University of Alberta

Movement of wolves (*Canis lupus*) in response to human development in Jasper National Park, Alberta.

by

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Abstract

Wolves are wary carnivores that occupy enormous territories. In mountainous regions, increasing levels of human activity may degrade wolf habitat and obstruct wolf movement among valleys. In this study, I quantified wolf preference or avoidance of areas near human development, determined the effect of human development on path tortuosity, and tested whether linear developments were barriers to movement. My assistants and I snow tracked the movements of two wolf packs for two winters near the town of Jasper in Jasper National Park, Alberta. Wolves strongly avoided high trail and road density and strongly selected for low-use trails. They were variable in their response to high-use roads, high-use trails, and low-use roads but generally showed stronger avoidance of high-use features than low-use features. Path tortuosity increased in areas of high trail and road density and wolves avoided crossing all linear features, particularly high-use roads. Based on these results, managers should limit human activity, including trail-use, in areas of high conservation concern.

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Chapter 1. General Introduction

This chapter introduces the rationale and research approach for questions addressed in chapters two and three. I created these two chapters as self-sufficient papers to be submitted directly to peer-reviewed journals. Therefore, introductions to these chapters duplicate much of the information presented in this introduction.

Increasing levels of human activity threaten animal populations throughout the world (Saunders et al. 1991; Meffe & Carroll 1994). Most research has focused on the ecological effects of roads rather than other developments such as trails, railway lines, or resorts because roads are one of the leading causes of habitat degradation, habitat fragmentation, habitat loss, and direct mortality (Trombulak & Frissell 2000). Roads occupy 1% of the United States land area, yet may affect ecological processes in approximately 20% of the country (Forman 2000). While the ecological effects of roads are clearly important, the cumulative effects of lesser-studied developments surrounding towns, such as trails, resorts, and railway lines, may also cause habitat degradation and fragmentation. Hikers, for example, have been shown to disturb Bighorn sheep (*Ovis canadensis*; Papouchis et al. 2001), and proximity to trails affected predation rates on artificial quail nests (*Callipepla spp*; Miller & Hobbs 2000). However, more research is required to determine what types and levels of human activity a variety of animals avoid. Moreover, we need to understand how animals move through these areas to determine whether habitat fragmentation constrains important movement, like dispersal, between habitat patches (With & Crist 1995; Keitt et al. 1997; Schultz 1998; Turchin 1998; Brooker et al. 1999; With & King 1999; Roland et al. 2000).

Several studies have examined the response of animals to human development by developing resource selection functions that compare habitats which species use to available habitats (Johnson 1980; Manly 1993). Most of these studies found that animals avoid roads and areas of high road density. For example, grizzly bears, wolves, elk, and caribou avoided areas with roads (Mace et al. 1996; Mladenoff et al. 1995, 1999; Rowland et al. 2000; Dyer et al. 2001). While most species avoided roads, wolves in remote regions selected for roads because they provided easy travel routes across their territory (Thurber et al. 1994; James & Stuart-Smith 2000). This suggests that avoidance of roads and other developments may be highly species and context-specific.

Studies linking fine-scale movement behaviour to habitat quality have generally measured movement behaviour either in terms of path complexity (tortuosity) or willingness to cross inhospitable habitats. For deer mice (*Peromyscus maniculatus*), caribou (*Rangifer tarandus*), and many species of insects, path tortuosity increases in areas of high quality habitat (Crist et al. 1992; Miyatake et al. 1995; Stapp & Van Horne 1997; Odendaal et al. 1998; Schultz 1998; Bergman et al. 1999; Kindvall 1999; Schultz & Crone 2001). Path tortuosity also increases during the denning period for wolves (Bascompte & Vilá 1997) and for insects with a uniform, versus clumped, distribution of resources (Wiens et al. 1995). If human activity degrades habitat quality, then species should travel quickly and with relatively straight paths in areas of high human activity. While this prediction has not been tested, other fine-scale movement studies have addressed the permeability of roads and forest gaps to movement. Bird studies in the form of mark-recapture, playback, relocation, and modeling experiments, suggest that forest gaps, like roads, agricultural fields, and forestry cutblocks, impede the movement of some forest dependent species (Desroches & Hannon 1997; St. Clair et al. 1998; Brooker et al. 1999; Bélisle & St. Clair 2001). Moreover, the structure of gaps in landscapes may be more important than patch structure to animal dispersal (With & King 1999). Other studies examining barrier effects have compared the frequency with which animals cross roads to a null model of road crossings. In these studies, black bears (*Ursus americanus*), caribou (*Rangifer tarandus caribou*), and hedgehogs (*Erinaceus europaeus*) crossed high-use roads less often than expected, while low-use roads and seismic lines did not seem to affect their movement patterns (Serrouya 1999; Dyer 1999; Rondinini & Doncaster 2002). Together, these studies indicate that although roads, and possibly other developments, occupy a small area, they may have a large effect on animal movement.

The effects of human developments are particularly problematic in mountainous areas. Here, rugged topography and deeps snows confine the movement of animals to the valley bottoms where people also concentrate their activity (Noss et al. 1996). Therefore, there is high potential for human activity to obstruct animal movement across or between valleys (Clevenger & Waltho 2000; Bélisle & St. Clair 2001). Wolves are a wary species susceptible to these habitat fragmentation effects (Weaver et al. 1996; Mladenoff et al. 1995, 1999). They often travel over thirty kilometers in a day within territories than encompass several valleys and approximately 1,000 km^2. Consequently, wolf movement through areas with human activity is necessary for their local persistence.

The town of Jasper (population 4,500) in Jasper National Park, Alberta, is a popular destination for tourists and outdoor enthusiasts. Like many communities within the Rocky Mountains, Jasper lies at the confluence of several valleys. Wolf packs near Jasper must circumvent or travel through human development when travelling among valleys. Therefore, Parks Canada is concerned that existing or future levels of development will impede wolf and other carnivore movement. To better manage the effects of human development on wolves, they need to identify the following: (a) the types and levels of human activity that will degrade wolf habitat or impede wolf movement; (b) areas where the combination of rugged topography and human development may obstruct wolf movement among valleys; and (c), the potential effects of future habitat restoration or development on wolf movement.

To address these needs, this study has three research objectives. In Chapter 1, I identify wolf selection or avoidance of specific types and levels of human activity. In Chapter 2, I examine both the effects of human development on the tortuosity of wolf paths and the permeability of linear features (roads, trails, railway lines) to wolf movement. This study focussed on the winter movements of two wolf packs for two winters (1999-2000, 2000-2001). To record the movement of wolves, we followed their tracks in the snow while recording our own positions with hand held Global Position Systems (GPS). Tracking efforts were concentrated within 25 kilometers of Jasper and thus encompass areas of high and low-levels of human activity.

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Chapter 2

Spatial response of wolves to roads, trails, and human developments in Jasper National Park, Alberta.

INTRODUCTION

Increasing levels of human activity threaten animal populations throughout the world (Saunders et al. 1991; Meffe & Carroll 1994). The effects of human activity may be intensified in mountainous regions because people concentrate their activities along the valley bottoms, which also provide the best habitat for many species (Noss et al. 1996). While human activities may cause direct mortality, habitat degradation, and habitat loss (Meffe & Carroll 1994), they also may inhibit animal movements between valleys where high levels of human activity abut rugged topography. To mitigate this habitat fragmentation effect, it is necessary to determine the spatial response of animals to developments such as roads, trails, resorts, and towns (Beier & Noss 1998).

Most research has focussed on the ecological effects of roads rather than other developments such as trails, railway lines, or resorts because roads are one of the leading causes of habitat degradation, habitat fragmentation, habitat loss, and direct mortality (Trombulak & Frissell 2000). Forman (2000) estimated that while roads occupy 1% of the United States land area, they affect ecological processes in approximately 20% of the country. While the ecological effects of roads are clearly important, the cumulative effects of trails and other developments surrounding towns also may cause habitat degradation and fragmentation. The few existing studies on trails show that they are of potential conservation concern. Bighorn sheep (*Ovis canadensis*) in Utah, for example, fled more often from hikers than from vehicles (Papouchis et al. 2001) and predation rates on artificial quail nests (*Callipepla californica*) depended on proximity to trails (Miller & Hobbs 2000). The combined effects of roads, trails and other human developments may be most problematic for carnivores because these species occur in low densities and occupy large home ranges that encompass multiple anthropogenic obstacles to movement (Noss et al. 1996). Wolves (*Canis lupus*) may be particularly susceptible to these effects because they are generally wary of people and in mountainous areas winter movements of wolves are confined by deep snows to the valley bottoms (Weaver et a. 1996). Because people also concentrate activities along the valley bottoms, there is high potential for their activities to affect wolf movement.

Only a few studies have examined how wolves respond to human developments, and roads were the primary focus of these studies. The response of wolves to roads can be partitioned according to two scales of analysis. Large scale studies of territory selection, commonly referred to as 2nd order selection (Johnson 1980), have been used to predict areas for wolf recolonization and persistence in Minnesota, Wisconsin, and Michigan. In Minnesota, wolf packs persist in areas with low densities of people and with low road densities (< 0.58 km/km^2; Thiel 1985; Mech et al. 1988). In Wisconsin and Michigan, wolves established and persisted in territories with road densities below 0.45 km/km^2 (Mladenoff et al. 1995, 1999). These studies suggest that it is not the roads per se that wolves avoid, but the positive correlation between road density and number of encounters with humans. Consequently, in areas of high road density, wolves are also subject to higher mortality from vehicles and illegal hunting.

While it is important to identify areas for successful wolf recolonization at a broad scale, it also is important to understand the spatial response of wolves to roads at a finer scale. The spatial response of wolves to roads within their territory, identified as 3rd order selection (Johnson 1980), is the scale at which management decisions are typically made to conserve local populations. Recent studies at this scale show that wolves select areas close to roads because these features provide easy travel routes across their territory. In Alaska, wolves selected areas close to all roads with the exception of a heavily used mining road, which they avoided (Thurber et al. 1994). In northern Alberta, wolves selected areas close to roads and seismic lines (James & Stuart-Smith 2000). Because of the structural similarity between seismic lines and trails, wolves likely selected areas close to low-use trails. While the studies at two scales of analysis show seemingly contradictory results, they occurred in areas with different densities of people. The fine-scale studies (wolves select roads) occurred in remote areas whereas the landscape studies (wolves avoid roads) occurred in populated areas. Therefore, it is important to identify the fine-scale response of wolves to roads in a populated area where wolf populations are most threatened. Furthermore, no studies have assessed the response of wolves to trails and other developments surrounding populated areas.

The town of Jasper (population 4,500) in Jasper National Park, Alberta, is a popular destination for tourists and outdoor enthusiasts. Like many communities within the Rocky Mountains, Jasper lies at the confluence of several valleys. Wolf packs near Jasper must move through narrow pinch points to travel among valleys. Consequently, the territories of these wolves encompass both high and low-levels of human activity. In this study, I determined the fine-scale, spatial response of two wolf packs to roads, trails, railway lines, resorts, and topographic features around Jasper. I compared the habitat characteristics of wolf paths and random points using multiple logistic regression (Manly et al. 1993). More specifically, I paired random points with wolf points and used match case-control logistic regression rather than standard logistic regression to isolate the movement decisions of wolves while estimating resource selection (Hosmer & Lemeshow 2000). I used the results to create a habitat model that identifies areas of conservation concern. The results of this study will help managers identify barriers to the movement of wolves and other wary species.

METHODS

Study area. This study focused on the movements of two wolf packs throughout two winters (1999-2000, 2000-2001). The territories of both packs extended between 20 and 50 km along the four valleys that converge upon the town of

Jasper. The study area included a portion of these two territories, approximately 25 km each side of Jasper (Figure 2-1). The outer limits of the study area coincided with park boundaries, prominent geographic features, and wolf territorial boundaries. While the study area encompassed 2900 km^2, only 572 km^2 lay below 1600 m (valley bottom is 1020 meters) and ninety-nine percent of wolf movements also lay below 1600 m. The number of wolves in Pack 1 (west and northeast of Jasper) ranged from seven to ten individuals whereas the number of wolves in Pack 2 (south and southeast of Jasper) ranged from two to three individuals.

Wolves in Jasper National Park prey mainly on elk (*Cervus elephus*), deer (*Odocoileus* spp.), and moose (*Alces alces*), but occasionally take big-horned sheep, caribou (*Rangifer tarandus*), and mountain goat (*Oreamnos americanus*). Valley bottoms, where wolves and their prey occur, are dominated by open lodgepole pine (*Pinus contorta*) forests that are interspersed with douglas fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), poplar (*Populus balsamifera*), white spruce (*Picea glauca*), and small meadow complexes. Sides of the valleys are dominated by englemann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Snow depths along the valley bottoms are generally shallow and range from 5 to 40 cm.

The study area includes 759 km of trails and 292 km of roads including a railway line. A major transportation highway with substantial freight-truck traffic runs

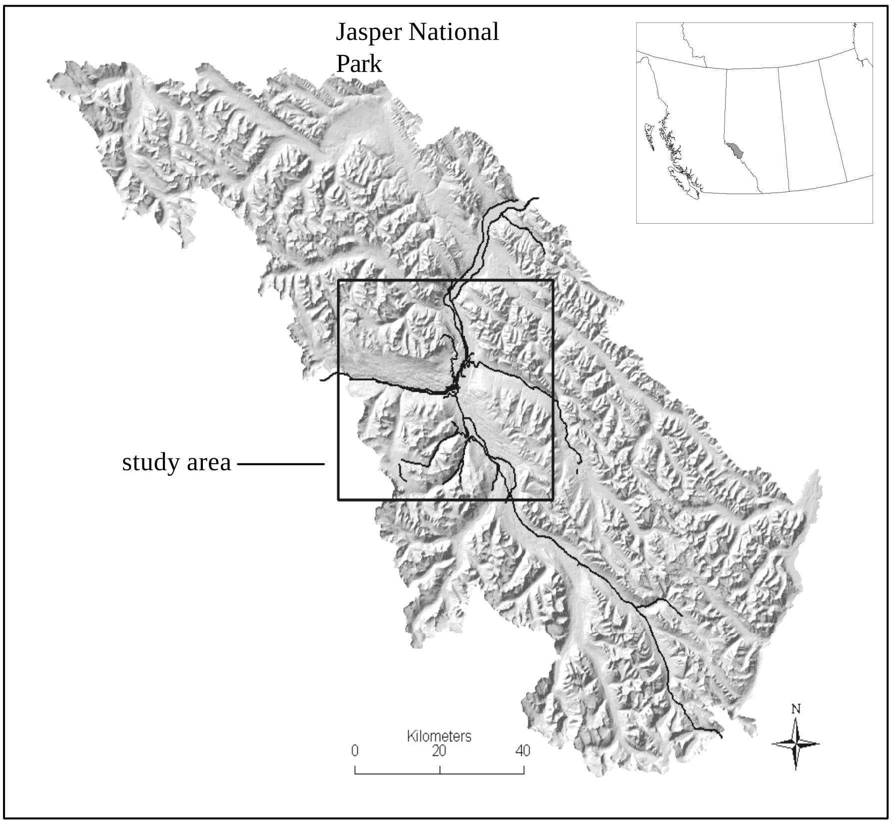

Figure 2-1. Map of study area within Jasper National Park, Alberta, Canada.

through the study area from northeast to west. This highway is neither divided nor fenced. Several secondary highways extend throughout Jasper National Park. Jasper received 1,288,788 vehicles in 2000, a 22 % increase from 1990 (Parks Canada Highway Services, unpublished data). There is marked seasonal variation in traffic volume and vehicle traffic quadrupled from 56,174 vehicles in February to 216,404 vehicles in August, 2000. Trail networks are concentrated within 10 km of the Jasper townsite but are rapidly expanding as people, particularly mountain bikers, create their own trails through the study area.

Field Methods. To record the movements of these two wolf packs, my assistants and I followed their tracks in the snow and simultaneously recorded positions with a hand-held global positioning system (GPS; Trimble GeoExplorer 3®). We initially located wolf tracks by conducting both cross-valley transects and road surveys. Once we found wolf tracks, we followed the tracks during the daylight hours, often returning to the same track on several successive days until snow-conditions deteriorated. Fresh wolf tracks were backtracked so as not to interfere with natural movement patterns. The tracking sessions were exported into ArcInfo® (ESRI 2000) for data preparation and then transferred to S-Plus® for statistical analysis (Venebles & Ripley 1999). Because single wolves may respond differently to roads and trails than packs of wolves, I excluded tracks of single wolves from the analysis.

Statistical Analysis. The spatial response of wolves to roads and trails may be influenced by habitat quality near the roads and trails. Therefore, I measured wolf preference and avoidance of several habitat variables in addition to measures of human use (Table 2-1). For this analysis, I used matched case-control logistic regression (Appendix I: equation 3) rather than standard logistic regression (Appendix I: equation 1). While standard logistic regression has been used extensively to model habitat selection of animals (Pereira & Itami 1991; Manly et al. 1993; Mladenoff et al. 1995, 1999; Mace et al. 1996; Peeters & Gardeniers 1998), matched case-control logistic regression has only recently been applied to the field of ecology (Compton et al. 2002). However, this method is considered to be one of the most important statistical techniques in medicine (Breslow 1996). Matched case-control logistic regression is similar to standard logistic regression in that use (case) points are coded as one and available (control) points are coded as zero. However, unlike standard logistic regression, matched case-control logistic regression pairs controls with cases by some stratifying variable (Hosmer & Lemeshow 2000). This pairing, which is analogous to a paired t-test, minimizes variance associated with the stratified variable and incidentally reduces autocorrelation problems inherent in spatial and temporal data. In essence, matched case-control identifies the difference between each case and its set of control points rather than the overall distribution of case and control points. This difference is expressed by a β coefficient for each predictor variable. The β coefficients, which are calculated using conditional maximum likelihood

Table 2-1. Predictor variables used for resource selection analysis. Boldface variables were used to create candidate models for model averaging.

Variable	Description	Transformation	
		Pack 1	Pack 2
Habitat predictors			
Elevation	meters above sea level (range 1020 m to 1750 m)		
Slope	degrees		
Cosine of aspect	radians; southwest = 1, northeast = -1		
Distance to water	km		
Forest type	lodgepole pine, spruce, douglas fir, aspen, open shrub/meadow/water		
Human use predictors			
Trail density	km/km^2; radius of 0.2, 0.5, **1.0**, 1.5 km		
Road density	km/km^2; radius of 0.2, 0.5, **1.0**, 1.5 km		
Distance to railway	km; max of 0.2, 0.5, 1.0 m, **no maximum**	sqrt()	
Distance to high-use road*	km; max of 0.2, 0.5, 1.0 m, **no maximum** high-use > 10,000 vehicles per month		
Distance to low-use road*	km; max of 0.2, **0.5,** 1.0 m, **no maximum** low-use < 10,000 vehicles per month	no max	sqrt(0.5)
Distance to high-use trail*	km; max of 0.2, 0.5, 1.0 m, **no maximum** high-use = several trail users per day		
Distance to low-use trail*	km; max of 0.2, 0.5, 1.0 m, **no maximum** low-use = trail not used every day		sqrt()
Distance to accommodation*	km; max of 0.2, 0.5, 1.0 m, **no maximum** Accommodation includes resorts, commercial facilities, and the town of Jasper		
Distance to town*	km; max of 0.2, 0.5, 1.0 m, no maximum		

* When far from human developments, the variables distance to road, trail, accommodation, or town may have little effect on wolf movement. Therefore, I tested each of these predictors with maximum values of 0.2, 0.5, and 1.0 kilometers such that the maximum replaced all values larger than the maximum.

estimation, indicate the direction of habitat selection and are interpreted similarly to coefficients from standard logistic regression.

In this analysis, I simplified wolf paths into discrete steps of 1000 m, selected those points as cases, and then created 10 controls for each case (Figure 2-2). I avoided shorter separation distances because they would constrain control points to lie within a similar (short) distance of the wolf path, and therefore increase the similarity between the two types of points and ultimately underestimate wolf resource selection. I further decreased the similarity between wolf and control points by prohibiting the controls from landing on wolf paths. However, to maximize the realism of control points I restricted the controls to areas outside the town limits and to elevations below 1600 m. Because the number of controls per case does not increase Type I error in match case-control logistic regression (Hosmer & Lemeshow 2000), I created 10 controls per case to estimate the habitat available to wolves at each step.

Model selection. To create the best predictive model of the paths selected by wolves, I followed the model averaging approach of Burnham & Anderson (1998) which consists of several steps. First, I created a list of likely predictor variables (Table 2-1), excluded inferior or redundant variables, and tested for non-linearity in the remaining variables. For all preliminary model comparisons I used likelihood ratio tests where differences in deviance between models follow a chi-squared distribution. I tested for non-linearity using fractional polynomials where

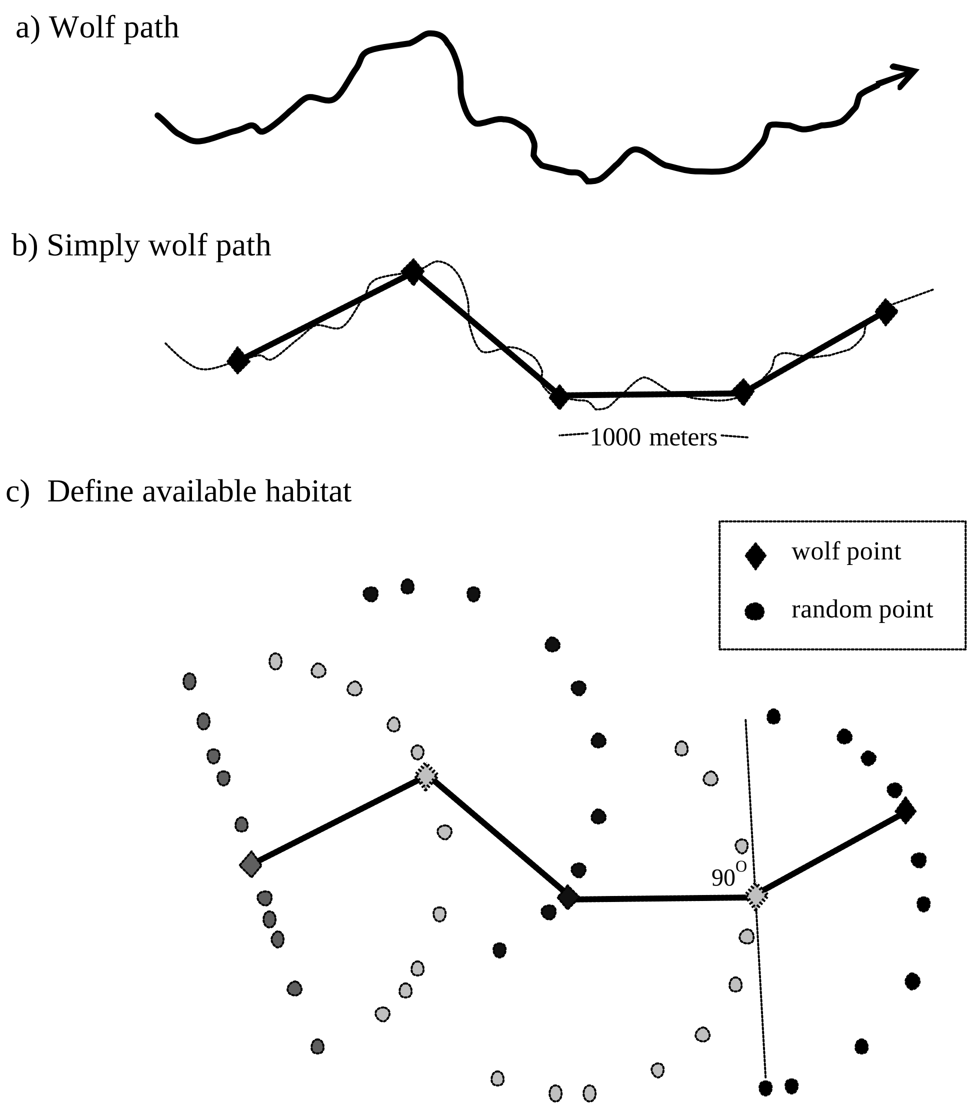

Figure 2-2. For the match case-control logistic regression 10 controls (random points) were paired with each case (wolf point). Wolf paths (a) were first simplified into a series of wolf points separated by 1000 meters (b). To avoid bias potentially associated with the start of each path, I defined the first step as a random point along the first 500 m of the path. To create the controls (c), random turning angles between plus and minus 90^{0} were added to the previous direction of travel.

transformations cost two degrees of freedom in likelihood ratio tests (Hosmer & Lemeshow 2000). After testing for non-linearity, I tested for interactions among likely pairs of variables. Next, I created 24 sets of likely variable combinations, called candidate models, and compared these models to one another using Akaike Information Criterion (AIC). To do this, I first identified the best-predicting model as the one with the lowest AIC (Appendix I: equation 8). Then I ranked the other models by subtracting from their AIC the lowest AIC. I used this difference in AIC (ΔAIC) to calculate the Akaike weights (Appendix I: equation 9) of each model, which reflects the relative strength of each model. I selected all models with ΔAIC less than 2.0 and a cumulative Akaike weight less than 0.90 as strong candidate models. Finally, I used the readjusted Akaike weights from this set of strong models and created a single averaged model with model-averaged coefficients (Appendix I: equation 10) and standard errors (Appendix I: equation 11). These standard errors account for variance both within and among the models. Consequently, these standard error estimates are larger than error estimates for a single model and inflate Type II error when examining the significance of individual predictors. Because the model averaging approach produces coefficients and standard errors from several strong models, averaged models are better predictors than single-best models across both space and time (Burnham & Anderson 1998).

I used the model-averaged β coefficients to evaluate the response of wolves to each covariate (i.e., habitat characteristic). While these β coefficients indicate selection or avoidance of a resource, they do not indicate the relative importance of that resource to wolf movement. Thus, I calculated the relative importance of each variable by comparing the deviance of the averaged model to the deviance of the model without each variable (Appendix I: equation 7).

Model diagnostics. In match case-control logistic regression the response variable equals one (y = 1) for all strata. Therefore, goodness-of-fit statistics for overall model performance are difficult to compute (Zhang 1999). I assumed a conservative estimate of model fit by calculating the Hosmer & Lemeshow goodness-of-fit statistic (Hosmer & Lemeshow 2000; Appendix I: equation 5) for a standard logistic regression model.

An important assumption of both match case-control and standard logistic regression is that the selected points are independent. A lack of independence causes models to underestimate standard errors and thus increases the likelihood of Type I error in significance tests (Hall et al. 1995). To test the assumption independence, I created predictions from a preliminary model and then examined the partial autocorrelation structure of the residuals (Menard 1995). If these residuals were strongly autocorrelated, I used a variance inflation factor to protect against Type I error (Cox & Snell 1989; Burnham & Anderson 1998; Appendix I: equation 6). This variance inflation factor, which is estimated using the goodness-of-fit statistic, inflates variance estimates and adjusts AIC estimates by reducing the deviance estimates. If residuals were not autocorrelated, I did not use variance inflation factors.

RESULTS

Over the course of two winters, we snow tracked the two wolf packs 1,390 km (Figure 2-3). Wolves traveled along roads, trails, and railway lines 16% of the time and traveled through the forests, rivers, and meadows the other 84% of the time. We accumulated 91 tracking sessions for pack 1 and 86 tracking sessions for pack 2. The length of tracking sessions ranged from 0.5 to 30 km with a median length of 5.6 km. Simplifying the wolf paths into a series of points separated by 1,000 m produced 374 wolf points for pack 1 and 359 wolf points for pack 2.

Human-use predictors were measured several ways and the strongest of these predictors were used to create the candidate set of models (Table 2-1). The way in which the strongest predictors were measured reflects the spatial extent that human development influence wolf movement. For instance, I measured trail and road density surrounding each point with radii of 200, 500, 1000, and 1500 m. Models using a radius of 1,000 m explained the most deviance, and therefore the cumulative effects of trails and roads appear to extend well beyond their physical footprint. Similarly, I measured distance to trail, road, and railway with maximum values of 200, 500, 1000 m with no maximum. A maximum of 500 m substantially increased model performance for distance to low-use trails ($\chi^2 = 10$, df = 1, p-value = 0.001 for Pack 2) but maximum values did not increase model performance for other predictors. Thus, Pack 2 showed the strongest selection

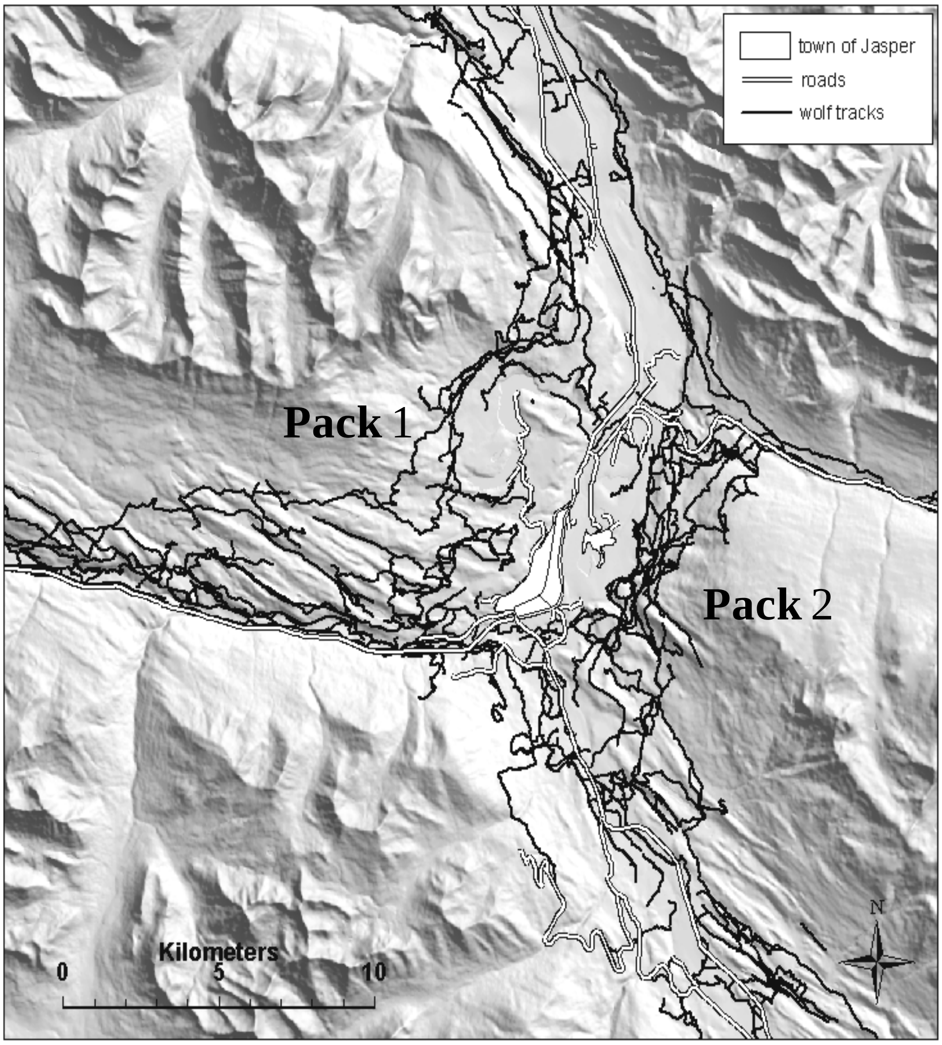

Figure 2-3. Wolf routes around the town of Jasper from two winters of snow tracking (November 1999 - March 2001). Pack 1 occupies the territory west and north of Jasper while Pack 2 occupies the territory south and east of Jasper.

Table 2-2. Match case-control logistic regression: best models ranked by ΔAIC from the best model. Model inclusion was based on ΔAIC < 2.0 and cumulative AIC < 0.9. The number of predictor variables in each model indicated by 'k'; 'x' indicates variables omitted from a model.

ΔAIC	AIC weight	k	elev.	slope	aspect	dist. to railway	dist. to high-use road	dist. to low-use road	dist. to high-use trail	dist. to low-use trail	dist. to accomm-odation	road density	trail density
Pack 1													
0.0	0.25	10						x					
0.29	0.21	9					x	x					
1.47	0.12	10					x						
1.55	0.11	11											
1.59	0.11	9						x			x		
1.61	0.10	10									x		
1.95	0.09	9						x					x
Pack 2													
0.00	0.33	7				x	x		x		x		
0.24	0.29	8				x	x				x		
1.18	0.13	7			x	x	x				x		
2.0	0.12	8				x			x		x		
2.0	0.12	9				x					x		

when within 500 m of a low-use road and little selection beyond. Fractional polynomial tests for non-linearity showed that distance to railway (Pack 1), distance to low-use trail (Pack 2), and distance to low-use road (Pack 2) were best explained by a square-root function (χ^2= 10, df = 1, p-value = 0.01) for railway; (χ^2= 14, df = 1, p-value = 0.001) for roads; (χ^2= 32, df = 1, p-value < 0.001) for trails). These square-root transformations indicated that wolves showed a strong selection near the linear feature but little preference or avoidance elsewhere. I also tested whether wolf selection for proximity to trails and roads was dependent on the density of both trails and roads by the interaction of these two variable types. Because these interactions created unstable models with large standard errors, I subsequently omitted them from the candidate set of models. After selecting the strongest human-use predictors I created the candidate set of models.

Seven of the 24 candidate models were selected as strong models for Pack 1 and five of the 24 candidate models were selected as strong models for Pack 2 (Table 2-2). From these strong models, I created an averaged model for each pack (Table 2-3). As a conservative estimate of overall fit, the Hosmer & Lemeshow (2000) goodness-of-fit statistics for models created using standard logistic regression indicated that the observed and expected frequencies of cases and controls did not differ within each percentile (χ^2= 9.09, df = 8, p-value = 0.33); (χ^2= 7.98, df = 8, p-value = 0.44) for Pack 2) and the models therefore had reasonably strong overall fit. Tests for independence showed that the residuals were weakly correlated at the first lag (partial autocorrelation coefficient = 0.23

Table 2-3. Match case-control logistic regression: averaged model coefficients, standard errors, and Wald statistic.

	Coefficient β^{ave}	Std. Error $se(\beta^{ave})$	Wald* $\beta^{ave} / se(\beta^{ave})$
Pack 1	n = 481 wolf points; 4810 control points		
elevation	-0.0064	0.0010	6.3
slope	-0.0281	0.0065	4.3
cosine(aspect)	0.332	0.076	4.4
dist.railway$^{0.5}$	-1.239	0.452	2.7
dist. high-use road	0.261	0.269	1.0
dist. low-use road	0.062	0.119	0.5
dist. high-use trail	0.322	0.154	2.1
dist. low-use trail	-0.950	0.244	3.9
dist. accomodation	0.247	0.194	1.3
road density	-1.268	0.233	5.4
trail density	-0.238	0.144	1.7
Pack 2	n = 467 wolf points; 4670 control points		
elevation	-0.0058	0.0010	6.0
slope	-0.0321	0.0086	3.7
cosine(aspect)	0.0129	0.0861	1.5
dist. high-use road	0.007	0.045	0.15
dist. low-use road$^{0.5}$	-2.114	0.388	5.5
dist. high-use trail	-0.133	0.174	0.8
dist. low-use trail$^{0.5}$	-2.126	0.272	7.8
road density	-0.547	0.173	3.2
trail density	-0.717	0.102	7.0

* $P[Z_{(2)}>1.64] = 0.10$

for Pack 1 and 0.25 for Pack 2) but showed little correlation thereafter. Because autocorrelation was weak and variance inflation factors were close to one, I did not adjust variance estimates or AIC values in the analysis.

Both wolf packs selected terrain with low elevations, flatter slopes, and southwest aspects (Table 2-3). The two packs were variable in their response to some human developments but similar in their response to others. The two packs differed in that Pack 1 avoided low-use roads and high-use trails whereas Pack 2 selected areas near these features. Furthermore, Pack 1 avoided areas close to accommodations and selected for areas close to railway lines whereas Pack 2 showed neither preference nor avoidance for these features. The two packs were similar in that they both selected areas with low trail or road density, areas far from high-use roads, and areas near low use trails. When examining the univariate response of wolves to trail density, the wolves strongly selected trail densities below 0.75 km/km^2, were variable in their response to trail densities between 0.75 – 2.5 km/km^2, and strongly avoided trail densities above 2.5 km/km^2.

There were several additional differences in the relative importance of each predictor between packs. Among the habitat variables I examined, elevation was the most important predictor for both packs (Figure 2-4), but aspect was a stronger predictor for Pack 1 than Pack 2. On the whole, the human use variables were better predictors for Pack 2 than Pack 1 and among these variables, road

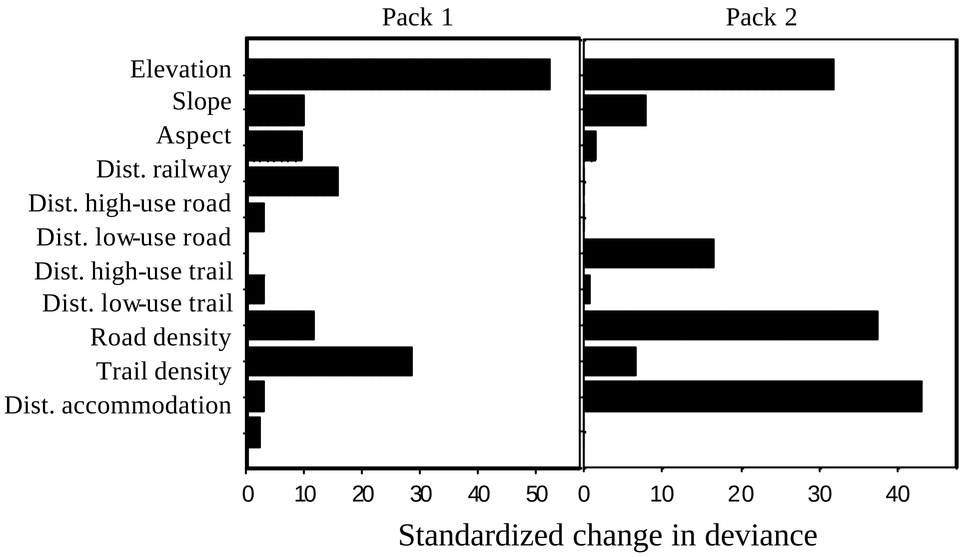

Figure 2-4. Relative importance of each predictor variable in the averaged models. Model performance is measured by the difference in deviance of the averaged model to the model without the predictor. This difference is standardized by the total deviance explained by the averaged model.

variables were stronger predictors than trail variables for Pack 1 but weaker predictors than the trail variables for Pack 2. Some variables resulted in coefficients with large standard errors and were, therefore, relatively weak contributors to prediction. For instance, Pack 1 showed weak avoidance of areas close to high-use trails, low-use roads, and accommodations. Pack 2 showed weak avoidance of high-use roads and a weak preference for high-use trails. All other human-use variables were relatively strong predictors.

The combination of empirical data and resource selection functions they generate can be used to produce a predictive map that highlights areas of conservation concern for land managers. Thus, I applied the results of the averaged models to create a map depicting the relative probability of wolf occurrence throughout the study area (Figure 2-5). Such predictive maps enable managers to identify visually areas of high and low quality wolf habitat, outline pinch points to movement, and generate predictions from potential management actions. This map highlights the habitat degradation from trails, roads, and accommodations both north and southeast of Jasper. The map also helps to emphasize the narrow movement corridors around these areas.

DISCUSSION

Both packs selected terrain with low elevations, flatter slopes, and southwest aspects. Wolves likely selected these terrain features because they contain the shallowest snow depths and highest prey abundance within the study area (Telfer

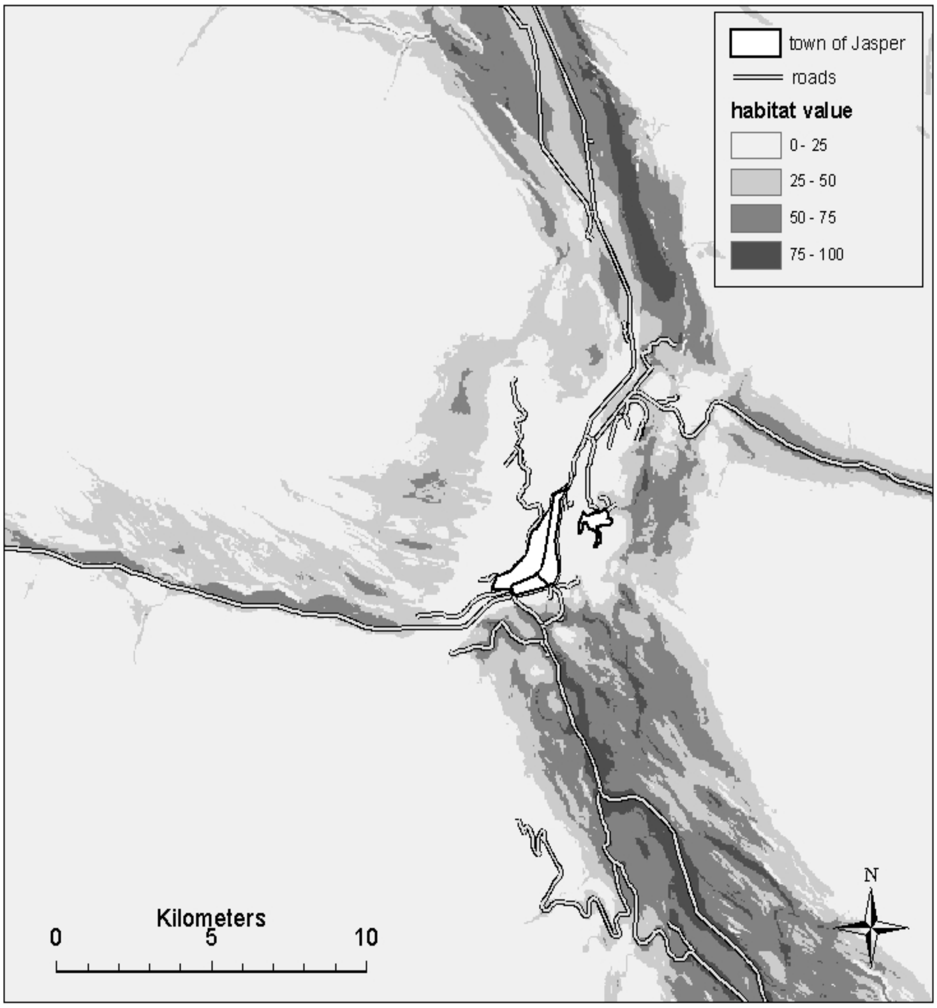

Figure 2-5. Wolf habitat map around Jasper, Alberta. To create this map I generated predictions using a 1:1 match case-control logistic regression equation. I classified each location and associated habitat attributes as the case and defined the control as the median value of wolf locations. Thus, the map shows probability of wolf occurrence relative to the median value of wolf observations, which has a habitat value of 50.

& Kelsall 1984; Huggard 1993). Wolf behaviour toward roads and trails generally depended on the level of human activity associated with those features. Both packs selected for areas near low-use roads and trails but either avoided or showed weak selection for high-use linear features. The square-root transformations of the distance to railway, low-use trail, and low-use road suggests that wolves show little preference for these features until they decide to use them as travel routes. This apparent tendency of wolves to travel along railway lines, roads, and trails was verified frequently by observation during the study and supports results from previous research in Alaska and northern Alberta (Thurber 1994; James & Stuart-Smith 2000). However, in this study wolves avoided areas with high densities of roads and trails, presumably because they are more likely to encounter people in these areas. Again, this supports previous research in which wolves selected territories with low road densities (Thiel 1985; Mech et al. 1988; Mladenoff et al. 1995,1999) and avoided high-use roads within their territory (Thurber 1994). In summary, wolves selected for areas with low elevations, shallow slopes, southwest aspects, and areas with low-levels of human activity, but selected for areas near low-use roads, trails, and railway lines and these results are consistent with both scales of previous study.

Much the variability between wolf packs to human-use predictors likely can be attributed to differences in availability (Manly et al. 1993), correlation among predictors, or variability in wolf behaviour. For instance, the railway line and high-use road, which run through the center of Pack 1's territory, occupy the periphery of Pack 2's territory. Consequently, these were weak predictors for Pack 2 but not Pack 1. Correlation among predictors also explains why some predictors were not important to model performance. For example, while wolves did not travel close to town, distance to town was not an important predictor because it is associated with high trail and road densities that absorbed much of the variation. Variability in wolf behaviour might also explain why Pack 2 showed stronger selection for areas close to roads and trails. Pack 1 traveled along these roads and trails (4 km on roads, 32 km on trails) less frequently than Pack 2 (41 km on roads, 63 km on trails). Importantly, while these packs varied in their selection for roads and trails, both packs clearly avoided areas of high trail and road density.

Pack 1 showed stronger avoidance of roads than trails, perhaps because of the dangers inherent in them. Wolves are subject to direct mortality form collisions with vehicles along high-use roads but not trails. Since 1992 at least 41 wolves have been killed by collisions with vehicles and trains in Jasper (Parks Canada unpublished data). Consequently, wolves generally may have a stronger aversion to roads than trails. Furthermore, most roads receive higher traffic volumes than trails. Therefore, wolves are more likely to encounter people on roads than trails. Surprisingly, Pack 2 showed similar aversion to high trail and road densities, and trails were generally more important to model performance than roads. This may have occurred because the secondary roads that run through the study area receive relatively little traffic, particularly at night.

No other wolf studies have specifically addressed the response of wolves to trails and so interpreting the strong avoidance of high-density trails by wolves in this study covers novel ground. However, James & Stuart-Smith (2000) found that wolves select areas close to seismic lines, which are structurally similar to trails. The further suggestion that too much human activity lessens trail appeal is indirectly supported by other studies which show that trails generally can degrade wildlife habitat (e.g. Papouchis et al. 2001). Moreover, Miller et al. (2001) found that mule deer and three species of songbirds flushed at greater distances from hikers who traveled off-trail versus on-trail. These related studies suggest that wildlife generally show the strongest flight response from off-trail activities, perhaps due to the unpredictability of human encounters there.

Off-trail use is increasing rapidly around Jasper and has resulted in the creation of many new trails, often near areas of high trail density, towns, and resorts. Many of these trails permeate narrow wildlife corridors and if human-use on these trails continues to increase within the corridors it may block wolf movement among valleys. Other animals that avoid areas of high road density, such as such as grizzly bears (*Ursus arctos horribilis*; Mace et al. 1996) and cougar (*Felis concolor*; Beier 1993), would also likely avoid areas of high trail density. Because this trail-use is increasing across the continent and is likely to obstruct the movement of several shy species, it is in urgent need of further investigation.

My main results, which indicate that wolves select areas close to roads and trails but avoid areas of high road and trail density, may be weakly confounded by two sources. First, wolf avoidance of trails and roads could be caused by their attraction to their prey, which have been shown to avoid roads (James & Stuart-Smith 2000; Johnson et al. 2000; Rowland et al. 2000; Dyer et al. 2001; Papouchis et al. 2001). In Jasper, however, many ungulates concentrate their movements along roads and even within the town limits making this confounding effect unlikely. The second, more likely, confounding factor is that roads, trails, and prime wolf habitat occur in similar areas. More specifically, roads and trails are typically built at low elevations often along waterways, on dry southwest aspects, or relatively flat land. These are the same areas preferred by both wolves and their prey, and this similarity may partially explain why wolves select areas close to trails and roads. Moreover, this association between roads, trails, and topography suggest that my estimates of road and trail avoidance are conservative.

There are two additional reasons that my estimates of trail and road avoidance are likely conservative but these effects will require further study. First, this study occurred during winter when trails and roads receive less than a quarter of their summer traffic. Wolves may show much greater avoidance during summer when human contact is so much more likely. Furthermore, in summer snow does not constrain the movements of wolves to valley bottoms and thus near roads and trails. Consequently, wolves would be free to show a stronger aversion to trail and road density. Second, this study did not examine the temporal effects of human activity on wolf movement behaviour. For instance, while wolves in this study sometimes preferred areas close to roads and trails, they may only travel in these areas at night when levels of human use are low. Night use is typical of wolves that occupy territories with high levels of human activity in Italy, presumably as a means of avoiding encounters with humans (Ciuci et al. 1997). Because trails and roads degrade wolf habitat beyond their physical footprint (Forman 2000), they have very important implications for wolf conservation along the confined valleys of mountainous regions.

Conservation implications. The wolves in this study avoided areas of high trail and road density that typically occur at low elevations in the mountains. Wolves are, in this way, excluded from some of the most productive habitat. This result could affect the fitness of wolves in two ways. First, wolves may then have less success hunting because they are forced to travel in areas of lower prey abundance, which in turn may affect wolf reproductive potential (Boertje & Stephenson 1992) and wolf density (Fuller 1989). Second, trails, roads, and other developments may also cause complete habitat loss through habitat degradation or isolation. Trails, roads, and resorts already degrade large tracts of habitat north and south of town. If trails continue to expand to the base of steep-sided mountains and within narrow movement corridors, then wolves may no longer be able to travel between valleys and will therefore be unable to access large tracts of habitat and its prey resources. The effects of habitat loss, degradation, and fragmentation associated with trails and roads are not limited to wolves and would undoubtedly affect complex ecological interactions among trophic levels (e.g. Boyce 1998).

This is the first study to show that wolves avoid areas of high trail density as well as areas of high road density within their territories. Recreational use within many mountain communities is expected to continue to increase and this use, even within protected areas, can cause habitat degradation and habitat fragmentation. Maintaining the conditions necessary for movement among valleys by wolves and other wary species will require careful management of road density, trail density, and levels of human use around mountain communities.

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Appendix I. Computational equations used for (A) standard logistic regression, (B) match case-control logistic regression, (C) evaluation of model performance, and (D) model creation with Akieke Information Criterion (AIC).

(A) Standard logistic regression

n = number of cases + number of controls
Probability that subject with data x is the case.

$\pi(x) = \exp(b'x) / (1 + \exp(b'x))$
(equation 1)

$b'x = b_0 + b_1 x_1 + b_2 x_2 + \ldots + b_i x_i$
i = number of predictors
b_i = coefficient for predictor i
x_i data for predictor i from subject n
y_i = value of response for subject n (y_i = 0 or 1)

Log-likelihood = $\Sigma_{i=1 \text{ to } n} \{y_i \ln[\pi(x_i)] + (1 - y_i)\ln[1 - \pi(x_i)]\}$ (equation 2)

Deviance D

$D = -2$ (log-likelihood)

Deviance for null model D_{Null}

$D_{Null} = -2\, n \ln[0.5]$

(B) 1-*M* matched case-control logistic regression

M = number of controls
k = number of cases
Partial likelihood $\pi(x_{k1})$ for case k is interpreted as the probability that subject with data x_{k1} is the case relative to M controls with data x_{k2}, x_{k3}, ..., x_{kM}.

$\pi(x_{k1}) = \exp(b'x_{k1}) / (\exp(b'x_{k1}) + \exp(b'x_{k2}) + \ldots + \exp(b'x_{kM}))$
(equation 3)

Partial log-likelihood = $\Sigma_{i=1 \text{ to } k} \ln[\pi(x_i)]$ (equation 4)
(likelihood for cases only)

Deviance D

$D = -2$(partial log-likelihood)

Deviance for null model D_{Null}

$D_{Null} = -2\, k \ln[1 / (1 + \text{number of controls})]$

(C) Model performance

Hosmer and Lemeshow goodness-of-fit statistic (standard logistic regression)

$C' = \Sigma_{k=1 \text{ to } g} \{(\Sigma_{j=1 \text{ to } n'} y_j) - n' \pi_{ave}\}^2 / \{n'\pi_{ave}(1 - \pi_{ave})\}$ (equation 5)

g = number of quantiles for estimated probabilities
n' = number of observation in category g
π_{ave} = average of probabilities in category g
χ^2 distribution with $g - 2$ degrees of freedom
high p value indicates strong overall fit

Variance inflation factor = C’ / *df* (equation 6)

Standardized change in deviance (relative importance of predictor *i* to model performance)

Standardized deviance = 100 * (D_i – D) / (D_{Null} – D) (equation 7)

D_i = deviance of model without predictor *i*

(D) AIC and model averaging (Burnham & Anderson 1998)

AIC = -2 (Log-likelihood) + 2K + 2K(K + 1) / (n – K – 1) (equation 8)

K = 2 + number of predictor variables

n = sample size (for matched case-control logistic regression this is number of cases k)

AIC_{min} = model with lowest AIC

$\Delta AIC_r = AIC_r - AIC_{min}$

R = number of models

r = model r

Akieke weight ω_i

$\omega_r = \exp(-0.5\Delta AIC_r) / (\Sigma_{r=1 \text{ to } R} \exp(-0.5\Delta AIC_r))$ (equation 9)

model averaged coefficient b_i^{ave}

$b_r^{ave} = \Sigma_{r=1 \text{ to } R}\ \omega_r\ b_r$ (equation 10)

model averaged standard errors se(b_i^{ave})

$se(b_r^{ave}) = (\Sigma_{r=1 \text{ to } R}\ \omega_i\ [var(b_r) + (b_r - b_r^{ave})^2]^{0.5})^{0.5}$ (equation 11)

Chapter 3

Path tortuosity and the permeability of linear features to wolf movement.

INTRODUCTION

Human developments are an immense problem the world over because they degrade habitat quality for many species. Of the many types of human developments, roads are one of the most well-studied and problematic sources of habitat degradation and habitat fragmentation (Forman 2000; Trombulak & Frissell 2000). While roads are known to degrade habitat quality for many organisms (Mace et al. 1996; Mladenoff et al. 1999; Rowland et al. 2000; Dyer et al. 2001), few studies have quantified the effects of roads and other human developments on fine-scale movement behaviour (e.g. Bélisle & St. Clair 2001; Rondinini & Doncaster 2002). Studies of movement behaviour may identify sources of disturbance not identifiable with traditional habitat-use studies (Caro 1998). Moreover, animal movement through poor quality habitats or places where human activity is concentrated may determine whether habitat fragmentation constrains important movement, like dispersal, between habitat patches (With & Crist 1995; Keitt et al. 1997; Schultz 1998; Turchin 1998; Brooker et al. 1999; With & King 1999; Roland et al. 2000).

Studies linking fine-scale movement behaviour to habitat quality have generally measured movement behaviour either in terms of path complexity (tortuosity) or willingness to cross inhospitable habitats. Several factors appear to influence path tortuosity including foraging behaviour, habitat quality, habitat complexity, and stage of life history. Weins et al. (1995) found that the distribution of food resources affects the optimal foraging strategy and, therefore, the tortuosity of insect paths. To maximize foraging efficiency, species with a clumped distribution of resources, such as harvester ants (*Pogonomyrmex occidentalis*), travel in more tortuous paths than those species with an even distribution of resources, such as beetles (*Eleodes* spp.) and grasshoppers (Orthoptera:Acrididae). Similarly, Spanish goats (*Carpa hircus*) had more tortuous paths than white-tailed deer (*Odocoileus virginianus*), likely because of differences in foraging strategies and social behaviour (Etzenhouser et al. 1998). In addition, path tortuosity depends on habitat quality. Beetles, grasshoppers, ants, butterflies, mice, and ruminants minimize their time in poor quality habitat by increasing the directionality of movement and/or speed of travel (Crist et al. 1992; Miyatake et al. 1995; Stapp & Van Horne 1997; Etzenhouser et al. 1998; Odendaal et al. 1998; Schultz 1998; Kindvall 1999; Schultz & Crone 2001). In addition to the effects of foraging strategy and habitat quality, path tortuosity also depends on the stage of life history. The tortuosity of wolf paths in Spain increased during the denning season and decreased for dispersing wolves (Bascompte & Vilá 1997). Similarly, the tortuosity of caribou paths decreased during seasonal migrations (Bergman et al. 2000). None of these studies have directly assessed the influence of human developments on path tortuosity. However, wolves in Poland traveled faster, and likely with more directional persistence, on trails, roads, and frozen rivers than through the forest (Musiani et al. 1998).

Studies of bird and mammal movement have addressed the permeability of forest gaps and roads to movement. Bird studies in the form of mark-recapture, playback, and relocation experiments, suggest that forest gaps in the form of roads, agricultural fields, and forestry cutblocks impede the movement of some forest dependent species (Desroches & Hannon 1997; St. Clair et al. 1998; Brooker et al. 1999; Bélisle & St. Clair 2001). Moreover, the structure of gaps in landscapes may be more important than patch structure to animal dispersal (With & King 1999). Other studies examining barrier effects have compared the frequency with which animals cross roads to a null model of road crossings. In these studies, black bears (*Ursus americanus*), caribou (*Rangifer tarandus caribou*), and hedgehogs (*Erinaceus europaeus*) crossed high-use roads less often than expected, while low-use roads and seismic lines did not seem to affect their movement patterns (Serrouya 1999; Dyer 1999; Rondinini & Doncaster 2002). Together, these studies indicate that although roads occupy a small area, they may have a large effect on animal movement.

The effects of human development on animal movement are particularly problematic in mountainous areas. Here, rugged topography and deep snows confine the movement of animals to the valley bottoms where people also concentrate their activity (Noss et al. 1996). Therefore, there is high potential for human activity to obstruct animal movement across or between valleys (Clevenger & Waltho 2000; Bélisle & St. Clair 2001). Wolves are a wary species that may be susceptible to these habitat fragmentation effects (Weaver et al. 1996; Mladenoff et al. 1999). They often travel over thirty kilometers in a day within territories than encompass several valleys and approximately 1,000 km^2. Consequently, wolf movement through areas with human activity is necessary for their local persistence.

In this study, I address the effects of human development on the fine-scale movement of wolves around the mountainous town of Jasper, Alberta. I examine the effects of human development on wolf movement behaviour in two ways. I first determine whether wolves, other species in poor quality habitat, travel with more directional persistence in areas with high levels of human activity. At the same time I account for other factors, such as terrain ruggedness and proximity to predation sites, that may also influence directional persistence. I then test whether linear features such as high and low-use roads, trails, and a railway line present barriers to wolf movement. For this analysis I compare the frequency with which actual wolf and simulated random paths cross these features.

METHODS

Study area. This study focused on the movements of two wolf packs throughout two winters (1999-2000, 2000-2001; Figure 3-1). The territories of the packs extended between 20 and 50 km along four valleys that converge upon the town of Jasper in Jasper National Park, Canada. The study area included a portion of these two territories, approximately 25 km each side of Jasper. The outer limits of the study area coincided with park boundaries, prominent geographic features, and wolf territorial boundaries. While the study area encompassed 2900 km^2, only 572 km^2 lay below 1600 m (valley bottom is 1020 m) and 99 percent of wolf movements also lay below 1600 m (Whittington pers. data). The number of wolves in Pack 1 (west and northeast of Jasper) ranged from 7 to 10 individuals whereas the number of wolves in Pack 2 (south and southeast of Jasper) ranged from 2 to 3 individuals.

Wolves in Jasper National Park prey mainly on elk (*Cervus elephus*), deer (*Odocoileus* spp.), and moose (*Alces alces*), but occasionally kill big-horned sheep (*Ovis canadensis*), caribou (*Rangifer tarandus*), and mountain goat (*Oreamnos americanus*). The valley bottoms, where wolves and their prey occur, are dominated by open lodgepole pine (*Pinus contorta*) forests interspersed with douglas fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), poplar (*Populus balsamifera*), white spruce (*Picea glauca*), and small meadow complexes. The sides of the valleys are dominated by englemann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Snow depths along the valley bottoms are generally shallow and range from 5 to 40 cm.

The study area includes 292 km of roads, 759 km of trails, and a railway line. A major transportation highway with substantial freight truck traffic runs through the study area following the valleys northeast and west of the townsite. This highway is neither divided nor fenced and received 1,288,788 vehicles in 2000, a 22 % increase from 1990 (Parks Canada Highway Services, unpublished data). There is marked seasonal variation in traffic volume; vehicle traffic quadrupled from 56,174 vehicles in February to 216,404 vehicles in August 2000. Several secondary highways also extend throughout Jasper National Park. Trail networks are concentrated within 10 km of the Jasper townsite but are rapidly expanding as people, particularly mountain bikers, create their own trails throughout lower elevations in the study area.

Roads and trails were divided into two categories: high or low-use. High-use roads received more than 10,000 vehicles per month in February. Low-use roads received less than 10,000 vehicles per month and had marked diurnal variation in traffic volume. High-use trails received foot traffic on a daily basis whereas low-use trails received infrequent or no foot traffic. The railway line received approximately 30 freight and passenger trains each day.

Field Methods. To record movement of these two wolf packs, my assistants and I followed their tracks in the snow and simultaneously recorded these positions with hand held global positioning systems (GPS; Trimble GeoExplorer3®). We initially located wolf tracks by conducting cross-valley transects and road surveys. Once we found wolf tracks, we followed the tracks during the daylight hours, often returning to the same tracks on several successive days until snow-conditions deteriorated. Fresh wolf tracks were backtracked so as not to interfere with natural movement patterns. The tracking sessions were exported into ArcInfo® (ESRI 2000) for data preparation and then transferred to S-Plus® for statistical analysis (Venebles & Ripley 1999). I excluded tracks of single wolves from the analysis because they may respond differently to roads and trails than packs of wolves. I analyzed each pack separately and then pooled the data if the results were similar between packs.

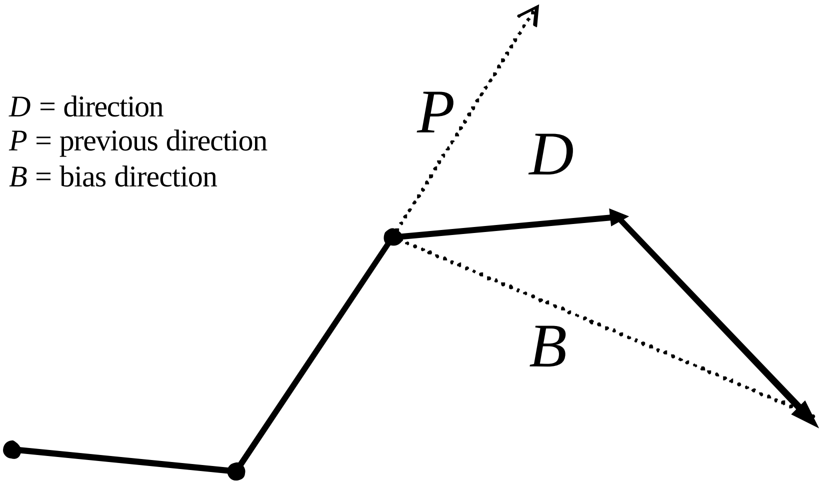
Statistical Analysis.

Path tortuosity. Path tortuosity is quantified as the ratio between path length and the net displacement (Turchin 1998). This ratio may be scale-dependent, so I measured tortuosity for path segments of three lengths: 0.5, 1.0, and 5.0 km. I then used multiple linear regression to determine the effects of topography and human development on tortuosity. Each path segment had a single measure of tortuosity, yet passed through many habitat types. For the analysis, I used the median or variance of these habitat types measured at 100 m intervals. Predictor variables for the analysis were variation in aspect and elevation, and the medians for distance to predation site, trail and road density (measured with radii 1.0 km), distance to high and low-use roads and trails, distance to railway line, and distance to accommodation. Variables were tested for non-linearity. At each scale of analysis, I identified the best linear regression model using forward stepwise regression. To compare the relative importance of predictor variables, the β coefficients and standard errors were re-scaled so that all standard errors equaled one (Menard 1995).

Path segments were randomly selected from within the wolf paths. For wolf paths much longer than the path length of interest, I selected several non-overlapping path segments. I minimized autocorrelation between successive path segments of length L by first partitioning the wolf path into lengths of $2L$ and then randomly selecting one segment from within each partition. Partial autocorrelation coefficients in the linear models were low for the first lag (0.04, 0.06, and 0.19 for path segments of 0.5, 1, and 5 km respectively) and therefore satisfied the assumption of independence.

Barriers to movement. I tested whether wolves circumvent and avoid crossing linear features by comparing the frequency with which wolves and a null model of random paths crossed linear features (high and low-use roads and trails, and a railway line). For a valid comparison between wolf and random paths, the shape of the paths should be similar except for their responses to linear features. Other studies using this approach (e.g. Serrouya 1999; Dyer et al. 2001; Rondinini & Doncaster 2002) failed to test for similarity in shape of the random and actual paths. Accordingly, I created random paths based on the best of a series of random walk models. Below, I define four random walk models, then describe how I: (a) compared the models; (b) tested the validity of the best model to wolf paths; (c) paired random paths to wolf paths; and (d) compared the frequency with which wolf and random paths crossed linear features.

When testing and creating a random walk model, the paths of an organism are first simplified into a series of points (Turchin 1998). Straight lines between successive points are called steps, and each step consists of a length and direction. The difference in direction of two steps creates a turn angle. The shape of a path depends on the magnitude and autocorrelation of these turn angles. Random walk models quantify the influence of directional persistence and external (directional) bias on step direction. Four common types of random walk models include uncorrelated, correlated, biased, and correlated+biased random walks (Turchin 1998, Schultz & Crone 2001). The simplest of these is the uncorrelated random walk in which the predicted direction of each step is a random direction between 0 and 360 degrees. This model creates highly tortuous and circular paths and was not included in this analysis. I tested the fit of the following three models (Figure 3-1). Correlated random walks models predict that the direction of present step will equal that of the previous step and therefore show strong directional persistence. These models are common in the literature (e.g. Kareiva & Shigesada 1983) and are theoretically linked to models of population dispersal (Turchin 1998). Biased random walks model the influence of external factors on movement direction. In one type of biased random walk, organisms move toward a particular destination such as a nest, hive, den, or high quality habitat. For this model, the predicted direction of travel is the direction toward the bias point (e.g.



(1) Correlated random walk	$\boldsymbol{D = P + error}$
(2) Biased random walk	$\boldsymbol{D = B + error}$
(3) Correlated + biased random walk	$\boldsymbol{D = (1-b)\,P + (1-b)\,B + error}$ $(0 < b < 1)$

Figure 3-1. Three types of random walk models based on directional persistence and directional bias.

Schultz & Crone 2001). Finally, the correlated+biased random walk models the influence of both directional persistence and directional bias on an organism's movement (Schultz & Crone 2001). This model predicts a weighted average of previous and bias directions. Optimal weights for these two factors are solved with the constraint that they sum to one. For this analysis, I simplified wolf paths into a series of points separated by 250 m and defined bias directions as the end point of each path. I chose step lengths of 250 m to balance the strong negative autocorrelation inherent with shorter step lengths against the loss of resolution and ability to detect the crossing of linear features with larger steps.

To compare the relative fit of the three models to wolf paths, I calculated the difference between the observed and predicted directions of travel (residuals) for each wolf step, and summed these differences for all steps (residual sum of squares). Because directions are circular in nature (e.g. 400 degrees equals 40 degrees), I programmed the computer to adjust the residuals such that they lay between +/- 180 degrees (Jammalamadaka & SenGupta 2001). I identified the best of the three models using log-likelihood and Akaike Information Criterion (AIC), where

$$\text{log-likelihood} = -0.5n\log(\text{RSS}/n)$$

$$\text{AIC} = -2(\text{log-likelihood}) + 2K$$

and n is the number of observations, RSS is the residual sum of squares, and K is the number of parameter estimates (Burnham & Anderson 1998). Finally, I compared directly the net-displacement of wolf paths to random paths generated from the best model for path lengths of 5, 10, and 15 km. To create random paths, I successively added steps to the previous steps according to the equations defining each model. The direction of each step was determined by calculating the predicted direction of travel and adding a randomly selected residual (error).

Using the best random walk model, I created one hundred random paths for each wolf path to define the expected number of times wolves would cross linear features given random movement. The random paths were paired with wolf paths based on path length, start location, and end location. The length of each random path was identical to its paired wolf path. Start and end locations of the wolf and random paths were similar but not identical to avoid Type II error. The distribution of wolf paths was likely biased away from areas the wolves avoided such as areas with high trail and road density (Chapter 2). I avoided this bias by creating a random start location within one kilometer of the wolf start location. I then created an end location (bias direction) within 45 degrees of the actual wolf bias direction. This angle represents the 75% confidence limits on the differences between the individual and average directions of wolf steps. As a final step in creating realistic random paths, I prohibited the paths from entering the town limits where wolves never travel. Similarly, the start and end locations of each random path favored habitats where wolves most commonly travel. When creating either a start or end location, I first generated two locations, determined the habitat value of each, and then used the location with the better habitat value for the random path. Habitat values were based on a resource selection function comprised of elevation, slope, and aspect (Chapter 2). Random paths were created with Arc Macro Language (AML) in ArcInfo®. Once I generated one hundred random paths for each wolf path, I overlaid five types of linear features (high and low-use roads and trails, and railway line) and counted the number of times each path crossed these features.

I determined whether wolves avoid crossing linear features by comparing the frequency with which wolf and random paths crossed each feature type. The number of crossings per path fit neither a gaussian nor poisson distribution because a high proportion of the paths did not cross linear features. Therefore, I changed the number of crossings to a binomial variable of either crossed or not crossed. I first tested whether wolves generally avoided crossing linear features by calculating the proportion of wolf and random paths that crossed each feature type and then running a t-test (paired by feature type) on the differences between the wolf and random proportions. Next, I tested whether the likelihood of wolf crossing depended on feature type. For this test, I used logistic regression to maintain the pairing between the wolf and random paths. Here, the dependent variable was the wolf path (crossed = 1, not crossed = 0) and the independent variables were availability of linear features (proportion of random paths that crossed) and feature type. If feature type and its interaction with availability failed to improve model performance, I concluded that wolves were equally likely to cross all feature types. Conversely, if feature type or its interaction with availability improved model performance, the likelihood of wolves crossing a linear feature depended on the type of linear feature. In this case, I compared linear features by examining the β coefficients and 95% confidence limits of the dummy variables. Based on the habitat selection responses of wolves to the linear features in Chapter 2, I predicted that wolves would cross high-use roads and trails (features that wolves avoided) less than expected, but would cross low-use roads and trails and the railway line (features selected) more often than expected.

RESULTS

Over the course of two winters, we snow tracked the two wolf packs 1,390 km (Figure 3-2). The wolves traveled along roads, trails, and railway lines 16% of the time and traveled through the forests, rivers, and meadows the other 84% of the time. We accumulated 91 tracking sessions for pack 1 and 86 tracking sessions for pack 2. The length of tracking sessions ranged from 0.5 to 30 km with a median length of 5.6 km.

Path tortuosity. Models of path tortuosity were similar for both packs. Therefore, I pooled their data for analyses. At all three scales of analysis (path segments of 0.5, 1, and 5 km), the tortuosity of wolf paths increased near predation sites, in rugged topography (high variation in elevation or aspect), and near high levels of human activity (Figure 3-3). Distance to predation site, variation in elevation, and

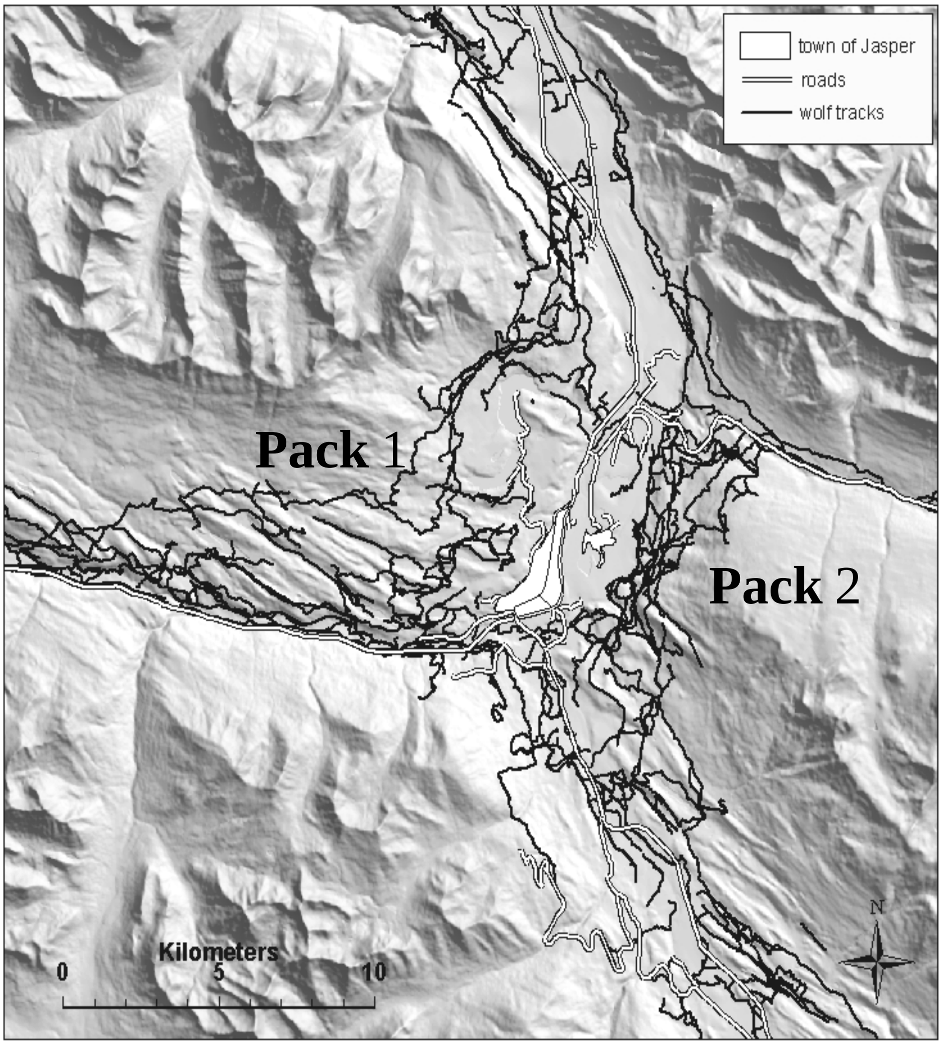


Figure 3-2. Wolf routes around the town of Jasper from two winters of snow tracking (November 1999 - March 2001).

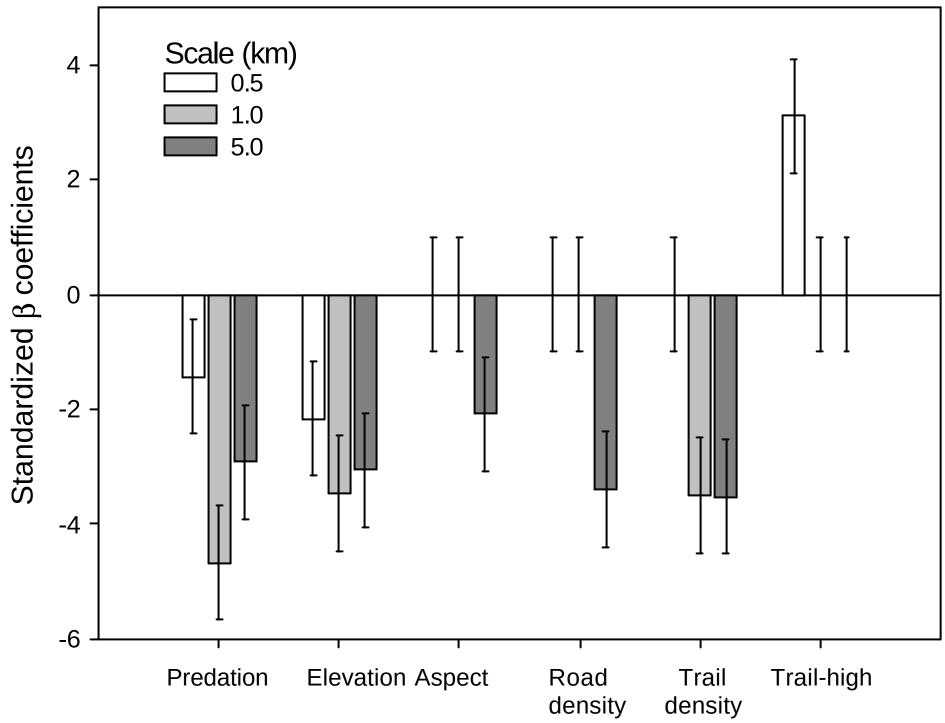


Figure 3-3. Standardized b coefficients ± one standard error for linear regression models predicting path tortuosity. Independent variables are inverse distance to predation site (predation), variation in elevation (elevation), variation in cosine of aspect (aspect), road density, trail density, and distance to high-use trail (trail-high). Models were created for path segments of 0.5, 1, and 5 km.

distance to high-use trail or trail density were strong covariates in all three scales of analysis. The main difference among them was that tortuosity increased in areas with high variation in aspect and high road density for 5 km paths, but not for 0.5 or 1 km paths. Surprisingly, distances to low-use roads and trails, on which wolves traveled almost 16% of the time and which showed a trend for attraction in the previous analysis, were not important predictors of tortuosity.

Model performance varied greatly among the three scales of analysis. Performance increased substantially with path length (r^2 = 0.03, 0.14, 0.51 and n = 667, 321, 54 for paths of 0.5, 1, and 5 km respectively). While the predictability of the finer scale models was poor, all models explained much more of the variation than a model with no covariates (ANOVA: 0.5 km paths, $F_{3,663}$ = 6.1, p < 0.01; 1 km paths, $F_{3,317}$ = 16.7, p < 0.01; 5 km paths, $F_{5,48}$ = 9.8, p < 0.01). The significance of these models and the consistency of predictor variables among scales lend strength to the results of this analysis.

Barriers to movement. The random walk model containing a weighted average of directional persistence and directional bias most closely resembled wolf paths (Table 3-1). This resemblance, however, was not consistent for wolf paths of different lengths. Random paths generated from this model were slightly more tortuous than wolf paths at 5, but not at 10 or 15 km. Net-displacements of random paths were an average of 0.4 km shorter than wolf paths at 5 km (two sample t-test, t-value = 4.0, df = 1801, p < 0.001) but had similar net-

Table 3-1. Performance of three random walk models as measured by Akaike Information Criterion (AIC). AIC values were calculated using the residual sum of squares (RSS) and the number of parameter estimates (K).

Model	RSS	K	ΔAIC
0.3 * Directional bias + 0.7Directional persistence	1062	3	0
Directional persistence (correlated random walk)	1304	1	563
Directional bias (biased random walk)	1662	1	1233

displacements at 10 (t-value = 0.19, df = 716, $p = 0.85$) and 15 km (t-value = 0.40, df = 433, $p = 0.65$).

Wolf paths crossed linear features less often than random paths (Figure 3-4; t-test paired by feature type: t-value = 7.25, df = 4, $p = 0.002$). Overall, 24.3% of wolf paths and 34.0% of random paths crossed linear features. The likelihood of wolves crossing a feature depended on availability and feature type (likelihood ratio tests: availability, $\chi^2 = 384$, df = 1, $p < 0.001$; feature type, $\chi^2 = 19.9$, df = 4, $p < 0.001$). Availability was measured as the proportion of the 100 random paths that crossed each feature type. The interaction between availability and feature type failed to improve model performance ($\chi^2 = 3.13$, df = 4, $p = 0.54$) and was therefore excluded from further analysis. Availability was the strongest predictor of wolf crossings and as availability increased, wolves were more likely to cross linear features (β coefficient = 5.3, s.e. = 0.4). Both wolf packs were consistent in their response to high-use roads, high-use trails, and low-use trails but differed in their response to railway lines and low-use roads (Figure 3-5). Compared to Pack 2, Pack 1 was on average 6.3 times more likely to cross the railway line and 3.5 times less likely to cross low-use roads. When data for these packs was pooled, the wolves were 2.2 (95% C.L. = 1.2, 4.4) times more likely to cross low-use roads than high-use roads and 3.7 (95% C.L. 1.9, 7.2) times more likely to cross low-use trails than high-use roads. There was no difference in their response to high-use roads, high-use trails, and railway lines. Nor was there a difference among high-use trails, railway lines, low-use roads, and low-use trails.

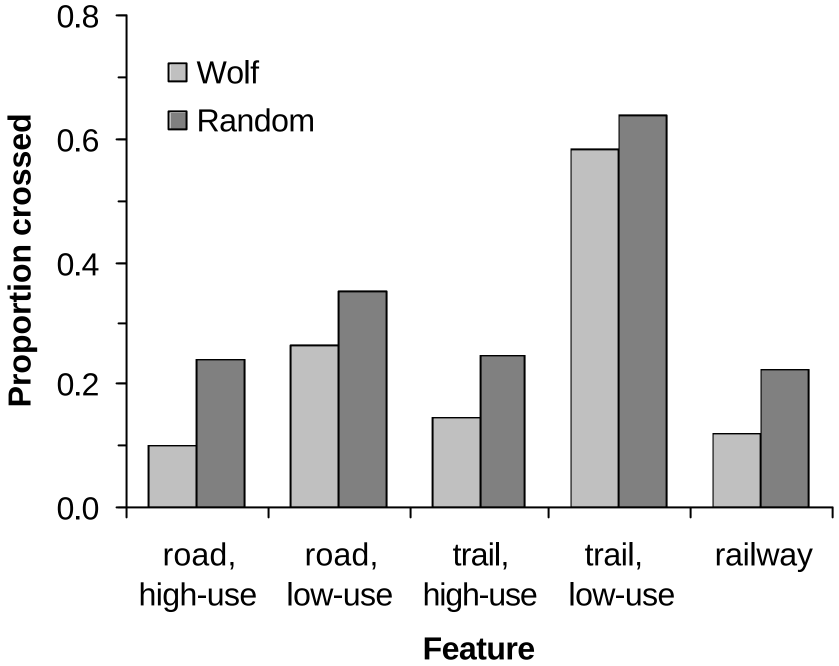


Figure 3-4. Proportion of wolf and random paths that crossed linear features.

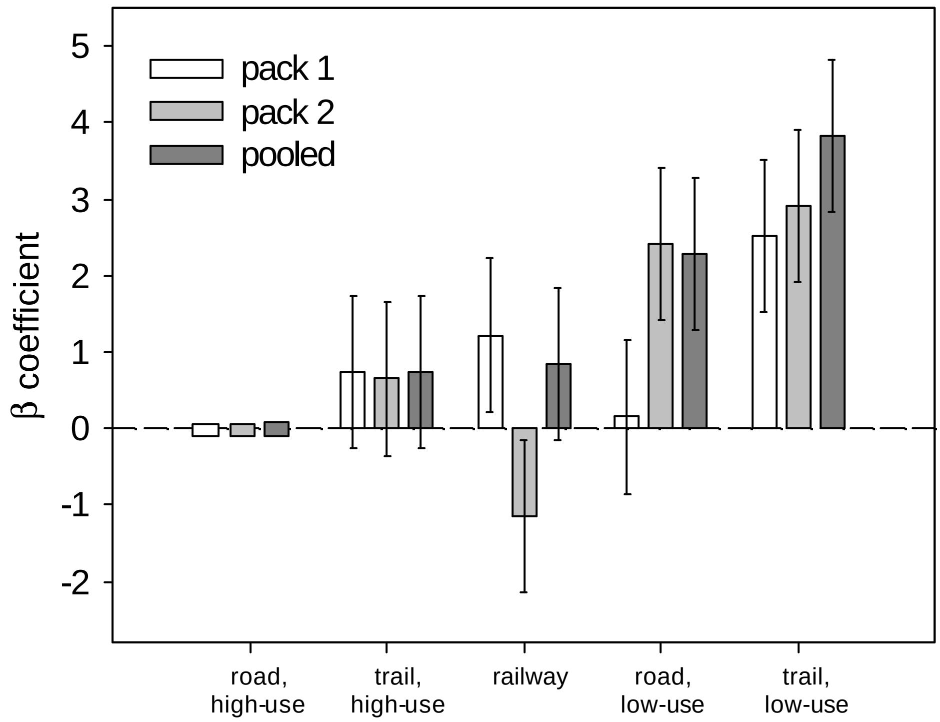


Figure 3-5. Standardized b coefficients $\pm$ one standard error of dummy variables within feature type. High-use roads were the reference category. Logistic regression models were created for each pack and packs pooled together.

The final pooled model (wolf cross ~ availability + feature type) had a close fit to the observed data (Hosmer and Lemeshow (2000) goodness-of-fit statistic: χ^2 = 5.5, df = 8, p = 0.70).

DISCUSSION

The tortuosity of wolf paths increased near predation sites and high-use trails as well as in areas containing rugged topography, high trail density, and high road density. These results both support and partially contradict the results of other studies where path tortuosity increased in high quality habitats (Crist et al. 1992; Miyatake et al. 1995; Odendaal et al. 1998; Schultz 1998; Kindvall 1999; Schultz & Crone 2001). Like these studies, the tortuosity of wolf paths increased near predation sites, which are associated with high quality wolf habitat. Unlike the other studies, the tortuosity of wolf paths also increased in areas with high trail and road density, which degrade habitat quality (Chapter 2). There are two possible explanations for this discrepancy. The first concerns the prey base because many elk in the study area congregate near human developments. If wolves were hunting elk in these areas, their path tortuosity may reflect wolf movement in high quality habitat. However, given the lack of correlation between distance to predation site and trail or road density (correlation coefficients < 0.01), this explanation is unlikely. Given wolf avoidance of areas near high-use trails and areas of high trail and road density, a more likely explanation is that wolves traveled in more circuitous paths within these areas to avoid contact with people. This explanation suggests that vegetation and topographic cover may facilitate animal movement through areas of high trail and road density.

Surprisingly, linear features that wolves used as travel routes, such as low-use roads, low-use trails, and the railway line, did not affect path tortuosity. Wolves travel faster on these features than through forest (Musiani et al. 1998), yet path tortuosity did not decrease as expected. This suggests that the wolves traveled short distances along these features, or that wolves travel with similar tortuosity through forests and on these features once variation in elevation or aspect are considered.

The performance of models predicting path tortuosity improved greatly from the smallest to largest scale of analysis (path segments of 0.5, 1, and 5 km). The finest-scale model explained very little of the variation in tortuosity. Therefore, while the path tortuosity increased near predation sites, high-use trails, and in rugged topography, other factors strongly influenced fine-scale movement of wolves. The largest-scale model explained much more variation in tortuosity. Consequently, the covariates had a much more predictable effect on tortuosity. Surprisingly, the largest-scale model included more covariates than the finer-scale models, even though significant variables are more difficult to obtain with small sample sizes.

In the barrier crossing analysis, none of the linear features were absolute barriers to wolf movement, yet wolves crossed all features less often than expected. This result was surprising given that the wolves previously selected for low-use trails, low-use roads, and railway lines (Chapter 2). While wolves may have avoided crossing these low-use features, it is more likely that other factors contributed to this result. First, linear developments usually parallel valley bottoms. When wolves travel long distances they may be more likely to travel parallel to rather than across valleys, and therefore are likely to move parallel to linear features. Second, there may be a cumulative effect of human development on the frequency of wolf crossings. Wolves may have avoided crossing low-use features that were embedded in areas of high trail or road density, which wolves avoid. Interestingly, the two wolf packs differed in their response to railway lines and low-use roads. These differences might be attributed to differing levels of availability. The railway line runs through the center of Pack 1's territory but is on the periphery of Pack 2's territory. Similarly, there are far fewer low-use roads in the territory of Pack 1 compared to that of Pack 2. As expected, the wolves together were more willing to cross low-use trails and roads than high-use roads. These results are similar to other barrier-crossing studies where black bears, caribou, and hedgehogs avoided crossing high-use features more so than low-use features (Serrouya 1999; Dyer 1999; Rondinini & Doncaster 2002). This result also supports other wolf studies, which suggest that wolves avoid encountering people traveling on linear features rather than the feature itself (Thiel 1985; Mech et al. 1988; Mladenoff et al. 1995,1999).

Even though roads received well over one hundred times the daily traffic of trails and presented wolves with a risk of mortality, trails had a larger effect on the tortuosity of wolf paths than roads and an equal barrier effect to movement. These results are similar to the relative effects of hikers and vehicles on bighorn sheep (*Ovis canadensis*) displacement. In Utah, bighorn sheep fled at least three times more often from hikers than from vehicles (Papouchis et al. 2001). Together, these studies suggest there may be a fundamental difference in how wolves and other animals perceive vehicles versus pedestrians. Although at least 41 wolves have died as a result of collisions with vehicles and trains in Jasper since 1992, three features may cause wolves to perceive people as greater threats than vehicles. First, as Papouchis et al. (2001) suggest, hikers are less predictable than vehicles and often directly approach animals. Second, vehicles appear relatively static compared to the body motions associated with animal and human movement. Consequently, it may be difficult for wolves to gauge the speed of vehicles, particularly on large, smooth highways. Third, people, but not vehicles have organic scent and may, therefore, be a stronger of a deterrent to wolf movement.

Regardless of the mechanisms for the difference between vehicles and pedestrians, this difference has important conservation implications. In areas where rugged topography or large water bodies confine animal movement, the density, distribution, and configuration of trails must be considered in order to maintain functional movement corridors. Moreover, these results suggest that wolves and some other animals either do not recognize, or have difficulty learning about the danger posed by vehicles. With aims to reduce vehicle-wildlife collisions, it would be interesting to pursue the mechanisms for this lack of response to vehicles.

This research suggests that the cumulative effects of trails, roads, and other developments are a potential conservation concern and merit further study. Future research should clarify the differing effects of food availability and human development on the tortuosity of animal paths, and should also further examine how cumulative effects of linear features affect the likelihood of animal crossing. In this study, the fine-scale movement decisions of wolves were affected by the level of human use on linear features and by the density of linear features. Therefore, land managers should consider the potential barrier effects of linear features that run across valleys and should maintain forest cover for animals in areas of high trail or road density.

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Chapter 4

General discussion and management recommendations.

In this chapter, I outline the most important results from the habitat and movement analyses (Chapters 2 and 3, respectively), then I identify important similarities and differences between this and other studies, and finally I propose specific management actions to enhance wolf movement in Jasper National Park.

In mountainous regions, such as Jasper National Park, people concentrate their activities in the valley bottoms (Noss et al. 1996). In this study, both wolf packs also selected for valley bottoms (low elevation), shallow slopes, and southwestern aspects. Therefore, human developments in this area had high potential to affect the movement of wolves. For analyses measuring (a) wolf preference or avoidance of areas near human activity, (b) the effect of human activity on path tortuosity, and (c) the permeability of linear features to movement, wolf movements were most affected by areas with high trail and road density and by high-use features. Wolves strongly avoided areas of high trail and road density and, when traveling through or around these areas, they traveled in more circuitous routes, presumably to minimize the probability of encountering people. The wolves were variable in their response to trail densities between 0.75 and 2.5 km/km^2 and strongly avoided trail densities greater than 2.5 km/km^2. Similarly, wolves avoided areas near high-use roads and trails, although Pack 2 (the smaller South Pack) showed weak selection for high-use trails. Conversely, wolves selected areas near low-use roads and trails, and the railway line, although Pack 1 (the larger Decoigne Pack) showed weak avoidance of low-use roads. Wolves crossed all linear features less often than expected, but were more likely to cross low-use trails and roads than high-use roads. Thus, linear features were partial, rather than absolute barriers to wolf movement. Overall, the deleterious effects of human development on wolf movement and habitat quality increased with levels of human-use and densities of development. Moreover, trails had a similar and sometimes stronger effect compared to roads in all three analyses even though roads received much higher traffic volumes and present a threat of mortality. Little is known about the effects of trails on animals in general, but the few studies that focused on trails, suggest that they degrade habitat quality (Miller & Hobbs 2000; Miller et al. 2001; Papouchis et al. 2001).

The variable response of wolves to roads in this study supported the context-dependent results of other studies. At the territorial scale, wolves in the northeastern United States selected territories with a low density of roads (Thiel 1985; Mech et al. 1988; Mladenoff et al. 1995, 1999). At a finer-scale, wolves in more remote areas of Alaska and northern Alberta selected areas near roads and seismic lines (Thurber et al. 1994; James & Stuart-Smith 2000), likely because these low-use features offer easy travel routes across their territories (Musiani et al. 1998). This study corroborated that apparent contradiction by showing that wolf preference or avoidance of roads depended on both their levels of use and density. In keeping with this result that anthropogenic linear features are useful travel routes to wolves as long as they do not contain high numbers of people, this study also found that wolves selected areas near railway lines but strongly avoided areas near high-use trails and areas with high trail density.

Few studies have examined directly the effects of human activity on path tortuosity. However, many studies show that path tortuosity increases in high-quality habitat (Crist et al. 1992; Miyatake et al. 1995; Stapp & Van Horne 1997; Etzenhouser et al. 1998; Odendaal et al. 1998; Schultz 1998; Kindvall 1999; Schultz & Crone 2001). In this study, two factors affected habitat quality: food abundance (as measured by predation sites and topography) and human activity. As predicted, the tortuosity of wolf paths increased near predation sites, which represented high-quality habitat. However, path tortuosity also increased in areas where habitat quality was degraded by high-use trails and high trail and road density. Surprisingly, low-use trails and roads did not affect path tortuosity even though wolves in this study selected these features and wolves in Poland increased their speed of travel on roads and trails (Musiani et al. 1998). Together, these results suggest that wolves move differently in habitats with low prey availability compared to habitats degraded by human developments. The tortuosity of paths decreases in areas of low prey abundance but increases near high levels of human activity. Research on other animals is required to determine if animals in general travel in more tortuous paths through human development.

The few studies comparing the frequency with which animal and random paths cross linear features indicate that high-use features impede animal movement more than low-use features (Serrouya 1999; Dyer 1999; Rondinini & Doncaster 2002). This study corroborates those results. However, wolves crossed all features less than expected, which suggests that the cumulative effects of several adjacent features may affect the willingness of animals to cross even low-use roads and trails (e.g. Bélisle & St. Clair 2001).

In this study, human activity in Jasper National Park clearly affected where and how wolves travel. This activity may limit wolf access to prey, displace wolves from predation sites, and disturb wolves from den sites. For example, within 20 km of Jasper there were very few areas that were both suitable for den sites and unaffected by people. Consequently, wolves may be forced to use inferior den sites. In 1999, the pups from one pack died because this wolf pack situated their new den site on poor, rocky substrate rather than on the sandy, loamy soil wolves generally prefer (Mech 1981). The wolves managed to dig a shallow den but it failed to provide a dry shelter. By limiting wolf access to den sites and prey, human activity likely affects the lifetime fitness of these wolves and may make the wolf population more vulnerable to other natural or anthropogenic effects.

Based on the results of this study, I identified areas that are particularly important for wolf movement around the town of Jasper. In doing so, I recognize that Parks

Canada has mandates to first protect biological communities and their ecological processes and second to facilitate enjoyment opportunities for people (National Parks Act 1998). Therefore, recommendations I make here are intended to prevent further habitat degradation and fragmentation in areas identified as high-quality wolf habitat or important movement routes among valleys. These areas currently receive low levels of human activity so management actions in these places would affect few people. In these recommendations I primarily target trail-use for two reasons. First, trails had an equal or stronger effect on wolf movement than did roads, but this effect was strikingly disproportionate to the number of people using the two feature types. Second, local residents are creating a rapidly expanding network of unofficial trails (often bicycle trails) throughout the study area (G. Mercer, unpublished data) and these have high potential to affect wolf movement if the levels of use and density of trails increases. I sectioned the following recommendations into two categories: those that primarily affect wolf movement and those that affect habitat quality.

Movement recommendations.

1. All human activity should be restricted from the important wolf movement corridors depicted in Figure 4-1. These movement corridors were defined as linear patches of habitat (Figure 2-5) that connect larger blocks of habitat (Beier & Noss 1998) known to be used frequently by wolves (Figure 2-3). These corridors provided wolves with rare movement routes between valleys and generally occurred where human activity abutted rugged topography.

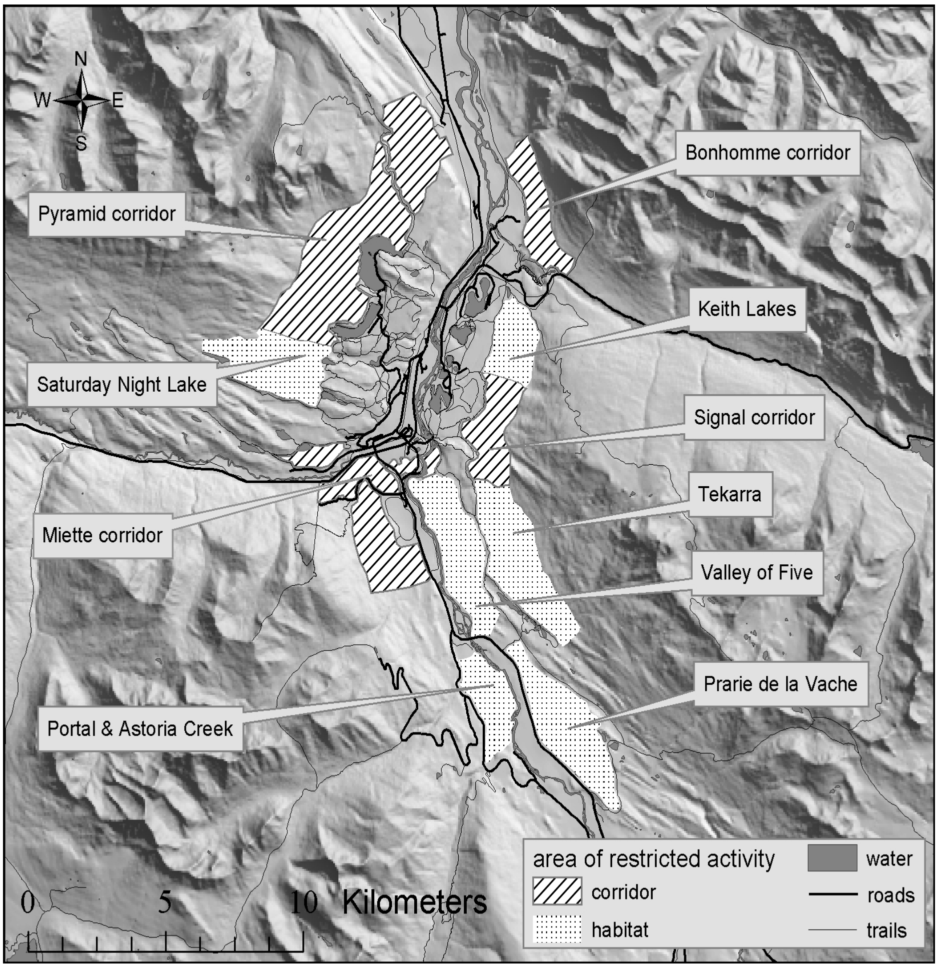

Figure 4-1. Movement corridors and high quality wolf habitat where human activity should be restricted.

Other investigations have also identified the importance of these corridors. A long-time warden in Jasper, Wes Bradford, initially identified many of the areas in Figure 4-1 as potentially important movement corridors in 1998. Moreover, preliminary results from the Three Valley Confluence Wildlife Movement Study and the Jasper Park Lodge Corridor Study show that these corridors are important for movement. These studies further indicate that while wolf displacement increases with levels of human-use, wolves quickly learn to use areas when levels of human use are reduced. Given the importance of movement corridors to wolf movement, there is a high risk that continued trail expansion into these narrow corridors would block the movement of wolves and other carnivores among the Athabasca, Miette, and Maligne Valleys. Conversely, reduced human use within in the corridors would likely greatly enhance wolf movement among the valleys. Recent trail development of unofficial trails within these movement corridors makes the protection of these corridors an immediate concern for Parks Canada.

2. A section of the pipeline to the Astoria Hydroelectric generator should be covered. Wolves south of Jasper traveled around rather than under this pipeline (Figure 2-3). Covering a section of this pipeline would enhance wildlife movement along the west side of the Athabasca Valley.
3. If Parks Canada decides to rehabilitate other areas for wolf movement, they should decommission poor and redundant trails and thus reduce trail densities to levels tolerated by wolves. They should maintain trail densities below 2.5 km/km^2 (measured with a radius of 1 km) for winter movement. Trail

densities tolerated by wolves are likely to be much lower in summer given the higher levels of human-use on the trails.

4. Parks Canada should implement the several planned initiatives that could enhance wolf movement around Jasper. First, Parks Canada plans to slow vehicle traffic on Highway 16 between 1 and 2 km west of town. Wolves and many other animals crossed this section of highway when traveling between the Miette and Athabasca Valley south of Jasper. Slowing traffic in this area would alleviate the high number of wildlife-vehicle collisions in this area. From 1990 through 1999 an average of 14.1 ($\pm$ 3.7 std. dev.) animals died each year as a result of collisions with vehicles and trains. These deaths occurred between 0.5 and 4.5 km west of Jasper. In the same area, Parks Canada plans to move the Whistler's Hostel closer to town and then close the road from Highway 93 to the Whistler's tramway during the winter. Implementation of this plan would greatly reduce levels of off-trail hiking and vehicle traffic in both winter and summer. Finally, closure of Highway 93A between Alpine Village and Tekerra Lodge would enhance wolf movement along the Miette River and across the Athabasca River toward Old Fort Point.
5. Parks Canada should conduct winter transects of the defined corridors to determine (a) changes in wolf use of the corridors and (b) the size of the wolf packs using the corridor. Pack 2 (the South Pack) has consisted of just two to three wolves for three years. This is an unusually small pack size given that most other wolf packs in Jasper number approximately seven wolves. That

small size may be evidence of the marginal movement potential and restricted den site availability through the central part of its territory.

Habitat recommendations.

1. Parks Canada should restrict public access in some areas of high quality wolf habitat. These areas, which I also outline in Figure 4-1, currently receive little human use and therefore represent some of the few undisturbed areas within 20 km of Jasper. During this study, wolves as well as many other species such as grizzly bears with cubs, cougar, wolverine, and moose used these areas. These areas contain relatively open forests which makes off-trail travel and the creation of new trails very easy. If Parks Canada does not restrict public access, there is a high probability that the ever-increasing network of unofficial trails will expand into these areas and severely degrade habitat quality. In fact, some trails have recently been created or enhanced in Prarie de la Vache (Wabasso Lake to Prarie de la Vache), Valley of Five (just north of Five Mile Bridge), Portal & Astoria Creek (Five Mile Bridge to Astoria Power Station), and around Keith Lakes. Parks Canada's ideal objective for these areas should be to accept infrequent but not regular visitation and prevent trail creation. In points 2 and 3, I recommend management actions to achieve this objective.
2. Parks should restrict all off-trail bicycle use. Many new trails appear to be created by bicyclists in the summer. Unlike hikers, bicyclists have difficulty crossing fallen trees and are, therefore, more likely to clear trails. Once a trail

is cleared through an area, the number of people visiting the area and using the trail appears to increase rapidly. Moreover, bicyclists travel at least 3 times as fast as hikers and therefore have the ability to travel further and degrade more habitat than hikers. Therefore, I recommend that Parks Canada first designate specific trails or areas where bicycling is allowed and then prohibit bicycling in other areas.

3. Hiker access to the habitat areas in Figure 4-1 should have seasonal restrictions. As a minimum, these areas should be closed to the public from mid-April through June when most species are breeding, denning, or calving. Parks Canada should monitor the levels of human activity in these areas and further restrict public access should these areas receive regular use.
4. The area at least 500 m surrounding wolf den sites should be closed to the public and all parks personnel, particularly from mid-April through mid-July. Wolf pups are usually born in late-April or early May. The wolf pups leave the den for a nearby rendezvous site 8-10 weeks later. If disturbed by people, wolves will often prematurely remove the pups from the den site and may abandon the use of that den in future years (Joslin 1967; Ballard et al.1987). Therefore, human activity near the den sites should not be permitted, particularly since there are few suitable areas for wolves to den in Jasper.
5. Large mammals killed by collisions with vehicles and trains should be placed in the waste transfer station. Prior to this study, Parks Canada removed ungulates killed by vehicles from primary highways and placed them off secondary highways where they could be fed upon by carnivores, such as

wolves. This practice only occurred during the winter when bears could not feed on the carcasses. In 1999, Parks Canada changed this practice within the study area and instead placed the carcasses into a fenced transfer station. Coincidentally, the number of wolves killed by collisions with vehicles and trains dropped from 6.2 wolves per year (std. err. = 2.7, n = 5, date =1994-1999) to 2.0 wolves per year (std. err. = 0, n = 2, date = 2000-2001). Therefore, I suggest Parks Canada continue to place road-killed carrion in the transfer station rather along secondary roads, tighten the fence around the transfer station to exclude coyotes, and continue to monitor rates of wolf mortality.

Implementation of the above recommendations requires an education program that will explain to the public the role of wolves in ecosystems and why the management actions are necessary to maintain wolf movement around Jasper. Parks Canada should simultaneously alleviate the need for new trails by improving existing trails and concentrating trail use in areas that already receive high levels of human use. Moreover, the work of the Jasper Trail Stewards Committee, a public organization that targets specific trails for improvement or rehabilitation, should be encouraged. In particular, this group should be involved in the public education for trail removal as well as the implementation of the goal to limit trail expansion.

This study was unique in that it used innovative methods of analyzing tracking data to address conservation issues. More importantly, this study was one of the first studies to identify the importance of trails to animal movement. However, future research is required to increase our understanding of how animals move in response to human developments. Here, I suggest two important areas future research. First, future research should clarify the effects of trails on the movement and habitat selection of a wider variety of species. Trails are commonly found around towns and within "green areas" of urban centers. Consequently, they have high potential to affect the movement and distribution of many different species. Second, while many studies, including this study, have examined the effect of roads on habitat selection, the results of these studies may be conservative because they did not address temporal effects. For instance, although wolves in this study traveled on lower use roads and trails, they may avoid traveling on these features during the day when there is a higher probability of encountering people. Therefore, future research should also examine how human developments affect the temporal movement and activity patterns of animals living in this and other habitats that are fragmented by human development.

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