Effects of Linear Developments on Winter Movements of Gray Wolves in the Bow River Valley of Banff National Park, Alberta

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EFFECTS OF LINEAR DEVELOPMENTS ON WINTER MOVEMENTS OF GRAY WOLVES IN THE BOW RIVER VALLEY OF BANFF NATIONAL PARK, ALBERTA

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Twice in this century, gray wolves (*Canis lupus*) were exterminated from the central and southern Rockies of Canada (Gunson 1992). The cause of these extirpations was direct persecution, primarily through hunting, trapping, and predator control programs. In recent years (since 1980) wolves have increased in numbers and recolonized areas from which they had been eliminated (Boyd *et al.* 1996). However, the security of newly recovered populations may be tenuous, because wolf ranges are heavily dissected by linear developments (i.e., highways, secondary roads, railways, and power line corridors). Highway mortality has become a primary cause of wolf mortality and there is accumulating evidence of habitat loss, fragmentation, and degradation related to roads (Purves *et al.* 1992, Paquet 1993). Ensured connectivity of quality habitats is important for survival of large carnivores (Beier 1993, Paquet and Hackman 1995, Doak 1995, Noss *et al.* in press), especially for those that face a high risk of mortality from humans or vehicles when travelling across settled landscapes (Noss 1992, Beier 1993).

Besides fragmenting and consuming critical habitat, linear developments provide access to remote regions, which allows humans to deliberately, accidentally, or incidentally kill wolves (Van Ballenberghe *et al.* 1975, Mech 1977, Berg and Kuehn 1982). Despite legal protection, 80% of known wolf mortality in a Minnesota study was human-caused (30% shot, 12% snared, 11% hit by vehicles, 6% killed by government trappers, and 21% killed by humans in some undetermined manner) (Fuller 1989). Mech (1989) reported 60% human-caused mortality in a roaded area (even after full protection), whereas human caused mortality was absent in an adjoining region without roads. On the east side of the Central Rockies between 1986 and 1993, human caused mortality was 95% of known wolf deaths. Of this, 36% were related to roads (Paquet 1993).

Linear developments may also be physical and/or psychological impediments to wolf movement. Road density and human density have been inversely correlated with viable populations of gray wolves in severa areas. Along the Ontario-Michigan border, distribution of breeding packs occurred only in Ontario. Except Cockburn Island, only lone wolves were found in areas close to the border or in Michigan. In Ontario, the density of roads in areas not occupied by wolves was greater than in areas occupied by wolves. Mean road density in Michigan, where no wolves resided, was also greater than in wolf-occupied areas of Ontario. High human densities, represented by road densities of > 0.6 km/km^2, were believed to be a barrier to wolf dispersal into Michigan (Jensen *et al.* 1986).

Studies in Wisconsin, Michigan, Ontario, and Minnesota have shown a strong relationship between road density and the absence of wolves (Thiel 1985, Jensen *et al.* 1986, Mech *et al.* 1988, Fuller 1989). Wolves generally are not present where the density of roads exceeds 0.58 km/km² (Thiel 1985 and Jensen *et al.* 1986, cf. Fuller 1989). In Minnesota, densities of roads for the primary range, peripheral range, and disjunct range of wolves all fell below a threshold of 0.58 km/km². These results, however, probably do not apply to areas on which public access is restricted. Mech (1989), for example, reported wolves using an area with a road density of 0.76 km/km², but it was next to a large, roadless area. He speculated that excessive mortality experienced by wolves in the roaded area was compensated for by individuals that dispersed from the adjacent roadless area.

The response of wolves to different road types and human presence at the boundaries of Kenai National Wildlife Refuge, Alaska, was examined in a study of radio-collared wolves (Thurber *et al.* 1994). Wolves avoided oilfield access roads open to public use, yet were attracted to a gated pipeline access road and secondary gravel roads with limited human use. Thurber *et al.* speculated that roads with low human activity provide easy travel corridors for wolves (see ??). The response of wolves to a major public highway was equivocal. Wolf absence from settled areas and some roads was thought to have been caused by behavioral avoidance rather than direct attrition resulting from killing of animals.

In the Bow River Valley of Banff National Park, Alberta wolf populations are being negatively affected by human activities that reduce habitat effectiveness, reduce populations of prey species, obstruct movements, and increase the risk of mortality (Purves *et al.* 1992, Paquet 1993). Traffic and recreational development will continue to increase within the region, stimulating a demand for additional roads, highways, railways, power line corridors, and increased visitor capacity (B. Leeson pers. commun.). Considering the probable threats to wolf survival, we require a better understanding of how movements of wolves are affected by linear infrastructure. Herein, we report on the behavioral response of wolves to the Trans Canada Highway, the Canadian Pacific Railway, Highway 1a, and the TransAlta powerline corridor. We assess whether wolves are displaced from areas next to these developments, and if these developments are barriers to movements. We also assess the use by wolves of underpasses designed to move wildlife across the Trans Canada highway safely.

STUDY AREA

We conducted the study in Banff National Park, Alberta between 01 November and 31 March in 1989-90 and 1992-1993. Our study focused on the Bow River Valley between Canmore and Lake Louise, a distance of approximately 80 km. The Bow River Valley is a 2-6 km wide glacial valley oriented northwest-southeast between mountain ranges rising to elevations of 3,000+ m. Small towns, roads and developments are scattered throughout the study area. Two major transcontinental transportation routes, the Trans Canada Highway (TCH) and Canadian Pacific Railway (CPR), traverse the Bow River Valley. The TransAlta Powerline also runs the length of the Bow Valley. The powerline corridor is approximately 30 m wide. The area underneath the line is kept clear of brush and trees. The powerline is serviced by truck, all terrain vehicle, and snow machine. The eastern 28 km of the TCH is 4-lane divided highway with speed limits up to 90 km/hour. Although the remainder of the highway (58 km) is double lane, speed limits are the same. The Trans Canada corridor in the unfenced 2 lane section averages 57 m (n = 30) in width, including the shoulders. Average daily traffic volume approaches 11,000 vehicles (Woods 1989). An additional 116 km of secondary roads is within the Bow River Valley (Woods 1991). Human use of the Bow River Valley is forecasted to double over the next 25 years because of new tourist developments and expansion of nearby urban centres (J. Otten pers. commun.).

Between 1983 and 1987, the eastern section of the highway was enclosed with a 2.4 m high, ungulate-proof fence. Underpasses and bridges were provided to help movement of ungulates between areas fragmented by the fenced highway (Woods 1991). The Spray River and Castle Mountain wolf packs recolonized the lower Bow River Valley in the mid 1980s, following an absence of >30 years (Paquet 1993). Portions of their home range comprised the unfenced 2-lane highway and 4 kms of the eastern terminus of the fenced highway. Within the latter area, movements across the highway were restricted to wildlife underpasses approximately 1 km apart. Wolves could also cross the highway by travelling beyond the end of the fence to use the surface of the road. In 1991, the Spray River Pack denned within 500 m of the highway and 200 m of the railway.

METHODS

We used the following general criteria to identify behavioral barriers: (1) movements of wolves were consistently concentrated along the edge of an impediment (Gates 1991); (2) wolf movements piled up at the margin of 2 contrasting landscape types (i.e., a 'dam effect'; Jagomagi *et al.* 1988); and, (3) movements in habitat on the other side of a barrier were minimal. We used winter snow-tracking and radiotelemetry to determine the response of wolves to the following potential natural and artificial linear barriers; TransAlta Power line corridor, Highway 1a, Canadian Pacific Railway, the Bow River, and Trans-Canada Highway. Patterns of activity were determined by recording the number and location of crossings (i.e., a line of tracks left by an animal) (Bider 1968). Ground observations were conducted when sufficient snow cover was present.

We categorized wolf tracks that approached within 50 m of a barrier and remained within 50 m for > 100 m, as an approach. If the tracks continued across a barrier, we recorded a crossing. When wolf tracks approach within 15 m of a potential barrier, we noted whether the tracks: intercepted the barrier and followed it for a minimum distance of 100 m; avoided the barrier by not crossing it and not moving parallel to it for a minimum distance of 100 m; crossed the barrier and continued the same course for a minimum distance of 100 m; intercepted and crossed the barrier, and followed it for a minimum distance of 100 m.

We also recorded wolf tracks at the Healy Creek and Five-Mile Bridge underpasses on the Trans Canada highway. We monitored the underpass and adjacent area daily at approximately 1000 and 1700 hrs. Outside the underpass, approaches were determined by new tracks in the snow. Only tracks within a 15-m zone were recorded. Inside the underpass we counted tracks in sand that was raked, which allowed us to confirm movements into the underpass. On occasion we could identify new wolf tracks inside the underpass, but snow conditions prevented us from verifying outside movements. We report those data but do not include them in our analysis.

We categorized wolf tracks into solitary, paired, and group approaches. We defined group approaches as tracks of ≥3 wolves. When wolves approached an underpass without passing through, we followed the tracks to determine if an alternate route was taken across the highway, or; the wolves were deterred, i.e., did not cross the highway.

We used radiotelemetry to monitor the daily movements of the Spray River Wolf Pack. We estimated the number of times the pack crossed the Trans Canada highway by overlaying the spatial distribution of point data. These data did not allow us to determine crossing points. We also used radiotelemetry to determine the use of 100, 200, 400, and 800 m buffer zones next to roads, highways, power line corridors, and pedestrian/horse trails.

Availability of suitable habitat could influence movements of wolves on either side of a potential linear barrier. Thus, we used a Geographical Information System to calculate the percentage composition of habitat next to barriers. We then tested the significance of the difference between the two percentages using the *G*-test of independence (Sokal and Rohlf 1995). We did not evaluate statistically juxtaposition and geometry of habitat patches, which could also influence travel patterns of wolves. We evaluated habitat at 100 m, 200 m, 400 m and 800 m spatial intervals on both sides of impediments for which wolves showed an aversion. Suitable wolf habitat was classified according to the Banff National Park Ecological Land Classification (section ?). For radiotelemetry data, we assumed that locations would be distributed in proportion to the area encompassed by each classification. The expected frequency for each classification was calculated by multiplying the number of observations by the proportion of the area each classification occupied.

We analysed frequency data by means of the *G*-statistic for goodness of fit and test of independence. *G*-values were adjusted using Williams' continuity correction (Sokal and Rohlf 1981). Replicated Goodness of Fit tests were use to examine frequency distributions of track patterns. The null hypothesis was that each pattern had an equal opportunity of occurrence. Therefore, expected values for each category were calculated as: 1/# categories * Total Observations. We also quantified behavioral responses to linear developments using Ivlev's Index of Electivy (Ivlev 1961). Ivlev's Index expresses the ratio of percentage occurrence divided by percentage expected. Electivity varies from -1 to +1, with values between 0 and +1 indicating preference and values between 0 and -1 indicating avoidance. The results of all statistical tests were considered significant at an α level ≤ 0.05.

RESULTS

Response to Linear Developments

The reaction of wolves to the TransAlta powerline corridor, Highway 1a, Canadian Pacific Railway, and Trans Canada Highway was consistent among years ($P > 0.05$) (Tables 1, 2, 3, 5). However, the response of wolves to the Bow River varied annually (G Williams = 10.63, df = 2, $P = 0.0052$) (Table 4). This was the result of increased crossings by individual wolves in 1991/92 while the river was frozen. Wolves travelling in groups crossed at the same frequency in 1991/92 as other years ($P = 0.3245$). The increased permeability of the frozen river suggests the river can be an impediment to travel. When the river was not frozen wolves often paralleled the shoreline until finding a convenient point of crossing (e.g., bridge, short distance between shores). On occasion wolves crossed by swimming.

Highway 1a and the railway were nearly transparent to movements of wolves (Fig. 1). Wolves usually crossed where they intersected or crossed after paralleling for a short distance. However, the powerline corridor and Bow River affected individual wolves and groups of wolves by changing their direction of travel (*G* Williams = 124.43, df = 4, P = 0.0; *G* Williams = 124.43, df = 4, P = 0.0, respectively) (Fig. 1). The powerline corridor appeared to provide a convenient route of travel, especially when snow-machines used to service the line compacted the snow (section ?).

The unfenced portion of the Trans Canada Highway was a serious barrier that wolves seldom crossed (Fig. 1). From radiotelemetry locations we could infer only 14 crossings in 4 years. No doubt other crossings occurred that we did not detect. Several attempts to cross the Trans Canada resulted in death or injury by collision with vehicles (n = 9) (section ?). These data are included as crossings in the summary tables.

A conspicuous contrast in the quality of habitat on either side of the highway might explain the reluctance of wolves to cross. That is, wolves may not be motivated to cross if habitat on one side is much better than the other. However, we found no significant difference (P > 0.05) in suitability of wolf habitat (section ?) on opposite sides of the Trans Canada (Table 6).

Table 1. Winter response of wolves to the TransAlta power line corridor in Banff National Park, Alberta. Monitoring was conducted between 01 November and 31 March, 1989-1992.

	DIRECTION OF TRAVEL			
	South to North		North to South	
CATEGORY	Approach	Pass	Approach	Pass
Individuals				
1989-90	16	10	19	8
1990-91	19	8	21	10
1991-92	14	8	15	9
Group				
1989-90	13	6	19	12
1990-91	21	10	23	13
1991-92	22	15	18	8

Table 2. Winter response of wolves to Highway 1a in Banff National Park, Alberta. Monitoring was conducted between 01 November and 31 March, 1989-1992.

	DIRECTION OF TRAVEL			
	South to North		North to South	
CATEGORY	Approach	Pass	Approach	Pass
Individuals				
1989-90	42	37	27	27
1990-91	71	70	33	28
1991-92	47	44	31	29
Group				
1989-90	21	21	17	14
1990-91	29	27	25	23
1991-92	31	30	28	26

Table 3. Winter response of wolves to the Canadian Pacific Railway in Banff National Park, Alberta. Monitoring was conducted between 01 November and 31 March, 1989-1992.

	DIRECTION OF TRAVEL			
	South to North		North to South	
CATEGORY	Approach	Pass	Approach	Pass
Individuals				
1989-90	24	13	8	3
1990-91	23	15	26	17
1991-92	31	21	39	29
Group				
1989-90	13	11	19	13
1990-91	29	17	25	13
1991-92	27	15	28	17

Table 4. Winter response of wolves to the Bow River in Banff National Park, Alberta. Monitoring was conducted between 01 November and 31 March, 1989-1992.

	DIRECTION OF TRAVEL			
	South to North		North to South	
CATEGORY	Approach	Pass	Approach	Pass
Individuals				
1989-90	27	8	19	7
1990-91	43	27	23	20
1991-92	41	14	19	2
Group				
1989-90	15	2	17	14
1990-91	21	17	25	23
1991-92	18	5	28	26

Table 5. Winter response of wolves to the Trans Canada Highway in Banff National Park, Alberta. Monitoring was conducted between 01 November and 31 March, 1989-1992.

	DIRECTION OF TRAVEL			
	South to North		North to South	
CATEGORY	Approach	Pass	Approach	Pass
Individuals				
1989-90	27	2	18	1
1990-91	33	1	35	2
1991-92	17	3	28	0
Group				
1989-90	17	2	23	1
1990-91	31	2	33	0
1991-92	33	3	28	2

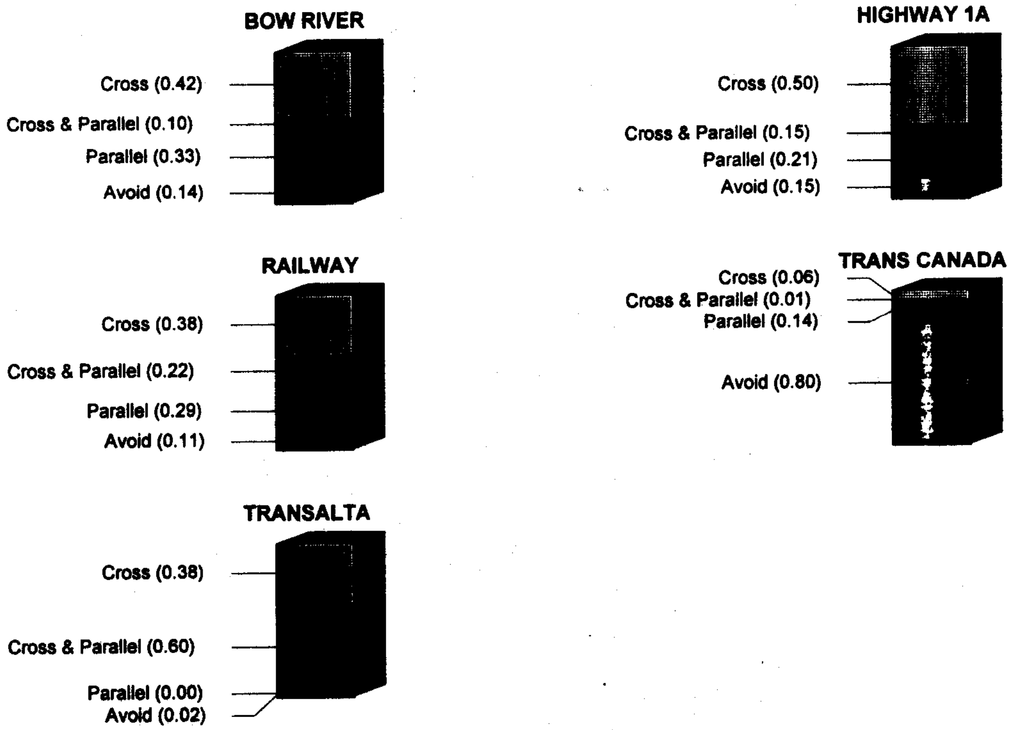


Figure 1. Winter response of wolves to linear developments in the Bow River Valley of Banff National Park, Alberta, 1989-1992. The Bow River is included as a potential natural impediment to movement.

Table 6. Winter ratings of wolf habitat in buffer zones north and south of the Trans Canada Highway between Lake Louise and Sunshine Interchange. This section of the highway is two-lane and unfenced. Ratings were derived from Banff National Park ELC for the period 1989-1993.

	HABITAT SUITABILITY					
BUFFER	V. High	High	Medium	Low	Rock/ice	Water
0-100m N	1.66 (15.3)	4.27 (39.4)	4.4 (40.7)		0.37 (3.4)	0.14 (1.3)
0-100m S	1.27 (18.1)	2.75 (39.2)	2.60 (37.1)		0.35 (5.1)	0.04 (0.5)
0-200m N	1.22 (15.3)	3.29 (41.2)	3.16 (39.6)		0.14 (1.8)	0.17 (2.1)
0-200m S	1.14 (14.3)	3.29 (41.4)	2.74 (34.4)	0.03 (0.4)	0.69 (8.6)	0.07 (0.9)
0-400m N	2.10 (13.1)	6.73 (41.9)	6.82 (39.6)		0.14 (1.8)	0.25 (2.1)
0-400m S	2.54 (15.8)	5.72 (35.7)	6.27 (39.2)	0.20 (1.0)	1.02 (6.4)	0.29 (0.6)
0-800m N	2.96 (9.12)	13.65 (42.1)	15.24 (47.0)		0.13 (0.4)	0.47 (1.5)
0-800m S	5.0 (15.4)	10.17 (31.3)	16.04 (49.4)	0.52 (1.6)	0.20 (0.6)	0.56 (1.5)

Use of Underpasses

For the 3 study seasons combined, we recorded 176 underpass approaches by solitary wolves, 27 by pairs of wolves, and 283 by groups (Tables 7 & 8). The mean number of wolves in group approaches was 5 (range 3-8). Solitary wolves and groups of wolves appeared to respond differently to the underpasses, although the difference was not statistically significant ($P = 0.018$). There was no significant change in group size between study years ($P < 0.05$). Track counts suggested that not all wolves were willing to use Healy Creek underpass. Wolves often approached the underpass and turned away at the entrance, entered part way and turned back, or paralleled the fence until it was possible to cross the road unobstructed (Fig. 2). Often (47% of observations) groups of wolves approached the underpass and only part of the pack went through. The remainder of the pack remained behind or crossed at Five Mile Bridge underpass and Sunshine Junction. Because we were unable to differentiate individuals by tracks, we cannot state with certainty which wolves avoided the underpass.

We recorded a significant annual change in the pattern of movements by groups of wolves through the Healy underpass (G = 10.865, df = 2, P = 0.0045) (Table 7). The proportion of approaches to complete passes through the Healy Creek underpass declined in 1990/91 for all categories and remained low in 1991/92. However, the most drastic change occurred within the group category (Table 7). This change in use of the underpass followed the death of a breeding female identified as a dominant pack member (Paquet 1993).

We also recorded tracks of black bear (n = 2), grizzly bear (n = 2), cougar (n = 2), lynx (n = 9), and wolverine (n = 3), that used the Healy Creek and Five Mile Bridge underpasses. For these species we did not determine the number of approaches.

Table 7. Winter use by wolves of the Healy Creek Underpass on the Trans Canada Highway, Banff National Park, Alberta. Monitoring was conducted between 01 November and 31 March, 1989-1992.

	DIRECTION OF TRAVEL			
	Vermillion to Healy		Healy to Vermillion	
CATEGORY	Approach	Passe	Approach	Pass
Individuals				
1989-90	13	11	16	8
1990-91	10	8	13	6
1991-92	23	9	17	10
Group				
1989-90	20	15	15	12
1990-91	33	10	21	2
1991-92	41	15	24	6

Table 8. Winter use by wolves of the Five-Mile bridge underpass on the Trans Canada Highway, Banff National Park, Alberta. Monitoring was conducted between 01 November and 31 March, 1989-1992.

	DIRECTION OF TRAVEL			
	South to North		North to South	
CATEGORY	Approach	Pass	Approach	Pass
Individuals				
1989-90	11	6	16	12
1990-91	8	5	9	7
1991-92	23	17	17	12
Group				
1989-90	11	9	17	14
1990-91	26	22	17	13
1991-92	31	26	27	19
Total				

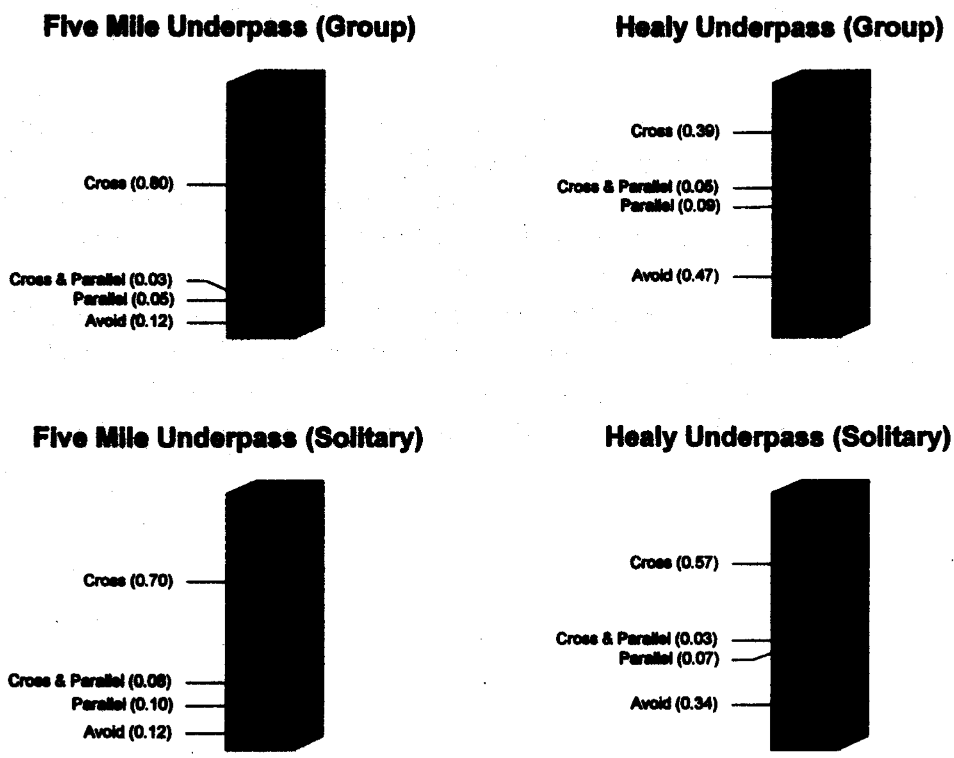
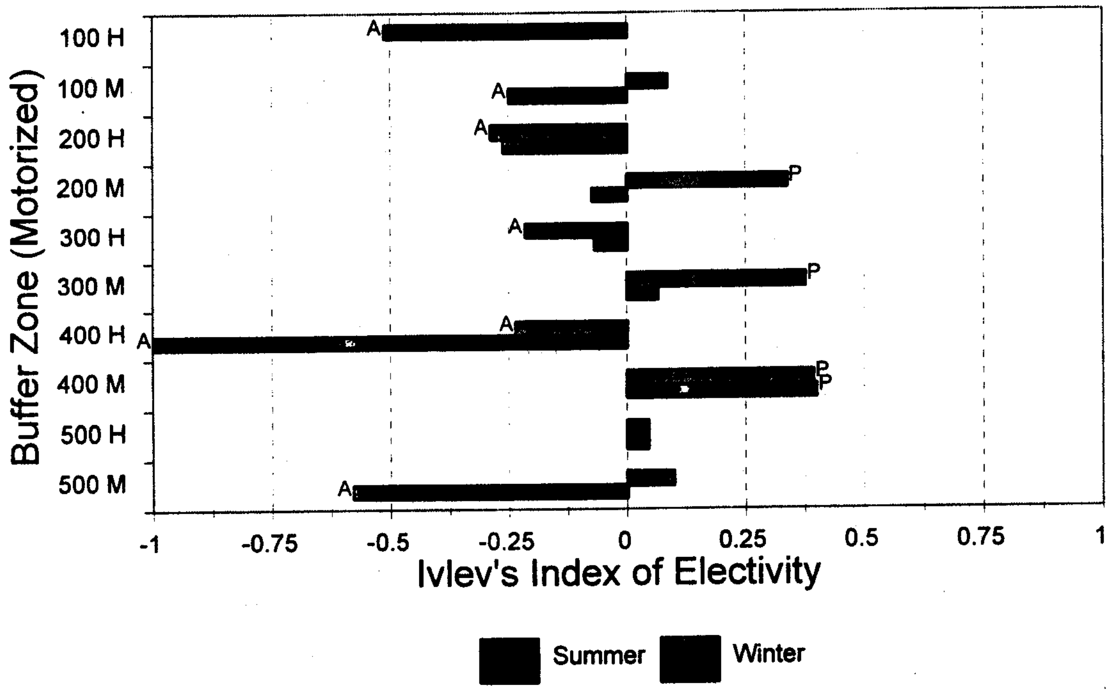


Figure 2. Winter response of wolves to wildlife underpasses along the Trans Canada Highway, Banff National Park, 1989-1993. A group was ≥3 individual wolves.

Displacement from Roads and Trails

In winter, the response of wolves to roads was to avoid areas where traffic volumes were high. Avoidance was evident to within 400 m of the disturbance ($P < 0.05$). A preference was shown for areas classified as medium traffic volumes ($P < 0.05$) (Fig. 3). A similar pattern of avoidance and preference occurred in summer, but the trend was less consistent and not always significant ($P > 0.05$) (Fig. 3). Although wolves may be attracted to high-use pedestrian trails during winter, the overall response to trails was equivocal. No clear or consistent pattern was evident in summer (Fig. 3).



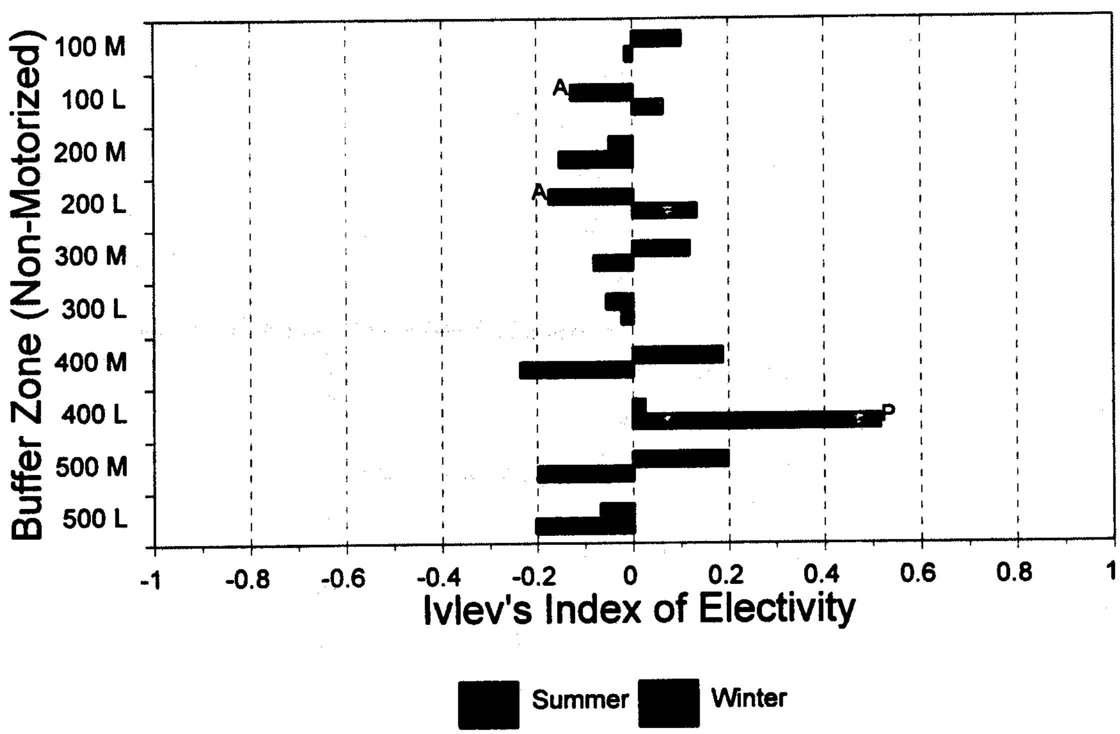


Figure 3. Response of wolves to motorized and nonmotorized roads and trails in the Bow River Valley of Banff National Park, Alberta, 1989-1993.

DISCUSSION

Historically, large scale extermination was the major threat to gray wolves in the Central Canadian Rockies. Now the most significant and pernicious ecological threats to wolf survival are related to loss, alienation, and alteration of habitat resulting from exploitation of natural resources, permanent facilities, and associated infrastructure. These activities and structures are contributing to the fragmentation of landscapes, occluding essential regional dispersal corridors[1], and creating impediments to inter- and intra-territorial movements (Paquet and Hackman 1993). Barriers such as highways and railways are exacerbating the landscape-related problems because they are also direct, and increasingly important, causes of mortality for wolves (Paquet 1993). Moreover, the permanence of these facilities has in many cases foreclosed future opportunities for restoration of impaired landscapes (Paquet and Hackman 1995).

Our results strongly suggest the Trans Canada Highway is a partial barrier to the movements of wolves across the Bow River Valley, which impedes the ability of wolves to disperse naturally across their existing range. The fragmented patchwork of habitats created by the highway likely alters territorial movements. High traffic volumes on the Trans Canada also appear to alienate wolves from using portions of the valley they might otherwise use. Infrastructures associated with the Trans Canada occlude movement through the Valley east of the Town of Banff. Moreover, the highway is the primary cause of wolf mortality (Paquet 1993). The combined consequence of obstruction, alienation, occlusion, and mortality is a reduction in the effectiveness of the Bow River Valley to support wolves.

Other linear developments also affect wolves. Rather than being impediments to movement, the Transalta powerline corridor and the CP Railway seem to redirect movements of wolves, i.e., wolves follow them. This is particularly true when snow depths are high. Whether this is disruptive has not been determined. At the very least, travel patterns probably deviate from what might occur in undisturbed landscapes. For the CP Railway, the immediate concern is that wolves are often killed by trains.

Wildlife underpasses are helpful in getting some wolves across the Trans Canada highway. However, during our study several underpasses were unused, others were used only by solitary wolves, and, for those used by individuals and packs, the consistency of crossings varied over time. This differential response was more pronounced for packs than individuals. As a species, wolves are highly adaptable and individually exhibit broad behavioral variability. Thus, use of underpasses may have been affected by pack composition and experience of pack members. Although we cannot show a causal relationship, we believe loss of a dominant breeding female in 1990 influenced the movements of other wolves. We noted a dramatic drop in use of the Healy Creek underpass following her death. Habituation and social transmission of information may be important in establishing consistent usage of underpasses.

The success of the underpasses in preserving natural ecological processes is difficult to measure without knowing something of the undisturbed norm. First, we can infer from observations elsewhere (including other areas of Banff National Park) that without physiographic constraints, wolves typically move across valleys through a broadly diffuse network of trails.

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[1]We use the term "corridor" synonomously with "landscape linkage" and "linkage zone."

Thus, we would expect that many trails once intersected what is now the footprint of the highway. Second, in undisturbed areas, movements of wolves across valleys are not selectively filtered. In the Bow River Valley some individuals and packs move freely through underpasses whereas others do not.

Thus, several potentially serious problems are not remedied by underpasses. First, the placement of the underpasses may not reflect natural crossings, forcing wolves reluctantly to modify travel patterns. Second, the number of natural crossings is dramatically reduced, depriving wolves of crossing alternatives. Again, wolves are forced to modify travel patterns to use underpasses. Third, not all wolves are willing to use underpasses, which creates a differential sieve that is selective for certain wolves. This could be disruptive of pack structure and cohesiveness. The ecological consequences of these disturbances are unknown. We can conclude that highways and underpasses alter movements of wolves, possibly affecting wolves adversely.

In summary, human population pressures and their associated land uses have supplanted large areas of natural habitat. Within the Bow River Valley the montane ecoregion comprises the highest suitability wolf habitat (Paquet 1993). However, more than 33% (48 km^2) of the montane is already occupied by permanent facilities, and wolves do not use > 16 km^2 situated east of the town of Banff. An additional 8 km^2 south of the unfenced portion of the Trans Canada highway is also not used. Reasons for avoidance of these montane areas are not well understood but are, at least in part, the result of impediments to movements caused by human structures (eg., highways, fences, buildings) and activities (Purves *et al.* 1992, Paquet 1993).

Based on conservative estimates of documented disturbance zones surrounding human activities (Paquet 1995), wolves are alienated from an additional 20 km^2 of montane habitat. In sum, wolves have been physically displaced, partially alienated, or blocked from using a minimum 92 km^2 of the Bow River Valley's montane, i.e., 62% of the best wolf habitat in the Bow River Valley. Much of the problem is the result of disruption from the Trans Canada highway.

LITERATURE CITED

Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. Conserv. Biol. 7:94-108.

Berg, W.O., and D.W. Kuehn. 1982. Ecology of wolves in north-central Minnesota. Pages 4-11 in F.H. Harrington and P.C. Paquet, eds. Wolves of the world. Noyes Publ., Park Ridge, N.J.

Bider, J.R. 1968. Animal activity in uncontrolled terrestrial communities as determined by a sand transect technique. Ecol. Monogr. 38:269-308.

Boyd, D.K., P.C. Paquet, S. Donelon, R.R. Ream, D.H. Pletscher and C.C. White. 1996. Dispersal characteristics of a recolonizing wolf population in the Rocky Mountains. *in* L.N. Carbyn ed, Second North American Symposium on Wolves, Edmonton, AB.

Doak, D.F. 1995. Source-sink models and the problem of habitat degradation: general models and applications to the Yellowstone Grizzly. Conserv. Biol. 9:1370-1379.

Fuller, T.K.. 1989. Population dynamics of wolves in north-central Minnesota. Wildl. Monogr. 105: 1-41.

Gates, J.E. 1991. Powerline corridors, edge effects, and wildlife in forested landscapes of the Central Appalachians. Pages 12-32 *In* (Rodiek, J.E. and E.G. Bolen, eds). Wildlife and habitats in managed landscapes. Island Press, Washington, D.C.

Ivlev, V.S. 1961. Experimental ecology of the feeding fishes. Yale University Press, New Haven, Conn.

Jagomagi, J., M. Kulvik, U. Mander, and V. Jachno. 1988. The structural-functional role of ecotones in the landscape. Ecologia 7:81-94.

Jensen, W. F.; Fuller, T. K.; Robinson, W. L. 1986. Wolf, *Canis lupus* , distribution on the Ontario-Michigan border near Sault Ste. Marie. Can. Field Nat.

Mech, L.D. 1977. Productivity, mortality, and population trends of wolves in northeastern Minnesota. J. Mammal. 58:559-574.

Mech, L.D. 1989. Wolf population survival in an area of high road density. Am. Midl. Nat. 121:387-389.

Mech, L. D., S. H. Fritts, G. L. Radde, and W. J. Paul. 1988. Wolf distribution and road density in Minnesota. Wildl. Soc. Bull. 16:85-87.

Noss, R.F., H.B. Quigley, M.G. Hornocker, T. Merrill, and P. Paquet. In press. Conservation biology and carnivore conservation in the Rocky Mountains. Conserv. Biol.

Noss, R.F. 1992. The wildlands project land conservation strategy. Pages 10-25 *in* Wild Earth (special issue), Plotting a North American wilderness recovery strategy. The Wildlands Project. Canton, N.Y. 88pp.

Paquet, P.C. 1993. Summary reference document - ecological studies of recolonizing wolves in the Central Canadian Rocky Mountains. Unpubl. Rep. by John/Paul and Assoc. for Canadian Parks Service, Banff, AB. 176pp.

Paquet, P.C. and A. Hackman. 1995. Large carnivore conservation in the Rocky Mountains: a long-term strategy for maintaining free-ranging and self-sustaining populations of carnivores. World Wildlife Fund-Canada, Toronto, Ontario. 53pp.

Purves, H.D., White, C.A., and Paquet, P.C. 1992. Wolf and grizzly bear habitat use and displacement by human use in Banff, Yoho, and Kootenay National Parks: a preliminary

analysis. Canadian Parks Service Rept. Banff, Alta. 54pp.
Sokal, R.R. and F.J. Rohlf. 1995. Biometry, Third ed. Freeman, San Francisco, CA. 887pp.
Sokal, R.R. and F.J. Rohlf. 1981. Biometry, Second ed. Freeman, San Francisco, CA. 859pp.
Thiel, R.P. 1985. Relationship between road densities and wolf habitat suitability in Wisconsin, Am. Midl. Nat. 113:404-407.
Thurber, J. M.; Peterson, R. O.; Drummer, T. D.; Thomasma, S. A. 1994. Gray wolf response to refuge boundaries and roads in Alaska. Wildlife Society Bulletin.; 22:61-68.
Van Ballenberghe, V., W. Erickson, and D. Byman. 1975. Ecology of the timber wolf in northeastern Minnesota. Wildl. Monogr.. 43. 43pp.
Woods, J. G. 1989. Second progress report: effectiveness of fences and underpasses on the Trans-Canada Highway and their impact on ungulate populations project. Sept. 1985 - May 1988. Unpubl. Rept. Environment Canada-Parks. 97pp.
Woods, J. G. 1991. Ecology of a partially migratory elk population. Ph.D. Thesis. University of British Columbia, Vancouver. 149pp.