The predator-prey dynamics of wolves and moose in the northern Columbia Mountains: spatial and functional patterns in relation to mountain caribou decline.

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Summary

Considerable effort has been made to quantify prey selection by wolves and to estimate kill rates to determine the effect that wolves have on ungulate populations, and therefore guide management decisions and direct conservation efforts. However, the majority of wolf-foraging studies occur in winter, when snow tracking enables researchers to more easily find kills from the air or on the ground. Investigating wolf prey selection and kill rates in other seasons may be important as studies have shown shifts in diet composition, greater prey diversity, and higher predation rates when compared to winter. Furthermore, there is the greatest potential for overlap between moose (the wolf's primary prey in the Columbia Mountains) and endangered mountain caribou during non-winter seasons. As a preliminary study, we used the GPS location data (May - August 2004) to determine the feasibility of quantifying summer predation patterns from GPS locations. Potential kill sites were identified from GPS clusters having ≥2 points that were <200 m apart. Of the 25 GPS clusters sites investigated, we found evidence of a large mammal predation event at 40% of the sites. The probability of a large mammal predation event being present at a GPS cluster site increased with the number of days a radio-collared wolf spent at the cluster and decreased if the cluster had been revisited over a number of non-consecutive days. Developing techniques that link GPS collar technology and animal behaviour could be important to increase our understanding of complex systems for the benefit of conservation and management efforts.

Although wolf foraging behaviour can be explained using kill rates and prey selection, landscape patterns can have important effects on the foraging efficiency of predators and can influence anti-predator strategies of prey. We compared locations of moose killed by wolves in winter to telemetry locations of live moose during winter, to identify landscape patterns that were associated with locations where wolves were likely to kill moose. Relative to live moose, killed moose were found >250 m further from a major water source (i.e. Goldstream River or Downie Creek). Dead moose were also at higher elevations, 30% closer to a seral edge, and in areas that contained 30% more logged forest, relative to live moose. However, variability was high, as evidenced by the large standard error of parameter estimates, and the winning multivariate model was the intercept-only (null) model. Nonetheless, the analysis identified some unique features of the study area, such as the probable use of open water as a refuge for moose. In other study areas during winter, most water bodies are frozen, which often facilitates foraging efficiency for wolves but does not provide an escape feature for moose. Ultimately our work on moose predation risk will be expanded to include non-winter seasons and contrasted with the caribou predation risk model being developed by other members of our research team (C. Apps, H. Wittmer, B. McLellan), to identify zones of shared predation risk between moose and caribou.

Introduction

Woodland caribou within the Southern Mountains National Ecological Area, that includes mountain caribou, are listed as Threatened (Committee on the Status of Endangered Wildlife in Canada), and Threatened or Endangered (Conservation Data Centre Red List) in British Columbia (B.C.; Mountain Caribou Technical Advisory Committee 2002). In a recent meta-analysis of mountain caribou populations in B.C., predation was identified as the proximate cause of this decline (Wittmer et al. 2004). This increased level of predation is linked to increasing amounts of young forests and fragmented habitat (Wittmer and McLellan, submitted).

Although wolf predation is not the main mortality factor implicated in the recent decline of the mountain caribou population near Revelstoke, B.C., recent increases in moose and wolf populations has led to concerns that encounters with mountain caribou will increase, leading to higher predation rates. A 2003 moose census documented a 100% increase (0.7 moose/km^2 to 1.54 moose/km^2) in moose densities over the past decade (Poole and Serrouya 2003). This increase has been attributed to a higher proportion of young seral stage forest on the landscape (Serrouya and D'Eon 2002), and possibly milder winters that facilitate overwinter survival. Since there has likely been a numerical response of wolves to the increased moose density, there may be a negative effect on the long-term persistence of mountain caribou populations in the region (Bergerud and Elliott 1998; Seip 1992). If management strategies for the recovery and maintenance of caribou herds are to be effective, a greater understanding of this complex predator-prey system in conjunction with the changing landscape is necessary.

Considerable effort has been made to quantify prey selection by wolves and estimate kill rates to determine the effect that wolves have on ungulate populations, guide management decisions, and direct conservation efforts (Huggard 1993; Hayes et al. 2000; Hebblewhite and Pletscher 2002; Kunkel et al. 2004; Smith et al. 2004). However, most of this research has been focused on the winter season, due to the logistical problems of wolf tracking in snow-free seasons. Investigating wolf prey selection and kill rates in other seasons may be important as past studies have shown shifts in diet composition, (Darimont and Reimchen 2002) greater prey diversity in the diet (Jedrzejewski et al. 2002) and higher predation rates (Sand et al. 2003) when compared to winter seasons. Furthermore, the potential for wolves to overlap with caribou range is greatest during the non-winter seasons, and more than 60% of caribou predation mortality occurs in the non-winter seasons (Wittmer et al., in press).

Summer kill rates and prey selection are traditionally investigated using intensive radio-tracking and scat analysis (Jedrzejewski et al. 2002). These techniques are costly, time intensive, and difficult in remote areas and potentially dangerous in areas with grizzly bear (*Ursus arctos*) populations. Recent advances in GPS radio-tracking technology have expanded the techniques used to determine prey selection and kill rates of carnivores. Using a combination of

intensive radio tracking and GPS location data, Sand et al. (2003) identified the summer predation patterns of Scandinavian wolves. Anderson and Lindzey (2003) estimated cougar predation rates from GPS clusters and developed a model to estimate predation events using GPS data.

Once the effects of predator foraging behavior on ungulate populations have been clarified, wildlife managers can attempt to manipulate the system using harvest management (and potentially other tools) to try and favour the threatened species. However, ecologists have argued that the spatial patterns of predator foraging can help explain the mechanisms behind prey selection and kill rates (Lima and Dill 1990). Several studies have linked landscape attributes to the location of prey kills sites (Kunkel and Pletcher 2000, Thogmartin 2000, Johnson et al. 2002) or predator/prey encounter and kill sites (Hebblewhite et al. in review). The results of these studies can help guide land-management decisions because some landscape features, such as the spatial configuration, distribution, and intensity of forest harvesting, road building, and other resource uses, can be manipulated by humans.

Our ultimate goal is to clarify wolf foraging patterns in the northern Columbia Mountains. More specifically, we had 3 objectives:
1) Determine the amount spatial overlap between caribou, wolves, and moose;
2) Determine the prey selection and foraging rates of wolves, and determine the feasibility of using GPS collars to quantify these parameters;
3) Describe stand and landscape-level factors that affect the foraging patterns of wolves on moose.

In this report we present the preliminary results of these objectives.

Methods

Study Area

The study area is in the Northern Columbia Mountain ecoregion in southeastern British Columbia (Demarchi 1996). The study area is bounded by Encampment Creek in the north and the town of Revelstoke in the south. The eastern and western boundaries extend to the heights of land surrounding the Lake Revelstoke reservoir.   Elevations range from 550 m to 3,050 m. The study area receives 946 mm of precipitation annually (425 cm of snow falls annually).

The study area is composed of a mosaic of forests, regenerating clear-cuts, riparian forests, shrublands, upper elevation basins, and avalanche chutes. Biogeoclimatic subzones within the study area range from Interior Cedar-Hemlock (variants ICHwk, ICHvk1, ICHmw3) in the valley bottoms and mid-elevations, to Engelmann Spruce-Subalpine Fir (variant ESSFvc) at approximately 1,280 m to 1,400 m (Braumandl and Curran 1992). The Alpine Tundra subzone occurs at elevations above the ESSF.

The ICH subzones are dominated by forests of western red cedar (*Thuja plicata)*, western hemlock (*Tsuga heterophylla*) and less commonly, Douglas-fir

(*Pseudotsuga menziesii*). The ESSF zone is comprised of coniferous forests of primarily Englemann Spruce (*Picea Engelmannii*) and subalpine fir (*Abies lasiocarpa*). Alpine meadows, shrublands, snowfields, glaciers and rock dominate the Alpine Tundra zone.

Moose are the most abundant ungulate species, with mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) occurring at lower densities in the southern portion of the study area (Poole and Serrouya 2003). Mountain goats (*Oreamnos americanus)* and mountain caribou are also found in the study area. Grizzly bears, black bears (*Ursus. americanus*), wolverine (*Gulo gulo*), wolves and cougars (*Felis concolor*) also occur.

Capture and Handling

Wolves were captured from 2003 to 2005 using modified foothold traps (Livestock Protection Co., Alpine Tex.) in the summer and helicopter net-gunning (Bighorn Helicopters Inc., Cranbrook, B.C.) in the winter. In 2004, two wolves were captured using modified foothold traps and five wolves were captured using a netgun fired from a helicopter. These wolves were affixed with 5 VHF LMRT-3 and 2 GPS 3300s collars (University of Alberta-Protocol 2004-09D; Lotek Inc.,Newmarket, Ontario). GPS collars were programmed to attempt position acquisitions every 3 hours. By February 2005, no wolves remained radio-collared, because of collar failure, dropped collars, possible dispersal, and death from trapping and hunting. In March 2005, 6 more wolves were captured in the study area and affixed with 2 VHF LRMT-3 collars, 1 Lotek GPS 3300s collar, and 3 remotely downloadable GPS collars (HABIT, Victoria, B.C.).

Spatial Overlap of Moose, Wolves, and Caribou

Ultimately our goal is to use resource selection functions (RSF) to quantify the spatial overlap among these 3 species. We plan to follow methods similar to Johnson et al. (2000), where they used RSF functions to quantify the degree of spatial separation of mule deer and elk. They compared the direction of parameter estimates for the same habitat variables for each species, and used the predictive equation for 1 species and tested it with data from the other species. In their case, the RSF for elk accurately predicted mule deer locations, but the converse did not hold, suggesting that mule deer avoided elk, but elk did not avoid mule deer (Johnson et al. 2000). However, the current amount of data for moose and particularly wolves did not warrant such an approach at this time. Until more data become available, we used a simpler approach by plotting the mean weekly elevation use of moose and caribou to examine the seasons where these species are most likely to come into contact with one another. Because sample sizes were small for wolves, we plotted the mean weekly elevational use of each wolf against the pooled data of moose and caribou.

GPS Radio-collar Cluster Analysis

Predation Site Investigation

     To identify GPS clusters, we calculated the distance between fixes using Arcview 3.3. These results were grouped into categories of 100 m and graphed using a histogram to determine a breakpoint that would represent the difference between resting/feeding distances and moving distances. A breakpoint of 200 m was visually estimated from the histogram. A cluster was defined as ≥2 locations less than 200 m apart. The average cluster location was delineated using the mean UTMs of all points making up the cluster. Twenty-nine clusters were randomly selected to be investigated in the field. Cluster sites were methodically searched for a minimum of 1 hour to find evidence of a large-mammal predation event. When kills were located, the species, age, and sex were recorded if possible. The incisor teeth, femur, and hair samples were taken to confirm age, nutritional condition and sex of the prey species (Sergeant and Pimlott 1959; Neiland 1970).

GPS Cluster Predation model

     Using binary logistic regression, we modeled the probability that a large-mammal predation event occurred at a GPS cluster site using 6 predictor variables pre-screened for mulitcollinearity. The probability of a large-mammal predation event being present (1) or not present (0) at the GPS cluster site was modeled as:

$$P_{PE} = \frac{\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n)}{1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n)}$$

where P_{PE} is the probability of a large-mammal predation event, β_0 is the regression constant and $\beta_1 \ldots \beta_n$ are coefficients estimated for variables $x_{1 \ldots} x_n$. (Hosmer and Lemeshow 2000). The predictor variables included GPS precision (% 3D locations), number of days the collared wolf spent at a cluster (DAY), if the wolf made multiple visits to the site (REVISIT; yes=1 or no=0), habitat type (HAB; forested, wetland, cutblock), time spent searching the area, and ground visibility (poor=1, good=0). Using Akaike's information criterion (AIC_c) for small sample sizes with no overdispersion (c), we assessed 8 *apriori* candidate models to identify the best model that predicted the probability of finding a large-mammal predation event at the cluster site.

     Using Δ_l values (Δ_l = AIC_i – minAIC), the candidate models were ranked and the strength of evidence for each model was determined (Burnham and Anderson 2001). The relative likelihood of an individual model given the data and the chosen set of candidate models was derived from the Akaike weights (*w*; Table 1). The assessment of the relative importance of the predictor variables was estimated from the set of models, rather than the best model, using the sum of the Akaike weights for each variable (w_+(j)) (Burnham and Anderson 2001). Due to small sample sizes, all data were used for model building. All statistical analyses were performed using SPSS 13.0 software (SSPS 2004).

Kill Rate Estimation

Radio-collared wolf packs were monitored using a combination of fixed-wing aircraft and ground-based winter tracking between November and March of 2003/04 and 2004/05. Two wolf packs, named the Downie and Goldstream packs after the major drainage in which they spend most of their time, were monitored for 1 and 2 winters respectively. Wolf locations and kill sites were sighted from the air using a fixed-wing aircraft. To augment aerial searching, wolves were tracked on the ground from the last known telemetry point to locate kills, document habitat use, determine wolf pack size, snow characteristics (depth, consistency) and wolf track sinking depth (Smith et al. 2004; Hayes et al. 2000). Mean pack size for the analysis was determined from visual counts during aerial telemetry (Hebblewhite et al. 2003).

When kills or scavenges were located, the species, age, and sex of the prey was recorded if possible. The incisor teeth, femur, and hair samples were also taken to confirm age, nutritional condition and to provide DNA of the prey (Neiland 1970; Sergent and Pimlott 1959). Criteria used to determine the difference between a kill or scavenge was based on research completed by Huggard (1993). Moose were categorized as calf (<1 yrs), subadult (1-2yrs) and adult (>3 yrs).

Kill rates and scavenge rates were estimated using the ratio estimation method (Hebblewhite et al. 2003). When attempting to estimate winter kill rates, the winter is often partitioned into sampled and unsampled time periods. These periods are often randomly distributed and of variable lengths due to weather and logistical constraints of maintaining a continuous tracking session. By accounting for these constraints, this method estimates kill rates using a linear model where β=kill rate, y_i =the number of kills in sampling interval i, and x_i = number of days in sampling interval i (Hebblewhite et al. 2003).   Therefore kill rate is estimated by,

$$\beta = \frac{\sum^n y_i}{\sum^n x_i}$$

where i=the sampling period, 1 to n, and n=total number of sampling periods. The ratio estimator approach was found to provide the least bias and most precise kill rate estimates when compared to other methods (Hebblewhite et al. 2003; Ballard et al. 1997; Dale et al. 1994). Total wolf kill rates are reported in kills/day/pack (k/d/p). Scavenge rates are reported as scavenges/day/pack (s/d/p).

To allow for greater comparisons among studies, we converted the number of prey to kilograms of prey killed per day per wolf (kg/d/w) using moose mass estimates from Hayes et al. (2000) and corrected for the percent of carcass consumed (65%, Hayes et al. 2000).

Landscape Attributes that Affect the Predation Risk of Moose by Wolves

We used locations of dead moose from the kill rate estimation section, plus other mortalities that did not form part of continuous tracking sessions, as our sample of where moose were killed by wolves. Telemetry data from radio-collared moose was our sample of where moose live. Each moose kill represented an independent data point, whereas individual live moose represented independent data points, with telemetry locations nested as subsamples within each live moose, to avoid pseudoreplication. The analysis was restricted to the winter season (Dec. 5 to May 10) because there were too few kill sites identified during the non-winter season. In a GIS we created a 200-m radius buffer around each kill site and telemetry location. This distance represents the approximate mean difference between where wolves encountered moose to where wolves successfully preyed on moose, as determined from snow-tracking sessions (Stotyn, unpublished data). Within each buffer, we queried digital forest cover and TRIM files to extract the percent cover of each tree species, percent of logged (<30 yrs old), riparian, and deciduous habitat, and mean values for stand age, canopy cover, elevation, and slope. We also used the point locations of kill sites and telemetry locations to extract the nearest distance to major water sources (e.g., Goldstream River, Downie Creek, Lake Revelstoke), all water sources (any small creek or major water source), all roads (including forestry mainlines, spur roads, and highways), and edge of early seral (< 30 yrs)/late seral forest types. We conducted univariate comparisons between kill sites and telemetry locations of live moose. To contrast the strength of different variables and account for potential interactions among variables, we conducted logistic regression analyses to predict the location of a kill site (y=1) relative to live moose sites (y=0), based on the aforementioned predictor variables. Similar to the GPS cluster analysis, we used AIC corrected for small sample sizes to gauge the strength of different models and particularly different variables, which may explain the location of moose kills.

Results

Spatial Overlap of Wolves, Moose and Caribou

The degree of elevational separation between moose and caribou was greatest during the "late winter" caribou season (January 11 to April 22; Apps et al. 2001; Figure 1), when caribou migrate to high elevations to access arboreal lichen, their primary winter food source. During summer, moose and caribou are more dispersed throughout the landscape, but on average, the elevational separation between the 2 species is at its minimum relative to the other seasons.

GPS Radio-collar Cluster Analysis

Predation Site Investigations

Potential kill sites were identified from GPS data downloaded from a LOTEK GPS_3300 collar retrieved in August 2004. The LOTEK GPS_3300 collar recorded wolf movements from March 10 to August 18th, 2004 and had a fix rate of 48.1%. Of those successful fixes, 62% were 3D and 38% were 2D fixes. There was evidence of a large mammal predation event at 40% of the sites investigated (Figure 2). Cluster sites were located in forested (52%), wetland (12%) and cutblock (40%) habitat types (Figure 2). Of the 29 GPS cluster sites identified, 4 were not investigated because of recent snow cover and poor accessibility. Sixty percent of the sites investigated were classified as having poor ground visibility due to leaf cover, dense forbs or snow cover. The identification of prey species, age, and body condition from hair and bones collected at the site are not complete at this time. Sites that had bones with evidence of human handling (saw marks) were assumed to be scavenged by wolves, and not included in the analysis.

GPS Cluster Predation Model

AIC values were used to rank the models using the smallest AIC value as an indicator of the best-supported model given the data (Table 1). Models with Δ_i ≤ 2 are considered to have substantial support and those models with $4 \leq \Delta_i \leq 7$ have reduced support.

The model (ϕ) = DAY + REVISIT was the best-fitting model based on AIC model selection (Table 1). The second ranked model, (ϕ) = HAB + DAY + REVISIT, had 11.6 times less support than the top ranked model (w_i/w_j = 11.6). The third model, (ϕ) = DAY, is two times less supported than the second ranked model. The last 5 models have considerably less support than the top 3 models. The best model (ϕ) = DAY + REVISIT correctly predicted clusters with a large mammal predation event 80% of the time. In this model, the probability of a large mammal predation event being present at a GPS cluster site increased with the number of days a wolf spent at the cluster (p=0.018) and decreased if the cluster had been revisited over a number of non-consecutive days (p=0.024; Table 3).

Based on AIC weights for individual variables, number of days (DAY) and revisit occurrence (REVISIT), were 12.4 times important than habitat and 247 times more important than the variables precision, ground cover, and search time in their ability to predict the occurrence of a large mammal predation event (Table 2).

Kill Rate Estimation

The territory size of the Goldstream and Downie wolf packs, determined from bi-weekly aerial monitoring, were 1001 km^2 (n=70) and 431 km^2 (n=26; MCP 95%; Figure 3), respectively. The pack size of the Goldstream and Downie wolf packs were 7 and 12 wolves respectively during winter tracking sessions.

Wolves were tracked for a total of 71 days in 20 sampling intervals, averaging 4.1 days each interval (Table 4). During these sampling intervals we located 15 kills and 14 scavenges. The average wolf-pack kill rate for the Goldstream pack was 0.207 k/d/p and 0.077 k/d/p for the Downie pack (Table 4). The average wolf-pack kill rate for both packs for all years was 0.16 k/d/p, all of which were moose, with the exception of one unidentified ungulate. The estimated number of kills for the entire winter (November 8 to April 30th) from both packs for all years is 24.8 kills per winter.

The average per capita consumption rates in kg prey killed/day/wolf (adjusted for percent edible and consumed) was 8.375 kg/d/w for the Goldstream and 1.55 kg/d/w for the Downie wolf pack. Scavenge rates for the Downie wolf pack was twice as high as the Goldstream pack at 0.25 and 0.13 s/d/p (Table 5).

There were no confirmed mortalities of mountain caribou during tracking sessions.   Further analysis of wolf scat and the use of stable isotope analysis may elucidate prey missed during tracking sequences. Using guard hair and bone collagen samples, stable isotope analysis has been used to determine the diet composition of wolves (Darimont and Reimchen 2002, Szepanski et al. 1999).   When a wolf consumes a prey item, the distinct carbon and nitrogen signature of the prey is deposited chronologically in inert tissues such as hair. This hair can be analyzed using stable isotope models to get an indication of relative prey consumption of each species consumed by wolves during that period of hair growth.

Landscape Attributes that Affect the Predation Risk of Moose by Wolves

During winter, we recorded 35 moose killed by wolves, and a total of 129 telemetry locations for 17 moose when they were alive. Unfortunately, several of the predation events and telemetry locations were found on private land (Beaumont Timber), where digital forest cover information was not readily available, so these locations were discarded from the analysis. We were left with 29 predation events and 96 telemetry locations for analysis.

Moose were killed an average of 895 m (SE=278.4) from a major water source, compared to live moose, which were found 633 m (SE= 134) from major water sources (Table 6). Dead moose were located 30% closer to seral edges (54.3 m [SE=22.6] vs. 77.9 m [SE=19.6]) and had 30% more logged forest within the 200-m buffer, relative to live moose. Moose were predated upon at an average of 839.6 m above sea level (asl; SE=52.2), compared to live moose, which were located at 780.1 m (SE=29.0) asl. The variance for most of the parameters we estimated was large, suggesting that higher sample sizes will be required to clarify these comparisons.

The multivariate modeling revealed that the intercept-only model (i.e., null model) was the most parsimonious, confirming that the variance of parameter estimates was too large to derive strong conclusions (Table 7). However, of the models that included covariates, the model with distance-to-major-water was the best, followed by elevation, and distance-to-early-seral edge. Greater distance-to-major-water and elevation were positively associated with finding a moose kill,

whereas moose were more likely to be killed with decreasing distance to early seral/late seral habitat edges.

Discussion

Spatial Overlap of Moose, Wolves, and Caribou

Our preliminary analysis of elevational overlap among the 3 species suggests that caribou are at the lowest probability of encountering moose and wolves during late winter (Allison 1998). Unfortunately, the wolf data is still too sparse to reliably quantify seasonal predation risk to caribou. However, if the moose elevation data is used as a surrogate for wolf locations, it appears that caribou are least threatened by wolves during late winter, and the greatest degree of threat occurs during late summer, with some risk during spring and early winter. Wittmer et al.'s (in press) provincial analysis of caribou mortality indicates that predation is greatest during spring and summer, and least during the 2 winter seasons, particularly during late winter.

GPS Radio-collar Cluster Analysis

Predation Site Investigations
We were able to successfully locate prey remains at 40% of the sites that were identified using GPS cluster analysis. This technique gave us the first look at summer wolf predation for packs in the northern Columbia Mountains. Using this technique in the future could elucidate summer predation patterns, increase sample sizes for prey selection studies, reduce field costs, and allow for the extrapolation of kill sites to estimating kill rates during all seasons.

As with any study that uses GPS data, one must be aware of the potential bias and problems inherent with this kind of data. In our study, the GPS collar had a low fix success rate (48.1%) relative to what has been reported elsewhere (84% and 88%; Mark Hebblewhite, Pers comm., Kim Lisgo, Pers. comm.). Poor GPS collar performance may be attributed to the interaction of steep terrain, dense canopy cover, seasonal ranges or animal behaviour (D'eon et al. 2002; Frair et al. 2004). Biases in GPS locations can introduce error and result in misleading conclusions. For example, uncorrected GPS bias could lead to the inference that steep slopes, or closed conifer forests have reduced predation risk, or that wolves spend less time in these habitats. An attempt to correct for these biases have been developed by Frair et al. (2004) and D'Eon (2003).

Additional sources of bias could be introduced due to the differences in sightability in different habitats. In some habitats, dense shrub and herb layers may hamper the ability to search for prey remains, therefore reducing the probability of detection. We attempted to reduce this source of bias by conducting detailed grid pattern searches during site visits. Difference in detectibility was included as a covariate in our models, but it was not a significant factor.

While other sources of bias may lead to underestimates of wolf predation rates, the inability to differentiate between a predation or scavenging event may lead to an over-estimate in kill rates. Baseline predation and scavenging rates for the study area have been determined using winter tracking in 2003 and 2004. These rates could be used as a correction factor when GPS cluster analyses are used to extrapolate kill rates in the future.

GPS Cluster Predation Model

With data gathered at GPS cluster sites we were able to develop a model that isolates important factors that can be used to predict large mammal predation events with future GPS data. The number of days spent the collared wolf spent at a cluster and whether the site was revisited over a number of occasions has been shown to be statistically significant in the model. What is the biological significance of these factors? The number of days a wolf pack spends near a moose kill is 2-4 days and less than 24 hours for a deer or caribou (Thurber and Peterson 1993; Hayes and Harestad 2000; Kunkel et al. 2004). Due to the prominence of moose on the landscape (3.54 moose/km^2; Poole and Serrouya 2003) and in the wolves' winter diet (Stotyn 2003), we can assume that moose make up a large proportion of the summer diet as well. Therefore, as the number of days spent at a location increases, so does the probability that a moose kill has occurred. Anderson and Lindzey (2003) also found the probability that a cougar killed a large mammal increased with the number of nights of cougar presence within a 200-m radius of the center point of the cluster.

The negative relationship between of the number of times a site is revisited by the GPS collared wolf may be due repeated dispersion of the prey remains, or these clusters favoured bedding or rendezvous sites.

GPS kill clusters may also help reveal important mechanistic differences in caribou mortality patterns across seasons that would be missed using solely patterns of spatial overlap. Although there is a high degree of spatial separation between caribou and wolves during late winter, with correspondingly less mortality (Wittmer et al. in press), this separation is not as pronounced during other seasons. Despite the lack of clear spatial separation between wolves and caribou during spring, summer, and early winter, there are pronounced differences in caribou mortality rates among these seasons. At a provincial scale, caribou have more than twice the chance of being killed in summer relative to early winter (Wittmer et al., in press). We hypothesize that the lack of predation in early winter is a function of predator foraging behaviour related to search times for primary prey. Holling's disk equation (1959) provides a mechanism to test this hypothesis, because the equation separates wolf behaviour into search times and handling times. The type II functional response asymptotic curve predicts that as prey density increases, search times are reduced, but handling times remain the same. The asymptote is reached because search times can become negligible at high prey densities, but handling time cannot be reduced because wolves cannot consume primary prey any faster. We predict that the discrepancy in mortality patterns between summer

and early winter is because moose are more dispersed during summer, resulting in greater search times by wolves, thereby increasing incidental encounters with caribou. Whereas in early winter, moose are more concentrated, so search times are expected to be lower, with less incidental encounters (and consequent predation) with caribou. Quantifying kill rates across different seasons using GPS clusters will help clarify this hypothesis because if the distance between kill clusters is greater during summer, we could infer greater probability of encounter with caribou.

We look forward to continuing this research and refining our predation model with the deployment of the three remotely downloadable GPS collars (HABIT, Victoria, B.C) in March 2005. If successful, these data may validate model predictions, increase sample size and reduced the time interval to investigating the site, possibly improving the identification of prey remains and probability of finding a kill at the site. Part of the model validation will include comparing kill rates determined from GPS clusters during winter with more traditional snow trailing and aerial-detection methods of estimating kill rates.

Kill Rate Estimation

When attempting to compare kill rates among studies, the per capita amount of biomass eaten by wolves per day is the desired parameter, because kill rates can vary with the prey size, wolf pack size and snow conditions of the study area (Jedrzejewski et al. 2002). The mass of prey killed/day/wolf in the Goldstream valley was within the range reported by Dale et al. (1995) and Ballard et al. (1987) of 4.1-12.0 kg/w/d and 4.5-14.9 kg/w/d respectively.

Kill rates were lower for the Downie wolf pack possibly due to the limited number of sampling intervals in 2004/05. Hebblewhite et al. (2003) suggest that 25% of the winter, sampled in ≥6-8 individual sampling intervals, is required to minimize sampling variation in kill rate estimates. Lower kill rates could also be due to the high scavenging rate obtained during those sampling intervals. Huggard (1993) found that wolves are opportunistic scavengers, independent of kill rates.   A high scavenge rate, especially in late winter when animals may die of other causes, may reduce kill rates because a substantial portion of the diet may be composed of scavenged food (Huggard 1993).

Winter wolf kill rates cannot be extrapolated to snow-free periods because of the influence of snow depth, seasonal pack cohesiveness, spatial arrangement of predators and prey, and changing prey vulnerabilities (Hebblewhite et al. 2003; Jedrzejewski et al. 2002; Thurber and Peterson 1993; Huggard 1993; Nelson and Mech 1986). We have attempted to address these limitations by developing models to locate kills in the summer using GPS location data. If successful, this information can be extrapolated to calculate summer kill rates by wolves.

Landscape Attributes that Affect the Predation Risk of Moose by Wolves

Ungulates use a number of behavioural adaptations to minimize predation risk including group living (Bertram 1978), dispersion (Bergerud and Page 1987),

and the selection of specific terrain conditions or habitat types (Kie 1999). Some habitat conditions afford protection to ungulates by providing escape terrain, such as steep slopes for mule deer, or rugged terrain used by mountain goats. Moose have been found to use islands or water bodies to minimize predation risk (Stephens and Peterson 1984, Leptich and Gilbert 1986, Jackson et al. 1991, Addison et al. 1993). In our study, we found that in winter, moose that ventured further from a major water source were more likely to be killed by wolves. It is likely that water bodies such as the Goldstream River or Downie Creek provide a refuge to moose because wolves have difficulty killing prey in water. This result contrasts with other moose-wolf study areas, where most water bodies freeze in winter, which provides increased travel and foraging efficiency for wolves.

Moose were also more likely to be killed at higher elevations, although elevation was correlated with distance-to-major-water (r=0.63), but the latter is likely the more mechanistic variable. Moose were more likely to be killed near seral edges, implying that moose that were either deep within clearcuts or old forests were less likely to be eaten by wolves. While trailing wolves in snow we often noted that they traveled in old forests adjacent to logged areas and other openings. As moose forage further into logged areas, it may become more difficult for wolves to locate them because of deeper snow and reduced visibility.

Proximity to logging roads did not seem to affect predation risk, although we did not have the data to differentiate between major, cleared logging roads and minor logging roads with deep snow. In Alberta, James and Stuart-Smith (2000) found that linear corridors facilitated wolf predation by providing faster travel routes for wolves.

Management Implications

As GPS-animal collar technology becomes more prevalent in wildlife studies it is important to develop methods that can take full advantage of this technology. Making the link between GPS locations and animal behaviour could be important to increase our understanding of complex systems for the benefit of conservation and management efforts.

Information on winter kill rates and scavenge rates can act as a baseline from which we can measure the effects of changing prey densities as a result of management scenarios, successional processes and changing climates.

Of special interest for conservation efforts is the spatial location of kill sites on the landscape in relation to terrain features, roads, the intensity and pattern of forest harvesting, habitat and human use. Information on the interaction of predation risk and landscape attributes may be used to define high and low risk habitats for moose and caribou with regards to wolf predation. Ultimately our work on moose predation risk will be expanded to include non-winter seasons and contrasted with the caribou predation risk model being developed by other members of our research team (C. Apps, H. Wittmer, B. McLellan) to identify zones of shared predation risk between the 2 species.

Acknowledgments

Literature Cited

Addison, E.M., R.F. McLaughlin, D.J.H. Fraser, and M.E. Buss. 1993. Observations of pre- and post-partum behaviour of moose in central Ontario. Alces 29:27–33.

Allison, B.A. 1998. The influence of wolves on the ecology of mountain caribou. M.Sc. thesis, University of British Columbia, British Columbia.

Anderson, C.R. and F.G. Lindzey. 2003. Estimating cougar predation rates from GPS location clusters. Journal of Wildlife Management 67**:** 307-316.

Apps C.D., B.N. McLellan, T.A. Kinley, and J.P. Flaa. 2001. Scale-dependent habitat selection by mountain caribou, Columbia Mountains, British Columbia. Journal of Wildlife Management 65(1):65-77.

Apps, C.D. and B.N. McLellan. Factors influencing the population fragmentation of mountain caribou populations. Submitted March 2005. Biological Conservation.

Ballard, W.B., L.A., Ayres, P.R. Krausman, D.J. Reed, and S.G. Fancy. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. Wildlife Monographs 135.

Ballard, W.B., J.S. Whitman, and C.L. Gardner. 1987. Ecology of an exploited wolf population in South-Central Alaska. Wildlife Monographs 54.

Bergerud, A.T. and J.P. Elliott. 1998. Wolf predation in a multiple-ungulate system in northern British Columbia. Canadian Journal of Zoology 76:1551-1569.

Bergerud, A.T., H.E. Butler, and D.R. Miller. 1983. Antipredator tactics of calving caribou: dispersion in mountains. Canadian Journal of Zoology 62**:**1566-1575.

Bergerud, A.T., and R.E. Page. 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. Canadian Journal of Zoology 65: 1597–1606.

Bertram, B.C.R. 1978. Living in groups: predators and prey. *In* Behavioral ecology: an evolutionary approach. *Edited by* J.R. Krebs and N.B. Davies. Blackwell Scientific Publications, Oxford. pp. 64–96.

Braumandl, T. F., and M. P. Curran. 1992. A field guide for site identification for the Nelson Forest Region. Victoria, British Columbia, Canada, Ministry of Forests.

Burnham, K.P., and D.R. Anderson. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. Wildlife Research 28:111-119.

Caughley, G., and A.R.E. Sinclair. 1994. Wildlife ecology and management. Oxford University Press, Don Mills, Ontario, Canada.

Dale, B.W., L.G. Adams, and R.T. Bowyer. 1994. Functional-response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. Journal of Animal Ecology 63:644-652.

Dale, B.W., L.G. Adams, and R.T. Bowers. 1995. Winter wolf predation in a multiple ungulate prey system, Gates of the Arctic National Park, Alaska. *In* Ecology and conservation of wolves in a changing world., *Edited by* L.N. Carbyn, S.H. Fritts, and D.R. Seip. pp. 223-230.

Darimont, C.T., and T.E. Reimchen. 2002. Intra-hair stable isotope analysis implies seasonal shift to salmon in gray wolf diet. Canadian Journal of Zoology 80:1638-1642.

Demarchi, D. A. 1996. An introduction to the ecoregions of British Columbia.   . Victoria, British Columbia, Canada, Wildlife Branch, Ministry of Environment, Lands and Parks.

D'Eon, R. G. 2003. Effects of a stationary GPS fix-rate bias on habitat-selection analyses. Journal of Wildlife Management. 67:858-863.

D'Eon, R.G., R. Serrouya, G. Smith, and C.O. Kochanny. 2002. GPS radiotelemetry error and bias in mountainous terrain. Wildlife Society Bulletin 30:430-439.

Frair, J.L., S.E. Nielsen, E.H. Merrill, S.R. Lele, M.S. Boyce, R.H.M. Munro, G.B. Stenhouse, and H.L. Beyer. 2004. Removing GPS collar bias in habitat selection studies. Journal of Applied Ecology 41:201-212.

Franke, K.A. 2004. Analysis of space-time-action systems in woodland caribou (*Rangifer tarandus*) using hidden Markov models. Ph.D thesis. University of Alberta. Edmonton, Alberta.

Hayes, R.D., A.M. Baer, U. Wotschikowsky, and A.S. Harestad. 2000. Kill rate by wolves on moose in the Yukon. Canadian Journal of Zoology 78:49-59.

Hayes, R.D., and A.A. Harestad. 2000. Wolf functional response and regulation of moose in the Yukon. Canadian Journal of Zoology 78:60-66.

Hebblewhite, M., Merrill, E.H., and McDonald, T.L. (In Review). Spatial decomposition of predation risk using resource selection functions:an example in a wolf-elk predator-prey system. Oikos.

Hebblewhite, M., P.C. Paquet, D.H. Pletscher, R.B. Lessard, and C.J Callaghan. 2003. Development and application of a ratio estimator to estimate wolf kill rates and variance in a multiple-prey system. Wildlife Society Bulletin 31:933-946.

Hebblewhite, M. and D. Pletscher. 2002. Effects of elk group size on predation by wolves. Canadian Journal of Zoology 80:800-809.

Holling, C.S. 1959. The components of predation as revealed by a study of small-mammal predation of the European sawfly. Canadian Entomology 91:293-320.

Hosmer, D.M., and S. Lemeshaw. 2000. Applied Logistic Regression . John Wiley & Sons, New York, NY.

Huggard, D.J. 1993. Effect of snow depth on predation and scavenging by gray wolves. Journal of Wildlife Management 57:382-388.

Jackson, G.L., G.D. Racey, J.G. McNicol, and L.A. Godwin. 1991. Moose habitat interpretation in Ontario. Ontario Ministry of Natural Resources, NWOFTDU Technical Report 52.

James, A.R.C. and A.K. Stuart-Smith. 2000. Distribution of caribou and wolves in relation to linear corridors. Journal of Wildlife Management 1:154-159.

Jedrzejewski, W., K. Schmidt, J. Theuerkauf, B. Jedrzejewska, N. Selva, K. Zub, and L. Szymura. 2002. Kill rates and predation by wolves on ungulate populations in Bialowieza Primeval Forest (Poland). Ecology 83: 1341-1356.

Kie, J.G. 1999. Optimal foraging and risk of predation: effects on behaviour and social structure in ungulates. Journal of Mammal. 80:1114-1129.

Kunkel, K.E., D.H. Pletscher, D.K. Boyd, R.R. Ream, and M.W. Fairchild. 2004. Factors correlated with foraging behavior of wolves in and near Glacier National Park, Montana. Journal of Wildlife Management 68:167-178.

Kuzyk, G. 2002. Wolf distribution and movements on caribou ranges in West-Central Alberta. B.Sc. thesis, University of Alberta, Alberta.

Leptich, D.J., and J.R. Gilbert. 1986. Characteristics of moose calving sites in northern Maine: a preliminary investigation. Alces 22:69–81.

Mountain Caribou Technical Advisory Committee. A strategy for the recovery of mountain caribou in British Columbia. 2002. Victoria, British Columbia, Ministry of Water, Land and Air Protection.

Neiland, K.A. 1970. Weight of dried marrow as indicator of fat in caribou femurs. Journal of Wildlife Management 34: 904-907.

Nelson, M.E. and D.L. Mech. 1986. Relationship between snow depth and gray wolf predation on white-tailed deer. Journal of Wildlife Management 50:471-474.

Poole, K., and R. Serrouya. 2003. Moose population monitoring in the Lake Revelstoke valley, 2002-2003. Revelstoke, BC: Downie Sawmills. 17 p.

Sand, H., O. Liberg, O. Johansson, P. Wabakken, B. Zimmerman, and P. Ahlqvist. 2003. Summer predation patterns of Scandinavian wolves. *In* World Wolf Congress 2003 - Bridging Science and Community. Banff, Alberta.

Seip, D.R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British-Columbia. Canadian Journal of Zoology 70:1494-1503.

Sergeant, D.E., and D.H. Pimlott. 1959. Age determination in moose from sectioned incisor teeth. Journal of Wildlife Management 23:315-321.

Serrouya, R., and R. D'Eon. 2002. Moose habitat selection in relation to forest harvesting in a deep snow zone of British Columbia. Prepared for Downie Timber Ltd., Revelstoke, British Columbia.

Smith, D.W., T.D. Drummer, K.M. Murphy, D.S. Guernsey, and S.B. Evans. 2004. Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995-2000. Journal of Wildlife Management 68: 153-166.

SPSS. 2004. SPSS 13.0 for Windows. Illinois, USA.

Stephens, P.W., and R.O. Peterson. 1984. Wolf-avoidance strategies of moose. Holarctic Ecology 7:239–244.

Stotyn, S. 2004. Revelstoke Caribou-Wolf Project: Year 2 Summary Report, April 2003-March 2004. Prepared for Downie Street Sawmills, Mnt. Revelstoke and Glacier National Parks, and Forest Innovation Investment. Revelstoke, British Columbia. 19 p.

Szepanski, M.M., M. Ben-David and V.Van Ballenberghe. 1999. Assessment of anadromous salmon resources in the diet of Alexander Archipelago wolf using stable isotope analysis. Oecologia 120: 327-335.

Thurber, J.M., and R.O. Peterson. 1993. Effects of population-density and pack size on the foraging ecology of gray wolves. Journal of Mammalogy 74: 879-889.

Wittmer, H.U., B.N. McLellan, D.R. Seip, J.A. Young, T.A. Kinley, G.S. Watts, and D. Hamilton. In Press. Spatio-temporal population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. Canadian Journal of Zoology.

Wittmer, H.U and B.N. McLellan. In review. Underlying mechanisms of the decline of an endangered large herbivore. Conservation Biology.

Wittmer, H. U., A. R. E. Sinclair, and B.N. McLellan. The role of predation in the decline and extirpation of woodland caribou. Oecologia . In Press.
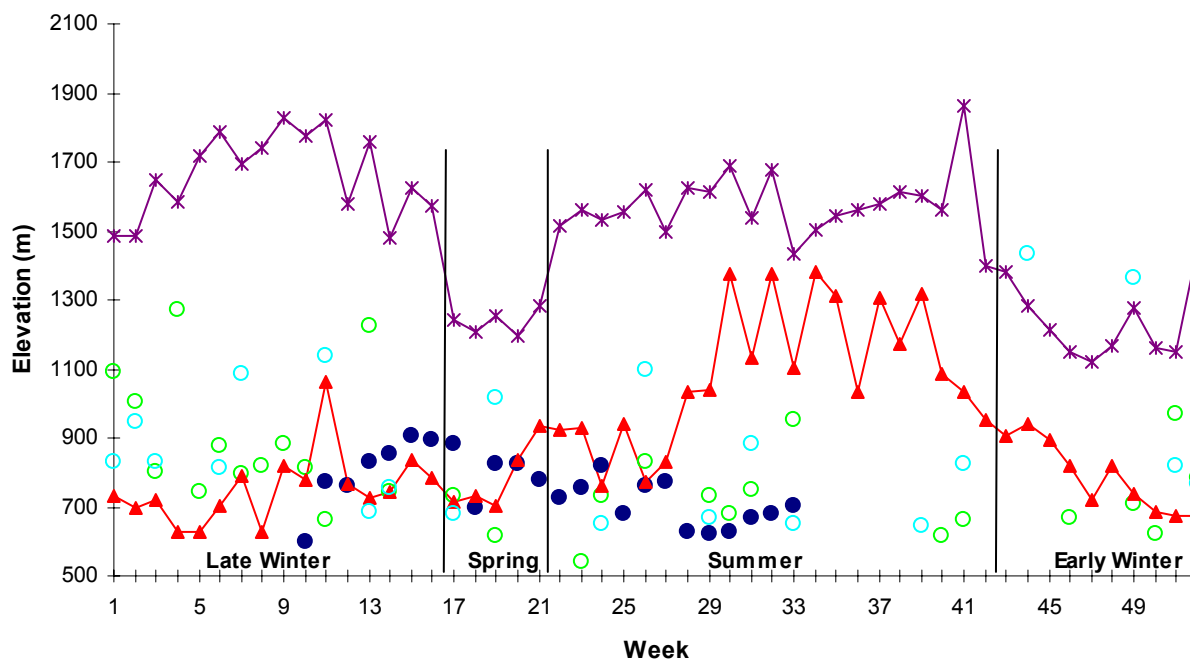
Figure 1. Mean weekly elevation use for mountain caribou (purple line; modified from Apps et al. 2001), moose (red line), and individual wolves (circles – each colour is an individual), in the northern Columbia Mountains, BC. Seasons identified are based on Apps et al.'s (2001) definition of mountain caribou seasons in the Columbia Mountains.

Figure 2. The number and success of cluster investigations in each habitat type in the northern Columbia Mountains, British Columbia.

Figure 3. Home ranges of three wolf packs (Red Rock, Goldstream and Downie) in the northern Columbia Mountains, British Columbia from telemetry locations gathered during 2003 to 2005 (MCP 95%).
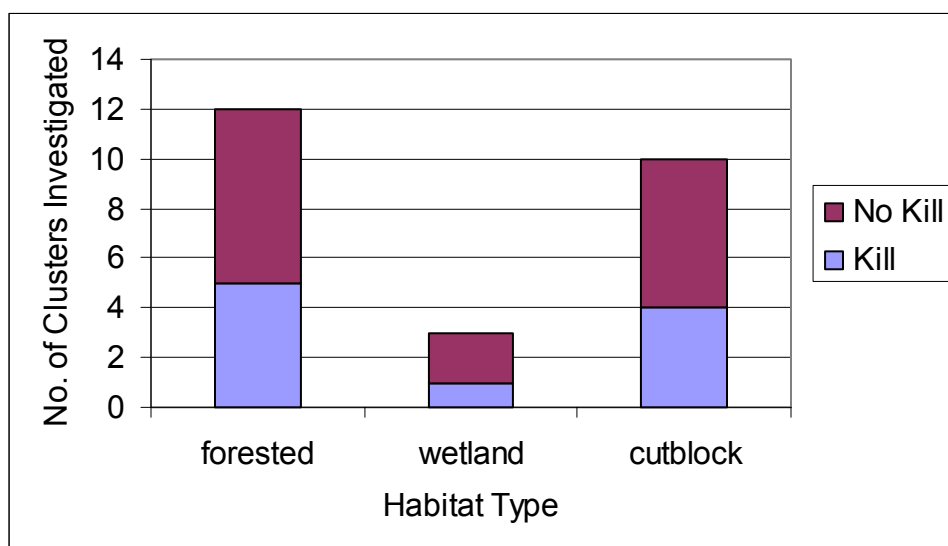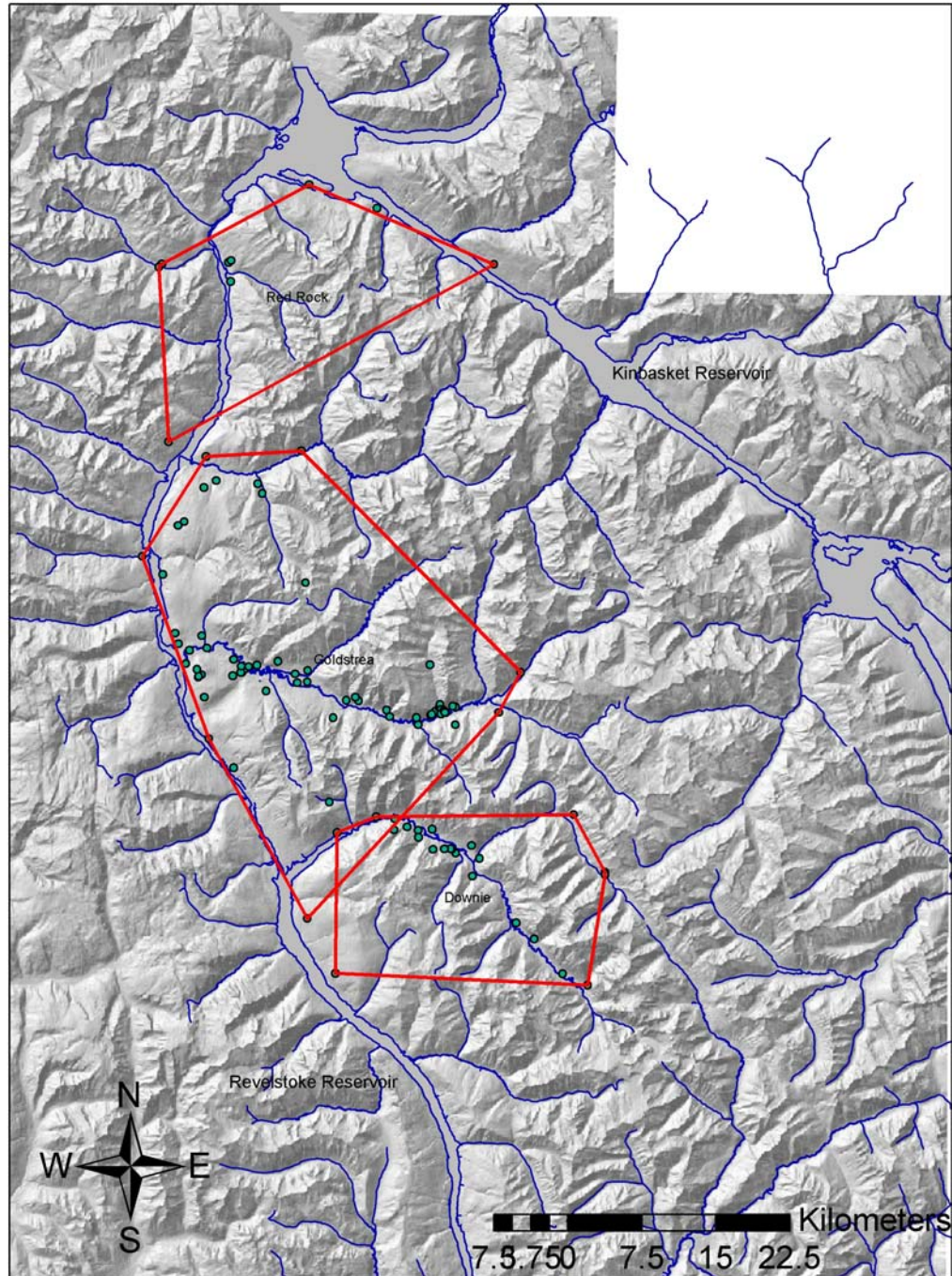
Table 1. Logistic regression models for GPS cluster site investigations in the northern Columbia Mountains, British Columbia, Canada. The top set of candidate models showing the model structure, maximized log likelihood (LL), the number of parameters (K), Akaike's information criteria for small sample sizes (AIC_c), change in AIC from the "best" fit model (Δ_i) and the Akaike weights (*w*). *Interaction terms for the specified variables.

Rank	Model Structure	LL	K	AIC_c	Δ_i	Wi
1	DAY[1]+REVISIT[2]	20.33	4	30.33	0.00	0.892
2	HAB[3]+DAY+REVISIT	18.55	6	35.22	4.89	0.077
3	DAY	32.01	2	36.55	6.22	0.040
4	DAY*REVISIT	30.74	3	37.88	7.55	0.020
5	PRE[4]	33.40	3	40.54	10.21	0.005
6	SEARCH[5]+GROUND[6]	31.46	4	41.46	11.13	0.003
7	HAB+DAY	31.56	5	44.72	14.39	0.001
8	DAY+HAB+GROUND+PRE +REVISIT+ SEARCH	17.84	9	47.84	17.51	0.000

[1], Number of days spent at the cluster site;[2], if wolves revisited the site (Y=1, N=0);[3],habitat class (forested, wetland, cutblock);[4], precision of fix (% 3D fix accuracy);[5], time spent searching the area;[6], ground visibility (good=0, poor=1).

Table 2. Multi-model inference of the importance of predictor variables in the identification of large mammal predation events using wolf GPS data in the northern Columbia Mountains, British Columbia, Canada.

Predictor variable	Predictor weight (w_{ij})
Days	0.991174
Revisit	0.990504
Habitat	0.078297
Precision	0.003555
Search time	0.003555
Ground cover	0.003555

Table 3. Highest-ranked logistic regression model for estimating the probability of finding a large mammal predation event at a GPS cluster site in the northern Columbia Mountains, British Columbia, Canada (N_{obs} = 25).

Variable	B	SE	P
Days	2.335	0.991	0.018
Revisit Site			
Yes	-6.013	2.656	0.024
Reference=No			
Constant	-4.502	1.616	0.030

Table 4. Data collected during winter snow-tracking used to estimate kill rates and per capita consumption rates for 2 wolf packs in the northern Columbia Mountains, British Columbia during 2003-2005. Kill rates were calculated using a ratio estimator as outlined by Hebblewhite et al. (2003). Total wolf kill rates in kills/day/pack (k/d/p), and kg prey killed/day/wolf (kg/d/w).

Wolf pack-year	# of sampling intervals (N)	Mean length in days (x_s)	# Days tracked (n)	% winter tracked [a]	# of kills (y_i)	Wolf pack size	Ratio-estimator kill k/d/p	rates kg/d/w [b]	Estimated total number of kills for the entire winter (Y) [a]
GOLD 03/04	9	4.89	44	25.14	9	6	0.205	7.17	35.8
GOLD 04/05	8	3.00	14	8.00	5	8	0.208	9.58	36.5
DOWNIE 04/05	3	4.33	13	7.43	1	12	0.077	1.55	13.5

[a] the entire winter is considered to be from Nov. 8 - April 30 to correspond to mountain caribou early and late winter delineation (175 days).
[b] number of prey to kilograms of prey killed per day per wolf using moose mass estimates from Hayes et al. (2000) and corrected for the percent of carcass consumed (65%, Hayes et al. 2000).

Table 5. Data collected during winter snow-tracking used to estimate scavenging rates for 2 wolf packs in the northern Columbia Mountains, British Columbia during 2003-2005. Scavenge rates were calculated using a ratio estimator as outlined by Hebblewhite et al. (2003). Total wolf scavenge rates in scavenges/day/pack (s/d/p), and scavenges/day/wolf (s/d/w).

Wolf pack-year	# sampling intervals (N)	Mean length in days (x_s)	# days tracked (n)	% winter tracked [a]	# of scavenges (y_i)	wolf pack size	Ratio-estimator scavenge s/d/p	rates s/d/w
GOLD ¾	9	4.89	44	25.14	8	6	0.182	0.030
GOLD 04/05	8	3.00	14	8.00	3	8	0.083	0.010
DOWNIE 04/05	3	4.33	13	7.43	3	12	0.250	0.021

[a] the entire winter is considered to be from Nov. 8 - April 30 to correspond to mountain caribou early and late winter delineation (175 days).

Table 6. Comparison of landscape factors around telemetry locations of live moose, compared to locations where wolves killed moose, in the northern Columbia Mountains, BC. Variables refer to the composition within a 200-m radius GIS buffer around each location, except distance variables, which were based on the point location.

Variable	Dead moose (N=29)		Live moose (N=16)		%
	Dead mean	Dead SE	Live mean	Live SE	difference[1]
Hemlock (%)	8.8	2.4	18.3	3.4	-51.9
Western red cedar (%)	35.9	3.7	30.0	3.0	19.7
Spruce (unclass) (%)	6.2	1.6	9.4	2.1	-33.7
Engelmann spruce (%)	13.5	3.0	8.4	2.4	61.3
Douglas-fir (%)	5.5	3.0	6.7	1.8	-18.3
Deciduous (%)	3.8	1.4	4.3	1.1	-12.3
Slope (%)	28.0	3.4	31.5	2.6	-11.1
Age (yr)	99.2	13.0	108.8	12.6	-8.8
Crown closure (%)	32.0	3.0	33.0	3.0	-3.0
Non-Productive Brush (%)	4.4	1.2	6.4	1.6	-31.6
Riparian (%)	6.9	2.7	5.4	1.9	27.2
Logged (%)	35.7	5.7	27.5	6.1	29.8
Elevation (m)	839.6	52.2	780.1	29.0	7.6
Distance to major water source (m)	894.6	278.4	632.8	134.0	41.4
Distance to any water source (m)	552.9	163.2	473.2	95.5	16.8
Distance to seral edge (m)	54.3	22.6	77.9	19.6	-30.3
Distance to road (m)	472.5	193.0	454.2	159.9	4.0

[1] Percent difference calculated for mean values as (dead – live)/live* 100% = "percent difference of the dead value from the live value."

Table 7. Logistic regression models to predict the probability of finding a moose predation event (1), relative to live moose (0). The top set (0-4 ∆AICc units of candidate models showing the model structure, maximized log likelihood (LL), the number of parameters (K), Akaike's information criteria for small sample sizes (AIC_c), change in AIC from the "best" fit model (Δ_i) and the Akaike weights (*w*). Direction of parameter estimate (+ or –ve) is given in brackets beside each variable.

Rank	Model Structure	-2LL	K	AIC_c	Δ_i	Wi
1	Null model	135.42	1	137.57	0.00	0.18
2	Distance to major water (+)	133.84	2	138.30	0.73	0.13
3	Elevation (+)	134.49	2	138.96	1.39	0.09
4	Distance to early seral (-)	134.71	2	139.17	1.60	0.08
5	Distance to major water (+) + Distance to early seral (-)	132.33	3	139.29	1.72	0.08
6	Riparian(%) (-)	134.88	2	139.35	1.78	0.07
7	Age (-)	135.16	2	139.62	2.05	0.06
8	Logged(%) (+)	135.31	2	139.77	2.20	0.06
9	Distance to road (+)	135.38	2	139.84	2.27	0.06
10	Distance to major water (+) + Logged(%) (+)	133.62	3	140.58	3.01	0.04