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SPATIAL RESPONSES OF WOLVES TO ROADS AND TRAILS IN MOUNTAIN VALLEYS

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Abstract. Increasing levels of human activity in mountainous areas have high potential to inhibit animal movement across and among valleys. We examined how wolves respond to roads, trails, and other developments. We recorded the movements of two wolf packs for two winters by following their tracks in the snow and simultaneously recording positions with a hand-held global positioning system. We then used matched case-controlled logistic regression to compare habitat covariates of wolf paths (cases) to multiple paired random locations (controls). This analysis emphasized the differences within pairs of cases and controls, rather than differences in their overall distribution, making it useful to assess fine-scale habitat selection and path data. Both packs selected low elevations, shallow slopes, and southwest aspects. They selected areas within 25 m of roads, trails, and the railway line and more strongly selected low-use roads and trails compared to high-use roads and trails. One pack strongly avoided distances between 26 and 200 m of high-use trails; otherwise, the wolves weakly selected or avoided this distance class. Both packs avoided areas of high road and trail density. We concluded that roads and trails have a cumulative effect on wolf movement and that management of trails, in addition to roads, may be needed to retain high-quality habitat for wolves, particularly in known movement corridors.

Key words: case control; Canis lupus; *Jasper National Park, Alberta, Canada; park management; path; resource selection; road; trail; wolf responded to roads and trails.*

INTRODUCTION

Increasing levels of human activity threaten animal populations throughout the world (Meffe and 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, they also may inhibit animal movements between valleys wherever high levels of human activity abut rugged topography. To mitigate this effect of habitat fragmentation, it is necessary to determine the spatial response of animals to anthropogenic developments such as roads, trails, resorts, and towns (Beier and Noss 1998).

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 and Frissell 2000). Forman (2000) estimated that while roads occupy 1% of the United States land area, they affect ecological processes in ~20% of the country. The ecological effects of roads are clearly important, yet 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. For example, bighorn sheep (*Ovis canadensis*) in Utah fled more often from hikers than from vehicles (Papouchis et al. 2001); some ungulates fled at greater distances from off-trail hikers compared to on-trail hikers (Taylor and Knight 2003); and distance to trail may affect which species are most likely to predate bird nests (Miller and Hobbs 2000). The combined effects of roads, trails, and other human developments may be problematic for carnivores because these species occur in low densities and occupy large home ranges that typically encompass multiple anthropogenic obstacles (Noss et al. 1996). Wolves (*Canis lupus*) may be particularly susceptible to these effects because they are generally wary of people, and in some areas deep snows seasonally confine the distribution of both wolves and their prey to the valley bottoms (Weaver et al. 1996). Because people also concentrate activities along the valley bottoms, there is high potential for their activities to affect wolf movement.

Studies examining the spatial response of wolves to human development can be partitioned according to two scales of analysis. Large-scale studies of territory selection have been used to predict areas for wolf recolonization and persistence in Minnesota, Wisconsin,

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PLATE. 1. Female wolf on bull elk carcass at Medicine Lake, Jasper National Park, Alberta, Canada. Photo credit: Caryl N. Utigard.

and Michigan (USA). Here, wolf packs established and persisted in territories with road densities below 0.58 km/km^2 (Thiel 1985, Mech et al. 1988) and 0.45 km/km^2 (Mladenoff et al. 1995, 1999). These authors suggested that it is not the roads per se that wolves avoid, but the positive correlations between road density and the likelihood of suffering mortality from hunters and collisions with vehicles.

While it is important to identify areas for successful wolf recolonization at a broad scale, it is also important to understand the spatial response of wolves to roads at a finer scale because this is the scale at which management decisions are typically made to conserve local populations. Studies at the finer scale suggest that wolves vary in their response to people. In many regions, wolves selected areas near roads, trails, and seismic lines because these features increased speed and ease of travel across their territory (Thurber et al. 1994, Musiani et al. 1998, James and Stuart-Smith 2000, Callaghan 2002). Moreover, some tolerated industrial activity near den sites (Thiel et al. 1998), fed predominantly at garbage refuse stations, or became habituated to people (McNay 2002). While some wolves have adapted to people, wolves in Alaska avoided a heavily used mining road (Thurber et al. 1994) and wolves in Poland avoided areas with high levels of human activity (Theuerkauf et al. 2003*a*, *b*). The apparent contradiction between avoidance of roads at larger scales of analysis and a tendency for attraction to them at the finer scale might be explained by differences in the density of people. The landscape studies (wolves avoid roads) occurred in populated areas, whereas most fine-scale studies in North America (wolves select roads and trails) occurred in remote areas. Therefore, it is important to identify the fine-scale response of wolves to roads in populated areas where wolf populations are most threatened.

The town of Jasper (population 4500) in Jasper National Park, Alberta, Canada, is a popular destination for tourists and outdoor enthusiasts. Like many communities in mountainous regions, Jasper lies at the confluence of several valleys. Human-use surrounding the town is increasing and in some places abuts the steep-sided mountains. Consequently, wolf packs near Jasper must navigate both humans and their infrastructure when traveling among valleys. In this study, we determined the fine-scale, spatial response of two wolf packs to roads, trails, railway lines, resorts, and topographic features within 25 km of Jasper. We compared the habitat characteristics of wolf paths and random points using multiple logistic regression (Manly et al. 1993). For greater precision, we paired random points with wolf points and used matched case-control logistic regression rather than standard logistic regression to isolate the movement decisions of wolves while estimating resource selection (Hosmer and Lemeshow 2000). In addition to determining the wolf response to anthropogenic features, we used the results to create a spatially explicit map of wolf habitat to identify areas of conservation concern. The results of this study are intended to help managers identify sources of habitat degradation and fragmentation for wolves and other wary species.

METHODS

Study area

This study focused on the movements of two wolf packs for two winters (1999–2000, 2000–2001). The territories of both packs extended between 20 and 50 km along the three valleys that converge upon the town of Jasper (Alberta, Canada). The study area included a portion of these two territories, ~20 km each side of Jasper (52°52′ N, 118°05′ W, elevation 970–2800 m

TABLE 1. Topographic and human-use covariates used for resource selection analysis (Jasper National Park, Alberta, Canada).

Variable†	Variable code	Description and/or units of measurement
Habitat predictors		
Elevation	ELEV	100 m; range: 1020–1750 m
Slope	SLOPE	degrees
Cosine of aspect	ASPCT	radians; southwest = 1, northeast = −1
Distance to water	WATER	km; lakes and rivers
Forest type	FOREST	lodgepole pine, spruce, douglas fir, aspen, open shrub/meadow, water
Human-use predictors		
Trail density	TR_DEN	km/km^2; radius of 0.2, 0.5, **1.0**, 1.5 km
Road density	RD_DEN	km/km^2; radius of 0.2, 0.5, **1.0**, 1.5 km
Distance to high-use road	RD_H	m; 0–25 m, 26–200 m, $>$ 200 m
Distance to low-use road	RD_L	m; 0–25 m, 26–200 m, $>$ 200 m
Distance to high-use trail	TR_H	m; 0–25 m, 26–200 m, $>$ 200 m
Distance to low-use trail	TR_L	m; 0–25 m, 26–200 m, $>$ 200 m
Distance to railway	RAIL	m; 0–25 m, 26–200 m, $>$ 200 m
Distance to accommodation	ACCOM	km; log(distance to accommodation + 1)

† Boldface variables were included in the final set of candidate models.

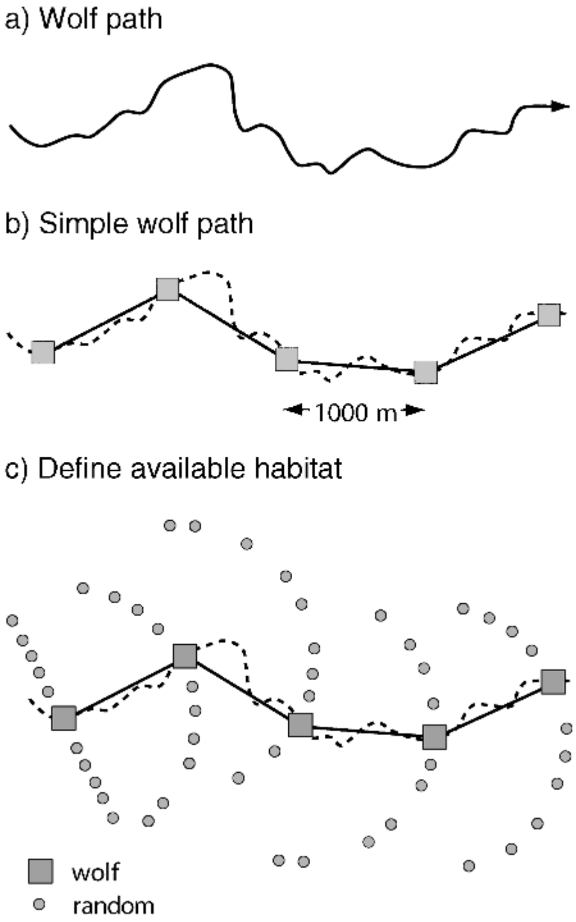

FIG. 1. For the matched case-control logistic regression, 10 controls (random points) were paired with each case (wolf point). Wolf paths (a) were first simplified into a series of wolf points separated by 1000 m (b). To avoid bias potentially associated with the start of each path, we defined the first step as a random point along the first 500 m of the path. To create the controls (c), random turn angles between +90° and −90° were added to the previous direction of travel. Ninety percent of actual wolf turn angles were $<90°$.

above sea level). 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 where 99% of wolf movements occurred. 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*; see Plate 1), deer (*Odocoileus* spp.), and moose (*Alces alces*), but occasionally kill bighorned sheep, caribou (*Rangifer tarandus*), and mountain goat (*Oreamnos americanus*) (Weaver 1994). Valley bottoms 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 (Holroyd and Van Tighem 1983).

The study area contained 759 km of trails and 292 km of roads including a railway line. A major transportation highway with substantial freight-truck traffic runs 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 also marked seasonal variation in traffic volume; 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 create their own trails throughout the study area (E. G. Mercer, *personal observation*). Human use on

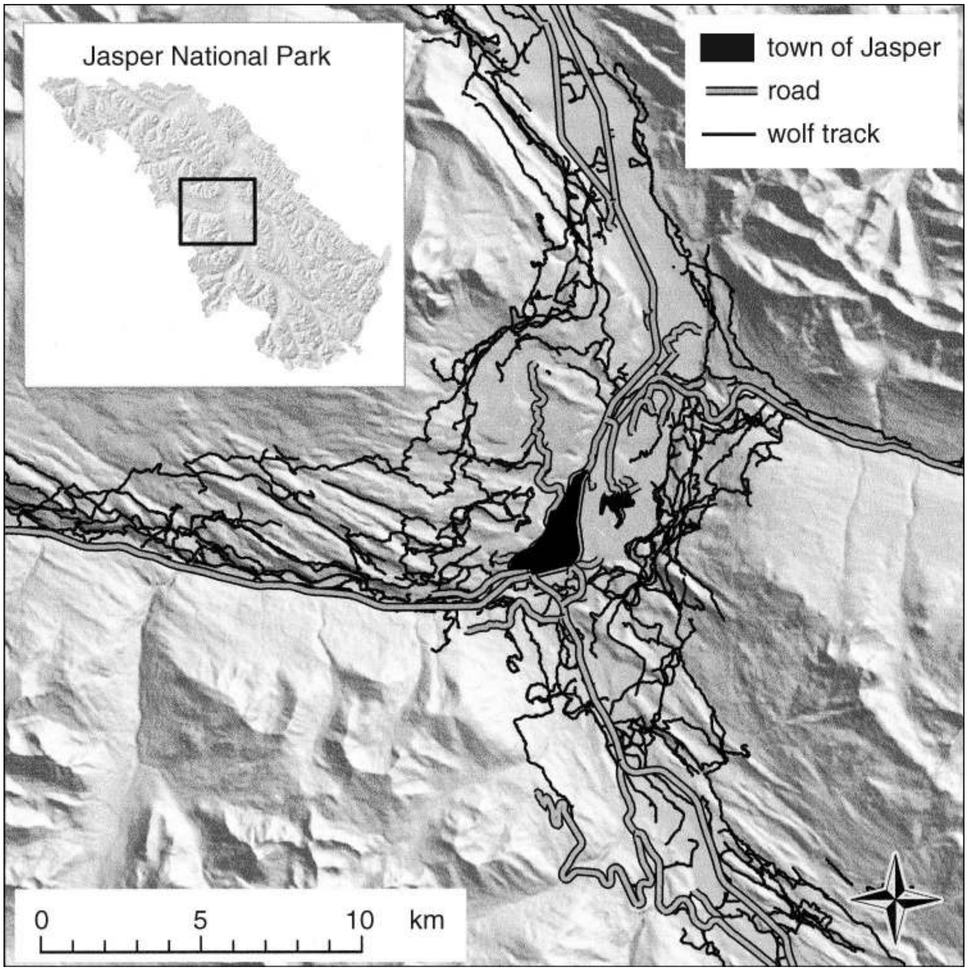

FIG. 2. Wolf routes around the town of Jasper from two winters of snow tracking (November 1999–March 2001). Pack 1 (7–10 individuals) occupied the territory west and north of Jasper, while Pack 2 (2–3 individuals) occupied the territory south and east of Jasper.

many of these trails increased 20-fold from winter to summer 2000 (Parks Canada, *unpublished data*).

Field methods

To record the movements of these two wolf packs, we followed their tracks in the snow and simultaneously recorded positions with a hand-held global positioning system (GPS; Trimble GeoExplorer 3 [Sunnyvale, California, USA]) every 25 m. GPS positions were differentially corrected to remove position error associated with scrambled satellite signals (selective availability, which occurred until 1 May 2000). 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 (<24 hours old) 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 R version 1.7.0 (Ihaka and Gentleman 1996) for statistical analysis.

Statistical analysis

The spatial response of wolves to human developments may be influenced by habitat quality near these developments. Therefore, we measured wolf preference and avoidance of several topographic variables in addition to measures of human use (Table 1). Elevation, slope, and aspect were derived from a digital elevation model with a resolution of 25 m. Aspect was sine-transformed such that southwest aspects with higher levels of solar incidence equaled 1 and northeast aspects with lower solar incidence equaled −1. The relative importance of aspect for resource selection is slope dependent, therefore aspects with slopes <5° were assigned a neutral value of 0. Road and trail densities (kilometers per square kilometer) were measured as the length of road/trail within a radius of 0.2, 0.5,

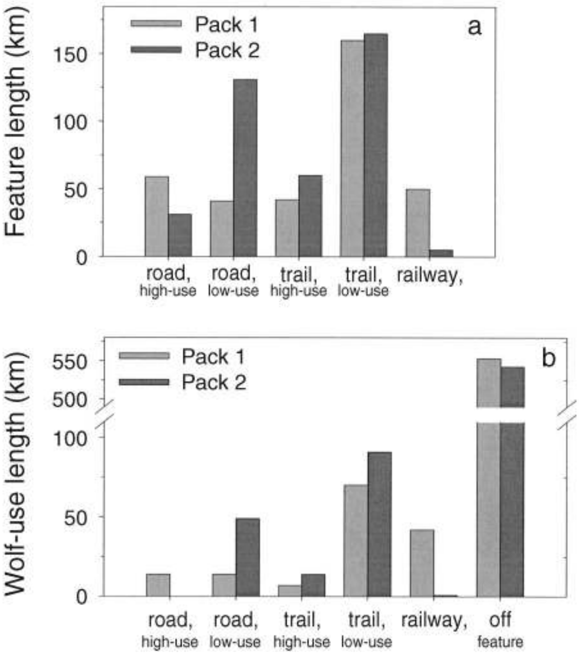

FIG. 3. Length of roads, trails, and railway line (a) within the study area and (b) used by wolves. Seventy-nine percent of the wolf paths were at least 25 m from roads, trails, and the railway line (i.e., off feature).

1.0, or 1.5 km divided by the respective area of the circle. We reclassified distances to roads, trails, and the railway line into categories of 0–25, 26–200, and >200 m to differentiate between wolf selection/avoidance of the linear feature and the surrounding habitat. We defined distances >200 m as our reference category. Roads and trails were categorized as high or low use. High- and low-use roads were estimated to receive ≥10 000 and <10 000 vehicles per month in February, respectively. High-use trails received foot traffic on a daily basis in winter, whereas low-use trails received infrequent or no foot traffic in winter. Accommodations included commercial facilities both within and outside the town site. This predictor was log-transformed because we expected that wolves would avoid areas near these features and that the influence of these features would decrease exponentially with distance.

For the analysis, we used matched case-control logistic regression rather than standard logistic regression. While standard logistic regression has been used extensively to model habitat selection of animals (Pereira and Itami 1991, Manly et al. 1993, Mladenoff et al. 1995, 1999, Mace et al. 1996), matched case-control logistic regression has only recently been applied to the field of ecology (e.g., Compton et al. 2002). However, this method is considered to be one of the most important statistical techniques in medicine (Breslow 1996) and may have many untapped applications in ecology. 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 multiple control points with each case using a stratifying variable (Hosmer and 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 estimation, indicate the direction of habitat selection and are interpreted similarly to coefficients from standard logistic regression.

In our analysis, we simplified wolf paths into discrete steps of 1000 m, selected those points as cases, and then created 10 controls for each case (Fig. 1). We 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. We further decreased the similarity between wolf and control points by prohibiting the controls from landing on actual wolf paths. However, to maximize the realism of control points we restricted the controls to areas outside the town limits and to elevations below 1600 m where we knew wolves to plausibly occur. Because the number of controls per case does not increase Type I error in matched case-control logistic regression (Hosmer and Lemeshow 2000), we created 10 controls per case to more thoroughly estimate the habitat available to wolves at each step. We determined step direction for the controls as a random turn angle between −90 and +90 degrees, which represent the 75% confidence interval of the turn angles made by wolves.

Model selection

To create the best predictive model of the paths selected by wolves, we followed the model-averaging approach of Burnham and Anderson (2002). We first tested for collinearity among explanatory variables and redundant variables by identifying correlation coefficients greater than 0.7 or variance inflation factors greater than 3 (Fox 2002). We then created 34 candidate models based on likely combinations of the remaining explanatory variables. Elevation, slope, aspect, and distance to low-use trail were included in all candidate models. We selected the most likely candidate models using $\Delta AIC_c < 4$ (Akaike information criterion with correction for small sample size [Burnham and Anderson 2002]), then calculated model-averaged coefficients and unconditional standard errors to create a final predictive model. We determined the relative im-

TABLE 2. Selected set of candidate models, by wolf pack (selection based on $\Delta\mathrm{AIC_c} < 4$).

Model	D
Pack 1; $n_1 = 481$, $n_0 = 4810$	
ELEV + SLOPE + ASPCT + RD_DEN + TR_DEN + RD_L + TR_L + RAIL	2078.9
ELEV + SLOPE + ASPCT + RD_DEN + TR_DEN + TR_L + RAIL	2083.5
ELEV + SLOPE + ASPCT + RD_DEN + TR_DEN + RD_H + RD_L + TR_L + RAIL	2077.7
ELEV + SLOPE + ASPCT + RD_DEN + TR_DEN + RD_H + TR_L + RAIL	2082.2
ELEV + SLOPE + ASPCT + RD_DEN + TR_DEN + RD_L + TR_H + TR_L	2078.8
Pack 2; $n_1 = 467$, $n_0 = 4670$	
ELEV + SLOPE + ASPCT + RD_DEN + TR_DEN + RD_L + TR_H + TR_L	1981.1
ELEV + SLOPE + ASPCT + RD_DEN + TR_DEN + RD_L + TR_L	1988.2
ELEV + SLOPE + ASPCT + RD_DEN + TR_DEN + RD_H + RD_L + TR_H + TR_L	1980.2
ELEV + SLOPE + ASPCT + RD_DEN + TR_DEN + RD_L + TR_H + TR_L + RAIL	1980.2

Notes: Definitions of column heads: D = deviance; K = number of estimatable parameters; $\mathrm{AIC_c}$ = Akaike information criteria value, corrected for small sample site; $\Delta\mathrm{AIC_c}$ = $\mathrm{AIC_c}$ distance from top-ranked model, w = Akaike weight. The number of cases (n_1) and number of controls (n_0) are indicated for each pack.

portance of each explanatory variable by summing renormalized Akaike weights from the selected models. Separate analyses were conducted for each wolf pack.

Model diagnostics

In matched 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). We assumed a conservative estimate of model fit by calculating the area under the receiver operating characteristic curve (ROC) for the top-ranked model (Hosmer and Lemeshow 2000). For another simple metric, we calculated the proportion of wolf locations that had larger predicted values than their paired random locations. We also calculated robust variance and standard-error estimates of the regression coefficients in our final model by jackknifing wolf points grouped by wolf path.

RESULTS

Over the course of two winters, we snow tracked the two wolf packs 1390 km (Fig. 2). 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 1000 m produced 481 wolf points for Pack 1 and 467 wolf points for Pack 2.

Wolves traveled within 25 m of roads, trails, and railway lines 21% of the time and traveled through the forests, rivers, and meadows the other 79% of the time (Fig. 3). Both wolf packs traveled five times farther on low-use trails than high-use trails, yet only Pack 2 traveled farther on low-use roads than high-use roads. Pack 2 rarely traveled on high-use roads and the railway line. These features, however, ran along the periphery of its territory.

Road and trail densities were measured using radii of 0.2, 0.5, 1.0, and 1.5 km. Preliminary models that included road and trail densities measured with a radius of 1.0 km had lower $\mathrm{AIC_c}$ values than models using a radius of 0.2, 0.5, or 1.5 km and were therefore used in the final set of candidate models.

The results from the matched case-control logistic-regression models indicated several candidate models had reasonable support compared to the top-ranked model (Table 2). When these models were averaged, both wolf packs selected for lower elevations, flatter slopes, southwestern aspects, and areas with lower road and trail density (Table 3). Both packs selected for areas within 25 m of roads, trails, and the railway line, but they selected low-use features more strongly than high-use features. They both selected and avoided areas 26–200 m from these features. As indicated by the Wald statistics, selection or avoidance of these areas was weak, although Pack 2 strongly selected areas 26–200 m from low-use trails and strongly avoided areas 26–200 m from high-use trails. The main differences between the two packs were high-use trails and low-use roads had less influence on the movements of Pack 1 compared to Pack 2. Conversely, the railway line had more influence on Pack 1 than Pack 2. When the values representing variable importance were averaged for the two packs, road density, trail density, and low-use trails were included in all selected models and were therefore equally important explanatory variables. Other variables ranked from most to least important were low-use road, railway, high-use trail, and high-use road.

As a conservative estimate of overall model fit, we calculated the ROC (receiver operating characteristic) value for the top-ranked model from each pack. The ROC values for Pack 1 (0.70) and Pack 2 (0.72) indicate that the models performed reasonably, but not exceptionally, well at discriminating between wolf and random locations. Overall, 67% and 70% of wolf locations for Pack 1 and 2, respectively, had predicted probabilities larger than their paired random locations.

Given that the strength of wolf avoidance for high road/trail density occurred on a continuum, we identified the density at which wolves begin to avoid road/trail density by comparing the densities of the wolf

TABLE 2. Extended.

K	AIC_c	ΔAIC_c	w
12	2103.0	0.0	0.35
10	2103.5	0.5	0.27
14	2105.8	2.8	0.09
12	2106.3	3.3	0.07
14	2106.9	3.9	0.05
12	2005.2	0.0	0.56
10	2008.2	3.0	0.12
14	2008.3	3.1	0.12
14	2008.3	3.1	0.12

locations to the paired random locations. More specifically, we first determined whether each wolf location had higher or lower road/trail densities than each of the 10 paired random locations. When wolf and random locations were equal, wolf locations were randomly assigned a positive or negative difference. We then classified the random locations into 0.5 km/km^2 intervals and calculated the proportion of wolf locations that were greater than the paired random locations. Examined thus, wolves began selecting lower road and trail densities when the available road and trail densities exceeded 1.0 km/km^2 (Fig. 4). Both packs traveled through areas with road/trail density greater than 1.0 km/km^2, yet only 10% of the wolf locations exceeded road densities of 1.3 km/km^2 and trail densities of 2.9 km/km^2. To provide context for these values, consider that road/trail densities were measured with a radius of 1 km. The density for locations at the junction of two linear roads/trails therefore equals 1.3 km/km^2. Thus, our results suggest that wolves avoided both road and trail intersections, but were less likely to travel through high densities of roads than trails.

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, we applied the results of the averaged models to create a map depicting the relative probability of wolf occurrence throughout the study area (Fig. 5). Such predictive maps enable managers to visually identify areas of high- and low-quality wolf habitat, outline compressed areas or ''pinch points'' to movement, and generate predictions from hypothetical management actions. This map highlights the habitat degradation from trails, roads, and accommodations both north and southeast of Jasper. The map also emphasizes the narrow movement corridors around these areas.

DISCUSSION

Both wolf packs selected terrain with low elevations, flatter slopes, and southwest aspects. Wolves likely selected these terrain features because they contained the shallowest snow depths and highest prey abundance within the study area (Telfer and Kelsall 1984, Huggard 1993). Similar to other studies (Thurber et al. 1994, Musiani et al. 1998, James and Stuart-Smith 2000, Callaghan 2002), wolves in this study also used linear features as travel routes. The wolves selected areas within 25 m of roads, trails, and a railway line, and showed stronger selection for low-use features than high-use features. At the same time, they showed variable selection or avoidance for the areas 26–200 m from features. This suggests that the wolves selected these features because they offered easy travel routes across their territory and not because they were associated with surrounding high-quality habitat. Yet, given that 79% of wolf movements were greater than 25 m from these features, the majority of their movements

TABLE 3. Model-averaged regression coefficients (β), standard errors (SE), Wald statistics (β/SE), and relative importance of each explanatory variable (w_+).

	Pack 1				Pack 2				Pack 1+2
Variable	β	1 SE	Wald	w_+	β	1 SE	Wald	w_+	Mean w_+
ELEV	−0.685	0.112	−6.1	1.00	−0.668	0.129	−5.2	1.00	1.00
SLOPE	−0.029	0.007	−4.0	1.00	−0.034	0.009	−3.8	1.00	1.00
ASPCT	0.455	0.117	3.9	1.00	0.341	0.109	3.1	1.00	1.00
RD_DEN	−1.236	0.247	−5.0	1.00	−0.567	0.170	−3.3	1.00	1.00
TR_DEN	−0.254	0.133	−1.9	1.00	−0.409	0.104	−3.9	1.00	1.00
RD_H 0–25	0.357	0.523	0.7	0.19	0.231	0.631	0.4	0.13	0.16
26–200	0.188	0.330	0.6	0.19	−0.437	0.482	−0.9	0.13	0.16
RD_L 0–25	0.810	0.466	1.7	0.59	1.520	0.257	5.9	1.00	0.79
26–200	−0.325	0.307	−1.1	0.59	0.331	0.230	1.4	1.00	0.79
TR_H 0–25	0.129	0.450	0.3	0.06	0.058	0.414	0.1	0.87	0.46
26–200	−0.004	0.312	0.0	0.06	−0.680	0.313	−2.2	0.87	0.46
TR_L 0–25	0.783	0.274	2.9	1.00	1.721	0.294	5.9	1.00	1.00
26–200	0.090	0.160	0.6	1.00	0.353	0.204	1.7	1.00	1.00
RAIL 0–25	1.410	0.451	3.1	1.00	0.812	0.829	1.0	0.13	0.56
26–200	0.053	0.311	0.2	1.00	−0.161	0.545	−0.3	0.13	0.56

Notes: The column heading w_+ indicates the sum of w in Table 2. The reference category for high- and low-use roads and trails and the railway line was distances farther than 200 m. Elevation, slope, aspect, and distance to low-use trail were included in all candidate models.

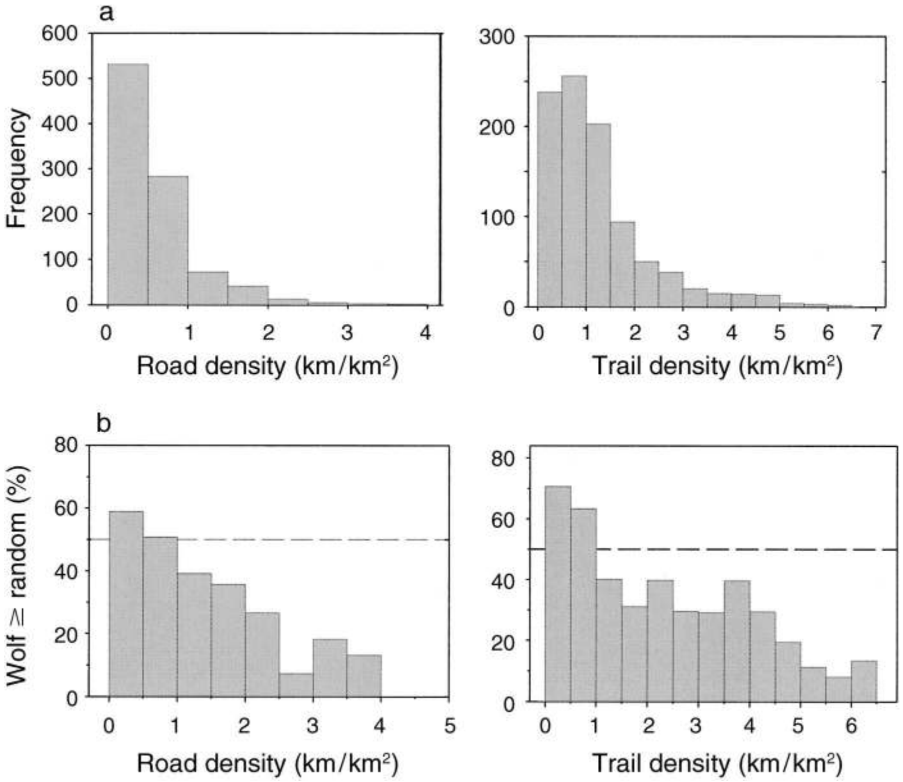

FIG. 4. (a) Frequency histograms of road and trail densities used by wolves. (b) Response of wolves to available road and trail densities. Responses were measured as the percentage of wolf locations that had larger road/trail densities than their paired random location. Differences of 0 between wolf and random locations were randomly assigned a positive or negative difference.

occurred in forests and meadows, and along waterways. Thus, wolves selected for linear features as opportunistic travel routes, but clearly did not require these features for movement across their territories.

Roads and trails had a cumulative effect on the distribution of wolves in Jasper (Alberta Canada). Other than one pack's avoidance of areas surrounding high-use trails, individual roads and trails had little negative effect on wolf movement. Yet, roads and trails had a cumulative effect such that wolves avoided areas of high road and trail density. Wolves in Jasper started to avoid both roads and trails when their density exceeded 1.0 km/km^2, yet the 90th percentiles of wolf locations occurred at considerably different densities for roads and trails (i.e., 1.3 and 2.9 km/km^2 for road and trail density, respectively). Thus, while both high densities of roads and trails degraded habitat quality, the density-impeded wolf movement was lower for roads relative to trails. This stronger aversion to roads than trails is not surprising given that roads received much higher traffic volumes than trails. However, the cumulative effects of trails on wolf movement and habitat use should not be underestimated given that there were almost twice as many trails as roads through the study area.

Wolves in this study avoided areas with a high probability of encountering people and were more likely to cross low-use roads and trails than high-use roads and trails (Whittington et al. 2004). These results support other research in which wolves minimized their probability of encountering people. For instance, wolves in Alaska avoided a heavily used mining road (Thurber et al. 1994), and the distances wolves in Poland were displaced from towns, roads, and trails depended on the number of people using them and the time of day (Theuerkauf et al. 2003*a*).

Wolves in this study were not subjected to legal or illegal hunting mortality, which would be expected to increase their wariness on both roads and trails. Instead, wolves were subject to mortality from collisions with vehicles and trains. At least 43 wolves from four packs in Jasper National Park have died from collisions with vehicles and trains in the last decade (Parks Canada, *unpublished data*). However, the relative risk of mortality from roads, trails, and the railway appeared to have little effect on the strength of wolf avoidance or selection for individual features. One explanation why wolves in Jasper avoided encounters with people on both roads and trails is that wolf packs along and outside the boundary of the Jasper National Park are sub-

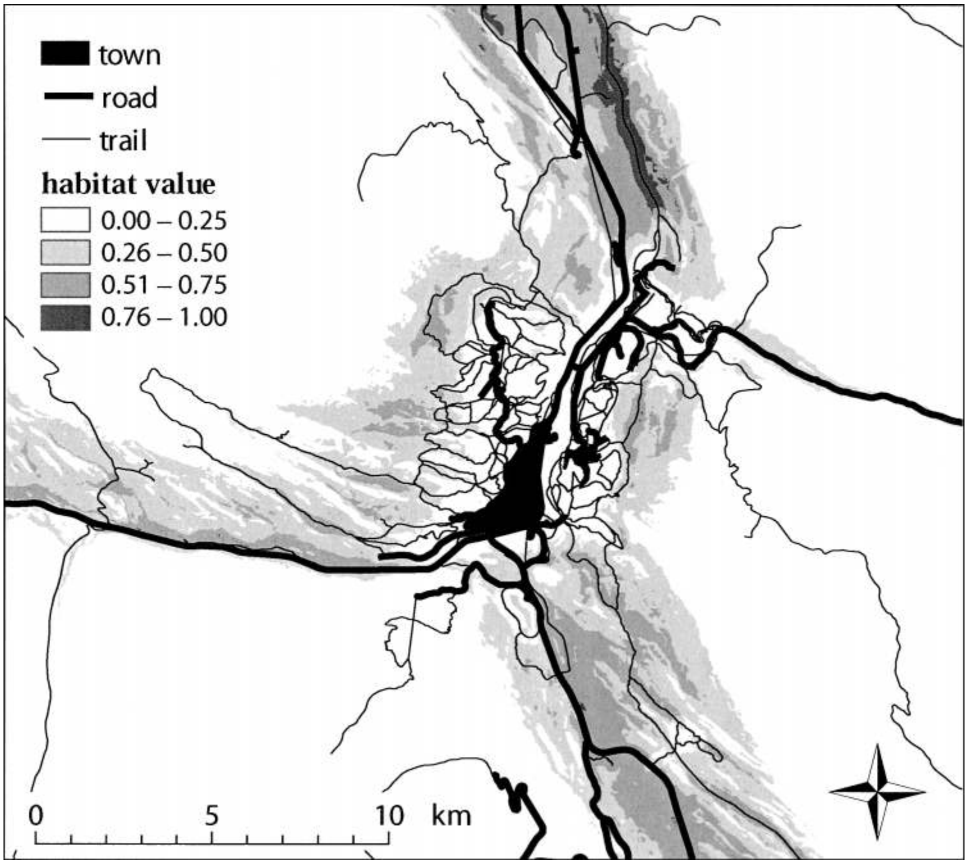

FIG. 5. Wolf habitat map around Jasper, Alberta, Canada. To create this map we generated predictions using a 1:1 matched case-control logistic regression equation. We classified each location and associated habitat attributes as the ''case'' and defined the ''control'' as the median value for the covariates of wolf locations. Thus, the map shows probability of wolf occurrence relative to the median value of wolf observations.

ject to legal hunting and trapping and incur high rates of mortality. Wolves bordering parks south of Jasper had an average annual survival rate of 0.77 and hunting and trapping accounted for 50% of the wolf mortalities (Callaghan 2002). Wolves in Poland, which were subject to hunting and trapping, were displaced similar distances from trails as primary roads, but only during the daylight hours (Theuerkauf et al. 2003*a*). Hunting and trapping along the boundary of Jasper might also explain why wolves in this study were more wary than wolves in some other regions (McNay 2002).

Our main results, which indicated that wolves selected low-use roads and trails as travel routes but avoided areas of high road and trail density, suggest some obvious management implications. Before describing these, we must acknowledge that our results may be weakly confounded by four sources. First, this was a correlative study based on the data gathered from two wolf packs. Therefore, the behavior of wolves in this study area might not represent the behavior of the wider wolf population. Second, wolf selection or avoidance of packed trails created by researchers could potentially confound results. However, given Jasper's relatively shallow, unconsolidated snow, open forests, and dispersed prey, we suspect that the wolves rarely benefited from trails created by trackers. Third, wolf avoidance of trails and roads could be caused by their attraction to prey, which in other regions has been shown to avoid roads (James and Stuart-Smith 2000, Johnson et al. 2000, Rowland et al. 2000, Dyer et al. 2001, Papouchis et al. 2001). In Jasper, however, many ungulates concentrated their movements along roads and even within the town limits, making this confounding effect unlikely (Parks Canada, *unpublished data*). The fourth and final potential confounder is that human activity and prime wolf habitat occurred in similar areas, which could contribute to a positive association with low-use roads and trails. More specifically, roads and trails are typically built at low elevations often along waterways, on dry southwest aspects, or on 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 low-use trails especially. Consequently, this association between roads, trails, and topography could create conservative estimates of road and trail avoidance.

Despite these potentially confounding variables that might inflate the effects we measured, we think it likely that our estimates of trail and road avoidance are overly conservative for two reasons. First, this study occurred during winter when roads receive less than a quarter of their summer traffic and trails receive a twentieth of their summer use (Parks Canada, *unpublished data*). Wolves may be expected to show even greater avoidance during summer when human encounters are much more likely. Moreover, deep snow depths at higher elevations during our field seasons could further affect our avoidance estimates by constraining the movements of wolves to valley bottoms and, thus, near roads and trails. Without such constraints in summer, wolves would be free to show a stronger aversion to trail and road density. A second way that our study may have underestimated the extent of wolf avoidance of human features is caused by the lack of temporal information contained in snow-tracking data. For instance, while wolves in this study traveled close to roads and trails, they may have traveled in these areas at night when levels of human activity were low. Temporal avoidance is typical of wolves that occupy territories with high levels of human activity in Italy and Poland (Ciucci et al. 1997, Theuerkauf et al. 2003*a*).

Wolves have high dispersal and reproductive potential and they are therefore resilient to extinction in the absence of hunting and trapping (Weaver et al. 1996, Callaghan 2002). However, wolf avoidance of high road and trail density may ultimately affect wolves living in Jasper National Park in three ways. First, the steep topography of the areas surrounding Jasper townsite and its several anthropogenic extensions limit alternative routes wolves can employ. Forman (2000) cautioned that human activity generally degrades habitat far beyond its physical footprint, suggesting that roads, trails, and resorts, which are abundant both north and south of the townsite, already severely constrain wolf movement (Fig. 5). If the density of trails continues to increase along the base of steep-sided mountains and within narrow movement corridors, then these trails may further inhibit wolf movement among valleys. Second, beyond constraints of movement, the concentration of roads and trails at low elevations may exclude wolves from some of the most productive habitat where prey populations are highest. Unless wolves in Jasper become more tolerant of human activity as they have in Europe (e.g., Ciucci et al. 1997), loss of this habitat could substantially affect prey availability and their hunting success. A final reason for concern about the effects of anthropogenic disturbance in Jasper is that wolves are more likely to be disturbed from den and predation sites near high levels of human activity (Theuerkauf et al. 2003*b*, but see Thiel et al. 1998). During this study, Pack 2 failed to rear pups for three consecutive years. Few areas within the study area had both attributes preferred for denning (e.g., sandy, loamy soil) and security from disturbance.

In summary, roads, trails, and other human developments may cumulatively affect local distributions of wolves through habitat fragmentation, loss, and degradation and vehicle-caused mortality. Park management may seek to mitigate, slow, or even reverse these effects.

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