of nodes of resource concentration (deer or elk wintering areas) connected by inter-node routes (regular travel routes). Similar route - node patterns of movement and resource acquisition have been well developed in the discipline of human geography (Lowe and Moryadas 1975), and may be very applicable to wolf ecology (Weaver 1994). By using ground tracking data to document the movement patterns of wolves in the North Fork, these route - node patterns become clear. While the tracking data do not provide information on how long the animals spent in an area, it does provide an insightful perspective on habitat use by identifying areas where animals concentrated their movements and how those areas were connected.

Several questions regarding winter habitat selection by wolves in the North Fork remain unanswered. A variety of factors probably influence habitat selection and movement patterns. Winter severity and snow depth, variation in pack size, variation in home range size, and interactions with sympatric predators could all effect the ways

Figure 4-1: Total wolf use from ground tracking Nov. 1983 to Mar. 1994 (tracking routes with 100 m analysis corridor buffers), and approximate deer winter ranges from Rachel (1992).



Legend

Infrequent Use (wolves tracked in these areas <4 times)

Moderate Use (wolves tracked in these areas 4-10 times)

Heavy Use (wolves tracked in these areas >10 times)

Deer Winter Ranges

wolves utilize areas available to them. In addition, behavioral characteristics such as turning frequency or travel route complexity are likely to vary depending on whether the animal is within a patch of concentrated resource availability (e.g. deer winter ranges), moving between known patches, or exploring new areas. These factors could provide interesting starting points for future research.

Habitat selection is a process that is influenced by a variety of characteristics at many scales. Gardener et al. (1989) point out the dangers of extrapolating study results across scales. Hopefully this study can provide an example of how habitat preference studies can be conducted to overcome some of the shortcomings that have been identified for such studies in the past (Thomas and Taylor 1990, Aebischer et al. 1993). The combination of the ancient art of tracking with the high technology capabilities of GIS can combine to shed significant light on patterns of animal habitat use at a variety of scales.

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Appendix A: Wolf Ecology Project GIS data sets.

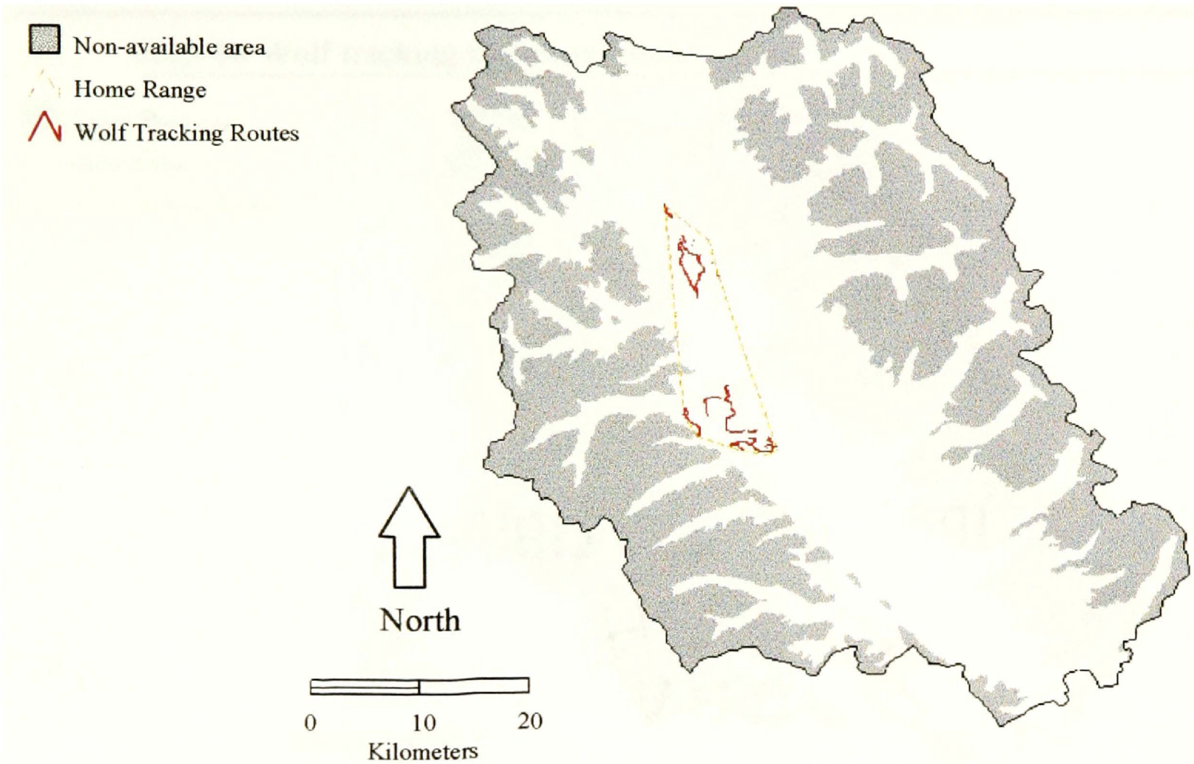
All winter wolf tracking information documented by the Wolf Ecology Project (WEP) of the University of Montana, from November 1983 to March 1994, was digitized using PAMAP GIS software (fig. A-1). Information entered into the GIS included tracking route, kill sites, bed sites, and ungulate track transects. A unique number was assigned to each tracking bout so non-spatial data, such as the wolf pack responsible for creating the tracks, number of wolves, date, etc., could be associated with each bout. Non-spatial data relating to tracking bouts were not entered into the GIS. Tracking routes, kill sites, bed sites, and track transects for each bout were entered onto separate layers. All layers were named (in PAMAP's select vector level window) with the tracking bout number and data type code (WT for wolf tracks, TT for ungulate track transects, BS for bed sites, and CS for carcass sites). Each winters data was entered into separate maps, though due to the 64-layer limit in PAMAP, some years required up to 4 maps to contain all of the data. In addition to the ground tracking data, radio-telemetry locations for each winter were merged into these maps as point databases (these layers were called WLFLOC followed by the year). Files for the tracking data maps were named WT followed by the year of the data and a letter if more than one map was needed for the years data (for example WT92A.*). A total of 18 separate maps were generated to contain all of the tracking data.

Two additional maps based on wolf ecology project data sets were generated. A map of all radio-telemetry locations (including data collected during all seasons) was generated and stored in the TELEDATA.* map files. A map of all carcass data, from WEP carcass data sheets, was generated and stored as a point data layer in the CARCMAP.* map files. This data was not merged with the yearly maps.

All of these maps are archived at the University of Montana on 4mm tape and 3.5in disk.

Figure B-2: Yearly wolf tracking routes and minimum convex polygon home ranges.

1983-84 Wolf tracking routes and home range



1984-85 Wolf tracking routes and home range

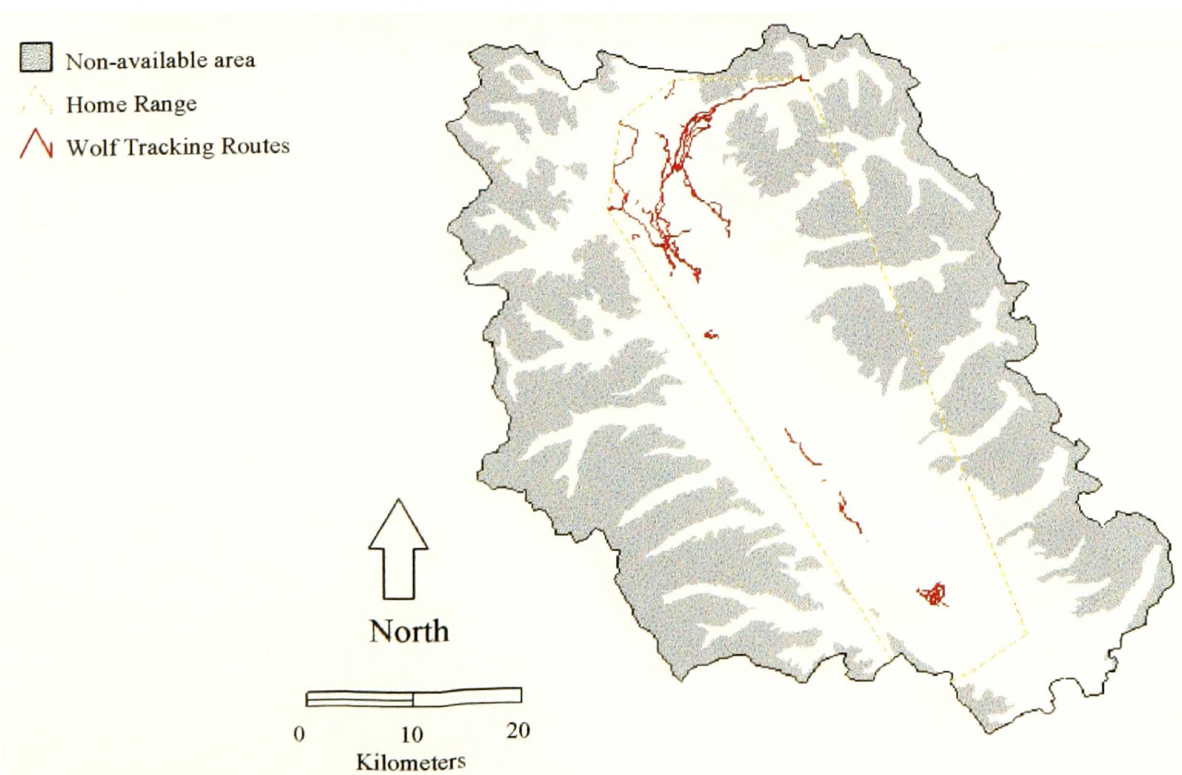
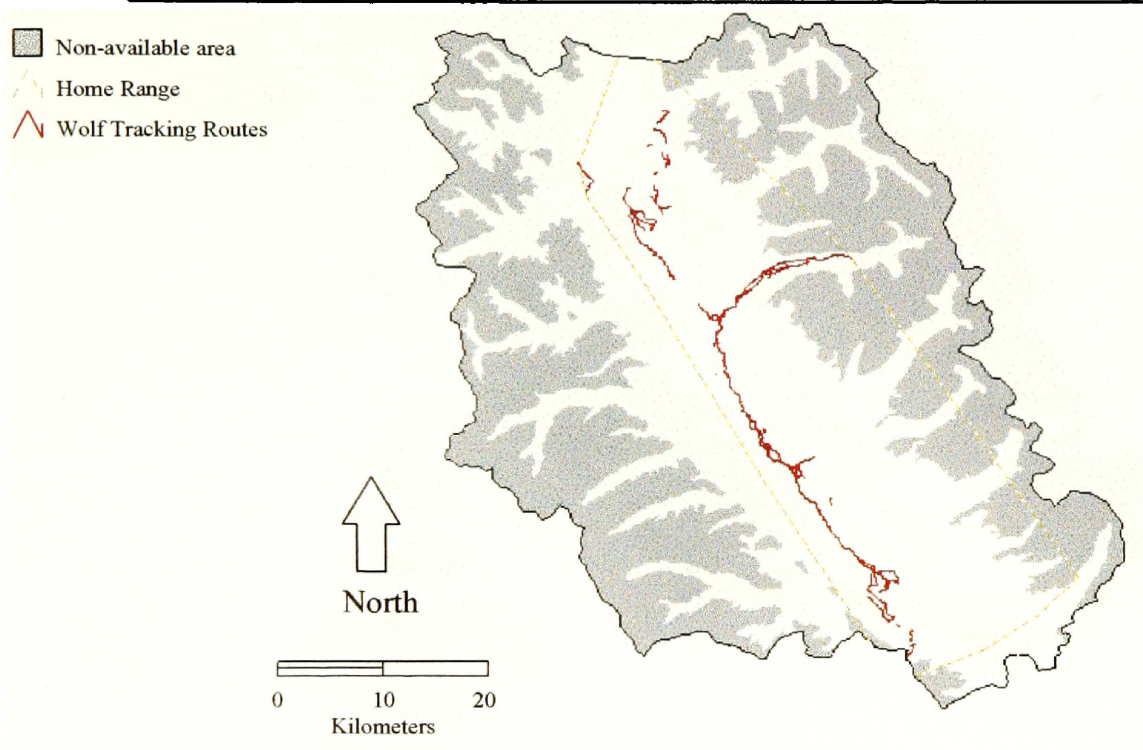


Figure B-2 (continued): Yearly wolf tracking routes and minimum convex polygon home ranges.

1985-86 Wolf tracking routes and home range



1986-87 Wolf tracking routes and home range

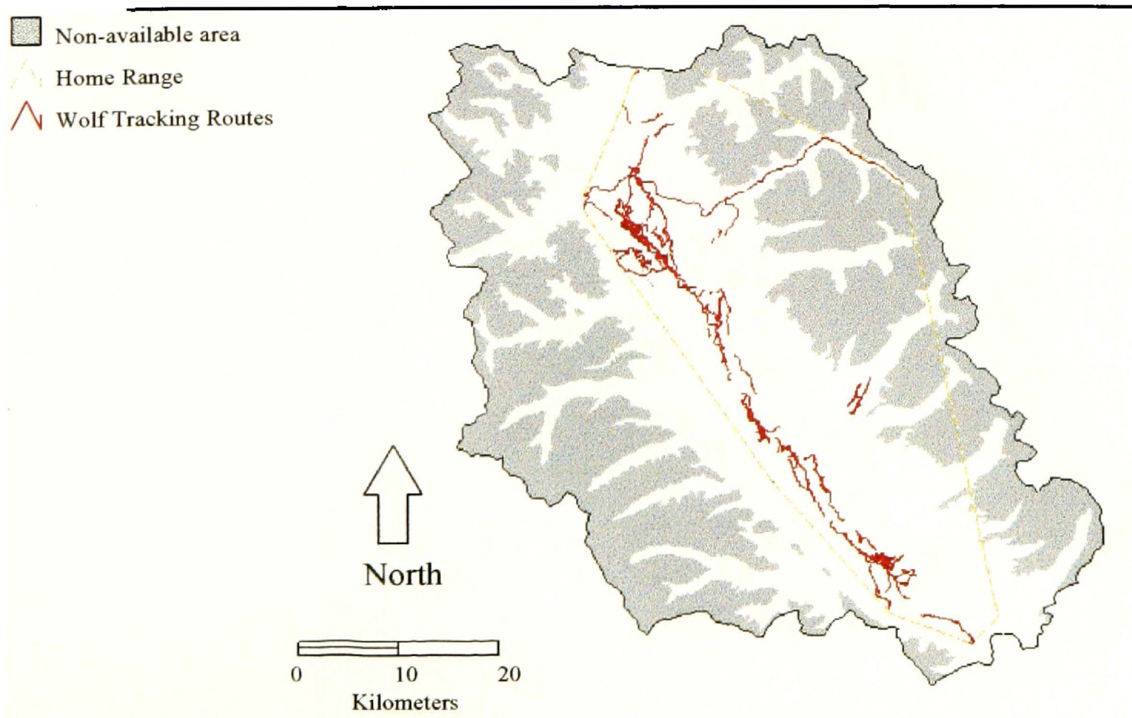
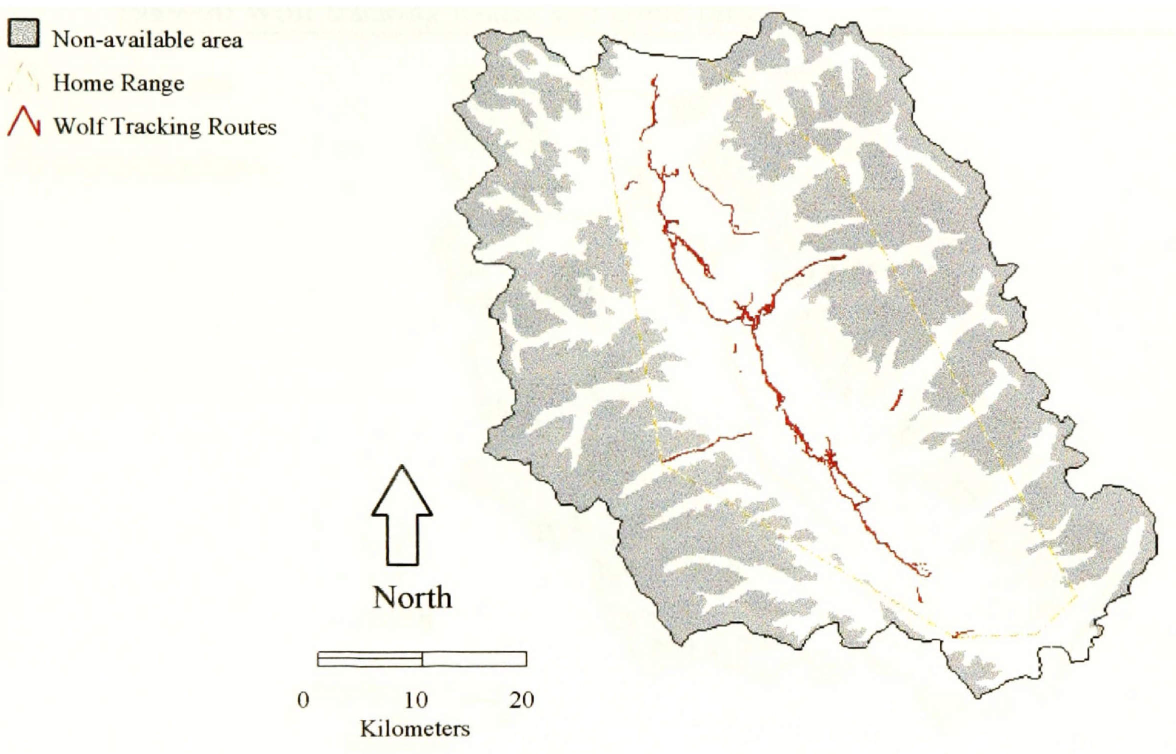


Figure B-2 (continued): Yearly wolf tracking routes and minimum convex polygon home ranges.

1987-88 Wolf tracking routes and home range



1988-89 Wolf tracking routes and home range

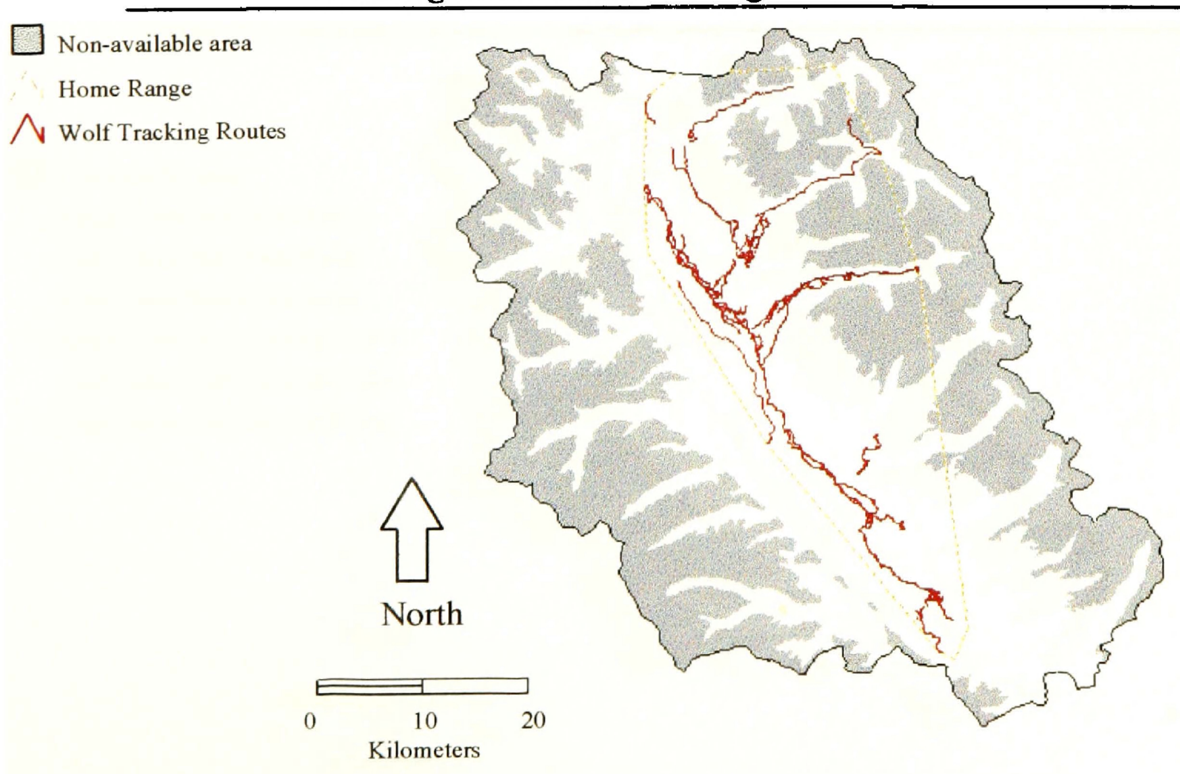
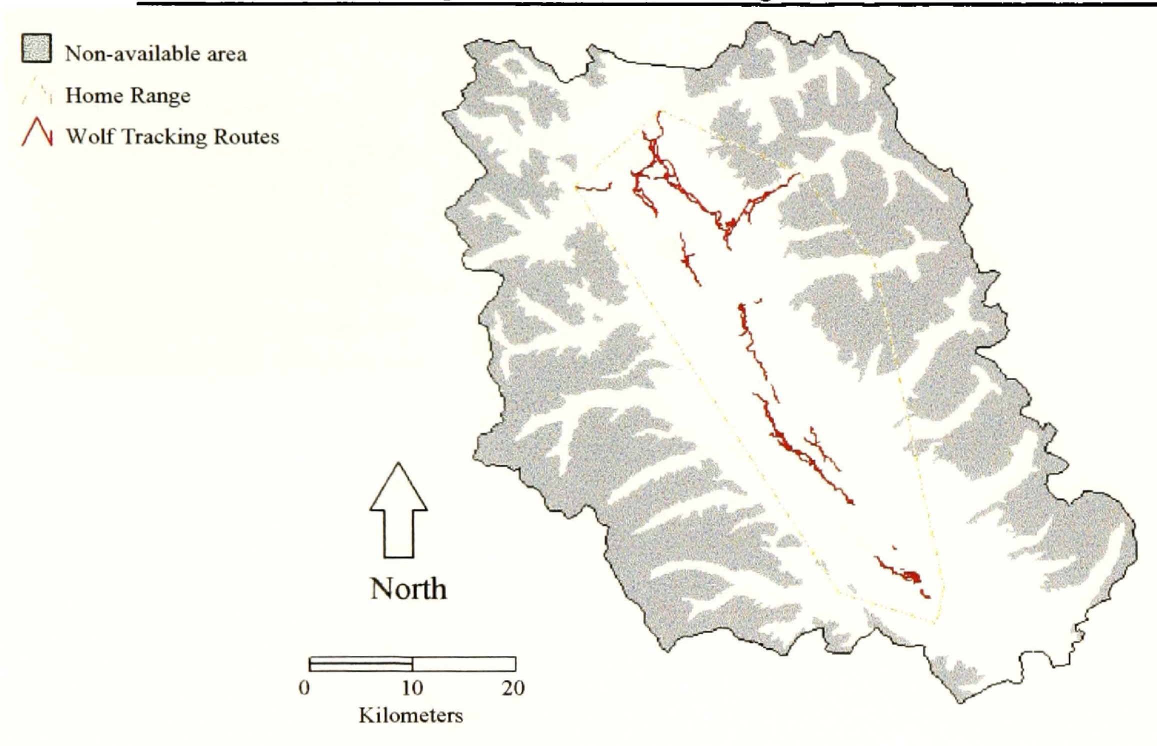


Figure B-2 (continued): Yearly wolf tracking routes and minimum convex polygon home ranges.

1989-90 Wolf tracking routes and home range



1990-91 Wolf tracking routes and home ranges

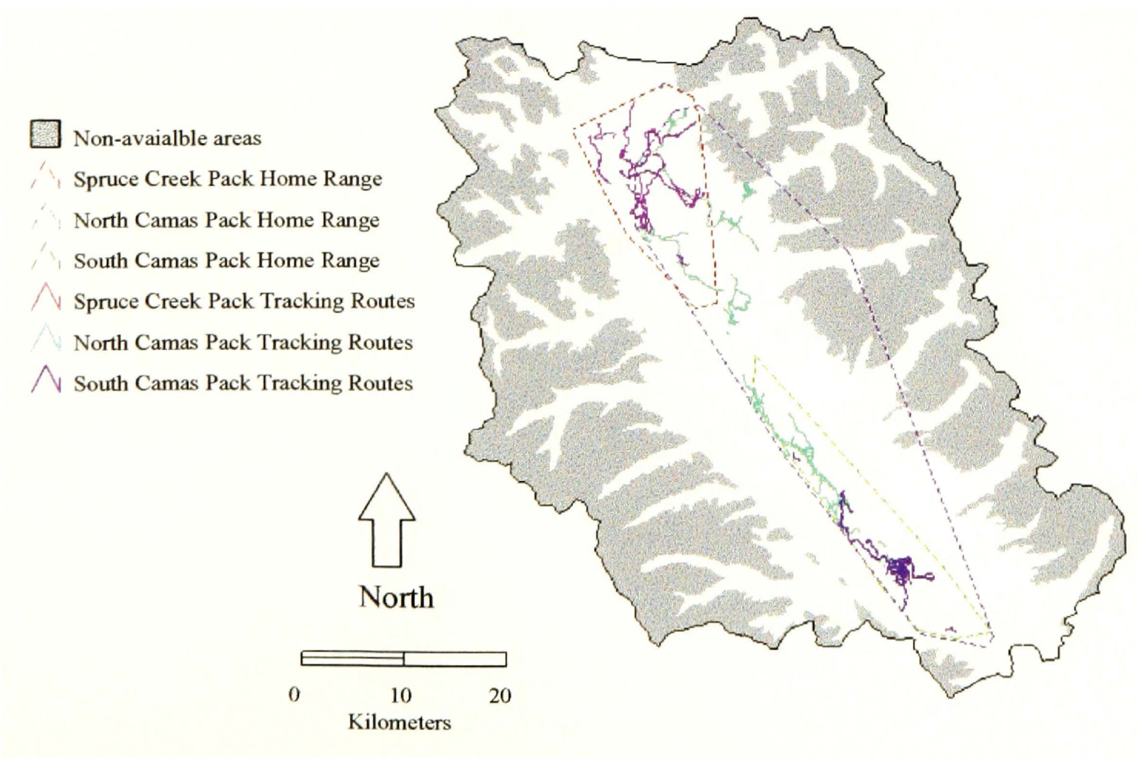
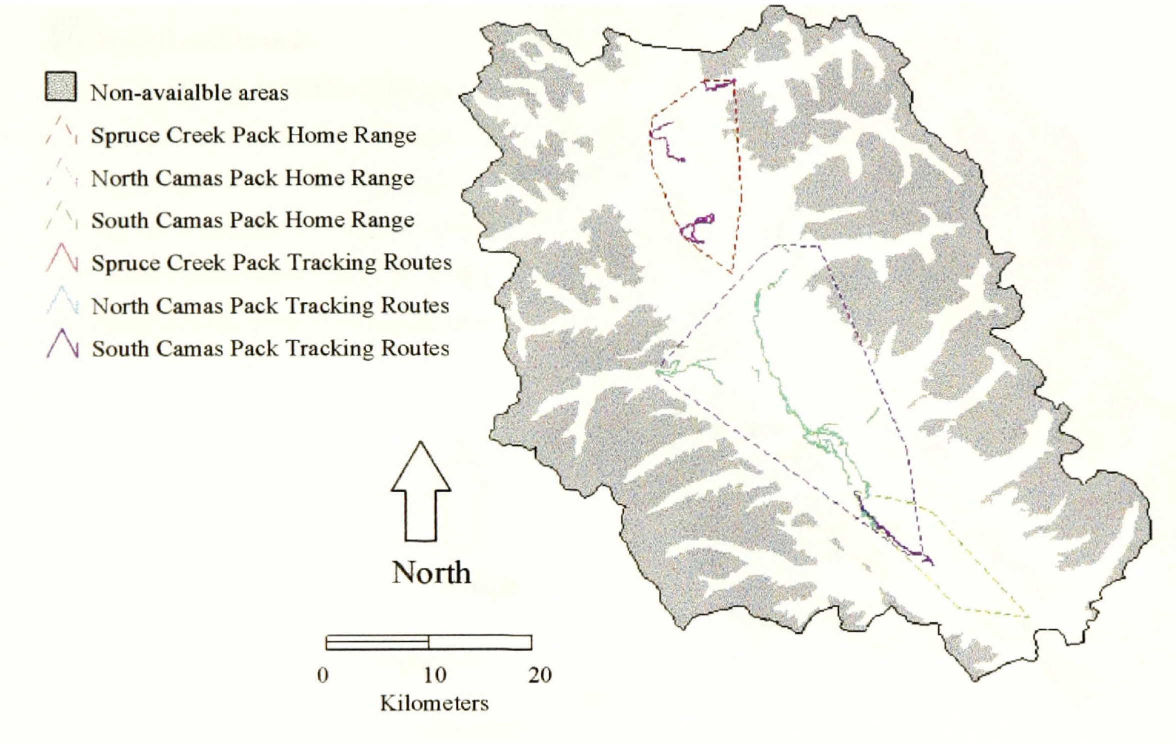


Figure B-2 (continued): Yearly wolf tracking routes and minimum convex polygon home ranges.

1991-92 Wolf tracking routes and home ranges



1992-93 Wolf tracking routes and home ranges

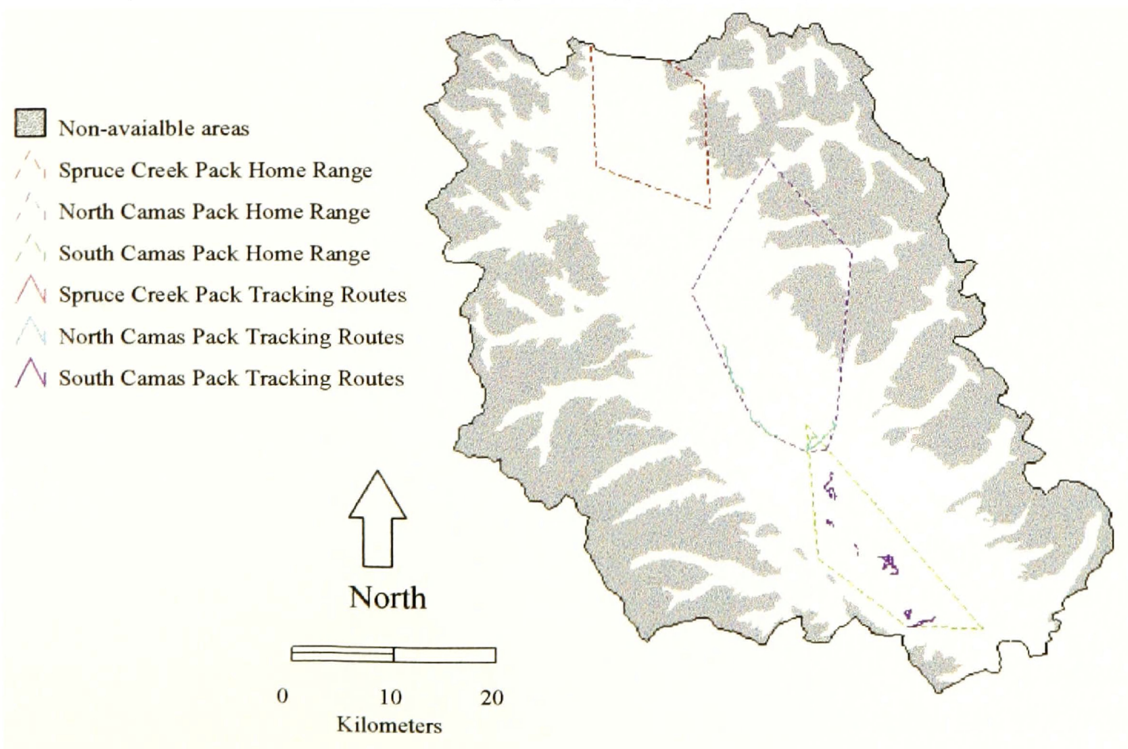
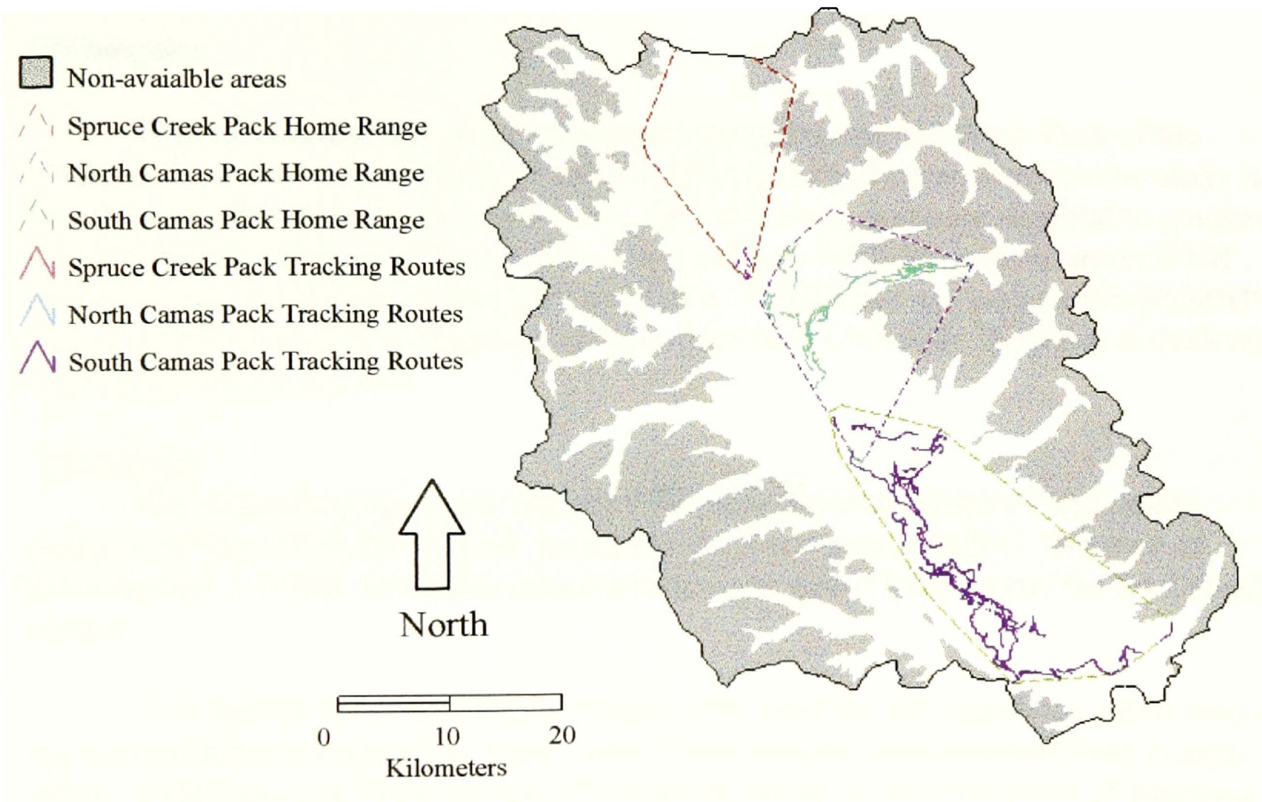


Figure B-2 (continued): Yearly wolf tracking routes and minimum convex polygon home ranges.

1993-94 Wolf tracking routes and home ranges



Appendix B: Habitat characteristic map layers for the North Fork of the Flathead River basin.

Introduction

Habitat characteristic map layers were generated for the North Fork of the Flathead River basin for analysis of habitat utilization by wolves. Because the study area encompasses the international border, two data sets were generally required to generate each layer. All habitat map layers were converted into NAD 27 map datum in UTM (zone 11) map projection, with a 50m pixel size. These maps are archived in PAMAP format at the University of Montana on 4mm tape and 3.5in disk. Graphics of each map layer are shown in fig. B-1.

Vegetation

The vegetation type layer was derived from classified landsat TM satellite imagery (White 1994) for the U.S. portion of the study area, and B.C. Ministry of Environment 1:20,000 terrestrial resource inventory maps (TRIM data) for the Canadian portion.

Two landsat thematic mapper images were used for the vegetation cover map of the United States portion of the study area. These images were obtained from Joseph White of the Numeric Terra-dynamic Simulation Group at the University of Montana (White 1994). One of the images contained classified information on vegetation types in the United States portion of the North Fork basin. The other contained information on the extent and intensity of the Red Bench fire of August 1988. The landsat images were obtained in ERDAS *.lan format using NAD 27 map datum and UTM (zone 12) projection. The ERDAS files were translated into Arc/Info GRID format and converted into NAD 27 map datum and UTM (zone 11) projection using the "reproject" function in Arc/Info. The resulting files were exported from Arc/Info as ERDAS lan files and imported into PAMAP. Pixel size was converted from 30m to 50m using the "change pixel size" function in PAMAP. To generate a post-fire vegetation cover map for the United States portion of the study area, the vegetation image and the Red Bench fire image were combined using the PAMAP "model linear surface" function. The vegetation cover image without the burn extent was used as the pre-fire vegetation cover map.

For the Canadian portion of the study area, vegetation cover information was derived from TRIM data. This data was originally generated from aerial photo interpretation and timber cruising conducted by the British Columbia Ministry of Environment. The TRIM data was translated from Intergraph GIS format into PAMAP vector layers, with database tags, using NAD 83 map datum and UTM (zone 11) projection. I copied the vector data and associated database tags into the North Fork template map in order to get the data translated into NAD 27 map datum and UTM (zone

11) projection. The vector files were then converted into polygons using a 10m pixel size to maintain connectivity of polygons with constrictions. Once the data was in polygon format, pixel size was converted to 50m using the "change pixel size" function in PAMAP. The TRIM data was reclassified to match the vegetation classes represented in the landsat TM image used for the United States portion of the study area using dominant tree species. The TRIM data and the landsat image were finally merged together to form single vegetation cover maps for the periods before and after the Red Bench fire. These layers are in the CANVEG.* and VEGOVL.* maps.

Vegetation classes represented were deciduous forest, *Pinus contorta* forest, *Pseudotsuga menziesii/Larix occidentalis* forest, *Abies lasiocarpa/Picea engelmanni* forest, shrub/meadows, bare ground, water, mixed, and burned.

Topographic Position

A topographic position layer was included to identify landform characteristics of areas used by wolves. Topographic position classes were determined based on landform shape, slope, and elevation above primary streams and rivers using the following model:

Topographic position class (Data Code) (Theme Value)	Criteria
Main Valley Bottom (MVB) (11)	slope <6% and in main valley
Lower Slope in Main Valley (MVL) (12)	slope >6%, <200m above river, and in main valley
Mid-upper slope in main valley (MVU) (13)	slope >6%, >200m above river, and in main valley
Side Valley Bottom (SVB) (14)	slope <6% and contiguous with areas within 150m of side streams or within 150m of side stream, not in main valley
Mid-upper slope in Side Valley (SVU) (15)	slope >6%, >150m above side stream
Bench, Terrace, or Saddle (BEN) (16)	slope <6%, not in main or side valley bottom
Lower Slope in Side Valley (SVL) (17)	slope >6%, not in main valley, <150m above stream
Ridgetop or Knoll (RDG) (18)	<100m from ridgelines (as determined by flat difference filter) and areas contiguous with ridgelines <6% slope

Input for this model was derived from U.S. Geological Survey (USGS) 1:24,000 and TRIM 1:20,0000 digital elevation models and hydrology data (as described for the distance to water layer). Four polygon layers were combined to provide the information to define the above classes. These polygon layers were:

1) Main valley; an outline of the main North Fork valley exclusive of side valleys, digitized by hand using a shaded aspect surface and contour lines to identify the valley.

2) Lower/Upper slopes; areas within 200 m elevation of the North Fork river and 150 m elevation of major tributaries were identified by hand and contour lines were copied to form the polygon boundaries.

3) Slopes; a slope surface was thresholded to identify areas with <6% slope using the "threshold surface values" function, then filtered using the "filter thematic cover" function to reduce noise.
4) Ridges and Knolls; ridges and other convex landforms were identified by running a DEM through a flat (all pixels weighted as 1) difference filter using the "filter surface cover" function (with a 5x5 pixel array for 1 iteration). The resulting surface was then filtered to reduce noise (using the "filter thematic cover" function). This generated a surface cover with each pixel having a Z-value indicating the average difference between it and it's surrounding pixels. Groups of pixels that were on average higher than their neighbors (those having values >1.5) were defined as ridges and converted into polygons.
5) Proximity to streams; areas within 150m of major tributaries to the North Fork River were identified using the "buffers from features" function.

Slope

The slope layer was derived from USGS 1:24,000 and TRIM 1:20,000 digital elevation models (DEMs) using the "derive slope" function.

Percent slope values were classified as flat (<5%), slight (5-15%), moderate (15-35%), steep (35-60%) and very steep (>60%).

Aspect

The aspect layer was derived from USGS 1:24,000 and TRIM 1:20,000 DEMs using the "derive aspect" function. Aspect values were classed as flat (<2% slope), north (338-22°), northeast (23-67°), east (68-112°), southeast (113-157°), south (158-202°), southwest (203-247°), west (248-292°), and northwest (293-337°).

Distance to water

The distance to water layer was generated from USGS 1:24,000 digital line graph data B. C. Ministry of Environment 1:20,000 TRIM data. Distance was derived using the "distance from features" function. Distance values were classified as <200 m, 200-500 m, 0.5 to 1 km, and >1 km.

Distance to open roads

The distance to open roads layer was derived from Flathead National Forest 1:24,000 cartographic feature files (CFFs) and 1:20,000 TRIM data. This layer represents distance to roads that were maintained as open roads during winter months, as well as distance to unmaintained roads that are within 2 km road distance of maintained open roads. The unmaintained roads that are within 2 km of open roads were included because these roads receive recreational use in the form of cross country skiing and snowmobiling that are usually confined to within a few kilometers of open roads. Also, many recreational and permanent residences used in winter are located along these unmaintained roads within a few kilometers of open roads. Two distance to open road layers were used during analysis to represent increasing development in the North Fork basin. Prior to fall 1990 includes primarily the main north fork road as open and maintained in winter, post fall 1990 includes a number of driveways and residential access roads that began to be maintained in winter around this time (Diane Boyd pers. commun.).

Generating the distance to open roads layers entailed two steps. First, I identified those roads within 2 km of roads that were maintained in winter. To do this I converted the original road layer, containing all roads maintained or not, into a surface cover in which the road pixels were assigned a Z-value of 1 and background pixels were assigned a Z-value of 2500. I then used the "buffers from features" function to identify areas within 2000 m of the roads maintained in winter, and weighted the spread function on the newly created road surface. In this manner, the software counted out 40 pixels from the maintained roads along the unmaintained road pixels (using the formula; distance / [pixel size x weight] = number of pixels included in buffer or 2000 m / [50 m x 1] = 40 pixels) but did not include any non-road pixels in the buffer (because 2000 m / [50 m x 2500] < 1 pixel). Once the roads within 2000 m of maintained roads were identified, the second step in the process was to use the "distance from surface" function to generate a surface representing distance from open roads and roads within 2000 m of open roads.

Distance values were classified as < 200 m, 200 - 500 m, .5 to 1 km, and > 1 km. These layers are in the RDDIST.* map.

Road Density

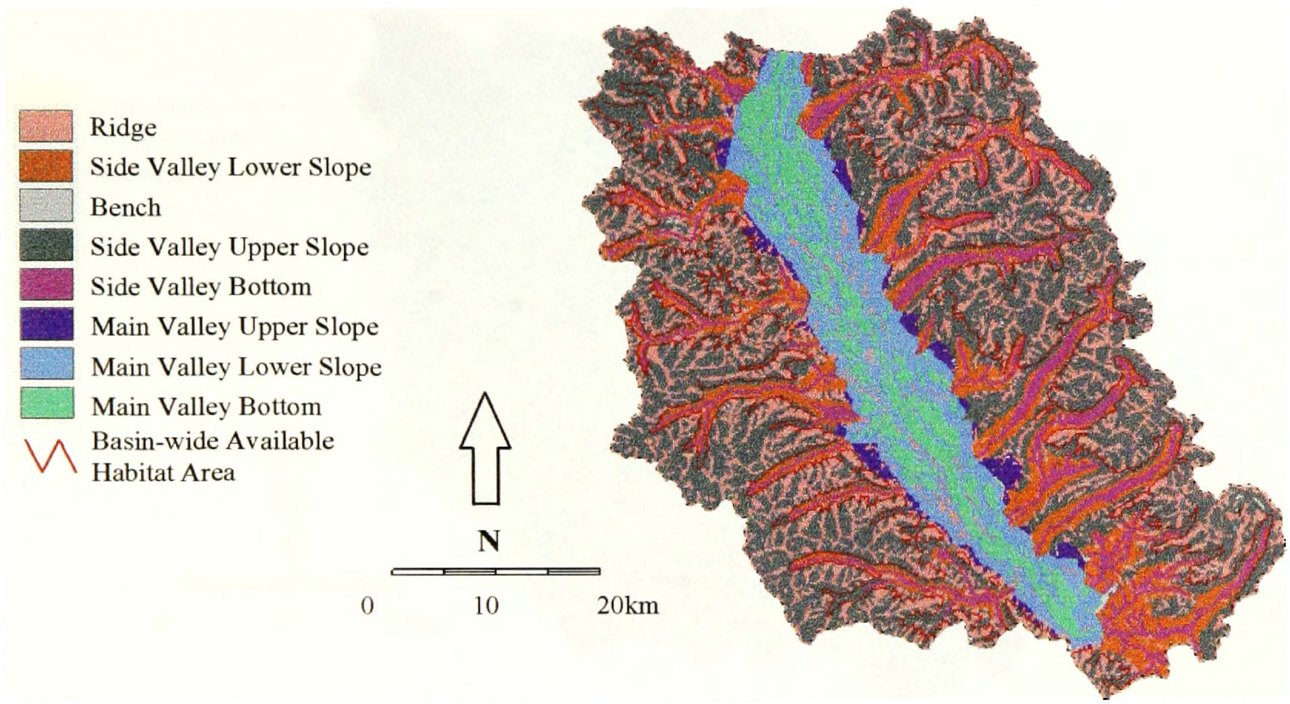
The total road density layer was also based on Flathead National Forest 1:24,000 CFF and 1:20,000 TRIM data. This layer represents the total road density of all roads both maintained and unmaintained in winter. It is important to note that this layer includes all roads in the CFF and TRIM files in the road density analysis. Many of these roads may be passable only by 4 wheel drive vehicles. Therefore road densities shown on this surface are not comparable to those reported by Mladenoff et al. (1995), Mech and Fritts (1988), or Theil (1985). These authors included only highly maintained paved and gravel roads in their analyses. I included all roads in the analysis because all roads except the main North Fork road are functionally closed in winter and I felt that total road density (including all roads) was an appropriate measure of at least seasonal human disturbance.

A road density surface was generated using the "focalsum" function in Arc/Info. I imported the north fork road vector layer into Arc/Info as a DXF file. All roads were imported and included in the analysis. To run the "focalsum" function, I used an Arc/Info aml written by Melissa Hart (1994) which I modified to conform with the configuration of my maps. First, the road vectors were converted to a raster cover. The focalsum function then counted the number of pixels corresponding to roads within a circular area as close to one square mile in area as possible given the 50m pixel size of my raster surface. Given that 1 mi^2 = 2,589,846.49 m^2 and the area of a circle equals $\pi(r^2)$, the radius of a 1 mi^2 circle is 907.95 m ($\sqrt{2,589,846.49/\pi}$). With a 50 m pixel size, a radius of 900 m or 18 pixels is the closest possible circle size. This yields a circle area of 2,544,690 m^2 or 0.986 mi^2. Some error is also introduced during the vector to raster conversion. Every pixel that has any portion of a road within it is designated to represent road presence, no matter what the distance of road within that pixel is. In order to correct for this error, I conducted a regression analysis using 1 mi^2 non-overlapping circles randomly placed across the roaded portion of the study area. After exporting the road density surface to PAMAP, I generated random center points for the circles by generating random x and y coordinates in Excel. I then imported these 200 coordinates into PAMAP as points and as polygon database tags. I digitized 1 mi^2 circles using the random points as the centroid for the circles. I converted the circles to polygons and overlaid the polygons on the road vector layers to determine the length of roads within each polygon. Because polygons are stored in raster format in PAMAP, the 1mi^2 circles became 0.986mi^2 when converted to 50 m pixels. The polygon database tags were then overlaid on the road density surface to determine the number of road pixels within the circle. I exported the resulting database to SPSS for Windows and conducted regression analysis to determine the best estimation of the road distance within each pixel. The resulting model was $y = 5.79 + 41.40x$ ($R^2 = 0.99$), thus indicating that each road pixel could best be estimated to contain 41.4 m of road. This measure of road distance was then used to create threshold tables for road density classification.

Road density values were classified as No roads, 0.01-2 mi/mi^2, 2-4 mi/mi^2, and >4 mi/mi^2.

Figure B-1: Habitat characteristic map layers and data classes.

Topographic Position



Aspect

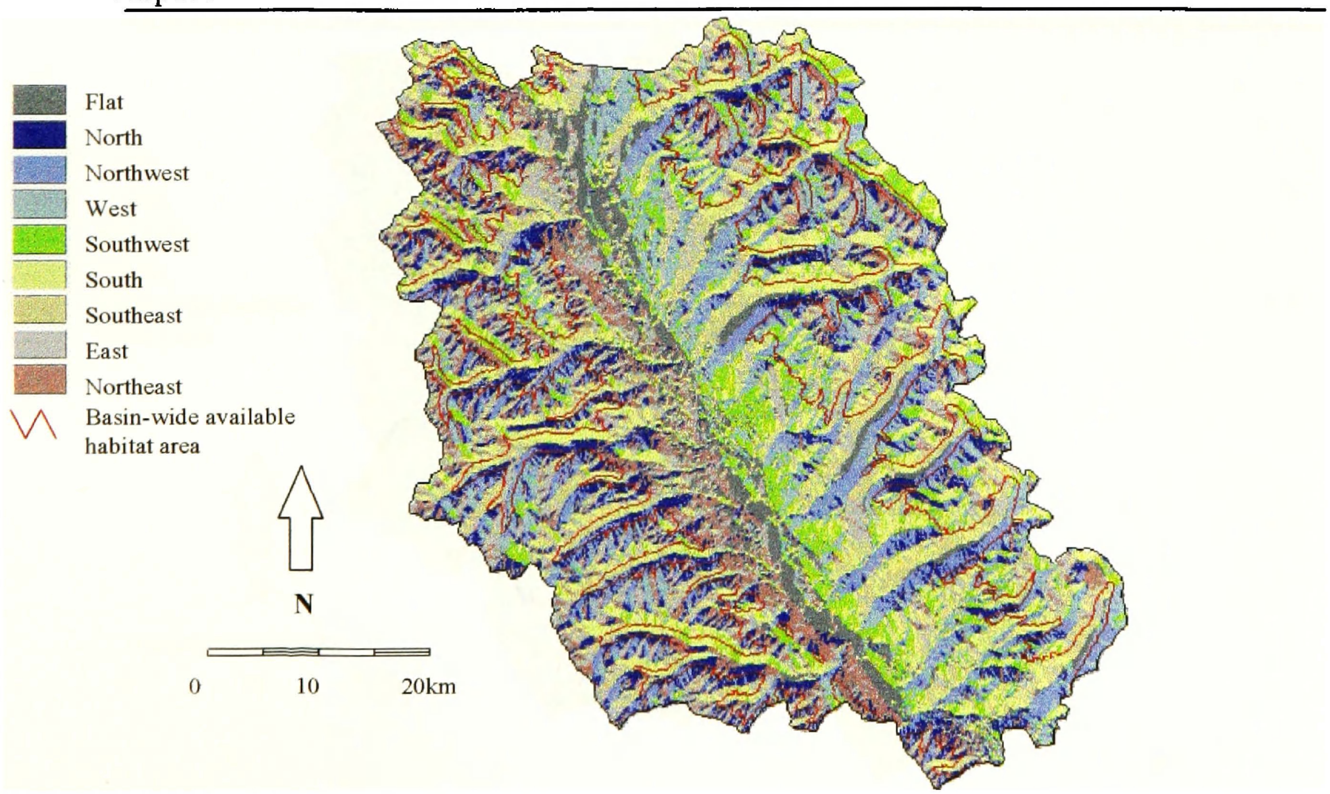
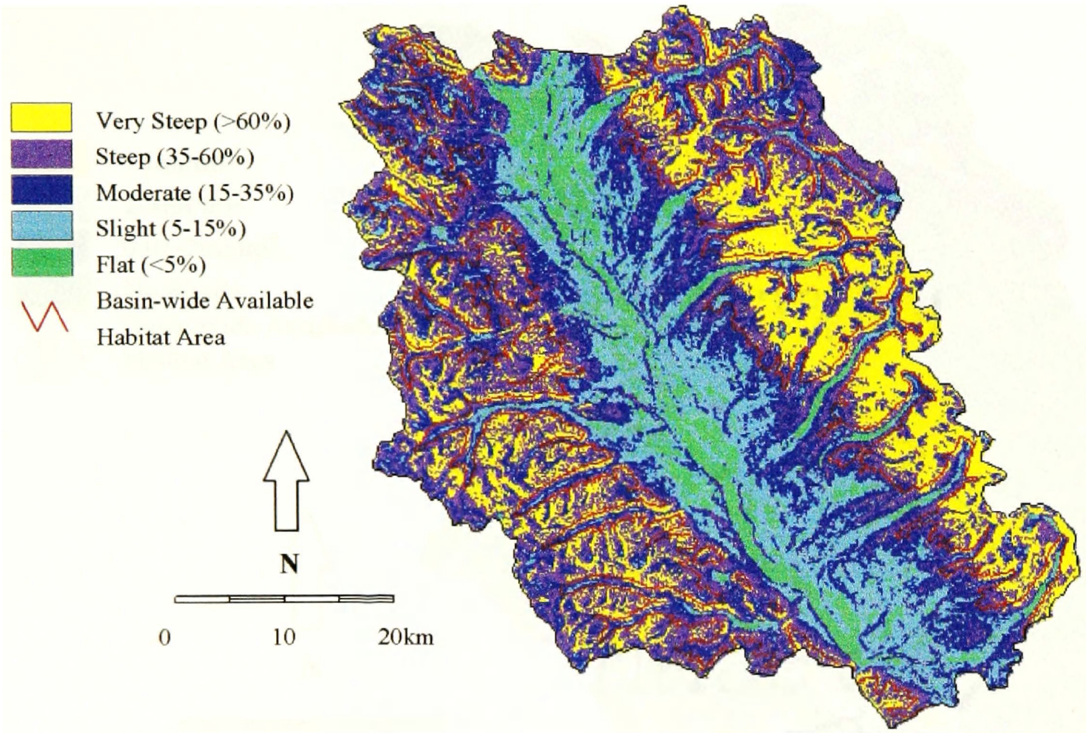


Figure B-1 (continued): Habitat characteristic map layers and data classes.

Slope



Distance to Water

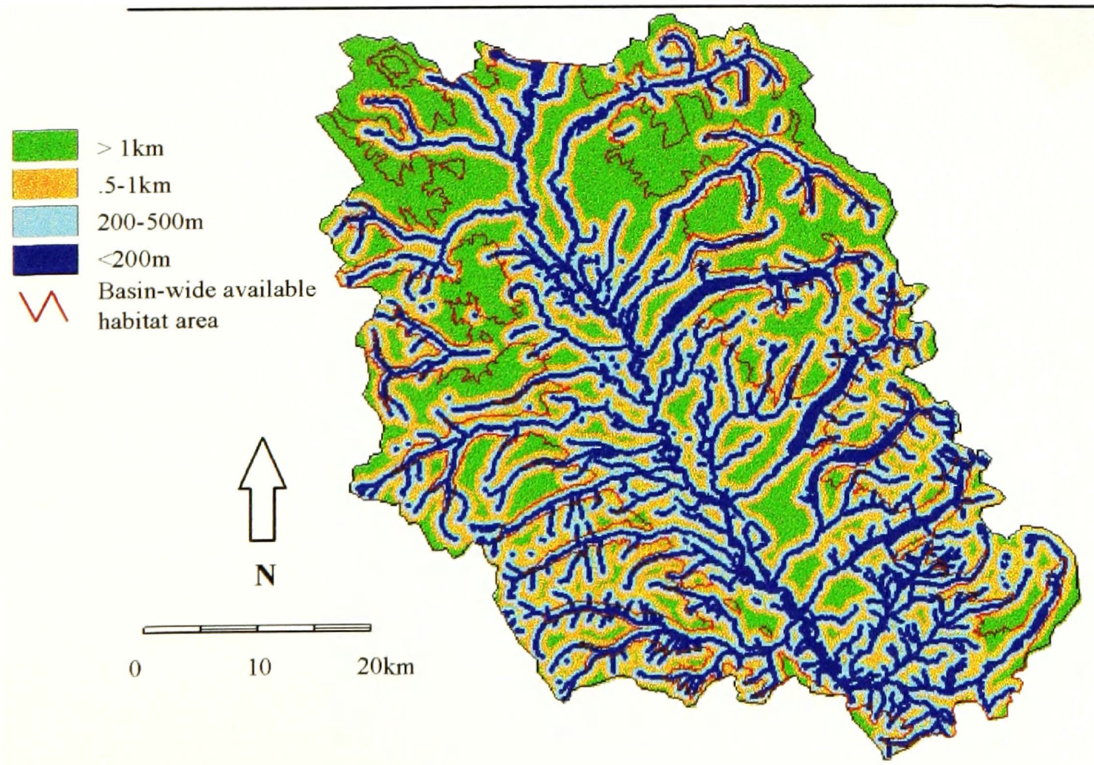


Figure B-1 (continued): Habitat characteristic map layers and data classes.

Road Density

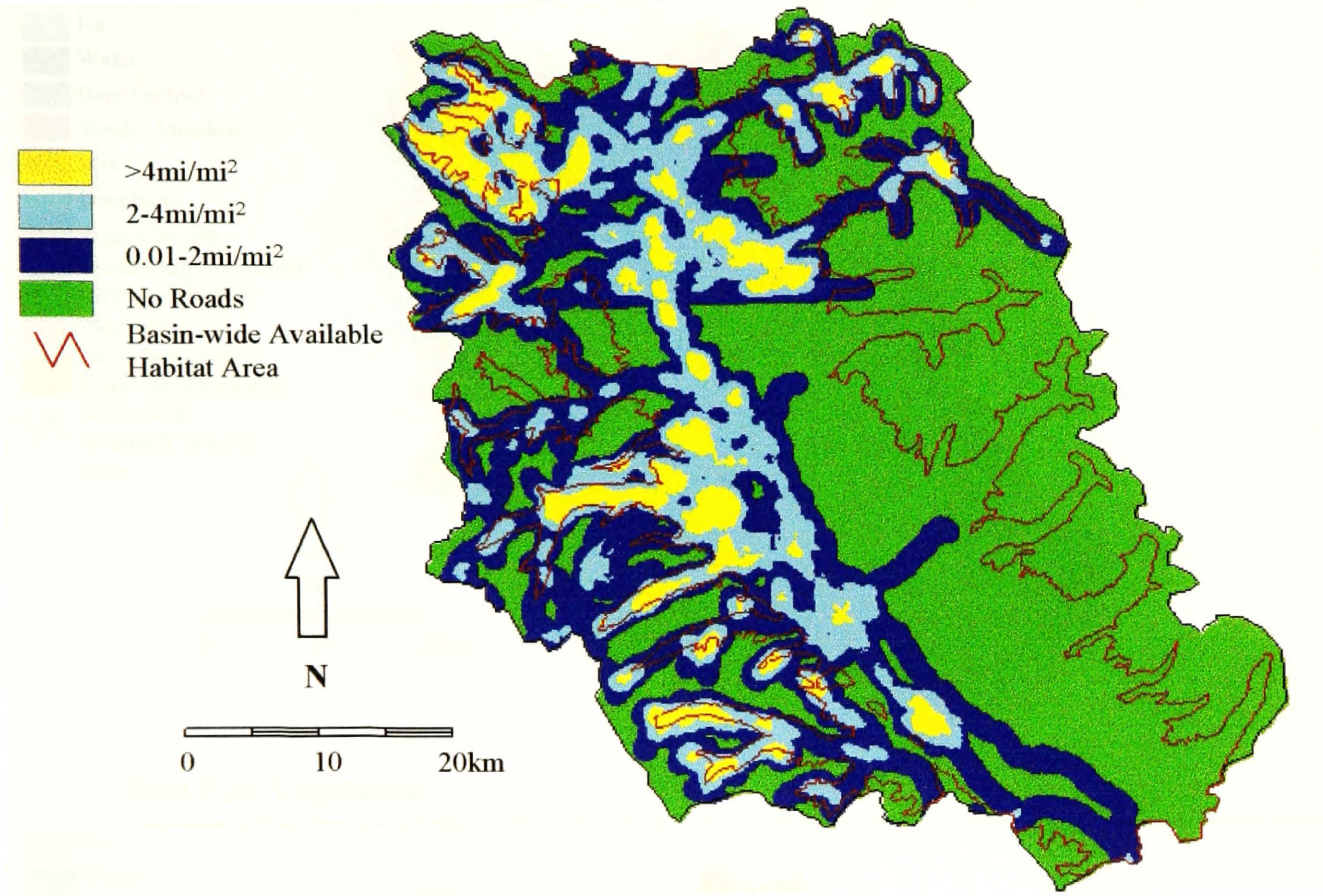
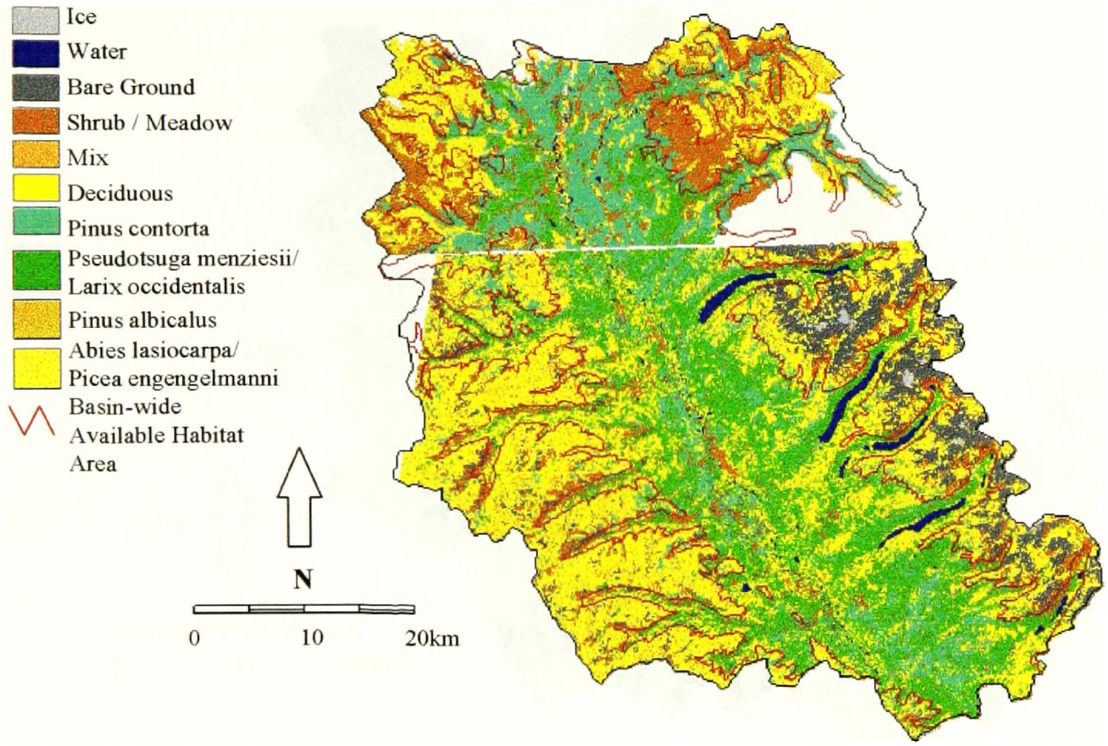


Figure B-1(continued): Habitat characteristic map layers and data classes.

Pre Fire Vegetation



Post Fire Vegetation

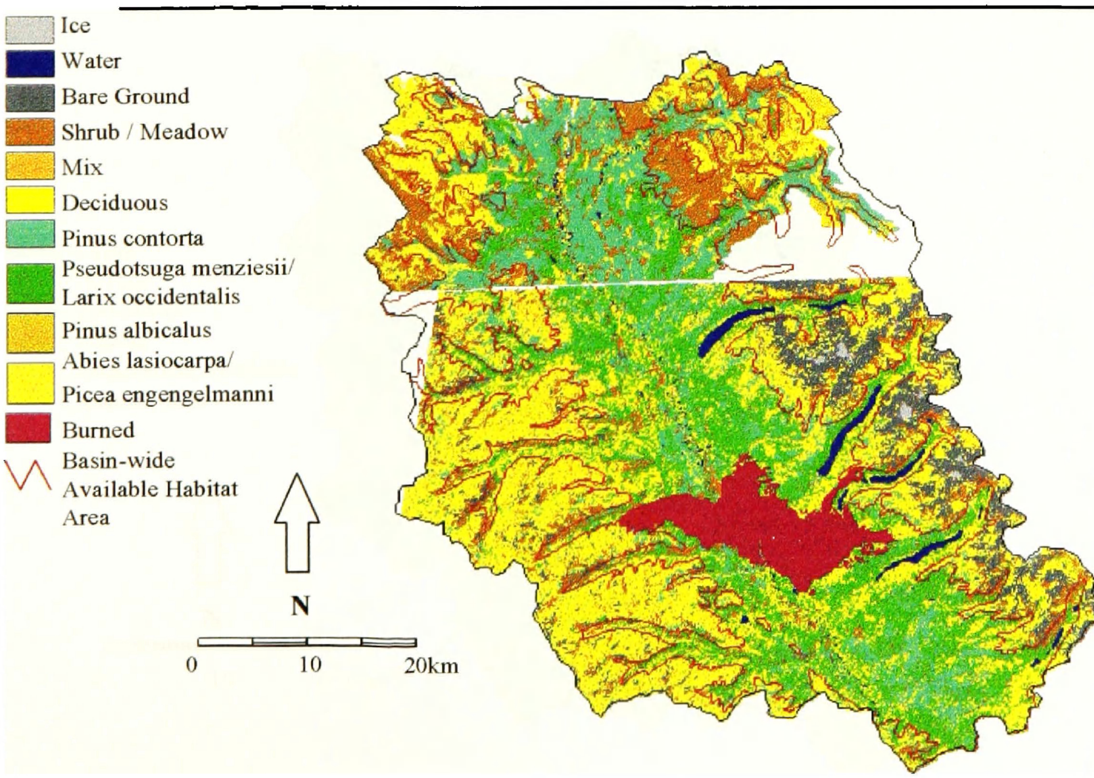
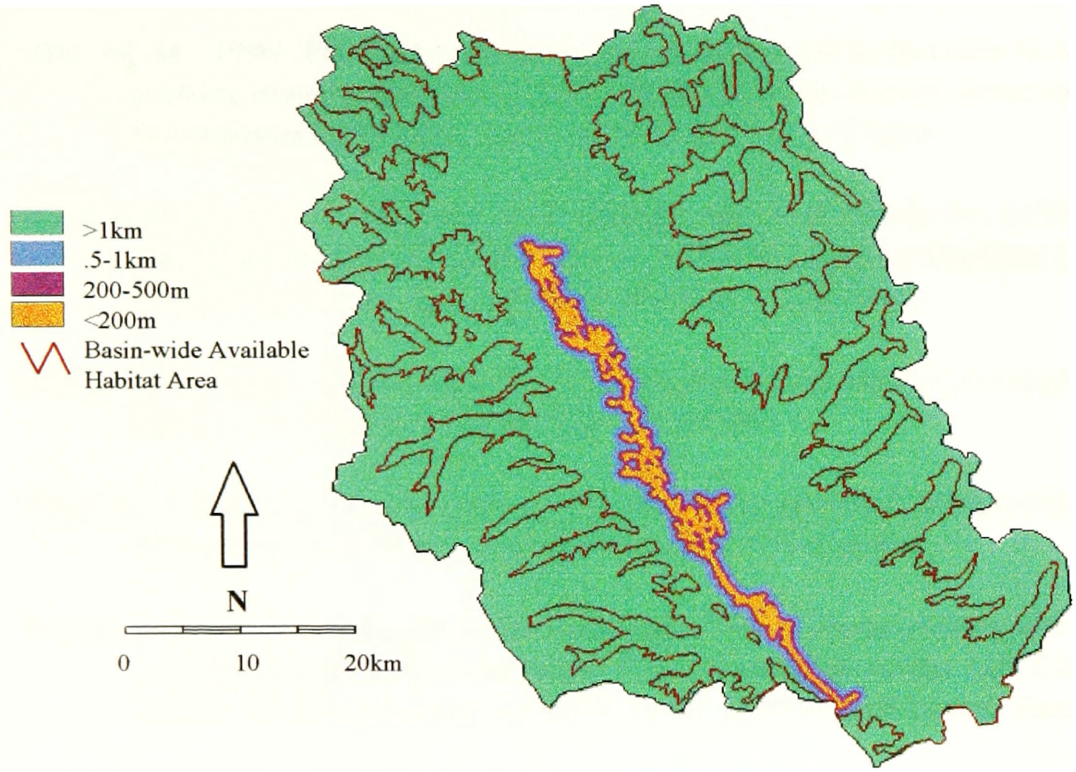
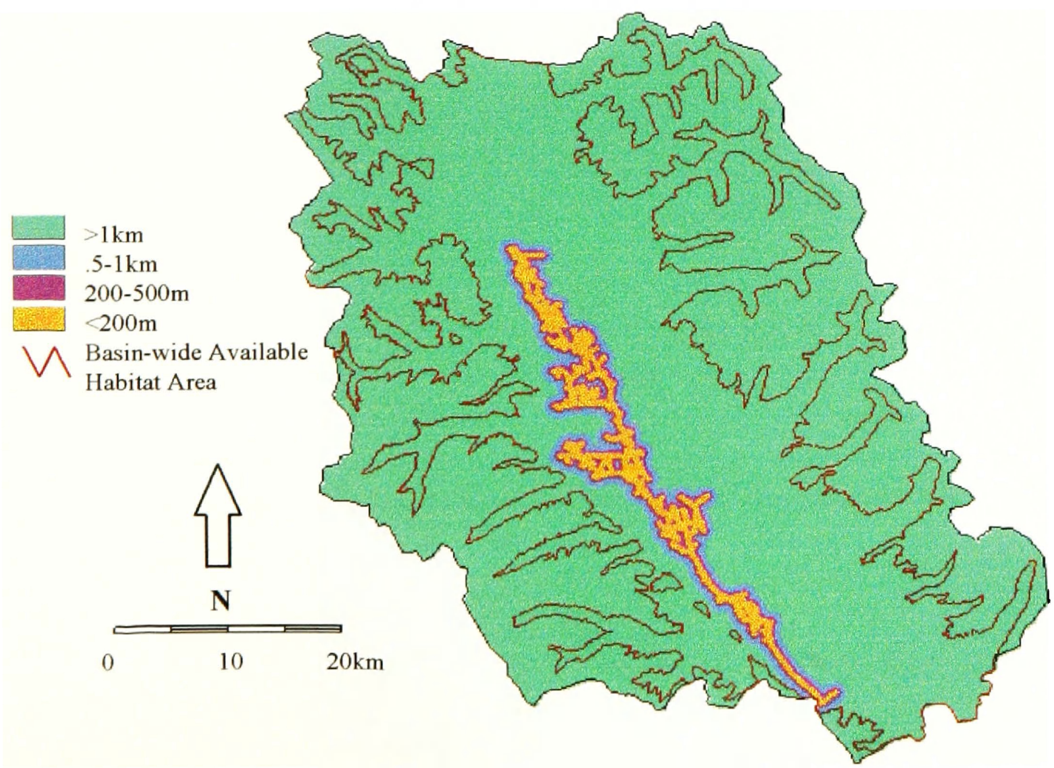


Figure B-1 (continued): Habitat characteristic map layers and data classes.

Distance to Open Roads (prior to 1990)



Distance to Open Roads (after 1990)



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Appendix C: Comparison of field mapping of wolf travel routes to GPS locations.

I attempted to quantify the accuracy of mapping of wolf tracking routes by comparing mapped routes to GPS locations. During March of 1994 I accompanied field technicians on short skiing or walking expeditions in the areas where wolves were normally tracked in the North Fork. The field technicians were instructed to map the route followed as they normally would while tracking wolves. At approximately one kilometer intervals we stopped and the field technicians noted our position on their topographic map while I obtained a location using GPS. Fifty-one locations were mapped. Locations mapped by the field technicians and using the GPS were both entered into the GIS and distances between paired GPS and field mapped locations calculated.

Points mapped by field technicians were on average 189.2m from recorded GPS points (standard deviation 180.8) (Table C-1). Because of selective availability (the periodic intentional degradation of GPS signals), single GPS locations have an average error of approximately 100m. These differences between field mapped and GPS locations are probably due to errors in both the GPS and field mapped locations. Without being able to differentially correct the GPS locations to eliminate the error introduced by selective availability, it is impossible to evaluate the level of error in field mapping. These results do however indicate that errors of up to 200m may not be uncommon for wolf travel routes mapped in the field.

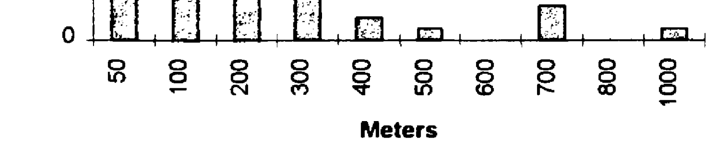


Figure C-1: Histogram of distance between field mapped and GPS locations.

Appendix D: Comparison of wolf ground tracking to radio telemetry locations.

To identify systematic bias in the ground tracking of wolves in the North Fork of the Flathead River basin, I compared the distribution of radio-telemetry locations to mapped wolf travel routes using adaptive kernal home ranges (Worton 1989). Adaptive kernal home ranges calculate the probability of locating a radio-collared animal in an area based on the distribution of locations previously recorded for that animal. If both the radio-telemetry data and the mapped wolf travel routes are unbiased, they should display similar spatial distributions (they are after all, samples of the same habitat utilization trajectory). In other words, approximately 30% of the mapped tracking should occur in the 30% adaptive kernal home range isopleth, 50% of tracking in the 50% isopleth, and so on.

I generated adaptive kernal home ranges for each pack-year using radio-telemetry locations for that pack collected between November 15 and March 31 of the year in question. Based on a 72 hour time to independence for wolf radio locations in the North Fork (Dan Pletscher pers. commun.), I eliminated telemetry locations for which less than 72 hours had elapsed since the previous used telemetry location. If there was a telemetry location determined from the air within 24 hours of a ground telemetry location, the aerial location was used and the ground location eliminated because aerial locations were less likely to be biased than ground locations.

Adaptive kernal home ranges were generated using CALHOME (Kie et al. 1994) software on 486 and pentium personal computers. Ninety-five, 75, 50, and 30 percent home range isopleths were identified. Files containing UTM coordinates for the home range isopleths were converted into GIS vector files using the "generate" function in Arc/Info, then exported as DLG files and imported into PAMAP for comparison with wolf travel routes. In PAMAP, I calculated the wolf travel route analysis corridor area (100 m buffers around mapped travel routes) within each home range isopleth and exported this data to Exel for analysis.

I conducted 2-sample t-tests (assuming unequal variance) to compare the mean percent of mapped tracking within each home range isopleth to percent expected. In general, less tracking occurred within each isopleth than was expected (Table D-1). Differences between observed and expected tracking within the 95% isopleth were not significant (two-tailed $P = 0.39$). Differences between observed and expected tracking within the 75%, 50%, and 30% isopleths were significant ($P < 0.01$). These statistics are suspect due to small sample size ($n=14$). Investigation of the distributions of the percentages of tracking within each isopleth indicate that, at least for the 50, 75, and 95 percent isopleths, these distributions are unimodal and centered near the expected values (Fig. D-1).

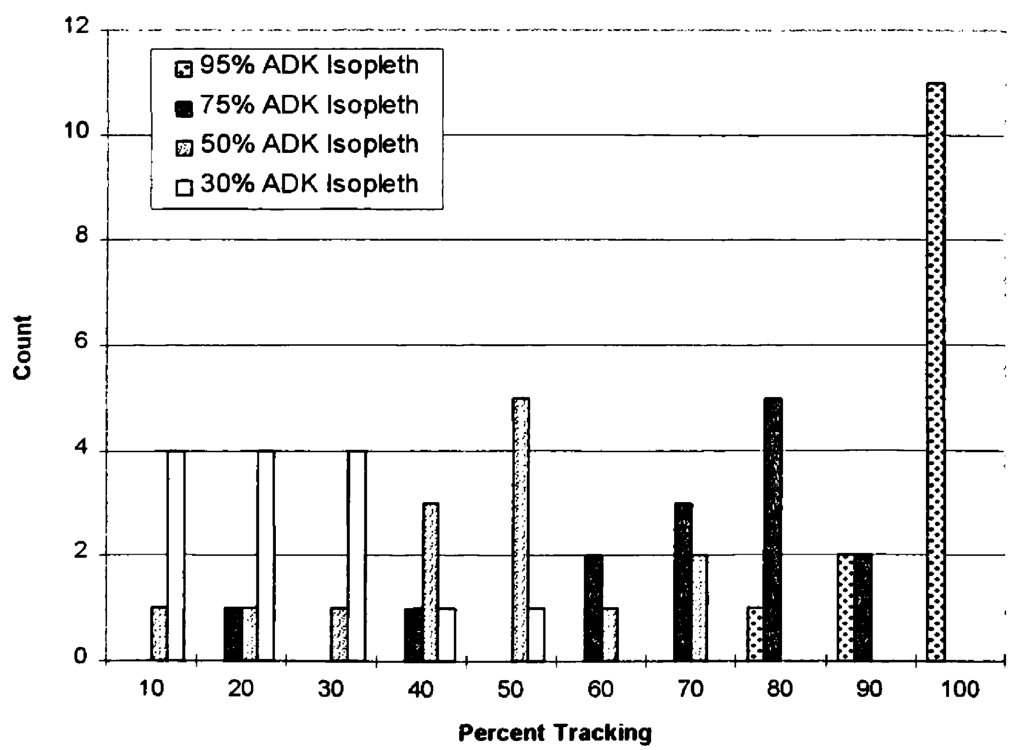
An important factor to take into consideration in this comparison is that ground tracking and radio-telemetry measure different things. Animal habitat utilization is a continuous trajectory through a 4 dimensional space (3 geographic coordinates and a time dimension). Radio-telemetry samples discrete points in that 4 dimensional space. Ground tracking samples continuous paths through the geographic coordinates, but does not allow for sampling the amount of time that the animal spent along the way. A field worker skiing along wolf tracks may easily ski past a bed site in 30 seconds where the wolves spent the better part of the previous day. This is probably particularly true for the 30 and 50 percent home range isopleths, which may represent areas that the wolves spend substantial periods of time in (e.g. Sullivan Meadow) but also make frequent short trips out of. Based on these considerations it is not surprising that the proportion of ground tracking within each home range isopleth is somewhat different from expected.

Another difficulty with this analysis is that the assumption that both the radio-telemetry and ground tracking are not biased. Each technique has it's own biases, and it is the differences in those biases that cause the differences in spatial distribution between the radio-telemetry and ground tracking data. For radio-telemetry, locations gathered from the ground are biased to areas in the main valley where radio signals can be monitored from the road. Twenty-eight point two percent of the telemetry locations used to determine these home ranges were ground locations. Potential sources of bias for mapping wolf travel routes are accessibility and ease of travel. It is possible that more tracking occurred in areas close to access points (bridges or easy crossing locations for the North Fork river) because less time in the day was taken up getting to these locations and more time could be spent on tracking. Ease of travel (for field workers) could also influence the distance of tracking recorded for certain areas. Areas where there are few obstacles and the snow is often consolidated (such as the Red Bench burn) facilitate skiing over long distances fairly rapidly compared to dense coniferous forest with heavy deadfall. While these factors probably effect ease of travel for the wolves as well, they probably influence ease of travel for field workers with 6ft appendages strapped to their toes substantially more.

Table D-1: Percent tracking observed within each ADK home range isopleth.

PACKYEAR	95%	75%	50%	30%
MAGC85	93.63	19.14	9.56	7.25
MAGC86	93.42	74.88	47.42	24.27
MAGC87	94.52	65.45	33.98	14.00
CAMA88	98.06	81.49	66.63	22.92
CAMA89	90.66	69.88	42.55	23.41
CAMA90	88.33	57.91	15.27	11.97
NCAM91	91.16	37.25	28.03	6.61
NCAM92	79.61	66.12	36.66	15.74
NCAM94	96.55	81.79	44.47	33.99
SCAM91	100.00	74.60	59.64	40.67
SCAM93	100.00	79.63	49.39	7.47
SCAM94	86.60	55.81	41.52	8.73
SPCR91	97.82	71.51	31.01	15.98
SPCR92	100.00	78.81	63.04	27.90
Mean	93.60	65.31	40.66	18.64
Standard Deviation	5.93	18.02	16.64	10.59

Figure D-1: Histogram of percent tracking within each adaptive kernal home range isopleth.



Appendix E: Compositional analysis of wolf habitat utilization data

Statistical analysis of the GIS data focused on comparing used areas to available areas at basin wide and home range scales. At the basin-wide scale, MCP home ranges were considered to be the used areas and the available habitat within the entire basin was considered to be available. At the home range scale, the tracking route analysis corridors were considered to be the used areas and the areas that were within the MCP home range of that pack for that year were considered to be available. All areas greater than 500 m in elevation above the North Fork of the Flathead River were excluded from analysis.

Univariate comparisons of used and available areas at these scales were conducted using compositional analysis (Aebischer et al. 1993). Compositional analysis is a statistical technique that focuses on the log-ratio analysis of compositions (Aitchison 1986). Pairwise difference matrices of log-ratios of used habitat types over a denominator used habitat type to log-ratios of the same available habitat type over the same denominator available habitat type were calculated for each pack-year (Table E-1) (Aebischer et al. 1993). Ranking matrices for used habitat types are generated by compiling summary statistics for the yearly pairwise difference matrices. The rows of the matrices are indexed by the habitat type used as the numerator in the log-ratio, and the columns by the denominator. The number of positive mean values in each row of the ranking matrix ranks the habitats in increasing order of relative use. Overall departure from random use across all habitat classes is determined using a multivariate analysis of variance type test. Significant differences between adjacent classes within the ranking can be detected using the ratio mean devided by the standard error, which gives a t value (Aebischer et al. 1993).

Each pack-year was used as the sample unit for the compositional analysis. In other words, the MCP home range for each year was compared to the available habitat within the basin, and the entire set of tracking for each pack each year was compared to that pack's home range for that winter. The reason for using the pack-year as the sampling unit was because of the questionable independence between subsequent tracking bouts. When one set of tracks were lost, another group of more recent tracks were commonly found in the vicinity of where the first set was lost. These consecutive tracking bouts often followed tracks left by the same group of wolves, but due to constraints imposed by snow conditions and time, a portion of the travel route could not be followed. Additionally, different tracking bouts were of different lengths. The longer the tracking bout, the better the representation of the wolves' habitat utilization trajectory. Rather than weighting the individual tracking bouts by length, it is more intuitive to group all the bouts attributed to a pack in a year into one composition. In this manner the longer bouts contribute more to the composition than the shorter bouts.

The following tables show the compositional anlaysis preference ranking matrices for the comparison of home ranges to available habitat within the North Fork drainage (Table E-2) and comparison of travel routes to home ranges (Table E-3).

Table E-1: Log-ratio difference matrix generated during compositional analysis are based on the mean difference between log-ratios. Rows of the matrix are indexed by the habitat characteristic used as the numerator in the log-ratio, and the columns by the denominator.

Habitat types (numerator)	Habitat types (denominator)			Positive values (total)
	1	2	*D*	
1		$\ln(x_{u1}/x_{u2}) - \ln(x_{a1}/x_{a2})$	$\ln(x_{u1}/x_{uD}) - \ln(x_{a1}/x_{aD})$	r_1
2	$\ln(x_{u2}/x_{u1}) - \ln(x_{a2}/x_{a1})$	. . .	$\ln(x_{u2}/x_{uD}) - \ln(x_{a2}/x_{aD})$	r_2
.	.	.	.	.
.	.	.	.	.
.	.	.	.	.
D	$\ln(x_{uD}/x_{u1}) - \ln(x_{aD}/x_{a1})$	$\ln(x_{uD}/x_{u2}) - \ln(x_{aD}/x_{a2})$		r_3

x_{ui} = the proportion of use observed in habitat i.

x_{ai} = the proportion of available habitat observed in habitat i.

r_i = the number of positive values in the row. This indicates the rank of use compared to availability for habitat i compared to all other habitats. Increased numbers of positive values indicated increased intensity of use.

Table E-2: Compositional analysis preference ranking matrices for comparison MCP home ranges to available habitat within the North Fork Drainage.

Topographic Position

Multivariate P < 0.001, n = 18

	Main Valley Bottom (MVB)	Main Valley Lower Slope (MVL)	Main Valley Upper Slope (MVU)	Side Valley Bottom (SVB)	Side Valley Upper Slope (SVU)	Bench (BEN)	Side Valley Lower Slope (SVL)	Ridge (RDG)	Use Rank
MVB									
MEAN		0.025	0.248	0.928	1.135	0.248	0.863	1.046	7
SE		0.071	0.111	0.169	0.190	0.295	0.181	0.147	
T VALUE		0.352	2.234	5.491	5.974	0.841	4.768	7.116	
P VALUE		0.729	0.039	0.000	0.000	0.412	0.000	0.000	
MVL									
MEAN	-0.025		0.223	0.903	1.110	0.223	0.838	1.021	6
SE	0.071		0.059	0.126	0.182	0.265	0.136	0.121	
T VALUE	-0.352		3.780	7.167	6.099	0.842	6.162	8.438	
P VALUE	0.729		0.001	0.000	0.000	0.412	0.000	0.000	
MVU									
MEAN	-0.248	-0.223		0.680	0.888	0.001	0.615	0.799	5
SE	0.111	0.059		0.104	0.190	0.221	0.102	0.117	
T VALUE	-2.234	-3.780		6.538	4.674	0.005	6.029	6.829	
P VALUE	0.039	0.001		0.000	0.000	0.996	0.000	0.000	
SVB									
MEAN	-0.928	-0.903	-0.680		0.207	-0.680	-0.065	0.118	2
SE	0.169	0.126	0.104		0.144	0.241	0.040	0.086	
T VALUE	-5.491	-7.167	-6.538		1.438	-2.822	-1.625	1.372	
P VALUE	0.000	0.000	0.000		0.169	0.012	0.123	0.188	
SVU									
MEAN	-1.135	-1.110	-0.888	-0.207		-0.887	-0.272	-0.089	0
SE	0.190	0.182	0.190	0.144		0.357	0.176	0.099	
T VALUE	-5.974	-6.099	-4.674	-1.438		-2.485	-1.545	-0.899	
P VALUE	0.000	0.000	0.000	0.169		0.024	0.141	0.381	
BEN									
MEAN	-0.248	-0.223	-0.001	0.680	0.887		0.615	0.798	4
SE	0.295	0.265	0.221	0.241	0.357		0.217	0.291	
T VALUE	-0.841	-0.842	-0.005	2.822	2.485		2.834	2.742	
P VALUE	0.412	0.412	0.996	0.012	0.024		0.011	0.014	
SVL									
MEAN	-0.863	-0.838	-0.615	0.065	0.272	-0.615		0.183	3
SE	0.181	0.136	0.102	0.040	0.176	0.217		0.105	
T VALUE	-4.768	-6.162	-6.029	1.625	1.545	-2.834		1.743	
P VALUE	0.000	0.000	0.000	0.123	0.141	0.011		0.099	
RDG									
MEAN	-1.046	-1.021	-0.799	-0.118	0.089	-0.798	-0.183		1
SE	0.147	0.121	0.117	0.086	0.099	0.291	0.105		
T VALUE	-7.116	-8.438	-6.829	-1.372	0.899	-2.742	-1.743		
P VALUE	0.000	0.000	0.000	0.188	0.381	0.014	0.099		

Table E-2 (Cont.): Compositional analysis preference ranking matrices for comparison MCP home ranges to available habitat within the North Fork Drainage.

Slope

Multivariate P <0.001. n = 18

	Flat	Slight	Moderate	Steep	Very Steep	Use Ranking
Flat						
MEAN		0.091	0.528	1.674	2.696	4
SE		0.093	0.105	0.256	0.522	
T VALUE		0.978	5.029	6.539	5.165	
P VALUE		0.342	0.000	0.000	0.000	
Slight						
MEAN	-0.091		0.437	1.583	2.605	3
SE	0.093		0.065	0.282	0.550	
T VALUE	-0.978		6.723	5.613	4.736	
P VALUE	0.342		0.000	0.000	0.000	
Moderate						
MEAN	-0.528	-0.437		1.145	2.168	2
SE	0.105	0.065		0.221	0.490	
T VALUE	-5.029	-6.723		5.181	4.424	
P VALUE	0.000	0.000		0.000	0.000	
Steep						
MEAN	-1.674	-1.583	-1.145		1.023	1
SE	0.256	0.282	0.221		0.279	
T VALUE	-6.539	-5.613	-5.181		3.667	
P VALUE	0.000	0.000	0.000		0.002	
Very Steep						
MEAN	-2.696	-2.605	-2.168	-1.023		0
SE	0.522	0.550	0.490	0.279		
T VALUE	-5.165	-4.736	-4.424	-3.667		
P VALUE	0.000	0.000	0.000	0.002		

Table E-2 (Cont.): Compositional analysis preference ranking matrices for comparison MCP home ranges to available habitat within the North Fork Drainage.

Aspect Multivariate P < 0.001 N = 18

	N	NE	E	SE	S	SW	W	NW	FLAT	Use Rank
N										
MEAN		0.095	-0.575	-0.799	-0.850	-1.233	-1.270	-0.835	-1.119	1
SE		0.129	0.127	0.104	0.090	0.136	0.154	0.087	0.188	
T VALUE		0.736	-4.528	-7.683	-9.444	-9.066	-8.247	-9.598	-5.952	
P VALUE		0.472	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
NE										
MEAN	-0.095		-0.670	-0.894	-0.946	-1.328	-1.365	-0.931	-1.214	0
SE	0.129		0.109	0.158	0.170	0.193	0.185	0.169	0.171	
T VALUE	0.736		-6.147	-5.658	-5.565	-6.881	-7.378	-5.509	-7.099	
P VALUE	0.472		0.000	0.000	0.000	0.000	0.000	0.000	0.000	
E										
MEAN	0.575	0.670		-0.224	-0.276	-0.658	-0.695	-0.260	-0.544	2
SE	0.127	0.109		0.090	0.125	0.140	0.092	0.110	0.097	
T VALUE	-4.528	-6.147		-2.489	-2.208	-4.700	-7.554	-2.364	-5.608	
P VALUE	0.000	0.000		0.023	0.041	0.000	0.000	0.030	0.000	
SE										
MEAN	0.799	0.894	0.224		-0.052	-0.434	-0.471	-0.037	-0.320	3
SE	0.104	0.158	0.090		0.043	0.062	0.075	0.035	0.112	
T VALUE	-7.683	-5.658	-2.489		-1.209	-7.000	-6.280	-1.057	-2.857	
P VALUE	0.000	0.000	0.023		0.243	0.000	0.000	0.305	0.011	
S										
MEAN	0.850	0.946	0.276	0.052		-0.382	-0.419	0.015	-0.268	5
SE	0.090	0.170	0.125	0.043		0.053	0.107	0.032	0.145	
T VALUE	-9.444	-5.565	-2.208	-1.209		-7.208	-3.916	0.469	-1.848	
P VALUE	0.000	0.000	0.041	0.243		0.000	0.001	0.645	0.082	
SW										
MEAN	1.233	1.328	0.658	0.434	0.382		-0.037	0.397	0.114	7
SE	0.136	0.193	0.140	0.062	0.053		0.100	0.069	0.128	
T VALUE	-9.066	-6.881	-4.700	-7.000	-7.208		-0.370	5.754	0.891	
P VALUE	0.000	0.000	0.000	0.000	0.000		0.716	0.000	0.386	
W										
MEAN	1.270	1.365	0.695	0.471	0.419	0.037		0.435	0.151	8
SE	0.154	0.185	0.092	0.075	0.107	0.100		0.088	0.083	
T VALUE	-8.247	-7.378	-7.554	-6.280	-3.916	-0.370		4.943	1.819	
P VALUE	0.000	0.000	0.000	0.000	0.001	0.716		0.000	0.087	
NW										
MEAN	0.835	0.931	0.260	0.037	-0.015	-0.397	-0.435		-0.284	4
SE	0.087	0.169	0.110	0.035	0.032	0.069	0.088		0.139	
T VALUE	-9.598	-5.509	-2.364	-1.057	0.469	5.754	4.943		-2.043	
P VALUE	0.000	0.000	0.030	0.305	0.645	0.000	0.000		0.057	
FLAT										
MEAN	1.119	1.214	0.544	0.320	0.268	-0.114	-0.151	0.284		6
SE	0.188	0.171	0.097	0.112	0.145	0.128	0.083	0.139		
T VALUE	-5.952	-7.099	-5.608	-2.857	-1.848	0.891	1.819	-2.043		
P VALUE	0.000	0.000	0.000	0.011	0.082	0.386	0.087	0.057		

Table E-2 (Cont.): Compositional analysis preference ranking matrices for comparison MCP home ranges to available habitat within the North Fork Drainage.

Distance to open roads (Multivariate P = 0.277, n = 18)

	<200m	200-500m	.5-1km	>1km	Use Rank
<200m					
MEAN		-0.559	-0.971	-1.645	0
SE		0.308	0.546	0.846	
T VALUE		-1.815	-1.778	-1.944	
P VALUE		0.087	0.093	0.069	
200-500m					
MEAN	0.559		-0.412	-1.087	1
SE	0.308		0.241	0.660	
T VALUE	1.815		-1.710	-1.647	
P VALUE	0.087		0.106	0.118	
.5-1km					
MEAN	0.971	0.412		-0.675	2
SE	0.546	0.241		0.635	
T VALUE	1.778	1.710		-1.063	
P VALUE	0.093	0.106		0.303	
>1km					
MEAN	1.645	1.087	0.675		3
SE	0.846	0.660	0.635		
T VALUE	1.944	1.647	1.063		
P VALUE	0.069	0.118	0.303		

Distance to water (Multivariate P < 0.001 N = 18)

	<200m	200-500m	.5-1km	>1km	Use Rank
<200m					
MEAN		-0.050	-0.238	-0.299	0
SE		0.019	0.044	0.127	
T VALUE		-2.632	-5.409	-2.354	
P VALUE		0.017	0.000	0.031	
200-500m					
MEAN	0.050		-0.188	-0.250	1
SE	0.019		0.033	0.123	
T VALUE	2.632		-5.697	-2.033	
P VALUE	0.017		0.000	0.058	
.5-1km					
MEAN	0.238	0.188		-0.061	2
SE	0.044	0.033		0.096	
T VALUE	5.409	5.697		-0.635	
P VALUE	0.000	0.000		0.534	
>1km					
MEAN	0.299	0.250	0.061		3
SE	0.127	0.123	0.096		
T VALUE	2.354	2.033	0.635		
P VALUE	0.031	0.058	0.534		

Table E-2 (Cont.): Compositional analysis preference ranking matrices for comparison MCP home ranges to available habitat within the North Fork Drainage.

Vegetation

Pre-fire (all years; '84 - '88 & Spruce Creek Pack) (Multivariate P = 0.077 N = 9)

	ABLA/ PIEN	PSME/ LAOC	PICO	DECID	MIX	SHUB/ MEAD	BARE GROUND	WATER	Use Ranking
ABLA/PIEN									
MEAN		-0.385	-1.056	-1.613	0.587	-0.719	0.076	-0.343	2
SE		0.077	0.381	0.503	0.402	0.317	0.156	0.279	
T VALUE		-5.000	-2.772	-3.207	1.460	-2.268	0.487	-1.229	
P VALUE		0.001	0.024	0.012	0.182	0.053	0.639	0.254	
PSME/LAOC									
MEAN	0.385		-0.671	-1.227	0.973	-0.334	0.461	0.043	4
SE	0.077		0.317	0.442	0.436	0.268	0.186	0.238	
T VALUE	5.000		-2.117	-2.776	2.232	-1.246	2.478	0.181	
P VALUE	0.001		0.067	0.024	0.056	0.248	0.038	0.861	
PICO									
MEAN	1.056	0.671		-0.557	1.643	0.337	1.132	0.713	6
SE	0.381	0.317		0.137	0.730	0.133	0.379	0.277	
T VALUE	2.772	2.117		-4.066	2.251	2.534	2.987	2.574	
P VALUE	0.024	0.067		0.004	0.055	0.035	0.017	0.033	
DECID									
MEAN	1.613	1.227	0.557		2.200	0.893	1.688	1.270	7
SE	0.503	0.442	0.137		0.849	0.209	0.483	0.391	
T VALUE	3.207	2.776	4.066		2.591	4.273	3.495	3.248	
P VALUE	0.012	0.024	0.004		0.032	0.003	0.008	0.012	
MIX									
MEAN	-0.587	-0.973	-1.643	-2.200		-1.307	-0.511	-0.930	0
SE	0.402	0.436	0.730	0.849		0.682	0.496	0.582	
T VALUE	-1.460	-2.232	-2.251	-2.591		-1.916	-1.030	-1.598	
P VALUE	0.182	0.056	0.055	0.032		0.092	0.333	0.149	
SHUB/MEAD									
MEAN	0.719	0.334	-0.337	-0.893	1.307		0.795	0.377	5
SE	0.317	0.268	0.133	0.209	0.682		0.302	0.304	
T VALUE	2.268	1.246	-2.534	-4.273	1.916		2.632	1.240	
P VALUE	0.053	0.248	0.035	0.003	0.092		0.030	0.250	
BARE GROUND									
MEAN	-0.076	-0.461	-1.132	-1.688	0.511	-0.795		-0.418	1
SE	0.156	0.186	0.379	0.483	0.496	0.302		0.257	
T VALUE	-0.487	-2.479	-2.987	-3.495	1.030	-2.633		-1.627	
P VALUE	0.639	0.038	0.017	0.008	0.333	0.030		0.143	
WATER									
MEAN	0.343	-0.043	-0.713	-1.270	0.930	-0.377	0.418		3
SE	0.279	0.238	0.277	0.391	0.582	0.304	0.257		
T VALUE	1.229	-0.181	-2.574	-3.248	1.598	-1.240	1.626		
P VALUE	0.254	0.861	0.033	0.012	0.149	0.250	0.143		

Table E-2 (Cont.): Compositional analysis preference ranking matrices for comparison MCP home ranges to available habitat within the North Fork Drainage.

Vegetation (Continued) *Post-fire ('89 - 94, SCR not included)* (Multivariate P = 0.043, n = 10)

	ABLA/ PIEN	PSME/ LAOC	PICO	DECID	MIX	SHUB/ MEAD	BARE GROUND	WATER	BURNED	Use Rank
ABLA/PIEN										
MEAN		-0.413	-0.137	1.473	-0.187	0.732	0.287	0.215	-0.829	4
SE		0.041	0.096	0.454	0.058	0.154	0.153	0.338	0.270	
T VALUE		-10.073	-1.427	3.244	-3.224	4.753	1.876	0.636	-3.070	
P VALUE		0.000	0.187	0.010	0.010	0.001	0.093	0.541	0.013	
PSME/LAOC										
MEAN	0.413		0.276	1.886	0.226	1.145	0.700	0.628	-0.416	7
SE	0.041		0.097	0.472	0.072	0.186	0.181	0.371	0.273	
T VALUE	10.073		2.845	3.996	3.139	6.156	3.867	1.693	-1.524	
P VALUE	0.000		0.019	0.003	0.012	0.000	0.004	0.125	0.162	
PICO										
MEAN	0.137	-0.276		1.610	-0.050	0.869	0.423	0.352	-0.692	5
SE	0.096	0.097		0.408	0.111	0.152	0.189	0.350	0.312	
T VALUE	1.427	-2.845		3.946	-0.450	5.717	2.238	1.006	-2.218	
P VALUE	0.187	0.019		0.003	0.663	0.000	0.052	0.341	0.054	
DECID										
MEAN	-1.473	-1.886	-1.610		-1.660	-0.741	-1.186	-1.258	-2.302	0
SE	0.454	0.472	0.408		0.470	0.348	0.488	0.479	0.481	
T VALUE	-3.244	-3.996	-3.946		-3.532	-2.129	-2.430	-2.626	-4.786	
P VALUE	0.010	0.003	0.003		0.006	0.062	0.038	0.028	0.001	
MIX										
MEAN	0.187	-0.226	0.050	1.660		0.919	0.474	0.402	-0.642	6
SE	0.058	0.072	0.111	0.470		0.177	0.150	0.313	0.318	
T VALUE	3.224	-3.139	0.450	3.532		5.192	3.160	1.284	-2.019	
P VALUE	0.010	0.012	0.663	0.006		0.001	0.012	0.231	0.074	
SHUB/MEAD										
MEAN	-0.732	-1.145	-0.869	0.741	-0.919		-0.446	-0.517	-1.561	1
SE	0.154	0.186	0.152	0.348	0.177		0.161	0.290	0.302	
T VALUE	-4.753	-6.156	-5.717	2.129	-5.192		-2.770	-1.783	-5.169	
P VALUE	0.001	0.000	0.000	0.062	0.001		0.022	0.108	0.001	
BARE										
MEAN	-0.287	-0.700	-0.423	1.186	-0.474	0.446		-0.072	-1.115	2
SE	0.153	0.181	0.189	0.488	0.150	0.161		0.242	0.343	
T VALUE	-1.876	-3.867	-2.238	2.430	-3.160	2.770		-0.298	-3.251	
P VALUE	0.093	0.004	0.052	0.038	0.012	0.022		0.773	0.010	
WATER										
MEAN	-0.215	-0.628	-0.352	1.258	-0.402	0.517	0.072		-1.044	3
SE	0.338	0.371	0.350	0.479	0.313	0.290	0.242		0.496	
T VALUE	-0.636	-1.693	-1.006	2.626	-1.284	1.783	0.298		-2.105	
P VALUE	0.541	0.125	0.341	0.028	0.231	0.108	0.773		0.065	
BURNED										
MEAN	0.829	0.416	0.692	2.302	0.642	1.561	1.115	1.044		8
SE	0.270	0.273	0.312	0.481	0.318	0.302	0.343	0.496		
T VALUE	3.070	1.524	2.218	4.786	2.019	5.169	3.251	2.105		
P VALUE	0.013	0.162	0.054	0.001	0.074	0.001	0.010	0.065		

Table E-2 (Cont.): Compositional analysis preference ranking matrices for comparison MCP home ranges to available habitat within the North Fork Drainage.

Road Density

Mulitvariate P = 0.064, n = 18

	No roads	<2mi/mi^2	2-4mi/mi^2	>4mi/mi^2	Use Rank
No roads					
MEAN		-0.071	0.650	0.937	2
SE		0.220	0.470	0.464	
T VALUE		-0.323	1.383	2.019	
P VALUE		0.751	0.185	0.059	
<2mi/mi^2					
MEAN	0.071		0.721	1.007	3
SE	0.220		0.356	0.359	
T VALUE	0.323		2.025	2.805	
P VALUE	0.751		0.059	0.012	
2-4mi/mi^2					
MEAN	-0.650	-0.721		0.286	1
SE	0.470	0.356		0.152	
T VALUE	-1.383	-2.025		1.882	
P VALUE	0.185	0.059		0.077	
>4mi/mi^2					
MEAN	-0.937	-1.007	-0.286		0
SE	0.464	0.359	0.152		
T VALUE	-2.019	-2.805	-1.882		
P VALUE	0.059	0.012	0.077		

Table E-3: Compositional analysis preference ranking matrices for comparison travel routes to home ranges.

Topographic Position
(Multivariate P = 0.001, n = 14)

	Main Valley Bottom (MVB)	Main Valley Lower Slope (MVL)	Main Valley Upper Slope (MVU)	Side Valley Bottom (SVB)	Side Valley Upper Slope (SVU)	Bench (BEN)	Side Valley Lower Slope (SVL)	Ridge (RDG)	Use Rank
MVB									
MEAN		0.157	3.099	0.749	3.117	4.498	1.159	1.999	7
SE		0.059	0.622	0.186	0.741	0.604	0.324	0.214	
T VALUE		2.661	4.982	4.027	4.206	7.447	3.577	9.341	
P VALUE		0.020	0.000	0.001	0.001	0.000	0.003	0.000	
MVL									
MEAN	-0.157		2.942	0.592	2.960	4.341	1.002	1.842	6
SE	0.059		0.640	0.201	0.752	0.613	0.329	0.190	
T VALUE	-2.661		4.597	2.945	3.936	7.082	3.046	9.695	
P VALUE	0.020		0.001	0.011	0.002	0.000	0.009	0.000	
MVU									
MEAN	-3.099	-2.942		-2.350	0.017	1.399	-1.940	-1.101	2
SE	0.622	0.640		0.602	0.895	0.698	0.764	0.631	
T VALUE	-4.982	-4.597		-3.904	0.019	2.004	-2.539	-1.745	
P VALUE	0.000	0.001		0.002	0.985	0.066	0.025	0.105	
SVB									
MEAN	-0.749	-0.592	2.350		2.368	3.749	0.410	1.250	5
SE	0.186	0.201	0.602		0.682	0.628	0.279	0.249	
T VALUE	-4.027	-2.945	3.904		3.472	5.970	1.470	5.020	
P VALUE	0.001	0.011	0.002		0.004	0.000	0.165	0.000	
SVU									
MEAN	-3.117	-2.960	-0.017	-2.368		1.381	-1.957	-1.118	1
SE	0.741	0.752	0.895	0.682		0.753	0.687	0.649	
T VALUE	-4.206	-3.936	-0.019	-3.472		1.834	-2.849	-1.723	
P VALUE	0.001	0.002	0.985	0.004		0.090	0.014	0.109	
BEN									
MEAN	-4.498	-4.341	-1.399	-3.749	-1.381		-3.339	-2.499	0
SE	0.604	0.613	0.698	0.628	0.753		0.607	0.598	
T VALUE	-7.447	-7.082	-2.004	-5.970	-1.834		-5.501	-4.179	
P VALUE	0.000	0.000	0.066	0.000	0.090		0.000	0.001	
SVL									
MEAN	-1.159	-1.002	1.940	-0.410	1.957	3.339		0.839	4
SE	0.324	0.329	0.764	0.279	0.687	0.607		0.317	
T VALUE	-3.577	-3.046	2.539	-1.470	2.849	5.501		2.647	
P VALUE	0.003	0.009	0.025	0.165	0.014	0.000		0.020	
RDG									
MEAN	-1.999	-1.842	1.101	-1.250	1.118	2.499	-0.839		3
SE	0.214	0.190	0.631	0.249	0.649	0.598	0.317		
T VALUE	-9.341	-9.695	1.745	-5.020	1.723	4.179	-2.647		
P VALUE	0.000	0.000	0.105	0.000	0.109	0.001	0.020		

Table E-3 (Cont.): Compositional analysis preference ranking matrices for comparison travel routes to home ranges.

Slope

(Multivariate $P < 0.001$, $n = 14$)

	Flat	Slight	Moderate	Steep	Very Steep	Use Rank
Flat						
MEAN		0.394	0.884	1.463	2.119	4
SE		0.059	0.131	0.256	0.429	
T VALUE		6.678	6.748	5.715	4.939	
P VALUE		0.000	0.000	0.000	0.000	
Slight						
MEAN	-0.394		0.490	1.069	1.725	3
SE	0.059		0.101	0.211	0.389	
T VALUE	-6.678		4.851	5.066	4.434	
P VALUE	0.000		0.000	0.000	0.001	
Moderate						
MEAN	-0.884	-0.490		0.579	1.235	2
SE	0.131	0.101		0.199	0.415	
T VALUE	-6.748	-4.851		2.910	2.976	
P VALUE	0.000	0.000		0.013	0.012	
Steep						
MEAN	-1.463	-1.069	-0.579		0.656	1
SE	0.256	0.211	0.199		0.355	
T VALUE	-5.715	-5.066	-2.910		1.848	
P VALUE	0.000	0.000	0.013		0.089	
Very Steep						
MEAN	-2.119	-1.725	-1.235	-0.656		0
SE	0.429	0.389	0.415	0.355		
T VALUE	-4.939	-4.434	-2.976	-1.848		
P VALUE	0.000	0.001	0.012	0.089		

Table E-3 (Cont.): Compositional analysis preference ranking matrices for comparison travel routes to home ranges.

Aspect (Multivariate P < 0.001 N = 14)

	N	NE	E	SE	S	SW	W	NW	Flat	Use Rank
N										
MEAN		0.098	-0.110	-0.515	-0.729	-1.067	-0.684	0.122	-1.384	2
SE		0.173	0.199	0.165	0.126	0.214	0.219	0.153	0.211	
T VALUE		0.566	-0.553	-3.121	-5.786	-4.986	-3.123	0.797	-6.559	
P VALUE		0.580	0.589	0.008	0.000	0.000	0.007	0.439	0.000	
NE										
MEAN	-0.098		-0.207	-0.613	-0.826	-1.165	-0.781	0.024	-1.482	1
SE	0.173		0.192	0.227	0.188	0.199	0.216	0.192	0.169	
T VALUE	0.566		-1.078	-2.700	-4.394	-5.854	-3.616	0.125	-8.769	
P VALUE	0.580		0.299	0.017	0.001	0.000	0.003	0.902	0.000	
E										
MEAN	0.110	0.207		-0.406	-0.619	-0.957	-0.574	0.231	-1.275	3
SE	0.199	0.192		0.096	0.121	0.134	0.118	0.152	0.123	
T VALUE	-0.553	-1.078		-4.229	-5.116	-7.142	-4.864	1.520	-10.366	
P VALUE	0.589	0.299		0.001	0.000	0.000	0.000	0.151	0.000	
SE										
MEAN	0.515	0.613	0.406		-0.213	-0.551	-0.168	0.637	-0.869	4
SE	0.165	0.227	0.096		0.097	0.178	0.163	0.140	0.181	
T VALUE	-3.121	-2.700	-4.229		-2.196	-3.096	-1.031	4.550	-4.801	
P VALUE	0.008	0.017	0.001		0.045	0.008	0.320	0.000	0.000	
S										
MEAN	0.729	0.826	0.619	0.213		-0.338	0.045	0.850	-0.656	6
SE	0.126	0.188	0.121	0.097		0.132	0.131	0.097	0.149	
T VALUE	-5.786	-4.394	-5.116	-2.196		-2.561	0.344	8.763	-4.403	
P VALUE	0.000	0.001	0.000	0.045		0.023	0.736	0.000	0.001	
SW										
MEAN	1.067	1.165	0.957	0.551	0.338		0.383	1.188	-0.317	7
SE	0.214	0.199	0.134	0.178	0.132		0.052	0.108	0.078	
T VALUE	-4.986	-5.854	-7.142	-3.096	-2.561		7.365	11.000	-4.064	
P VALUE	0.000	0.000	0.000	0.008	0.023		0.000	0.000	0.001	
W										
MEAN	0.684	0.781	0.574	0.168	-0.045	-0.383		0.805	-0.700	5
SE	0.219	0.216	0.118	0.163	0.131	0.052		0.121	0.089	
T VALUE	-3.123	-3.616	-4.864	-1.031	0.344	7.365		6.653	-7.865	
P VALUE	0.007	0.003	0.000	0.320	0.736	0.000		0.000	0.000	
NW										
MEAN	-0.122	-0.024	-0.231	-0.637	-0.850	-1.188	-0.805		-1.506	0
SE	0.153	0.192	0.152	0.140	0.097	0.108	0.121		0.142	
T VALUE	0.797	0.125	1.520	4.550	8.763	11.000	6.653		-10.606	
P VALUE	0.439	0.902	0.151	0.000	0.000	0.000	0.000		0.000	
Flat										
MEAN	1.384	1.482	1.275	0.869	0.656	0.317	0.700	1.506		8
SE	0.211	0.169	0.123	0.181	0.149	0.078	0.089	0.142		
T VALUE	-6.559	-8.769	-10.366	-4.801	-4.403	-4.064	-7.865	-10.606		
P VALUE	0.000	0.000	0.000	0.000	0.001	0.001	0.000	0.000		

Table E-3 (Cont.): Compositional analysis preference ranking matrices for comparison travel routes to home ranges.

Distance to roads

(Multivariate P = 0.001, n = 14)

	<200m	200-500m	.5-1km	>1km	Use Rank
<200m					
MEAN		-0.214	-0.891	0.290	1
SE		0.259	0.299	0.514	
T VALUE		-0.826	-2.980	0.564	
P VALUE		0.424	0.011	0.582	
200-500m					
MEAN	0.214		-0.677	0.504	2
SE	0.259		0.148	0.339	
T VALUE	0.826		-4.574	1.487	
P VALUE	0.424		0.001	0.161	
.5-1km					
MEAN	0.891	0.677		1.181	3
SE	0.299	0.148		0.324	
T VALUE	2.980	4.574		3.645	
P VALUE	0.011	0.001		0.003	
>1km					
MEAN	-0.290	-0.504	-1.181		0
SE	0.514	0.339	0.324		
T VALUE	-0.564	-1.487	-3.645		
P VALUE	0.582	0.161	0.003		

Table E-3 (Cont.): Compositional analysis preference ranking matrices for comparison travel routes to home ranges.

Distance to water

(Multivariate P = 0.006, n = 14)

	<200m	200-500m	.5-1km	>1km	Use Rank
≤200m					
MEAN		0.173	0.328	0.895	3
SE		0.074	0.115	0.183	
T VALUE		2.338	2.852	4.891	
P VALUE		0.036	0.014	0.000	
200-500m					
MEAN	-0.173		0.155	0.723	2
SE	0.074		0.067	0.153	
T VALUE	-2.338		2.313	4.725	
P VALUE	0.036		0.038	0.000	
.5-1km					
MEAN	-0.328	-0.155		0.568	1
SE	0.115	0.067		0.124	
T VALUE	-2.852	-2.313		4.581	
P VALUE	0.014	0.038		0.001	
≥1km					
MEAN	-0.895	-0.723	-0.568		0
SE	0.183	0.153	0.124		
T VALUE	-4.891	-4.725	-4.581		
P VALUE	0.000	0.000	0.001		

Table E-3 (Cont.): Compositional analysis preference ranking matrices for comparison travel routes to home ranges.

Vegetation

Pre-fire (all years; '84 - '88 & SPCR) (Multivariate P = 0.430, n = 8)

	ABLA/ PIEN	PSME/ LAOC	PICO	DECID	MIX	SHUB/ MEAD	BARE GROUND	WATER	Use Rank
ABLA/PIEN									
MEAN		0.337	0.042	0.600	0.782	-0.264	-0.584	-0.439	4
SE		0.150	0.288	1.031	0.641	0.283	0.250	0.256	
T VALUE		2.247	0.146	0.582	1.220	-0.933	-2.336	-1.715	
P VALUE		0.059	0.888	0.579	0.262	0.382	0.052	0.130	
PSME/LAOC									
MEAN	-0.337		-0.295	0.263	0.445	3.347	-3.177	-0.198	3
SE	0.150		0.227	0.982	0.528	0.871	0.356	0.173	
T VALUE	-2.247		-1.300	0.268	0.843	3.843	-8.924	-1.145	
P VALUE	0.059		0.235	0.797	0.427	0.006	0.000	0.290	
PICO									
MEAN	-0.042	0.295		0.558	0.740	-0.306	-0.626	-0.481	3
SE	0.288	0.227		0.774	0.539	0.152	0.310	0.275	
T VALUE	-0.146	1.300		0.721	1.373	-2.013	-2.019	-1.749	
P VALUE	0.888	0.235		0.494	0.212	0.084	0.083	0.124	
DECID									
MEAN	-0.600	-0.263	-0.558		0.182	-0.864	-1.184	-1.038	1
SE	1.031	0.982	0.774		0.905	0.807	0.964	0.923	
T VALUE	-0.582	-0.268	-0.721		0.201	-1.071	-1.228	-1.125	
P VALUE	0.579	0.797	0.494		0.846	0.320	0.259	0.298	
MIX									
MEAN	-0.782	-0.445	-0.740	-0.182		-1.046	-1.365	-1.220	0
SE	0.641	0.528	0.539	0.905		0.486	0.448	0.429	
T VALUE	-1.220	-0.843	-1.373	-0.201		-2.152	-3.047	-2.844	
P VALUE	0.262	0.427	0.212	0.846		0.068	0.019	0.025	
SHUB/MEAD									
MEAN	0.264	-3.347	0.306	0.864	1.046		-0.320	-0.175	4
SE	0.283	0.871	0.152	0.807	0.486		0.210	0.190	
T VALUE	0.933	-3.843	2.013	1.071	2.152		-1.524	-0.921	
P VALUE	0.382	0.006	0.084	0.320	0.068		0.171	0.388	
BARE GROUND									
MEAN	0.584	3.177	0.626	1.184	1.365	0.320		0.145	7
SE	0.250	0.356	0.310	0.964	0.448	0.210		0.103	
T VALUE	2.336	8.924	2.019	1.228	3.047	1.524		1.408	
P VALUE	0.052	0.000	0.083	0.259	0.019	0.171		0.202	
WATER									
MEAN	0.439	0.198	0.481	1.038	1.220	0.175	-0.145		6
SE	0.256	0.173	0.275	0.923	0.429	0.190	0.103		
T VALUE	1.715	1.145	1.749	1.125	2.844	0.921	-1.408		
P VALUE	0.130	0.290	0.124	0.298	0.025	0.388	0.202		

Table E-3 (Cont.): Compositional analysis preference ranking matrices for comparison travel routes to home ranges.

Vegetation *Post-fire ('89 - 94, SCR not included)* (Multivariate P = 0.133, n = 10)

	ABLA/ PIEN	PSME/ LAOC	PICO	DECID	MIX	SHUB/ MEAD	BARE GROUND	WATER	BURNED	Use Rank
ABLA/PIEN										
MEAN		-0.016	-0.243	-0.029	0.742	-1.066	-0.999	-0.914	-0.528	1
SE		0.064	0.162	0.356	0.469	0.192	0.155	0.259	0.271	
T VALUE		-0.250	-1.500	-0.081	1.582	-5.552	-6.445	-3.529	-1.948	
P VALUE		0.808	0.168	0.937	0.148	0.000	0.000	0.006	0.083	
PSME/LAOC										
MEAN	0.016		-0.227	-0.013	0.758	1.984	-2.456	-0.590	-0.512	3
SE	0.064		0.117	0.326	0.491	0.500	0.251	0.363	0.247	
T VALUE	0.250		-1.940	-0.040	1.544	3.968	-9.785	-1.625	-2.073	
P VALUE	0.808		0.084	0.969	0.157	0.003	0.000	0.139	0.068	
PICO										
MEAN	0.243	0.227		0.214	0.985	-0.823	-0.756	-0.670	-0.285	4
SE	0.162	0.117		0.269	0.492	0.154	0.271	0.391	0.278	
T VALUE	1.500	1.940		0.796	2.002	-5.344	-2.790	-1.714	-1.025	
P VALUE	0.168	0.084		0.447	0.076	0.000	0.021	0.121	0.332	
DECID										
MEAN	0.029	0.013	-0.214		0.771	-1.038	-0.970	-0.885	-0.499	3
SE	0.356	0.326	0.269		0.543	0.361	0.464	0.573	0.357	
T VALUE	0.081	0.040	-0.796		1.420	-2.875	-2.091	-1.545	-1.398	
P VALUE	0.937	0.969	0.447		0.189	0.018	0.066	0.157	0.196	
MIX										
MEAN	-0.742	-0.758	-0.985	-0.771		-1.809	-1.742	-1.656	-1.270	0
SE	0.469	0.491	0.492	0.543		0.465	0.475	0.478	0.639	
T VALUE	-1.582	-1.544	-2.002	-1.420		-3.890	-3.667	-3.464	-1.987	
P VALUE	0.148	0.157	0.076	0.189		0.004	0.005	0.007	0.078	
SHUB/MEAD										
MEAN	1.066	-1.984	0.823	1.038	1.809		0.067	0.153	0.538	7
SE	0.192	0.500	0.154	0.361	0.465		0.239	0.336	0.311	
T VALUE	5.552	-3.968	5.344	2.875	3.890		0.280	0.455	1.730	
P VALUE	0.000	0.003	0.000	0.018	0.004		0.786	0.660	0.118	
BARE										
MEAN	0.999	2.456	0.756	0.970	1.742	-0.067		0.086	0.471	7
SE	0.155	0.251	0.271	0.464	0.475	0.239		0.198	0.321	
T VALUE	6.445	9.785	2.790	2.091	3.667	-0.280		0.434	1.467	
P VALUE	0.000	0.000	0.021	0.066	0.005	0.786		0.674	0.176	
WATER										
MEAN	0.914	0.590	0.670	0.885	1.656	-0.153	-0.086		0.385	6
SE	0.259	0.363	0.391	0.573	0.478	0.336	0.198		0.406	
T VALUE	3.529	1.625	1.714	1.545	3.464	-0.455	-0.434		0.948	
P VALUE	0.006	0.139	0.121	0.157	0.007	0.660	0.674		0.368	
BURNED										
MEAN	0.528	0.512	0.285	0.499	1.270	-0.538	-0.471	-0.385		5
SE	0.271	0.247	0.278	0.357	0.639	0.311	0.321	0.406		
T VALUE	1.948	2.073	1.025	1.398	1.987	-1.730	-1.467	-0.948		
P VALUE	0.083	0.068	0.332	0.196	0.078	0.118	0.176	0.368		

Table E-3 (Cont.): Compositional analysis preference ranking matrices for comparison travel routes to home ranges.

Road Density

(Multivariate $P < 0.001$, $n = 14$)

	No Roads	<2mi/mi^2	2-4mi/mi^2	>4mi/mi^2	Use Ranking
No Roads					
MEAN		-1.506	-0.788	-0.580	0
STD. ERROR		0.186	0.326	0.522	
T VALUE		-8.097	-2.417	-1.111	
P VALUE		0.000	0.031	0.287	
<2mi/mi^2					
MEAN	1.506		0.717	0.926	3
STD. ERROR	0.186		0.271	0.471	
T VALUE	8.097		2.646	1.966	
P VALUE	0.000		0.020	0.071	
2-4mi/mi^2					
MEAN	0.788	-0.717		0.209	2
STD. ERROR	0.326	0.271		0.343	
T VALUE	2.417	-2.646		0.609	
P VALUE	0.031	0.020		0.553	
>4mi/mi^2					
MEAN	0.580	-0.926	-0.209		1
STD. ERROR	0.522	0.471	0.343		
T VALUE	1.111	-1.966	-0.609		
P VALUE	0.287	0.071	0.553		

Appendix F: Steps for conducting stepwise multiple logistic regression on spatial data.

Multiple logistic regression is a statistical technique that examines the functional relationship between a binomial dependent variable and a set of independent variables that may be either discrete or continuous in their distribution (Trexler and Travis 1993). This technique is used frequently for analysis of wildlife habitat utilization data (e.g. Mladenoff et al. 1995, Pereira and Itami 1991). It is especially well suited for examining the characteristics of specific locations such as nest sites or observation points.

In my analysis of wolf home ranges and travel routes however, I desired to examine the characteristics of continuous portions of the landscape. Other investigators have conducted such analysis by calculating summary values (such as mean slope) to characterize the area that they are investigating. I did not feel that such techniques were appropriate for my analysis because they often do not identify important interactions between habitat characteristics (such as the combination of slope and aspect) where variables are summarized for large areas.

I determined that the best way to characterize wolf home ranges and travel routes was as a grid of points. Each point would be updated with data for wolf use (home ranges, and tracking routes) and habitat characteristics using GIS. The resulting point data set could then be exported to a statistics package for logistic regression. The primary problem with this method was that the points used to characterize the GIS data represented an arbitrary sub-sampling of this data. Significance within the final stepwise logistic regression model did not imply practical significance on the landscape because of the artificially inflated sample size in the point data sets. In fact, all variables were identified as significant (due to the artificially large sample size) in the final analyses.

I generated 2 sets of point grids To characterize the GIS data. I used a 400 m grid to characterize the minimum convex polygon home range areas and the available habitat within the basin. A 150 m grid of points was used to characterize the wolf travel route analysis corridors (areas within 100 m of mapped wolf travel routes). I generated the point grids in PAMAP by converting the basin-wide available habitat polygon into a surface layer. I used the "change pixel size" function to convert the basin-wide available habitat surface from 50 m pixel size to 400 m pixel size. Using the "export surface to ASCII" function, I exported the X,Y coordinates of the southwestern corners of the 400 m pixels into an ASCII file. I then pulled the X,Y coordinates back into PAMAP as point database tags using the "import from ASCII" function. I updated the resulting point database layer with values from habitat characteristic map layers and wolf use layers (home range and tracking routes). A similar procedure was used for the wolf tracking analysis corridors, but the analysis corridor surface was translated from 50 m to 150 m before being converted to points. A total of 10,500 points were sampled to characterize the basin-wide available habitat and home range areas, 10,500 points were sampled to characterize the wolf travel route analysis corridors.

Upon investigation of the data resulting from my first attempts at overlaying the point database with habitat characteristic data, I found that PAMAP had generated false data values for many of the points in the 400 m grid. These errors were caused because the points fell on the corners of pixels, so PAMAP extrapolated the values for these points from the values of the 4 adjacent pixels. I corrected this problem by shifting the points north and east 25 m so that the points fell in the center of pixels. The shift was done by pulling the ASCII X,Y coordinate files into Excel and adding 25 to each X and Y value. No errors were encountered using the 150 m grid (these points fell in the centers of pixels without being shifted).

Databases were structured so that a weighting variable and a use variable were included for each pack year. The use variable included a code indicating whether the pixel represented by that point had been included in a wolf travel route analysis corridor or home range for that year. The weighting variable contained the number of times that wolves had been tracked in the vicinity of that point for that pack that year.

The resulting data sets were then combined and a series of logistic regression analyses were conducted using SPSS for Windows. Stepwise multiple logistic regression was conducted comparing home ranges to the available area within the basin for each year using only points from the 400 m grid. Analysis for the winters of 1990-91 to 1993-94 combined the home ranges for the 3 packs in the North Fork and compared the combined home range area to the available habitat within the basin. I conducted the analysis this way because I assumed that if an area was occupied by one pack, it was not available to other packs within the basin, and I was primarily interested in characterizing the areas within the basin used by wolves, not necessarily the individual home ranges.

I also conducted stepwise multiple logistic regression comparing tracking route analysis corridors to minimum convex polygon home ranges for each pack each year. In the regression analysis, points within the travel route analysis corridors were weighted according to how many times wolves from that pack had been tracked in that area that year. Points from the 150 m grid representing travel route analysis corridors for that year were compared to points from the 400 m grid representing the home range for that pack that year.

In this manner 10 stepwise logistic regression analyses were conducted comparing wolf home ranges to the available habitat within the basin and 14 regression analyses were conducted comparing travel route analysis corridors to home ranges. The resulting logistic regression models were evaluated based on accuracy of identification of used and unused points and chi-square scores. Models that provided a balance between the minimum number of variables and the maximum predictive value were selected as the best. These best models were compared across years to identify which habitat characteristics were consistently predictive of wolf use. Results of this analysis are presented in Chapter 2 of this thesis.

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