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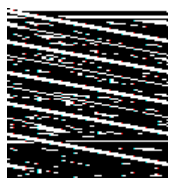
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# WINTER HUNTING PATTERNS OF WOLVES IN AND NEAR GLACIER NATIONAL PARK, MONTANA

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**Abstract:** Wolves (*Canis lupus*) will become an important mortality factor on ungulate populations as they recolonize the western United States. Innovative means of altering the wolf-ungulate dynamic to enhance either prey security or the predator population may be necessary to meet management objectives. From 1990 to 1996, we examined multiscale factors affecting hunting success of wolves during winter in a multi-prey system in northwestern Montana and southeastern British Columbia, Canada. Within their home ranges, wolves concentrated their hunting in wintering areas of white-tailed deer (*Odocoileus virginianus*). They used areas with features that facilitated travel (low snow and vegetative cover) and habitats that were favored by deer. Along their travel routes, wolves killed deer in areas with higher densities of deer and lower densities of elk (*Cervus elaphus*) and moose (*Alces alces*) than expected, based on occurrence of these prey. They killed deer in areas with greater hiding-stalking cover, less slope, and closer to water than expected, based on occurrence along wolf travel routes. More deer were killed in the main valley bottom and ravines than in other landscape classes located along travel routes. Within deer home ranges, wolves killed more deer at flatter sites and at sites with lower densities of deer.

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**Key words:** *Canis lupus*, detect, encounter, gray wolf, habitat, Montana, *Odocoileus virginianus*, predator-prey, spatial scale, white-tailed deer.

A basic theory of predation ecology is that the killing rate of a predator is a product of 3 factors: (1) the rate of prey encounter; (2) the rate of prey detection; and (3) the probability of a successful capture once prey is detected (Taylor 1984). These factors treat foraging and predation at different orders of selection or spatial scales. Predators must first search the landscape to locate patches of prey and then within those patches detect and successfully capture prey. How these 3 factors affect predator foraging and prey vulnerability have rarely been tested in large mammal systems. When they have been tested, researchers have focused on the third factor by examining how animal condition affects vulnerability of prey to capture (see Mech 1996 for a synopsis of this topic). However, predators (including large carnivores) do not kill only animals in poor condition (Kenward 1978, Temple 1987, O'Gara and Harris 1988, Porsin et al. 1988, Kunkel and Pletscher 1999), which suggests that encounter and detection rates are critical in determining capture success.

Habitat features and spatial relationships between predators and prey may affect selection

and vulnerability of prey, capture success (Bergeud et al. 1983, Stephens and Peterson 1984, Van Ballenberghe 1987, Bergeud and Snider 1988), and whether and how long predation limits prey density (Van Ballenberghe 1987, Bergeud 1992). Tanner (1975) modeled several predator-prey systems—including some with 5 species of ungulates—and reported that relatively long search times decreased predator kill rates and thereby added stability to predator-prey interactions. Populations with individuals spaced widely may support higher ungulate numbers, as may areas with ample escape habitat. Both conditions increase the searching time of predators.

Van Ballenberghe (1987), Lima and Dill (1990), and Skogland (1991) indicated that environmental heterogeneity significantly affected kill rates and that certain types of habitat may provide refugia from predation (Wolff 1981, Skogland 1991, Crawley 1992). Similarly, habitat structure and physiography may allow prey to detect predators before the predators are within killing distance (Elliot et al. 1977, Van Orsdal 1984) and allow prey to successfully escape predators.

As wolves recolonize portions of the western United States and elsewhere, they may at times be the primary limiting factor for some ungulate populations (Kunkel and Pletscher 1999). While the value of wolf control in increasing ungulate populations over the long term is debatable (Gas-

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away et al. 1992, Boutin 1992, Boertje et al. 1996, National Research Council 1997), wolf control is probably no longer an acceptable option due to social and political reasons (Boertje et al. 1995, Mech 1995). As a result, we examined alternative habitat and spatial factors that may alter wolf-ungulate dynamics. These relations may suggest how management of habitat and landscape can affect predation rates to meet various objectives for populations of predators and prey. Alternately, identifying factors affecting wolf foraging success may indicate ways to influence and manage wolf populations.

We examined foraging patterns of wolves hunting white-tailed deer, elk, and moose (*Alces alces*) in northwestern Montana from 1990 to 1996. Our objective was to determine the effects of spatial and habitat features on hunting success of wolves (and thereby vulnerability of prey). We hypothesized that: (1) wolves use travel routes that reduce search times (e.g., easy travel corridors); (2) they hunt in areas that have greater densities of preferred prey (elk; Kunkel 1997); (3) within areas of high prey densities, wolves use spatial and habitat features that maximize detection of prey (enhance visibility); and (4) wolves select habitat features that minimize escape of prey (e.g., deep snow, reduced prey group size).

## STUDY AREA

Our 3,000-km<sup>2</sup> study area was in the basin of the North Fork of the Flathead River, Montana and British Columbia, Canada. The valley of the Flathead River varied from 1,024 to 1,375 m in elevation. Land east of the Flathead River (south of Canada) was managed by Glacier National Park. West of the river, land ownership was a mosaic of Flathead National Forest, Coal Creek State Forest, and private property. The British Columbia portion of the study area was composed primarily of Crown (federal government) lands.

The climate is transitional between the northern Pacific coastal and the continental types. Mean temperatures ranged from -9°C in January to 16°C in July (Singer 1979). Snow normally covered the area from mid-November to mid-April. The annual maximum snow depth at the Pole-bridge Ranger Station averaged 65 cm (Singer 1979). Dense lodgepole pine (*Pinus contorta*) forests dominated most of the valley, but subalpine fir (*Abies lasiocarpa*), spruce (*Picea* spp.), western larch (*Larix occidentalis*), and Douglas-fir (*Pseudotsuga menziesii*) communities existed throughout the valley. Meadows and riparian

areas were dispersed throughout the study area. Detailed descriptions of vegetative communities in this area were provided by Habeck (1970), Jenkins (1985), and Krahmer (1989).

Density of deer was approximately 5 times greater than density of elk and 8 times greater than density of moose (Kunkel et al. 1999). Approximately 12 wolves/1,000 km<sup>2</sup> and 70 cougars (*Puma concolor*)/1,000 km<sup>2</sup> occur there (K. E. Kunkel and T. E. Ruth, unpublished data). Grizzly bear (*Ursus arctos*) density was estimated as 64 bears/1,000 km<sup>2</sup> for the Canadian portion of the study area (McLellan 1989), and black bear (*Ursus americanus*) density was approximately 200 bears/1,000 km<sup>2</sup> (B. N. McLellan, British Columbia Ministry of Forests, personal communication).

## METHODS

### Field methods

Wolves were trapped, sedated, and radiocollared following techniques described by Mech (1974) and Ream et al. (1991). Wolves were located from the ground or the air >4 times/week during winter (Nov–Apr). We followed wolf travel routes on skis or snowshoes 1–2 days after wolves left an area and searched for kills and measured habitat characteristics where wolves hunted and made kills.

Deer were captured (Clover 1956) and fitted with radiotransmitters containing mortality sensors. Females were monitored for mortality signals 2–3 times/week during winter and spring and 1–2 times/week during summer and fall. When a mortality signal was detected, the collar was located and the site and any remains were examined to determine cause of death. Mortality signals of radiocollared deer were usually investigated 1–4 days after death.

For all kills, predation was considered to be the cause of death when blood, subcutaneous hemorrhaging at wound sites, or sign of a struggle was found at the site. Evidence such as cougar or wolf hair, tracks, scats; presence of a buried carcass; plucked hair; bite marks and feeding pattern; and percent of carcass found was used to classify the predator responsible for death (O'Gara 1978, Kunkel 1997). The location of the carcass was considered the kill site unless it had been dragged.

Habitat variables were measured in a 30-m-radius plot centered on the kill site. Percent tree canopy coverage was estimated in 1993 by comparing tree canopy over the plot with schematic drawings presented in Unsworth et al. (1991) and placing it into 1 of 5 categories: (1) 0–10%, (2)

Table 1. Proportion of cover types at wolf kills, control sites, wolf routes, and systematic routes in and near Glacier National Park, Montana, for winters 1993–1996.

Cover type	Wolf kills	Control site	Wolf route <sup>a</sup>	Systematic route <sup>b</sup>
Open-shrub	0.10	0.09	0.12	0.09
Ice	0.11 <sup>c</sup>	0.09	0.02 <sup>c</sup>	0.00
Burned timber	0.04 <sup>d</sup>	0.05	0.19 <sup>d,e</sup>	0.09 <sup>e</sup>
Deciduous	0.03	0.03	0.04 <sup>f</sup>	0.10 <sup>f</sup>
Larch/Ponderosa	0.04	0.04	0.04	0.07
Douglas-fir	0.18	0.20	0.07	0.07
Lodgepole	0.05 <sup>g</sup>	0.07	0.13 <sup>g,h</sup>	0.22 <sup>h</sup>
Upland spruce	0.35 <sup>i</sup>	0.27	0.21 <sup>i</sup>	0.25
Lowland conifer	0.12	0.16	0.21 <sup>j</sup>	0.10 <sup>j</sup>
	n = 115	n = 93	n = 885	n = 512

<sup>a</sup> Significant difference ( $\chi^2 = 57.65$ ,  $df = 8$ ,  $P < 0.001$ ) between wolf kill and wolf route.

<sup>b</sup> Significant difference ( $\chi^2 = 80.82$ ,  $df = 8$ ,  $P < 0.001$ ) between wolf route and systematic route.

<sup>c</sup>  $P < 0.001$ .

<sup>d</sup>  $P = 0.10$ .

<sup>e</sup>  $P = 0.004$ .

<sup>f</sup>  $P < 0.001$ .

<sup>g</sup>  $P = 0.10$ .

<sup>h</sup>  $P < 0.001$ .

<sup>i</sup>  $P = 0.009$ .

<sup>j</sup>  $P < 0.001$ .

Table 2. Proportion of habitat structure categories at wolf kills, control sites, wolf routes, and systematic routes in and near Glacier National Park, Montana, for winters 1993–1996.

Structure	Wolf kills	Control site	Wolf route <sup>a</sup>	Systematic route <sup>b</sup>
Nonvegetated	0.12 <sup>c</sup>	0.08	0.01 <sup>c</sup>	0.01
Herbaceous	0.08	0.02	0.09	0.02
Shrub-seedling	0.03	0.08	0.05	0.02
Sapling	0.01	0.00	0.03	0.02
Pole-sapling	0.06 <sup>d</sup>	0.07	0.18 <sup>d</sup>	0.14
Young trees	0.45 <sup>e</sup>	0.41	0.38 <sup>e</sup>	0.35
Mature trees	0.26	0.33	0.24	0.44
	n = 111	n = 83	n = 391	n = 104

<sup>a</sup> Significant difference ( $\chi^2 = 50.05$ ,  $df = 6$ ,  $P < 0.001$ ) between wolf kill and wolf route.

<sup>b</sup> Significant difference ( $\chi^2 = 10.9$ ,  $df = 6$ ,  $P = 0.09$ ) between wolf route and systematic route.

<sup>c</sup>  $P < 0.001$ .

<sup>d</sup>  $P = 0.01$ .

<sup>e</sup>  $P = 0.007$ .

11–30%, (3) 31–50%, (4) 51–75%, and (5) 76–100%. The method was refined in the following years by counting the number of points under canopy cover at 2-m intervals along 2 (1 N-S, 1 E-W) 20-m perpendicular transects centered on the carcass and then placed into 1 of the above 5 categories. Percent hiding cover was determined by visually estimating the percent of a deer obscured at 30 m in the 4 cardinal directions from the carcass. Hiding cover was divided into the same 5 categories as canopy coverage. The mean of the cover classes from the 4 directions was considered the hiding cover for the site. In 1993, only an overall estimate for the plot was made and placed into 1 of the 5 categories. At the start of each field season, all project personnel spent a day in the field standardizing hiding cover classifications. Vegetation cover type at the site was classified based on the types developed by Jenkins and Wright (1988; Table 1). Structure of the dominant vegetation at the site was placed into 1 of 8 categories (Table 2). We recorded whether or not a different structure class could be seen from the center of the plot. The number of downed trees (>4 cm diameter) within 10 m north of plot center was recorded. The mean height above ground of these obstacles was determined by measuring the distance from the ground to the top of each log.

Snow depth was measured at 2-m intervals on a 10-m transect going north from plot center. When present, 5 representative prey track depths and 5 representative predator track depths (wolf or cougar) were measured within the plot. Slope at each plot was estimated using a clinometer, and aspect was recorded to the nearest degree. Topographic position (U.S. Forest Service code; Table 3) of each plot was also recorded.

To estimate relative densities of prey at the sites, we skied 2 100-m transects in opposite directions starting at plot center. At kill sites, we attempted to place these transects perpendicular to the travel route of the predator responsible for the kill. If the travel route was not known, and if the site was on an incline, the transects were oriented up and down the slope. If neither of these conditions applied, the transects went east and west. The distance to the first deer, elk, and moose track on each transect was recorded. If no track was encountered, the distance recorded was 100 m. The number of deer, elk, and moose tracks located on both transects (0, 1, or 2; only the first track on each transect was recorded) was divided by the distance to that track (e.g., 1/100

Table 3. Proportion of topographic classes at wolf kills, control sites, wolf routes, and systematic routes in and near Glacier National Park, Montana, for winters 1993–1996.

Topographic class	Wolf kills	Control site	Wolf route <sup>a</sup>	Systematic route <sup>b</sup>
Valley bottom <sup>c</sup>	0.27 <sup>d</sup>	0.29	0.15 <sup>d</sup>	0.11
Ravine	0.08 <sup>e</sup>	0.04	0.01 <sup>e</sup>	0.01
Lower slope <sup>f</sup>	0.07	0.18	0.15 <sup>d</sup>	0.33 <sup>g</sup>
Mid-upper slope <sup>f</sup>	0.05	0.07	0.10	0.11
Wide valley slope	0.24	0.17	0.32 <sup>h</sup>	0.05 <sup>h</sup>
Ridgetop-knoll	0.06	0.04	0.06	0.02
Bench-terrace	0.16	0.18	0.15	0.19
Creek bottom	0.08	0.05	0.06 <sup>i</sup>	0.16 <sup>j</sup>
	n = 110	n = 84	n = 391	n = 95

<sup>a</sup> Significant difference ( $\chi^2 = 33.42$ ,  $df = 7$ ,  $P = 0.002$ ) between wolf kill and wolf route.

<sup>b</sup> Significant difference ( $\chi^2 = 33.65$ ,  $df = 7$ ,  $P = 0.002$ ) between wolf route and systematic route.

<sup>c</sup> Main valley.

<sup>d</sup>  $P = 0.03$ .

<sup>e</sup>  $P = 0.001$ .

<sup>f</sup> Side valley.

<sup>g</sup>  $P = 0.008$ .

<sup>h</sup>  $P < 0.001$ .

<sup>i</sup>  $P = 0.005$ .

if 1 deer track was found at 90 m in 1 direction and no deer track was found along the opposite 100-m transect) to obtain the number of deer, elk, and moose tracks/m. This value was divided by the number of days since the most recent snowfall of >5 cm to adjust for snowfall effects. When snowfall had not occurred for 7 or more days, we divided the value by 7 because we assumed that track deposition had plateaued by this time, and tracks started to deteriorate. Tracks were classified as either: (1) single animal; (2) light trail (2–3 animals); (3) medium trail (4–6 animals); or (4) heavy trail (packed trail or runway; >6 animals). The distance to a cervid trail (medium or heavy trail) was tabulated the same way as distance to the first track.

### Spatial Analysis

Universal transverse mercator (UTM) coordinates from a 1:24,000-scale map or from a global positioning system receiver were recorded at each habitat plot. These coordinates were entered into a geographic information system (PAMAP, ARCVIEW). Spatial and vegetative attributes were generated for each site from GIS

map layers of the study area created by Singleton (1995) and the Montana Cooperative Wildlife Research Unit Spatial Analysis Laboratory (Redmond 1996). These maps represented cover type, structure class, canopy coverage, modified normalized difference vegetation index (NDVI: a measure of absorption variation in middle infrared wavelengths that are known to be associated with canopy closure; Butera 1986, Redmond 1996), topographic position, slope, aspect, distance to open roads, distance to trails, and distance to water. A variable called *trawdis* (travel distance) was created to measure the distance to a linear feature that could be used by wolves for travel; this was the shortest of the distance to roads, distance to trails, or distance to water. We created cover type and structure class polygons from which we could estimate area and distance to edge of the polygon.

### Scales of Analysis

Because factors affecting vulnerability of prey and hunting strategies of wolves probably occur at different scales, we made comparisons at 3 different scales: (1) prey encounter; (2) prey detection and capture; and (3) prey capture.

**Prey Encounter.**—We skied track transects at 1-km intervals and measured habitat variables at sites spaced 3 km apart along systematic transects that followed hiking trails, roads (*trawdis* not used in the encounter scale analysis), and pellet transects (Kunkel 1997). These variables were compared to variables collected at 1-km intervals along wolf travel routes to test the null hypothesis that habitat and spatial variables where wolves chose to travel and hunt did not differ from what was available within their home range.

**Prey Detection and Capture.**—We tested the null hypothesis that habitat and spatial variables did not differ between sites along wolf travel routes and sites where wolves killed deer.

**Prey Capture.**—We tested the null hypothesis that habitat and spatial variables at kill sites did not differ from the same variables measured at another site within an area equivalent to a deer's home range; these control sites were randomly located 500 m in a random direction from wolf kill sites.

### Statistical Analysis

We used univariate analyses to test the null hypothesis that individual variables did not differ between paired site class comparisons (e.g., wolf kill sites vs. control sites). Because we were testing

different hypotheses with each comparison of site pairs, no adjustments of *P* values were necessary for these tests (Rice 1989). None of the interval scale variables was distributed normally (Lilliefors test; Norusis 1993) and no transformations successfully normalized them, so we used Kruskal-Wallis (KW) tests to compare these variables among sites. When large sample size was the suspected reason for rejection of the normality assumption, we also examined results of 2-sample *t* tests. When the KW test was significant ( $P < 0.10$ ), we compared sites using Mann-Whitney *U* statistics.

Snow depths were compared between sites by pairing sites examined on the same day. Because snow depths were not normally distributed but were symmetrical, we used the Wilcoxon Matched Pairs test to make comparisons. Categorical habitat variables were cross-tabulated by sites (e.g., travel vs. kill sites). We used Pearson's Chi-square statistic to test the null hypotheses of independence among categories. When  $>20\%$  of cells had expected values  $<5$ , we combined adjacent (similar) categories. We rejected null hypotheses when  $P \leq 0.05$ . Adjusted standardized residuals  $([\text{observed} - \text{expected}/\text{expected}^{0.5}]/\text{standard error})$  were used to identify significant cells (Haberman 1973). Probability values were ad-

justed by multiplying by the number of cell pairs in the cross-tabulation (Bonferroni adjustment: where overall  $P = 0.001$  and cell pairs = 5,  $0.001 \times 5 = 0.005$ ; Rice 1989).

## RESULTS

We captured and radiotagged 30 wolves in 3–4 packs from May 1992 through April 1996. Aerial counts made in May of each year indicated packs consisted of 5, 11, 3, and 4 wolves in 1992; 10, 7, 5, and 6 in 1993; 11, 3, and 7 in 1994; 10, 4, and 10 in 1995; and 12, 5, and 6 in 1996. We captured and radiotagged 67 female deer.

### Travel Routes

Wolves used areas for travel that had lower snow depths (median = 23.5 cm,  $n = 91$  vs. 31.5 cm,  $n = 81$ ; Mann-Whitney [MW]  $Z = -2.30$ ,  $P = 0.02$ ) and shallower deer track depths (median = 13.5 cm,  $n = 54$  vs. 16.0 cm,  $n = 70$ ; MW  $Z = -1.75$ ,  $P = 0.08$ ) than expected based on occurrence along systematic routes.

Wolves used areas for travel with 8% less elk (MW  $Z = -2.23$ ,  $P = 0.03$ ), 22% less hiding cover (MW  $Z = -5.30$ ,  $P < 0.001$ ), and 1.4 times more slope (MW  $Z = -11.90$ ,  $P = 0.05$ ; Table 4) than expected based on occurrence within their home

Table 4. Habitat and spatial variables associated with wolf kill and other sites in and near Glacier National Park, Montana, 1992–1996.

Habitat variables	Habitat category											
	Wolf kill			Control			Travel route			Systematic		
	$\bar{x}$	SD	<i>n</i>	$\bar{x}$	SD	<i>n</i>	$\bar{x}$	SD	<i>n</i>	$\bar{x}$	SD	<i>n</i>
Deer tracks/km	32.9	18.0	101	38.7	8.0	81	21.7	1.0	932	12.4	2.0	696
Elk tracks/km	0.3	0.0	102	2.3	0.0	81	2.4	0.0	933	2.6	1.0	696
Moose tracks/km	0.2	0.0	102	0.2	0.0	81	1.1	0.0	933	1.4	0.0	696
Aspect (degrees)	134.7	14.7	61	122.3	14.0	49	151.3	5.7	366	144.0	11.3	82
No. of deadfall encounters	28.3	4.4	54	30.0	3.7	48	19.4	2.8	47	27.2	2.7	95
Hiding cover (%)	12.8	0.7	62	12.3	0.7	50	10.4	0.2	387	13.4	0.5	95
Slope (degrees)	5.4	0.9	84	9.7	1.6	61	9.5	1.1	50	5.9	0.8	95
Trail distance (m)	167.7	9.5	27	139.7	14.1	24	155.0	3.3	364	na	na	na
NDWI <sup>a</sup>	6,630.0	1,731.0	115	6,001.0	1,910.0	90	2,370.0	575.0	369	3,455.0	1,208.0	111
SC edges <sup>b</sup>	667.0	52.0	115	585.0	56.0	90	699.0	37.0	368	1,062.0	111.0	111
SC area <sup>c</sup>	3,629.0	339.0	115	3,405.0	377.0	90	3,959.0	196.0	369	4,573.0	370.0	111
Trailw <sup>d</sup>	228.0	24.0	115	238.0	30.0	90	353.0	15.0	369	na	na	na
Road distance (m)	1,858.0	123.0	371	1,952.0	256.0	90	1,720.0	123.0	371	na	na	na
Trail distance (m)	1,465.0	104.0	116	1,359.0	113.0	90	1,645.0	66.0	371	na	na	na
Stream distance (m)	349.0	33.0	116	340.0	38.0	90	387.0	18.0	371	na	na	na

<sup>a</sup> Normalized difference vegetation index.

<sup>b</sup> Distance (m) to edge of structure class polygon.

<sup>c</sup> Area of structure class polygon.

<sup>d</sup> Distance (m) to closest road, trail, or stream.

range. Lower slopes in side valley bottoms were 0.45 times as abundant, and creek bottoms were 0.32 times as abundant along travel routes than within home ranges. Wide valley slopes were 6.4 times more common along travel routes than within home ranges (Table 3). Burned timber was 1.8 times more abundant, and lowland conifer cover type was 2.1 times more abundant along travel routes than within home ranges. The deciduous cover type was 0.40 times as abundant and lodgepole pine cover type was 0.59 times as abundant along travel routes as within home ranges (Table 1). Wolves hunted in areas with 32% less modified NDVI than occurred within home ranges (MW  $Z = -1.87$ ,  $P = 0.06$ ; Table 4) and in areas 37% closer to the edge of structure class polygons (MW  $Z = -2.50$ ,  $P = 0.012$ ; Table 4).

During 1993, wolves selected areas for travel with 5.3 times more deer ( $\bar{x} = 0.21$  vs. 0.004, MW  $Z = -3.15$ ,  $P = 0.002$ ), 10 times more elk ( $\bar{x} = 0.003$  vs. 0.0003, MW  $Z = -4.70$ ,  $P < 0.001$ ), and 40 times more moose ( $\bar{x} = 0.001$  vs. 0.00003, MW  $Z = -4.61$ ,  $P < 0.001$ ) than occurred along systematic routes.

#### Kill Site versus Travel Route

The difference between depth of deer tracks and wolf tracks was significantly greater along wolf travel routes than at kill sites (median = 6.5 cm vs. median = 3.0 cm;  $n = 26$ , Wilcoxon  $Z = -2.386$ ,  $P = 0.02$ ). Wolf tracks were shallower along travel routes than at kill sites (median = 3 cm vs. median = 4 cm;  $n = 29$ , Wilcoxon  $Z = -1.722$ ,  $P = 0.09$ ). Snow depth at kill sites and along wolf travel routes were similar (median = 21.5 cm vs. median = 22 cm;  $n = 44$ , Wilcoxon  $Z = -0.671$ ,  $P = 0.50$ ), as were deer track depths at kill sites and along wolf travel routes (median = 11 cm vs. median = 11 cm;  $n = 35$ , Wilcoxon  $Z = -0.411$ ,  $P = 0.68$ ).

Wolves killed deer at sites with 1.5 times more deer (MW  $Z = -9.166$ ,  $P < 0.001$ ), 0.13 times as many elk (MW  $Z = -3.658$ ,  $P = 0.0003$ ), and 0.18 times as many moose (MW  $Z = -2.913$ ,  $P = 0.004$ ; Table 4) as expected based on occurrence of these prey along travel routes. Hiding cover was 1.2 times greater at kill sites than along travel routes (MW  $Z = -3.50$ ,  $P = 0.0005$ ), and kill sites had 37% less slope than travel routes (MW  $Z = -2.51$ ,  $P = 0.01$ ). The non-vegetated structure class was 12 times more abundant and young tree class was 1.6 times more abundant at kill sites than along travel routes. The pole-sapling structure class was 0.28 times as abundant at kill sites than along wolf routes (Table 2). Ice was 5.5

times more abundant and upland spruce was 1.7 times more abundant at kill sites than along travel routes (Table 1). Burned timber was 0.25 times as abundant and lodgepole pine was 0.38 times as abundant at kill sites than along travel routes. The valley bottom class was 1.8 times more common, and ravines were 8 times more common at wolf kills than along travel routes (Table 3). Wolves killed deer at sites with 2.8 times more NDVI (MW  $Z = -3.92$ ,  $P = 0.0001$ ) than travel routes and 0.90 from the distance to water as found along travel routes (MW  $Z = -1.79$ ,  $P = 0.07$ ; Table 4).

#### Wolf Kill Site versus Control Site

Snow depths were similar at kill sites and control sites (median = 28 cm vs. median = 29 cm,  $n = 71$ , Wilcoxon  $Z = -0.67$ ,  $P = 0.500$ ) as were deer-track depths (median = 14.5 cm vs. median = 16,  $n = 50$ , Wilcoxon  $Z = -0.48$ ,  $P = 0.633$ ), wolf-track depths (median = 0.5 cm vs. median = 0.5,  $n = 16$ , Wilcoxon  $Z = -1.54$ ,  $P = 0.12$ ), and the difference between wolf- and deer-track depths (med = 0.0 vs. 0.0,  $n = 16$ , Wilcoxon  $Z = -1.12$ ,  $P = 0.26$ ).

Kill sites had 44% less slope than control sites (MW  $Z = -2.37$ ,  $P = 0.02$ ; Table 4), and were 1.2 times farther from deer trails than were control sites ( $x = 1.65$ ,  $P = 0.10$ ).

## DISCUSSION

### Prey Encounters

Habitat and spatial features used by wolves varied among the scales examined, and these features probably optimized the ability of wolves to encounter, detect, and capture prey. As predicted, within their home ranges, wolves chose to travel in areas with features that facilitated travel (reduced snow and vegetative cover) or that enhanced an encounter with prey (cervid winter ranges; Kunkel 1997). The wolves selected topographic, cover, and slope classes similar to those selected by prey within winter ranges (Keay and Peek 1980; Jenkins and Wright 1988; Krahnert 1989; Rachael 1992; Pauley et al. 1993; K. Kunkel, unpublished data). Contrary to 1 of our predictions, wolves used areas for travel with greater densities of deer and lower densities of elk. The most abundant prey in the study area is deer (Jenkins and Wright 1988, Kunkel et al. 1999), and wolves concentrated their hunting in deer winter ranges where elk were less abundant (Bureau 1992, Kunkel 1997). Along travel routes, wolves preyed on more elk than deer (Kunkel 1997) but probably chose to hunt in deer winter

ranges because deer were the most abundant prey in the study area. Areas where deer wintered were the same from year to year (and thus predictable), while areas where elk wintered were more variable (Bureau 1992, Huggard 1993, Kunkel 1997).

### Prey Detection and Capture

Habitat and spatial features affecting capture success appeared to be more important to wolf predation success than features that affected prey detection. We predicted that wolves would select hunting areas with good prey detectability. However, our analysis suggested that predator concealment was more important for wolf success in hunting deer. This may have resulted from wolves relying more on scent than vision to detect prey (Mech 1966a), or high densities of deer in wintering areas assured that detection was not a limiting factor.

Wolves were more successful killing deer in dense stalking-hiding cover. A primary antipredator strategy of deer is to detect predators and maximize distance so they can elude them (Mech 1966a, 1970, 1984; Lingle 1992). Differences in alert behavior indicate that deer in dense vegetation are more wary than deer in open areas (LaGory 1987). Experiments in our study area showed that deer fed more often in areas with sparse cover (Kotler et al. 1994, Kunkel 1997).

Wells and Bekoff (1982) indicated that canids were more successful killing in areas of sparse cover. However, in Yukon Territory, coyotes were more successful hunting hares (*Lepus americanus*) in dense habitats than in more open habitats, probably because these habitats allowed coyotes to approach hares to within killing distance (Murray et al. 1995). This strategy may have been used because the sustained speed of coyotes did not permit successful capture of hares (Curio 1976). The same may be true for wolves chasing deer in deer yards. Nelson and Mech (1993) reported that greater than 90% of the observations of wolves chasing deer and moose in Minnesota resulted in escape by the prey. The availability of escape trails and the confusion provided by other deer likely produce escape advantages for deer (Sweeney et al. 1971, Crist 1981, Nelson and Mech 1981). For wild dogs (*Lycaon pictus*), the reduced flight distance of male gazelles (*Gazell thomsoni*) probably was the most important factor accounting for the higher rates of hunting success on this group (Fanshawe and Fitzgibbon 1993). Wolves certainly are capable

of killing prey in areas without stalking cover, but we believe that when wolves hunt deer concentrated in wintering areas, wolves are much more successful when they can closely approach their quarry without detection.

Concentration in wintering areas by deer facilitates escape along runways, predator detection, predator confusion during pursuit, sharing of predation risk (lower predator:prey ratios), and familiarity of escape terrain (Geist 1981, Nelson and Mech 1981, Mech 1984, Messier and Barrette 1985). The relative importance of these various mechanisms is not clear. Messier and Barrette (1985) suggested that density of runways may be the most influential mechanism for deer-coyote systems. Successful coyotes relied on cornering deer in deep snow away from runways. Wolves, however, rely much less on such conditions for capture success. Within the range of snow depths occurring over the course of our study, snow depth was not related to wolf kill success. Higher kill rates away from trails, however, suggest that these are important as deer escape routes in wolf habitat. The benefits of predator detection, terrain familiarity, and predator confusion (Nelson and Mech 1981, Messier and Barrette 1985) provided by trails appear to be relatively more important mechanisms than is reduced snow depths along trails.

Sloped terrain may help deer to detect and avoid wolves. Bihakow (1982) and Murie (1944) reported that when red deer (*Cervus elaphus*), caribou (*Rangifer tarandus*), and Dall sheep (*Ovis dalli*) were above wolves, or if they ran uphill, wolves did not pursue. Wolves in this and other studies also made more kills in ravines and closer to water and on ice (Pimlott 1967, Mech and Frenzel 1971, Bihakow 1982, Mech 1984).

In summary, the element of surprise (as provided by stalking cover) appears to be a very important factor affecting predation success of wolves in our study. Prior to our work, only anecdotal evidence existed for the value of surprise to wolves. Prey condition was assumed to be the primary factor affecting success. The relative value of predator detection and prey quality could not be evaluated in our study, but Kenward (1978) showed that surprise interacted with prey condition to determine attack success of goshawks (*Accipiter gentilis*) on pigeons (*Columba palumbus*).

We found that habitat and landscape features affected wolf hunting success and therefore probably affected the functional response of wolves. Whether these features can be manipulated to

affect the kill rate of wolves remains to be tested. Such manipulations may simply result in longer and more careful searches by wolves (McCullough 1979, Wood and Hand 1985) to maintain the same kill rate, or they may result in changes in selection of prey in poorer condition (Potvin et al. 1988).

Very little is known about how habitat and landscape features in the Rocky Mountains (or elsewhere) influence the security of cervids in relation to predators. Few behavioral decisions an animal makes are as critical as predator avoidance. Most studies of habitat preference tell us nothing about whether the habitats are critical for survival (White and Garrott 1990). This study provides evidence that use of some habitats resulted in lower probabilities of predator-caused mortality for deer. Multivariate analysis of these data further supports these results (Kunkel 1997). The next step should be to manipulate habitat components and structure and monitor resulting survival and kill rates.

## MANAGEMENT IMPLICATIONS

Results from this work indicate several avenues for management to influence hunting success of wolves. Strategies in western North America where impacts of wolves on deer are a concern could be focused on ways to reduce wolf predation of deer. In areas where prey such as deer are overabundant, the opposite approach could be taken. Hunting success of wolves preying on deer could probably be reduced by concentrating deer in a few large deer yards or wintering areas with high deer density as opposed to several smaller lower-density areas (Messier and Barrette 1985, Patterson and Messier 2000). This might be accomplished through manipulation of food and cover in selected winter ranges. Deciduous browse and low evergreen shrubs or lichens might be optimal (Singer 1979, Jenkins and Wright 1987). Predator detection and escape and predator-adaptive behavioral changes (i.e., resource depression; Charnov et al. 1976, Hugdard 1993, Kunkel 1997) would likely be optimized under this strategy. However, the increased presence of hunting wolves may reduce foraging by deer due to their increased levels of wariness. The effect of such a strategy on deer exposure to their other primary predator, cougars, would require more research.

Control of fire in the Rocky Mountains has resulted in forest succession, which has increased cover to favor predators (Barrett and Arno 1982).

Similar anthropogenic changes explain declines in waterfowl (Clark and Nudds 1991), bighorn sheep (*Ovis montanus*; Berger and Welhausen 1991), and moose (Bergerud 1981). Prior to the arrival of Europeans, lightning-caused and Indian-caused fires produced habitats in many portions of the Rockies that were more open than they are today (Barrett and Arno 1982). In fact, 1 of the reasons hypothesized for use of fire by Indians was to reduce camouflage for enemies (Barrett and Arno 1982). Prescribed burns in deer winter ranges can reduce stalking cover and improve browse production. Fires must be managed to reduce undergrowth and small trees but to maintain snow mitigation structure (canopy) provided by large trees. Within open areas, interspersed of dense hiding cover might facilitate deer escape. More research is needed to determine the optimum arrangement of such cover.

To further reduce wolf kill rates, areas surrounding winter ranges could be managed to reduce ease of wolf travel. Contiguous blocks of dense timber with few trails and roads could aid in this (Bergerud 1981, McNay and Voller 1995).

Peck et al. (1982) noted the lack of knowledge about the role of security cover in maintaining deer populations. Despite this, management recommendations for deer winter range in the Rocky Mountains have largely failed to include the role of predators in habitat use by deer (Keay and Peck 1980, Jenkins and Wright 1988, Pauley et al. 1993; but see McNay and Voller 1995 for black-tailed deer [*Odocoileus hemionus*]). We advocate applying our recommended prescriptions as integral parts of management programs (MacNab 1983, Walters and Holling 1990, Clark and Nudds 1991) that include measuring wolf predation rates or deer survival rates. Excluding the role of predators in deer habitat analysis may create especially difficult management scenarios (i.e., prolonged depressed densities of prey; Boertje et al. 1996) where wolves recolonize the western United States and elsewhere.

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