Determining wolf summer predation patterns using GPS cluster analysis: a preliminary report.

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Abstract

As a preliminary study, we used the GPS location data (May – September 2004) from one wolf collar to determine the feasibility of determining 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 wolf spent at the cluster ($P = 0.024$) and decreased if the cluster had been revisited over a number of non-consecutive days ($P = 0.018$). 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.

Introduction

Efforts have been made to quantify wolf prey selection 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 rates of predation (Sand et al. 2003) compared to winter seasons.

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, difficult in remote areas and dangerous in areas with bear 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 be able to estimate predation events using future GPS data. Wolf movement patterns such as travel rate per hour, turn angle and distance between locations were used to train models that successfully predicted observer-confirmed wolf kill sites (Kuzyk 2002; Franke 2004).

Investigating summer wolf predation patterns could also be an important factor in the recovery of mountain caribou (*Rangifer tarandus*) and the management of moose (*Alces alces*) populations in the North Columbia Mountains, B.C. As an anti-predator strategy, mountain caribou spatially separate themselves from predators and other ungulate species to reduce their risk of predation (Bergerud et al. 1983). In the summer, mountain caribou come into increasing contact with predators and other ungulate species and therefore experience higher mortality rates (Wittmer et al. In Prep; Seip 1992).

In the following paper, we present the preliminary results that attempt to investigate summer wolf predation patterns in the North Columbia Mountains from GPS cluster sites using techniques employed by Anderson and Lindzey (2003).

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, extensive clearcut areas, 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 subzone is dominated by forests of western redcedar (*Thuja plicata)*, western hemlock (*Tsuga heterophylla*) and Douglas-fir (*Pseudotsuga menziesii*). The ESSF landscape is comprised of coniferous forests of Englemann Spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Alpine meadows, shrublands, snowfields, glaciers and rock dominate the Alpine Tundra subzone.

The most abundant ungulate species in the area is moose, 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 R. 2003). Mountain goats (*Oreamnos americanus)* and mountain caribou are also found in the study area. Grizzly bears (*Ursus arctos*), black bears (*U. americanus*), wolverine (*Gulo gulo*), wolves and cougars (*Felis concolor*) occur throughout.

GPS Collars

Six wolves were captured using a netgun fired from a helicopter (Bighorn Helicopters Inc., Cranbrook, B.C.) and affixed with VHF LMRT and GPS_3300 collars in March 2004 (University of Alberta-Protocol 2004-09D; Lotek Inc.,Newmarket, Ontario). Collars were programmed to attempt position acquisitions once every 3 hours. Potential kill sites were identified from GPS data downloaded from a LOTEK GPS_3300 collar retrieved in August 2004.

Predation Site Investigation

To identify GPS clusters, I calculated the interfix distance between fixes using Arcview 3.3. These results were binned into groups of 100 m and graphed to determine a breakpoint in the data that would represent the difference between resting/feeding and moving. A breakpoint of 200 m was visually estimated from the histogram. A cluster was defined as >2 locations and less than 200 m apart. The average cluster location was delineated using the weighted mean of points. Twenty-nine clusters were randomly selected to be investigated in the field.

Cluster sites were methodically searched for a minimum of 1 hour for evidence of a large mammal predation event at the GPS cluster site. When kills were located, the species, age, and sex were recorded. 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).

Predation model

Using binary logistic regression, I 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, if the wolf made multiple visits to the site (yes=1 or no=0), habitat type (forested=0, 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), I assessed 8 a-priori candidate models to identify the best model that predicted the probability of finding a large mammal predation event at the cluster site. .

Using Δ_I values ($\Delta_I = AIC_i - \text{min}AIC$), the candidate models were ranked and the strength of evidence for each model was determined (Burnham and Anderson 2001). I also calculated Akaike weights (*w*), which provide a measure of the relative likelihood of an individual model given the data and the chosen set of candidate models. 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 was used for model building. Future data will be used to increase sample size and verify the model predictions. All statistical analyses were performed using SPSS 13.0 software (SSPS 2004).

Results

GPS Collars

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.

Predation Site Investigations

There was evidence of a large mammal predation event at 40% of the sites investigated (Figure 1). Cluster sites were located in forested (52%), wetland (12%) and cutblock (40%) habitat types. Of the twenty-nine GPS cluster sites identified, 4 were abandoned due to 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 completed at this time. We did not include sites where cut bones were found, as they were assumed to be a scavenging event.

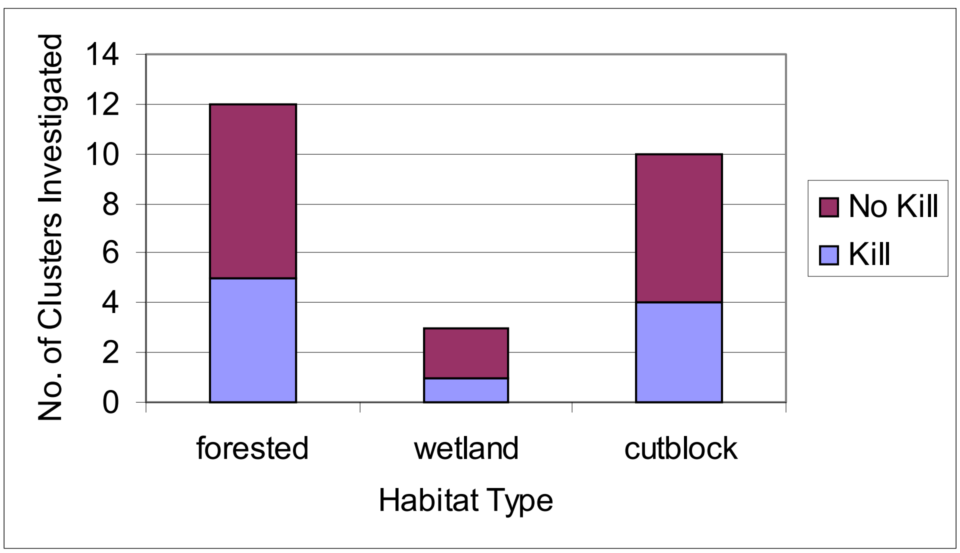

Figure 1. The number and success of cluster investigations in each habitat type in the North Columbia Mountains, British Columbia.

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 $\Delta_i \leq 2$ 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 chosen as the best fit model using AIC model selection (Table 1 and 3). The second ranked model (ϕ) = HAB + DAY + REVISIT has 11.6 times less strength of 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.

The variables, number of days and revisit occurrence, are 92% more important than habitat and 99.7% more important than the variables precision, ground cover, and search time in its ability to predict the occurrence of a large mammal predation events (Table 2).

Discussion

GPS Collars

Poor GPS collar performance in the study area may be attributed to the interaction of steep terrain, dense canopy cover, season and animal behaviour (D'eon et al. 2002; Frair et al. 2004). Fix rate success for wolves affixed with Lotek GPS_3300 collars in other studies range from 84% and 88% in Banff National Park, Alberta and western Alberta respectively (Mark Hebblewhite, Pers comm., Kim Lisgo, Pers. comm.). These biases in GPS locations can introduce error and influence resource selection models resulting in misleading assessments. For example, GPS bias could lead to the inference that closed conifer forests have reduced predation risk, or that wolves spend less time in these habitats. Data should be corrected to reduce the effects of GPS bias before proceeding with fine scale analysis using GPS location data (Frair et al. 2004).

Although remote downloadable GPS collars (HABIT, Victoria, B.C.) were available for deployment, collars were not successfully deployed due to poor capture success. This would have increased our 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.

Predation Site Investigations

The dense shrub and herb layer in some habitats hampered the ability to search for prey remains therefore reducing the probability of detection. It is also important to visit sites before fall to ensure that ground visibility is optimal.

The methods used to identify clusters could be improved using programs such as the Arcview extension “tracking analyst” (Anderson and Lindzey 2003). This would provide a repeatable, non-bias method for identifying GPS cluster sites.

The coarse GPS fix schedule (8 locations/day) limits the analysis to the location of large mammal predation events only. A more detailed picture of wolf diet may emerge if GPS fix schedules were increased. This method does not differentiate between a predation or scavenging event which may lead to over-estimates of wolf predation rates.

Predation Model

What is the biological significance of the number of days spent at a cluster and whether the site was revisited over a number of occasions? 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 R. 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 increase so does the probability that a moose kill has occurred. Anderson and Lindzey (2003) also found that the probability that a cougar killed a large mammal increased with the number of nights of cougar presence within a 200 m radius.

The negative relationship of the number of times a site is revisited is difficult to explain. This relationship may be due to the lack of evidence of a kill if the site has been visited multiple times. Therefore, researchers may infer that no kill has been made at the site. Wolf behaviour may also complicate the analysis, as cluster points may represent bedding, dennning or rendezvous sites.

The number of variables and categories used in the analysis was restricted by the small sample size. Additional data from GPS cluster site investigations will be used to increase sample size and validate model predictions.

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.

Using techniques such as GPS cluster analysis to investigate wolf predation patterns would increase sample sizes for prey selection studies, reduce field costs, elucidate summer predation patterns, and allow for the extrapolation of kill sites to kill rates.

Of special interest for conservation efforts is the spatial location of kill sites on the landscape in relation to terrain features, roads, 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. With this increased knowledge we can alter the patterns of human use on the landscape and make informed management decisions.

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Table 1. Logistic regression models for GPS cluster site investigations in the North 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	*W*i
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=0, 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 North 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 North 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