Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia

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Abstract: We compared habitat features at sites where wolves (*Canis lupus*) killed moose (*Alces alces*), sites 500 m from kills, telemetry locations of moose, and random sites, to examine the influence of logging and other landscape features on the vulnerability of moose to predation by wolves in southeastern British Columbia during the winters of 1984–1985 through 1995–1996. Moose-kill sites were located farther from the edges of seedling and pole size-class patches than telemetry locations. Road density was lower and wolf use was higher in areas where kill sites occurred than in areas where relocation or random sites occurred. Kill sites were located at lower elevations than relocation or random sites. A logistic regression model using road density, elevation, distance from trails, and distance from size-class polygon edges successfully classified 94.5% of sites as either kills or locations. Moose density was greater and hiding-cover levels were lower at kill sites than at control sites. Forest harvest practices in this study area apparently did not increase the vulnerability of moose to wolf predation.

Résumé : Nous avons comparé les propriétés de l'habitat à divers sites où des Loups gris (*Canis lupus*) ont tué des Orignaux (*Alces alces*), à des endroits situés à 500 m des sites précédents, à des sites de repérage télémétrique d'orignaux, et à des sites aléatoires; notre objectif était d'examiner l'influence de la coupe du bois et d'autres propriétés du paysage sur la vulnérabilité des orignaux à la prédation par les loups dans le sud-est de la Colombie-Britannique au cours des hivers de 1984–1985 à 1995–1996. Les points de prédation se trouvaient plus loin des bordures des terrains contenant des jeunes pousses et des arbres au stade perche que les sites de repérage télémétrique. Les points de prédation se trouvaient dans des zones comportant moins de routes, à des altitudes plus basses et dans des zones plus achalandées par les loups que les sites de repérage ou les sites aléatoires. Un modèle de régression logistique tenant compte de la densité des routes, de l'altitude, de la distance des sentiers et de la distance des bordures du polygone des classes de taille a permis de classifier correctement 94,5% des sites comme sites de prédation ou sites de repérage. La densité des orignaux était plus élevée et la couverture protectrice se trouvait à un niveau plus bas aux points de prédation qu'aux sites témoins. Les procédures de coupe utilisées dans la région ne semblent pas avoir augmenté la vulnérabilité des orignaux à la prédation par les loups.

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Introduction

Forest management practices have often led to forest fragmentation (Hunter 1990). One of the hypothesized outcomes of this fragmentation is the exposure of animals to increased predation. Higher levels of predation on bird nests occur when patch size is reduced and edge is increased (Wilcove et al. 1986; Paton 1994). Little research has been done to examine this phenomenon in large mammal predator–prey systems.

Bergerud (1981) hypothesized that, as logging reduces the size of residual forest patches and increases the density of roads, the travel and searching efficiency of large carnivores

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is enhanced. Bergerud (1988) postulated that part of the decline in woodland caribou (*Rangifer tarandus*) numbers to low levels in British Columbia was due to harvest practices that concentrated caribou in small patches that were easily accessible to wolves (*Canis lupus*) traveling on roads. Langley and Pletscher (1994) found that moose (*Alces alces*) calving areas in northwestern Montana were characterized by greater levels of hiding cover than were random sites.

Conversely, the control of fire may have resulted in forests with increased stalking cover for predators. Kunkel (1997) found that deer are killed more frequently by cougars (*Puma concolor*) and wolves in areas where hiding-cover levels were greater, possibly as a result of predators being able to approach prey closely before being detected.

Particular habitat features may also provide refuges that act at a finer scale to reduce detection and capture of prey (Wolff 1981; Skogland 1991; Crawley 1992). Other habitat features may allow prey to detect and successfully evade predators before the predators are within killing distance (Elliot et al. 1977; Van Orsdal 1984). These may be particularly important for moose (Stephens and Peterson 1984).

The effects of habitat alteration, particularly of cutting practices and roads, on ecosystem sustainability in terms of

ungulates and their predators is unknown. A knowledge of how habitat and spatial factors affect vulnerability of prey may suggest how wildlife managers can manage habitats and landscapes in order to affect predation rates, to meet objectives for populations of both predators and prey. We examined how habitat and landscape features, particularly as they are modified by logging, affect predator–prey relationships in a wolf–moose system. To do so, we compared habitat variables at sites where wolves killed moose with habitat variables at sites where we located radio-tagged moose and at random sites.

Methods

Study area

Our study was conducted in the North Fork of the Flathead River drainage in southeastern British Columbia (49°N, 114°30′W) from December 1984 through April 1996. The MacDonald Divide formed the western border of the study area and the Continental Divide the eastern border. The valley bottom varied in width from 4 to10 km and rose in elevation from 1200 m asl in the south to 1375 m asl in the northern part of the study area.

The climate of this area is transitional between a northern Pacific coastal type and a continental type. Mean monthly temperatures ranged from –9°C in January to 16°C in July (Singer 1979). Snow normally covered the area from mid-November through mid-April. Average maximum snow depth at the Polebridge Ranger Station (23 km south of the international border) was 65 cm. Dense forests of lodgepole pine (*Pinus contorta*) dominated most of the North Fork valley, but subalpine fir (*Abies lasiocarpa*), spruce (*Picea* spp.), western larch (*Larix occidentalis*), and Douglas-fir (*Pseudotsuga menziesii*) communities existed throughout the valley. Abundant meadows and riparian areas were dispersed throughout the study area. Detailed descriptions of vegetative communities in this area were provided by Jenkins (1985) and Krahmer (1989).

One pack of 6–12 wolves occupied the study area (ca. 35 wolves/ 1000 km^2). Langley (1993) estimated that the moose density was 0.42–0.55/km^2. Moose were the primary prey item for wolves; elk (*Cervus elaphus*) and white-tailed deer (*Odocoileus virginianus*) made up a smaller portion of their diet.

During the first half of this century, wildfires burned most of the study area. In the late 1970s and early 1980s, 13% of the study area was clearcut, and the open road density is 69 km/100 km^2 (B. McLellan, British Columbia Forest Service Research Branch, personal communication). The primary roads in the study area received only snowmobile use during winter. No humans reside year-round in the study area.

Field methods

The methods for capturing and handling wolves and moose for our study were approved by the University of Montana's Animal Care and Use Committee and met the standards set by the Canadian Council on Animal Care. Wolves were captured, sedated, and radio-collared following techniques described by Mech (1974) and Ream et al. (1991). Wolves were located from the ground or from the air approximately once per week during winter (December–April) to determine their travel routes. Tracks were found by bisecting the area between consecutive daily locations of wolves. We followed these routes forward and backward on snowmobiles (when wolves traveled along roads), skis, snowshoes, or on foot to locate kills of non-radio-collared cervids and to estimate habitat and spatial variables of areas where wolves hunted and made kills. To minimize our effects on wolf behavior, we did not work in areas where we knew wolves were present.

Moose were captured in January and December 1990, using darts filled with 3.9 mg of carfentanil (Meuleman et al. 1984) and 0.25 mg of rompun fired from a helicopter (Langley 1993). Carfentanil was reversed with 6 cc (1 cc = 1 mL) of naloxone. Moose were net-gunned (i.e., captured by a hand-held gun that shoots a canister-held net) from a helicopter in December 1993. Females were fitted with radio transmitters containing mortality sensors and were located from the ground or from the air approximately once per week during winter (December–April).

To measure the accuracy and precision of bearings used for triangulating ground locations of moose, an independent observer placed radio collars at various locations in the area where we typically located radio-tagged animals (Kunkel 1997). All project personnel located these collars using the same technique that was used to locate moose. Mean bearing error (bias) and standard deviation (precision) were calculated following White and Garrott (1990, p. 82). Triangulations of test collars were plotted using LOCATE II software (Pacer Ltd. 1990). Confidence ellipses were generated for each location using Tukey's estimator (Lenth 1981).

Moose were monitored for mortality signals 2–3 times/week. When a mortality signal was received, the collar was located and the site and any remains were examined to determine cause of death. Mortality signals of radio-collared animals were usually investigated 1–4 days after death. 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 hair, tracks, scats, presence of buried carcass, plucked hair, kill and feeding pattern, and percentage of carcass found was used to classify the predator responsible for death (O'Gara 1978; Kunkel 1997).

The location of the carcass was considered to be the kill site unless track or other site evidence indicated otherwise. Beginning in 1992, habitat variables were measured in a 30-m radius plot centered on the kill site and at "control sites" located 500 m in a random direction from the moose-kill sites. Canopy cover was estimated by counting the number of points under the forest canopy at 2-m intervals along two (1 N–S, 1 E–W) 20-m perpendicular transects centered on the carcass, and then placed in one of five categories: (1) 0–10%, (2) 11–30%, (3) 31–50%, (4) 51–75%, and (5) 76–100%. The percentage of hiding cover was estimated by visually estimating the percentage (using the same five cover classes as canopy coverage) of a moose that would be obscured at 30 m in the four cardinal directions from the carcass. The mean of the cover classes from the four directions was considered to be the hiding cover for the site (J. Lyon, United States Department of Agriculture, Forest Service, personal communication). At the start of each field season, all project personnel spent a day in the field standardizing canopy and hiding-cover classifications.

Vegetation cover type at the site was classified based on the types developed by Jenkins and Wright (1988). We combined these into three classes: lodgepole, mixed xeric, and mixed mesic (Table 1). The dominant vegetation at the site was placed into one of 4 size-class categories (Table 1). To examine the effects of edge, we recorded whether a different size class could be seen from the plot center. The number of downed logs (>4 cm in diameter) that had to be stepped over while walking 10 m N from the plot center was recorded. The mean height of these logs was determined by measuring the distance from the ground to the top of each log. The slope at each plot was estimated using a clinometer. The topographic position of each plot was recorded as: main valley bottom, ravine, side valley lower slope, side valley upper slope, wide valley slope, ridgetop, bench, or creek bottom (Kunkel 1997).

To estimate relative densities of prey at the sites, we skied two 100-m transects in opposite directions starting at the plot center. We attempted to position these transects perpendicular to the wolf travel route. If the travel route was not known and if the site was on an incline, the transects were positioned perpendicular to the

Table 1. Habitat and spatial classes (%) at kill, relocation, and random sites in the upper Flathead Basin, British Columbia, 1985–1996.

Sites	Canopy				Size class[a]					Cover type			
	Low (15–39%)	Medium (40–69%)	High (70–100%)	n	Seedling (<12.7 cm)	Pole (12.7–22.9 cm)	Medium tree (23.0–53.3 cm)	Large tree (>53.3 cm)	n	Lodge pole	Mixed xeric	Mixed mesic	n
Kill	52	44	4	27	19	26	41	15	27	28	28	44	18
Relocation	47	43	9	76	12	33	44	11	75	17	36	47	53
Random	40	47	12	202	13	32	33	22	196	52	16	33	89

[a]Diameter at breast height for trees.

topography. If neither of these conditions applied, the transects were positioned east and west. The distance to the first deer, elk, and moose track on each transect was recorded. We did not record tracks that were known to be those of the dead moose. If no track was encountered, the distance recorded was 100 m. The number of deer, elk, and moose tracks located on the two transects (0, 1, or 2; only the first track on each transect was recorded) was divided by the distance to that track (e.g., 1/190, if one deer track was found at 90 m in one direction and no deer track was found along the opposite 100 m transect) to obtain the number of deer, elk, and moose tracks per metre. This value was divided by the number of days since the most recent snowfall of >5 cm, to adjust for snowfall effects. We set 7 as the maximum number of days since snowfall, because after that time track deposition leveled off and tracks started to deteriorate (K. Kunkel, personal observation).

Geographic information system spatial analysis

Universal Transverse Mercator coordinates for habitat plots estimated from a 1 : 24 000 scale map or from a global positioning system receiver were entered into a geographic information system (PAMAP) along with 81 telemetry locations from 29 moose. Random sites were generated by PAMAP. Spatial and vegetative attributes were generated for each site (kill, control, location, and random) from geographic information system (GIS) map layers (30-m minimum mapping unit) created by Singleton (1995) and Redmond (1996). These included maps representing cover type, size class, and canopy coverage (Table 1); modified normalized difference vegetation index (a measure of absorption variation in middle infrared wavelengths that is associated with canopy closure; Butera 1986; Redmond 1996); slope; road density; distance to open roads; distance to trails; distance to water; and total wolf use. Wolf use was classed as low if no back-tracking routes of wolves were located in a 30-m pixel mapping unit and as high if ≥1 route was located in a mapping unit. To eliminate bias, we did not add back-tracking routes upon which we found moose kills to the total. We created polygons based on the size class of vegetation from which we could estimate the area of the polygon and the distance to the edge of the polygon. We created a prey density map layer by using the average density of all track transects that fell into 1 km² cadastral blocks. Track transects used for this purpose included those measured at kill sites and at 1-km intervals along wolf travel routes (Kunkel 1997). These were pooled across years.

Scales of analysis

Because factors affecting the vulnerability of prey and the hunting strategies of wolves probably occur at different scales, we compared habitat and spatial variables associated with kill sites with the same variables at sites occurring at 3 different scales: (*i*) to assess the effects of variables at a basin-wide level of sites available to wolves (<500 m above the river bottom; Singleton 1995), we tested the hypothesis that habitat and spatial variables (using data from GIS map layers) did not differ between moose-kill sites (1985–1996) and random sites within this area; (*ii*) to assess the effects of variables at the landscape level used by moose (the next finer scale of comparison), we tested the null hypothesis that habitat and spatial variables (using data from GIS map layers) did not differ between moose-kill sites (1985–1996) and locations of radio-tagged moose; and (*iii*) to assess variables at an individual moose home range level (the finest scale of comparison), we tested the null hypothesis that habitat and spatial variables (only those collected on the ground from 1992–1996) at kill sites did not differ from the same variables measured at control sites.

Statistical analysis

We used univariate analyses to test the null hypothesis that individual variables did not differ between each of the 3 pairs of site-

Table 2. Habitat and spatial variables associated with moose-kill (n = 28), relocation (n = 81), and random (n = 210) sites in the upper Flathead Basin, British Columbia, 1985–1996.

Variable	Kill sites			Relocation sites			Random sites		
	Mean	Median	SD	Mean	Median	SD	Mean	Median	SD
Distance from edge (m)									
All size classes	407	121	506	67[a]	45	66	633[b]	528	494
Seedling, pole size class	652	636	598	61[a]	42	63	526	426	475
Medium, large tree size class	230	67	349	75	58	69	765[b]	714	466
Distance to road (m)	717	387	897	425	275	416	663	460	731
Road density (km/100 km^2)	65	34	65	82[c]	89	51	90[b]	82	63
Size-class patch area (m^2)	2769	236	3 568	2592	659	3099	2174	219	3175
Distance to stream (m)	385	92	566	462	204	498	837[b]	475	800
Distance to trail (m)	902	209	1 174	854[c]	697	717	740	470	877
Elevation (m)	1218	1222	107	1337[a]	1301	82	1497[b]	1494	167
NDVI[e]	5744	317	16 330	1140	331	6132	355	359	168
Elk track density (tracks/m)	5[e]	0	9	13	0	25	12	0	32
Moose track density (tracks/m)	59[e]	10	153	36	10	65	56	8	112

[a]Kill site significantly different from relocation site (P < 0.05).
[b]Kill site significantly different from random site (P < 0.05).
[c]Kill site significantly different from relocation site (P < 0.10).
[d]Normalized difference vegetation index.
[e]n = 22 for kill sites; n = 37 for relocations; n = 63 for random sites.

class comparisons. Because we were testing different hypotheses with each comparison of site pairs, no adjustments of P values were deemed necessary for these tests (Rice 1989). None of the interval scale variables were judged normal based on the Lilliefors test (Norusis 1993) and no transformations successfully normalized them, so we used Mann–Whitney U (M–W U) tests to compare these variables between sites.

Categorical habitat variables were cross-tabulated by pairs of sites (e.g., kill sites versus control sites). We used Pearson's χ^2 statistic to test the null hypotheses of independence among categories. When >20% of the cells had expected values of <5, we combined adjacent (similar) categories. Adjusted standardized residuals ((observed – expected/expected$^{0.5}$)/standard error) were used to identify significant cells (Habermann 1973). We adjusted probability values with the Bonferroni technique (Rice 1989). We used M–W U and Pearson's χ^2 statistics to determine if there were differences in any variables based on month or method (aerial versus ground) of relocation.

We used stepwise logistic regression (Norusis 1993; Trexler and Travis 1993) to predict the probability of successfully classifying pairs of sites (dependent variable), using habitat and spatial variables found to be significant in the univariate tests (Capen et al. 1986). Two models with the following dichotomous dependent variables were examined: (*i*) random site or moose-kill site and (*ii*) moose relocation or moose-kill site. The sample size for the model comparing kill sites with control sites was too small for analysis. The least explanatory of the highly intercorrelated variables was removed during model building, to reduce the likelihood of inaccurate results due to multicollinearity (Trexler and Travis 1993). Independent variables were entered into the model at the 0.10 significance level and removed at the 0.11 level using the likelihood-ratio test (Norusis 1993). Wald's statistic was used to test whether the coefficient of individual classes of categorical variables was different from zero. Final models were assessed for reliability using goodness-of-fit maximum-likelihood estimates, accuracy of classification tables, estimates of R^{2logit} (Hair et al. 1995), and significance tests of coefficients (Norusis 1993; Trexler and Travis 1993). Initial overall prediction success values for classification tables resulted from predicting that all observations fell into one of the two site classes. For example, if 100 moose-kill sites and 200 locations were examined, all 300 of these sites would

be predicted to be moose-kill sites in the initial classification table. This would yield an overall prediction success of 33% (100/300), because all the moose-kill sites would have been classified correctly and all the locations would have been classified incorrectly.

Results

Four of 29 moose that were radio-collared in our study area were killed by wolves. While back-tracking wolves, we investigated the kill sites of an additional 24 moose that had been killed by wolves.

Average aerial telemetry error was 75 m (Langley 1993). Mean bearing error (bias), based on ground locations of test collars, was 1.6° and SD (precision) was 16.1° (n = 74 bearings). Mean distance error based on 27 locations of test collars (excluding one outlier) was 266.2 m (SD = 194.7 m). Mean area of confidence ellipses was 35.4 ha (SE = 3.4, n = 606).

Landscape characteristics derived from ground locations were similar to those from aerial locations, except for the topographic-class variable. More aerial locations (33%) than ground locations (7%) occurred on lower slopes in the main valley bottom class (χ^2 = 16.43, df = 7, P = 0.02). When only aerial locations were compared with kill sites, there was no difference in the distribution of topographic classes (χ^2 = 1.97, df = 3, P = 0.58). Because of this, we excluded this variable from further analyses.

Moose-kill sites versus random sites

The elevation at moose-kill sites was significantly lower than at random sites (M–W U = 419, P < 0.0001; Table 2). Moose-kill sites were closer to the edge of size-class polygons than random sites (M–W U = 1909, P = 0.003); when only seedling and pole size classes were examined, there was no difference between moose-kill (n = 12) and random (n = 105) sites (M–W U = 573, P = 0.61); when only medium- and large-tree size classes were examined, moose kills (n = 15) were closer than random sites (n = 119) to the

Table 3. Habitat and spatial variables associated with moose-kill and control sites in the upper Flathead Basin, British Columbia, 1992–1996.

Variable	Kill sites			Control sites		
	Mean	Median	SD	Mean	Median	SD
Deadfall height (cm)	13.7	0.0	33.4	11.4	0.0	25.3
Moose track density (tracks/m)	10.0	1.0	34.0	0.4	0.0	0.7
Degree of slope	7.9	4.0	8.7	12.1	5.5	15.7

edges of these polygons (M–W $U = 247$, $P < 0.0001$). The density of roads was lower at moose-kill than at random sites (M–W $U = 2181$, $P = 0.03$). Moose-kill sites were closer to streams than random sites (M–W $U = 1585$, $P < 0.0001$; Table 2).

There were more moose-kill sites than random sites in areas of high wolf use (57 vs. 16%) than in areas of low wolf use (43 vs. 84%; $\chi^2 = 26.4$, df = 1, $P < 0.0001$). The distributions of cover types ($\chi^2 = 3.6$, df = 2, $P = 0.16$), canopy classes ($\chi^2 = 2.53$, df = 2, $P = 0.28$), and size classes ($\chi^2 = 1.85$, df = 2, $P = 0.60$) were similar for kill sites and random sites (Table 1).

Moose-kill sites versus moose location sites

The distribution of moose locations and moose kills did not differ between average (<75 days per winter with >30 cm of snow on the ground; Kunkel and Pletscher 1999) and severe ($\chi^2 = 0.10$, df = 1, $P = 0.75$) winters. The elevation at moose-kill sites was significantly lower than at relocation sites (M–W $U = 374$, $P < 0.0001$; Table 2). Moose-kill sites were farther from the edge of size-class polygons than were relocation sites (M–W $U = 604$, $P < 0.001$; Table 2); when only seedling and pole size classes were examined, moose kills ($n = 12$) were farther than locations ($n = 34$) from the edge of these polygons (M–W $U = 46$, $P < 0.0001$); when only medium- and large-tree size classes were examined, there was no difference between moose-kill sites ($n = 15$) and location sites ($n = 41$; M–W $U = 258$, $P = 0.36$). The area of size-class polygons did not differ between kill sites and random sites (M–W $U = 1131$, $P = 0.98$; Table 2). The density of roads was marginally lower at moose-kill sites than at relocation sites (M–W $U = 881$, $P = 0.08$; Table 2) and moose-kill sites were marginally closer to trails than relocation sites (M–W $U = 883$, $P = 0.08$; Table 2).

There were more moose-kill sites than relocation sites in areas of high wolf use (57 vs. 31%) than in areas of low wolf use (43 vs. 69%; $\chi^2 = 6.1$, df = 1, $P = 0.01$). The distribution of cover types ($\chi^2 = 1.08$, df = 2, $P = 0.58$), canopy classes ($\chi^2 = 0.87$, df = 2, $P = 0.65$), and size classes ($\chi^2 = 0.34$, df = 2, $P = 0.84$) were similar for kill sites and location sites (Table 1).

Moose-kill sites versus control sites

The density of moose tracks was greater at moose-kill sites ($n = 13$) than at control sites ($n = 10$; M–W $U = 59$, $P = 0.03$; Table 3). Neither slope nor deadfall height differed between kill and control sites (M–W $U = 84$, $P = 0.21$; M–W $U = 89$, $P = 0.98$; respectively; Table 3). Edge was visible from a marginally greater percentage of moose-kill sites ($n = 14$) than control sites ($n = 13$; 71 vs. 39%, respectively; $\chi^2 = 2.97$, df = 1, $P = 0.09$). A marginally greater percentage of moose kills ($n = 16$) than control sites ($n = 12$) occurred

at sites with low levels of hiding cover (56 vs. 25%, respectively) ($\chi^2 = 2.73$; df = 1, $P = 0.09$).

The proportion of kill sites ($n = 20$) and control sites ($n = 14$) occurring where canopy cover was <50% (75 vs. 50%, respectively) did not differ significantly ($\chi^2 = 2.25$, df = 1, $P = 0.13$). Cover-type and size-class data from kill and control sites were too few for analysis.

Logistic regression

The simplest multivariable model that predicted ($\chi^2 = 89.8$, df = 1, $P < 0.00001$) the probability that a specific site within areas available to wolves would be a kill site (k) used elevation (Table 4):

$$k = \frac{1}{1 + e^{-z}}$$

where $Z = $ constant $+ B_1$ and B is elevation (Table 4).

A lower elevation increased the probability that the site would be a kill site. The model's overall prediction success increased from an initial value of 88.2% to a final value of 94.5% ($R^{2\text{logit}} = 0.505$).

The simplest multivariable model that predicted ($\chi^2 = 91.8$, 7 df, $P < 0.00001$) the probability that a specific site within areas used by radio-tagged moose would be a kill site (k) used road density, elevation, distance from trails, and distance from size-class polygon edges (Table 5). Lower road density, lower elevation, a lesser distance from trails, and a greater distance to the edge of the size-class patch increased the probability that a site would be a kill site. The model's overall prediction success increased from an initial value of 74.3% to a final value of 94.5% ($R^{2\text{logit}} = 0.696$). Only 6 sites were misclassified by this model.

Discussion

Data interpretation

We believe that our ground telemetry error was not too large to preclude our comparison of sites where wolves killed moose and moose locations, because this was a coarse-scale comparison. Additionally, we found no differences in results when we compared ground locations with aerial locations, except for the topographic-class variable. The sample size used for our comparisons of kill sites and control sites was very small and thus had low power. Because of this, differences may exist that we were unable to detect.

Factors affecting vulnerability

Factors affecting the vulnerability of moose were similar across the three scales examined. In general, moose were most vulnerable to predation in the areas of highest wolf use. These were generally sites at the lowest elevations,

Most studies of habitat are unable to indicate if the habitat selected is critical for survival (White and Garrott 1990). Our study takes a step in this direction. Our evidence indicates that moose are less likely to be killed by wolves at higher elevations, farther from trails, away from other moose, nearer to or within areas sheltered by large trees, and in areas with higher road density. The next research step should be to manipulate habitats and then compare survival rates of moose and (or) kill rates of wolves in these manipulated areas with the same parameters in control areas, to clarify whether various logging practices affect the sustainability of large mammal predator–prey systems.

Bergerud and Snider (1988) hypothesized that the spacing of predator and prey determines the predation rate and sets the equilibrium density of prey below that dictated by food. Humans may affect this relationship through habitat modifications that reduce the ability of prey to space out or away from predators (Bergerud 1992). Our research generally supports Bergerud (1992), but indicates there are additional complexities that influence the effects of habitat modifications by humans in moose–wolf systems. Further research is needed to more fully elucidate these confounding effects.

Acknowledgements

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