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Statistical Methods for Identifying Wolf Kill Sites Using Global Positioning System Locations

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ABSTRACT Accurate estimates of kill rates remain a key limitation to addressing many predator–prey questions. Past approaches for identifying kill sites of large predators, such as wolves (*Canis lupus*), have been limited primarily to areas with abundant winter snowfall and have required intensive ground-tracking or aerial monitoring. More recently, attempts have been made to identify clusters of locations obtained using Global Positioning System (GPS) collars on predators to identify kill sites. However, because decision rules used in determining clusters have not been consistent across studies, results are not necessarily comparable. We illustrate a space–time clustering approach to statistically define clusters of wolf GPS locations that might be wolf kill sites, and we then use binary and multinomial logistic regression to model the probability of a cluster being a non–kill site, kill site of small-bodied prey species, or kill site of a large-bodied prey species. We evaluated our approach using field visits of kills and assessed the accuracy of the models using an independent dataset. The cluster-scan approach identified 42–100% of wolf-killed prey, and top logistic regression models correctly classified 100% of kills of large-bodied prey species, but 40% of small-bodied prey species were classified as nonkills. Although knowledge of prey distribution and vulnerability may help refine this approach, identifying small-bodied prey species will likely remain problematic without intensive field efforts. We recommend that our approach be utilized with the understanding that variation in prey body size and handling time by wolves will likely have implications for the success of both the cluster scan and logistic regression components of the technique. (JOURNAL OF WILDLIFE MANAGEMENT 72(3):798–807; 2008)

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Although predation is recognized as a major factor influencing population dynamics and community structure (Schmitz et al. 1997), there remains substantial debate surrounding key issues such as limitation versus regulation of prey by predators (Eberhardt et al. 2003), type of predator functional responses (Abrams and Ginzburg 2000), importance of top-down effects on prey populations (Schmitz et al. 2000), and dynamics of switching in multi-prey systems (Abrams and Allison 1982, Patterson et al. 1998). A practical problem to resolving these issues is adequate quantification of actual kill rates of predators (i.e., prey animals killed/predator/unit time), which requires locating all kill sites made during continuous time intervals (Boutin 1992, Boyce 1993, Eberhardt 1997, Marshal and Boutin 1999, Eberhardt et al. 2003). Locating kill sites of wolves (*Canis lupus*) is particularly difficult because wolves range over wide areas, hunt in packs, and have shorter prey-handling times than do some other large predator species (Anderson and Lindzey 2003).

Past approaches for locating wolf kill sites have used either aerial or ground-monitoring of radiomarked wolves. Frequent (twice daily to every other day) relocations of radiocollared wolf packs via fixed- or rotary-winged aircraft have been used to locate kills, but this approach is costly and misses kills of small prey for which handling times are typically short (Messier and Crete 1985, Dale et al. 1994, Hayes et al. 2000, Smith et al. 2004, Sand et al. 2005). In addition, aerial monitoring is infeasible in areas where snow cover is lacking or highly variable, weather and terrain prevent regular flights, or sightability is poor due to extensive forest cover. The alternative to aerial monitoring to locate kills during winter has been continuous snow-tracking sessions (Huggard 1993, Kunkel 1997, Hebblewhite et al. 2004). Although ground-tracking has reduced the likelihood of missing kills, this approach depends on suitable snow conditions and usually results in small samples of kill sites across packs (Fuller 1989, Hebblewhite et al. 2004). Thus, current approaches remain limited by the need for adequate snow cover, open terrain, and road access and still require substantial financial investment to sample even relatively short time periods.

The recent advent of Global Positioning System (GPS) radiocollars for predators provides the potential to locate kill sites without the need for intensive aerial monitoring or tracking snow (Anderson and Lindzey 2003, Sand et al. 2005, Franke et al. 2006). However, these approaches have been met with variable success, have been thoroughly tested with wolves only for large prey species, and may require extensive field visitation to potential kill sites to determine kill rates. For example, Sand et al. (2005) estimated that as many as 32% of wolf-killed moose (*Alces alces*) would not be included in clusters that were defined by their decision rules. Further, characteristics of movement behaviors representing kill sites are likely to vary among predator species due to differences in predator-handling and resting behaviors and types of prey killed. As a result, a method that is effective for small ungulate prey species and minimizes field visits to potential kill sites is needed (Anderson and Lindzey 2003, Sand et al. 2005, Franke et al. 2006).

Our objective in this paper is to present a new approach that uses a space–time clustering algorithm adapted from epidemiology to identify clusters of wolf GPS locations and

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uses binary and multinomial logistic regression to model the probability of a cluster being a non–kill site, kill site of a small-bodied prey species, or kill site of a large-bodied prey species based on wolf movement characteristics. We also investigated whether site-specific environmental covariates can improve predictive success. We assessed the accuracy of our approach for predicting kill sites using an independent set of GPS-movement data and associated clusters collected from wolves in 4 packs.

STUDY AREA

We captured and collared wolves in a 25,000-km^2 area west of Rocky Mountain House about 200 km southwest of Edmonton, Alberta, Canada (52°27′N, 115°45′W). This area included crown lands under jurisdiction of the provincial government as well as portions of Banff and Jasper National Parks. Terrain consisted of moderate to steep hills and mountains ranging in elevation between 900 m and 3,100 m with elevation generally increasing towards the Rocky Mountains in an east to west gradient. The area was predominately conifer forest (52.1%), interspersed with small openings of forestry cut-blocks (5.7%), natural lowland (10.4%), subalpine meadows (3.1%), and stands of deciduous forest (2.7%) including aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*). Conifer forests were dominated by lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*) at moderate and high elevations and black spruce (*Picea mariana*) at lower elevations. Much of the western portion of the study area consisted of bare rock (20.1%) and permanent ice or snow (2.7%). Extensive oil and gas development, forest harvesting, and recreational activity (camping, snowmobiles, all-terrain vehicles, motorbikes, and off-road 4 × 4 vehicles) occurred throughout the majority of provincial lands. Access via trails, seismic-exploration lines, and roads was widespread across the area except at high elevations in mountainous regions in the west.

Wolves were managed as a furbearer and big-game animal on provincial lands and were subject to a 10-month hunting season and 6-month trapping season with no harvest quotas. Wolf populations in Banff and Jasper National Parks were protected except when they crossed park boundaries and were also subject to human-caused mortality in road and railway accidents. Major prey for wolves included elk (*Cervus elaphus*), moose, white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and feral horses (*Equus caballus*), which were present throughout the study area, and bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), and caribou (*Rangifer tarandus*), which were present only in the western portion of the study area. Although rarely killed by wolves, domestic livestock (primarily cattle) were available in eastern portions of the study area. Carcasses of road-killed ungulates were placed by trappers at bait stations distributed throughout provincial lands from December to March; however, we did not use these locations in our study.

METHODS

We captured 19 wolves from 13 packs in 2002–2006 (pack sizes: 3–17 wolves) via helicopter net-gunning during winter months and with modified foot-hold traps during summer (University of Alberta Animal Care Protocols No. 391305, 353112, and 411601). We physically restrained wolves captured with helicopter net-gunning, whereas we either physically restrained or chemically immobilized wolves captured in traps. We fitted 13 wolves with Lotek (Lotek Engineering, Newmarket, ON, Canada) 3300Sw store-on-board GPS collars (2002–2005), and 6 wolves with Lotek 4400S remote-downloadable GPS collars (2005–2006); both collar types featured the advanced-scheduler option. We programmed collars to collect locations at 15-minute, 30-minute, 1-, 2-, 4-, or 6-hour intervals during October–April. We downloaded data from model 3300Sw collars upon retrieval via remote-release mechanism, recapture of the wolf, or when wolves were harvested by trappers. We remotely downloaded data from model 4400S collars every 1–2 weeks during aerial telemetry flights. Global Positioning System collars collected 443–6,676 locations per wolf and remained on wolves for 41–180 days. Collars recorded locations on 90% (3300Sw model) and 82% (4400S model) of fix attempts, suggesting the influence of habitat-induced GPS bias was minimal (Frair et al. 2004). Previous trials using Lotek GPS collars in our study system indicate that 95% of locations fall within 114 m of the true position, with a Bessel distribution (*s* parameter) of 34 m (Hebblewhite 2006).

Our approach used 2 steps to identify wolf kill sites and 3 distinct wolf GPS data sets. First, we used GPS locations collected from 13 wolves at 25 different kill sites located by snow-tracking or aerial observations during the winters of 2002–2005 to constrain maximum values of a scan statistic in a space–time clustering routine for identifying clusters that represented potential kill clusters. Second, using GPS locations from 4 wolves fitted with remote-downloadable collars in winter 2005–2006, we identified potential kill clusters, visited a subset of these clusters in the field, and derived statistical models to predict the probability of an individual cluster being a non–kill site, a kill site of a small-bodied prey species, or a kill site of a large-bodied prey species based on space–time dimensions of the clusters and landscape features of the cluster site. We assessed accuracy of these models using the third data set of known kill sites from 4 GPS-collared wolves in 4 packs during March 2006.

To identify clusters of GPS locations that were potentially kill sites, we used a space–time permutation scan statistic (STPSS) available in the program SaTScan (Kulldorff et al. 2005). The STPSS was developed to detect clusters of disease cases, using both spatial and temporal dimensions (geographic location and day) of the disease incident to search for areas with an increased likelihood of a disease outbreak. We refer readers to Kulldorff et al. (2005) for details but describe here how we adapted this approach to identify clusters of wolf GPS locations that were potential kill sites. The STPSS detects spatially and temporally identified groups of events by centering a time–space cylinder on each event (e.g., disease incidents or GPS locations) in the dataset, with the diameter of the cylinder defining the geographical area of the cluster and the height of the cylinder defining the time interval in days. This process results in many overlapping cylinders, each of which is a potential cluster and has an explicit number of locations that exist within a specific user-defined spatial and temporal window. The STPSS uses a probability model to calculate expected number of locations in each space–time cylinder. For our application, we let c_{zd} = number of locations at geographic coordinate z during day d, and the total number of observed GPS wolf locations (C) is

$$C = \sum_{z}\sum_{d} czd \tag{1}$$

Expected number of GPS locations (U) at z on day d is

$$Uzd = \frac{1}{C}\left(\sum_{z} czd\right)\left(\sum_{d} czd\right) \tag{2}$$

However, in a GPS collar dataset (in which each location is geographically unique), the number of GPS locations at a unique z location across all days sums to equal one. Therefore, in our example, $U_{zd} = 1$. Expected number of locations U_A in a cylinder A is the summation of these expectations over all the location-days within that cylinder:

$$UA = \sum_{(z,d)\in A} Uzd \tag{3}$$

If we let c_A = observed number of locations in the cylinder, when there is no space–time interaction, n_A is distributed according to a hypergeometric distribution with mean U_A and probability function

$$P(cA) = \frac{\begin{pmatrix}\sum_{z\in A} czd \\ cA\end{pmatrix}\begin{pmatrix}N - \sum_{z\in A} czd \\ \sum_{d\in A} czd - cA\end{pmatrix}}{\begin{pmatrix}C \\ \sum_{d\in A} czd\end{pmatrix}} \tag{4}$$

When both $\sum_{z\in A} czd$ (no. of geographic locations within cylinder A) and $\sum_{d\in A} czd$ (no. of days within cylinder A) are small compared to C, c_A is approximately Poisson distributed with mean U_A. Therefore, the technique uses the Poisson Generalized Likelihood Ratio (GLR) as a measure of evidence that a given cylinder contains a cluster. We evaluated statistical significance for each cluster using Monte Carlo hypothesis testing. We compared the GLR for each cluster in the observed dataset to the maximum GLR obtained from 999 simulated datasets in which the dates and locations in the original dataset were randomized, and the resulting dataset then searched for clusters, identifying those that were significant at the 95% level.

Use of the STPSS to identify GPS-location clusters that have a reasonable probability of being a kill site requires a priori inputs that constrain the size of the cluster by the amount of time (days) that wolves spend at kills (handling time) and a distance radius (cluster spread). To obtain values for these inputs, we examined cluster dimensions of 25 known kill sites from the winters of 2002–2005 located during snow-tracking or aerial telemetry flights for which we had corresponding GPS locations from collared wolves (see Hebblewhite et al. 2004). We retrieved data from 2 GPS-collared wolves at 6 kills; we treated these data independently because handling time and cluster spread were not identical for the 2 wolves at each kill. We determined maximum time duration at a cluster based on the distribution of the number of days wolves spent at each kill, with the start of a kill event defined as the first GPS point within 200 m of the actual kill location and handling time defined as the number of continuous days that the GPS-collared wolf was within 200 m of the kill (Anderson and Lindzey 2003, Franke et at. 2006). For cluster spread radius, we visually inspected the frequency distribution of distances from the known kill site of GPS locations associated with the kill sites and chose the distance at which 75% of all locations occurred because wolves frequently appeared to leave and return to kill sites. Finally, because sampling intensity is likely to influence cluster identification, we evaluated the effect of GPS fix intervals on the ability of the STPSS to identify potential kill sites. We rarified GPS locations of 13 wolves where we obtained locations at 15-minute to 6-hour intervals to location frequencies of 15 minutes, 30 minutes, 1 hour, 2 hours, 4 hours, 6 hours, and 8 hours and ran the STPSS on each subset of data. We assumed that the STPSS correctly located a specific kill site if it identified a cluster whose geometric center was within 200 m of the actual kill location in the time window within which field observations indicated the kill had been made. We used chase sequences in snow or presence of rumen contents to indicate where prey had been consumed, and we considered this to be the kill-site location. We visually inspected confidence limits around the proportion of kills identified by the STPSS for each location frequency to assess the GPS fix interval needed to consistently locate wolf kills.

We applied the STPSS to GPS location data from 4 wolves in 4 packs during winter 2005–2006 to identify clusters that were possible kill sites, and we visited a randomly selected subset of 326 clusters (33–158/wolf) in the field within 45 days of occurrence to determine if they were kill sites. We uploaded geometric centers of the clusters into handheld GPS units, and field crews of 2–4 people conducted an extensive grid search by walking parallel circular transects, covering a 200-m radius area. We classified clusters where we observed no prey remains (e.g., hair, bones, and rumen contents) as non–kill sites. We classified clusters as kill sites when we found prey remains where time since death matched the date that the cluster was made, carcasses were disarticulated, and blood in the snow, chase sequences, or signs of a struggle indicated that the prey had been killed by wolves. We classified all known and suspected scavenging events and revisits to previously consumed carcasses as nonkills.

Modeling the probability of a site being a kill site consisted of 2 phases. Initially, we developed general, behavior models based only on cluster dimensions, such as handling time and distance spread (see below) of the cluster as covariates. Then we included landscape characteristics and human-use variables associated with kill sites in other studies to determine whether site-specific environmental covariates could improve classification success (Kunkel and Pletscher 2000, Anderson and Lindzey 2003, Sand et al. 2005). In both approaches, we compared a 2-step binomial logistic regression for modeling the probability that an identified cluster was a non–kill site versus a kill site to a multinomial logistic regression for modeling a non–kill site versus a kill site of large-bodied prey species (elk, moose, feral horse, cow) or a small-bodied prey species (deer, bighorn sheep; Hosmer and Lemeshow 2000). The multinomial logistic regression approach allows for simultaneous distinction of nonkills from small-bodied kills from large-bodied kills using a series of 2 equations but does not independently distinguish non–kill sites from kill sites and then kills of small-bodied species from kills of large-bodied species as does the 2-step binary logistic regression. Instead, the multinomial logistic regression approach relies on the joint probability of a cluster belonging to one of the 3 categories. We did not attempt to use models to identify kill sites by individual prey species because initial results indicated we had too few kill sites of some species to derive reliable models, but we discuss this possibility below. We recognize that overlap exists in body sizes of individuals within the 2 prey categories, but our goal was to assess the utility of the approach to identify kills of different prey species in a multiprey system.

Cluster dimensions in the models included 1) *distance spread*: average distance (m) of all wolf GPS locations within 1 km of the cluster from the cluster center during the time frame of the identified cluster; 2) *continuous handling time*: number of continuous days spent within 100 m, 200 m, or 1 km of the cluster center, number of hourly locations within 100 m, 200 m, or 1 km of the cluster center during these days, and percent of hourly locations within 100 m, 200 m, or 1 km of the cluster center during these days; 3) *discontinuous handling time*: number of days wolves were within 100 m, 200 m, or 1 km of the cluster center within a 30-day period, number of hourly locations within 100 m, 200 m, or 1 km of the cluster center during these days, and percent of hourly locations within 100 m, 200 m, or 1 km of the cluster center during these days; 4) *pack size:* maximum number of wolves known to be in the pack at the time the cluster was created; 5) *wolf sex:* sex of the GPS collared wolf; 6) *wolf age:* age of the GPS collared wolf, classified as pup–yearling or adult.

Environmental variables in the second set of models included elevation to the nearest meter, percent slope, aspect in degrees, and terrain ruggedness, all of which we measured at the geometric center of the cluster. We derived terrain ruggedness as the standard deviation of elevation values within 500 m of each cluster. We used abundance of well sites, roads, and trails as surrogates for human use. We recorded well sites as density (no./km^2) and roads and trails as total length (km) within a 5-km^2 square centered on the cluster, as well as distance (m) to nearest road, well site, or trail. We mapped data on human use from Indian Radar Satellite Imagery following Frair et al. (2005). Because we expected our ability to detect a kill at a site would decrease with time since the kill (Anderson and Lindzey 2003), we also incorporated *days to visit* as a covariate for the number of days that elapsed between the first location in a cluster and the date field crews visited the cluster to search for prey remains. We examined all variable combinations for collinearity, and we did not include in the same model those variables that were correlated at $r^2 \geq 0.7$. We selected the top logistic and multinomial models from a set of a priori models using Akaike's Information Criterion and assessed individual model classification of the binomial models by plotting the receiver-operating characteristic (ROC) curve (Fielding and Bell 1997, Burnham and Anderson 2002).

To assess model accuracy, we ran the STPSS on GPS locations from 4 wolves collected at 1-hour intervals during March 2006 and searched all resulting clusters for prey remains within 2 weeks of cluster formation using the procedures described above. We applied the top binary and multinomial logistic regression models from both modeling phases to these data and compared predicted kills to the results obtained from field visits.

RESULTS

We located 25 kill sites (10 elk, 8 moose, 5 deer, 1 feral horse, and 1 bighorn sheep) via snow-tracking wolves (14 kills) or during aerial telemetry flights (11 kills) that had associated GPS-collar locations from $\geq$1 wolf; we used these kills to derive inputs for the STPSS cluster routine. Based on inspection of the frequency distribution of average spread distances (Fig. 1), we selected a spread radius of 300 m to define the maximum radius over which SaTScan searched for potential clusters. Wolves returned to kill sites at least once per day for a maximum of 4 days (Fig. 1); therefore, we set the maximum time duration over which SaTScan searched for clusters to 4 days. Clusters identified by the STPSS at these kill sites included 2 to 85 wolf GPS locations, and the geometric centers of clusters associated with kill sites were always within 200 m of actual kill locations.

Using the above inputs, we found the percent of known kill sites identified by the STPSS model decreased with less frequent sampling, with the most rapid loss occurring between sampling intervals of 4–6 hours and <50% of kill sites identified with an 8-hour sampling interval (Fig. 2). Sampling intervals between 30 minutes and 2 hours provided the most similar results in cluster identification but approximately 10% of kill sites were still missed; we detected all kills using a 15-minute sampling interval. The technique successfully identified all kill sites of large-bodied prey species using sampling intervals up to 4 hours in length, but 17% (1

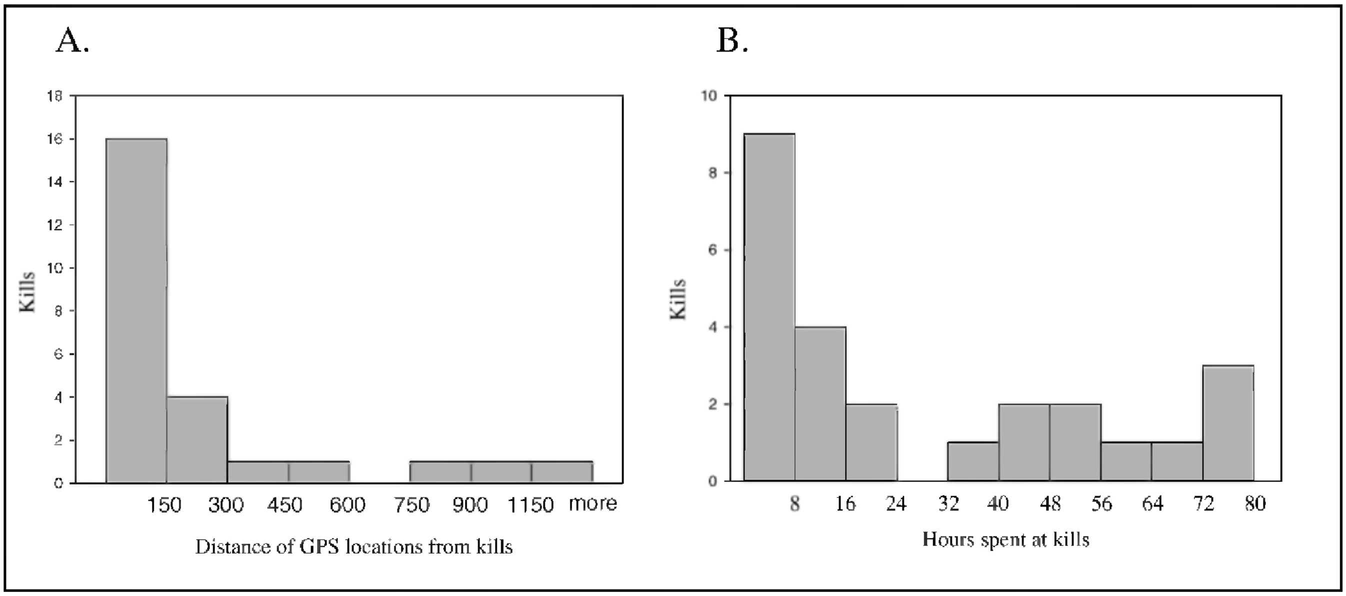

Figure 1. Space–time dimensions of clusters of wolf Global Positioning System (GPS) locations collected at kill sites from 2002 to 2005 in the central east slopes of the Rocky Mountains in Alberta, Canada. (A) Frequency distribution of the distances at which the 75th percentile of wolf locations were from of known kill sites during the handling interval. (B) Number of hours spent at kill sites by GPS collared wolves during the handling interval.

of 6) of kills of small-bodied prey were not identified as clusters even with a 30-minute sampling interval.

We visited a randomly selected subset of 326 movement clusters (33–158/wolf) identified using 1-hour data from 4 wolves in 4 different packs within 45 days of occurrence. Based on site visits, we classified 282 clusters as non–kill sites and 44 as kills, including 26 sites of small-bodied kills (26 deer) and 18 sites of large-bodied kills (12 elk, 5 moose, 1 cow).

There was little difference in the weight of evidence among the top 3 models for predicting either the probability of a cluster being a kill site or non–kill site (KNK) or the probability of an identified kill site being a large- or small-bodied species (KLS; Table 1). Variables most consistently found in KNK models included number of days (either continuous or noncontinuous) the wolf spent within 100 m of the cluster center and number of GPS locations within 100 m of the cluster center during the continuous handling interval (Table 1). In contrast, the number of continuous or noncontinuous days spent within 1 km of the cluster center was the variable most consistently found in the top KLS models (Table 1). Adding environmental covariates improved KNK model fit by up to 7.25 Akaike's Information Criterion (AIC) units, with the top model including negative responses to slope and seismic line density in addition to the cluster dimension metrics (Table 2, eq 6). Percent slope improved the KLS model fit by 1.71 AIC units with a higher probability of large kills in areas with more gentle terrain (Table 2, eq 8). Area under the curve (AUC) for the ROC plot for the top behavior-based KNK model was 0.85 with a probability cutoff for a site being a kill site of 0.12. The AUC for the ROC plot associated with top behavior-based KLS model was 0.89 with a cutoff of 0.36 for the probability of a kill site being one where a large-bodied species was killed.

In the multinomial approach, we used non–kill sites as the reference condition. We found that number of locations within 100 m of the cluster within the continuous handling interval was consistently identified in the top models although there was little difference in the weight of evidence among these models (Table 3). We used equation 9 to predict the probability of a cluster being a kill of a small-bodied prey and equation 11 to predict the probability of a cluster being a kill of a large-bodied prey. Adding environmental covariates improved model fit by up to 6.33 AIC

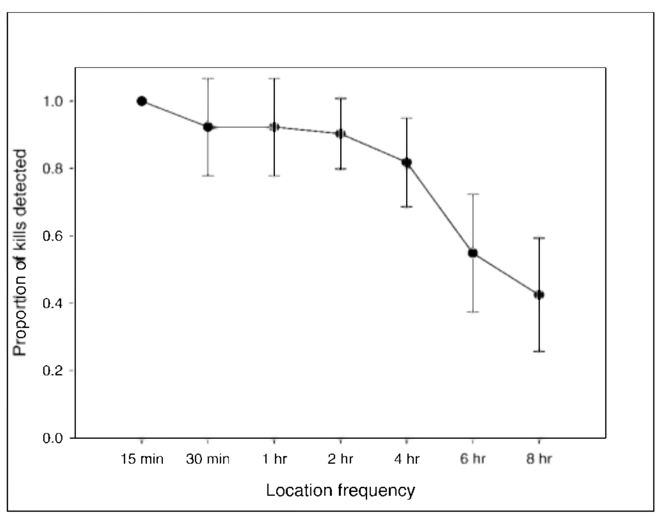

Figure 2. Proportion of kills detected by the space–time permutation scan statistic cluster-scan technique using wolf Global Positioning System data collected from 2002 to 2005 in the central east slopes of the Rocky Mountains in Alberta, Canada, at intervals of 15 minutes to 8 hours. Sample size is 13 kills for 15-minute–1-hour data and 31 kills for 2-hour–8-hour data.

Table 1. Top-ranked binomial logistic regression models for predicting wolf kill sites versus non–kill sites (KNK) and top models for predicting kill sites of small- (deer, sheep) versus large-bodied prey species (moose, elk, feral horse, domestic cow; KLS) from data on collared wolves in the central east slopes of the Rocky Mountains in Alberta, Canada, 2005–2006. Models are shown in order of decreasing rank with model log-likelihood (LL), number of estimated parameters (K), Akaike's Information Criterion (AIC), AIC difference (Δ_i), and AIC weight (w_i).

Rank	Variables	LL	K	AIC	Δ_i	w_i
KNK behavior						
1	$LOCS_{100}$[a], $DAYS_{NC-100}$[b]	−87.06	2	178.37	0.00	0.39
2	$LOCS_{100}$, $DAYS_{C-100}$[c]	−87.28	2	178.81	0.81	0.32
3	$LOCS_{100}$, $DAYS_{NC-100}$, $PCTLOCS_{C-1km}$[d]	−86.95	4	180.41	2.04	0.14
KNK site-specific						
1	$LOCS_{100}$, $DAYS_{NC-100}$, PKSIZE[e], SLP[f], DNSEIS[g]	−79.90	5	171.12	0.00	0.34
2	$LOCS_{100}$, $DAYS_{C-100}$, SLP, DNSEIS	−81.42	4	171.71	0.59	0.26
3	$LOCS_{100}$, $DAYS_{C-100}$, SLP	−83.26	3	173.03	1.91	0.13
KLS behavior						
1	$LOCS_{100}$, $DAYS_{NC-1K}$[h]	−21.84	2	47.93	0.00	0.35
2	$LOCS_{100}$, $DAYS_{NC-200m}$[i]	−22.04	2	48.34	0.41	0.29
3	$DAYS_{C-1K}$[j]	−23.55	1	49.18	1.25	0.19
KLS site-specific						
1	$LOCS_{100}$, $DAYS_{NC-1K}$, SLP	−19.85	3	46.22	0.00	0.50
2	$LOCS_{100}$, $DAYS_{NC-1K}$, SLP, DNWELL[k]	−19.17	4	47.21	1.00	0.30
3	$LOCS_{100}$, $DAYS_{NC-1K}$, DNSEIS	−21.34	3	49.19	2.97	0.11

[a] No. of 1-hr locations within 100 m of the cluster center during the continuous handling interval.
[b] No. of noncontinuous days spent within 100 m of the cluster center.
[c] No. of continuous days spent within 100 m of the cluster center.
[d] % of locations within 1 km of the cluster center during the continuous handling interval.
[e] Pack size.
[f] Slope (°).
[g] Density of seismic lines within 5 km^2 of the cluster center.
[h] No. of noncontinuous days spent within 1 km of the cluster center.
[i] No. of noncontinuous days spent within 200 m of the cluster center.
[j] No. of continuous days spent within 1 km of the cluster center.
[k] Density of well sites within 5 km^2 of the cluster center.

units (Table 3), with the top model including negative responses to slope and density of well sites (Table 2, eqs 10 and 12).

We assessed kill-site models using an independent set of 221 clusters identified from 4 wolves in 4 packs (6–11 kills/wolf) monitored intensively during March 2006. Based on site visits, 189 of the clusters were non–kill sites and 32 were kill sites that included 22 kills of small-bodied prey species (deer) and 10 kills of large-bodied prey species (4 moose, 3 elk, and 3 feral horses).

Overall, using the first binomial regression model (eq 5) we correctly identified 72% of the 221 clusters as being a kill or non–kill site with a commission error (identifying a non–kill site as a kill site) rate of 24% and an omission (identifying a kill site as a non–kill site) error rate of 4% (Table 4). With multinomial models (eqs 9 and 11) we correctly identified 88% of clusters as kill or non–kill sites, with a 2% commission error rate and a 10% omission error rate (Table 4). High overall success in cluster classification using the multinomial model was primarily due to correctly identifying non–kill sites at the expense of incorrectly classifying kill sites as nonkills (i.e., high omission error). For example, multinomial models misclassified 18 of the 22 (82%) kill sites of small-bodied prey as non–kill sites and misidentified 4 of 10 (40%) kill sites of large-bodied prey as non–kill sites (Table 4). In contrast, with the 2-step binomial models (eqs 5 and 7) about 2.5 times as many kill sites of small-bodied prey were identified (56) as actually existed (22), and twice as many large prey (19) were identified as existed (10) in the sample (Table 4). Nevertheless, all 10 large prey kill sites were correctly identified as kills using 2-step binomial regressions, whereas only 6 of 10 were identified using multinomial regression (Table 4).

Using models that included environmental covariates did not improve classification success despite their lower AIC values. In fact, the top binomial model used to classify clusters as kill sites or non–kill sites that included environmental covariates missed more kill sites (13 vs. 9) than did the model that included only cluster-dimension covariates (Table 4). Overall, omission and commission errors did not differ substantively between the model types, although the 2-step, behavior-based binomial models correctly classified the most kills (Table 4).

DISCUSSION

The STPSS was effective at identifying potential kill sites from wolf GPS data with 90–100% of actual kill sites identified when location intervals were relatively short ($\leq$2 hr), and all kills of large prey species detected when using location intervals of up to 4 hours. Because some kills of small-bodied prey (1 of 6) were missed even with 30-minute sampling intervals, the proportion of total kills detected in

Table 2. Coefficients of the highest ranked logistic regression models for predicting whether a wolf Global Positioning System location cluster represents a non–kill site, kill site, kill site of a small prey species (deer, sheep), or kill site of a large prey species (moose, elk, feral horse, domestic cattle) in the central east slopes of the Rocky Mountains in Alberta, Canada, 2005–2006.

	Binomial logistic regression				Multinomial logistic regression			
	Nonkill vs. kill		Small prey vs. large prey		Nonkill vs. small prey		Nonkill vs. large prey	
Variable	Behavior (eq 5)	Site-specific (eq 6)	Behavior (eq 7)	Site-specific (eq 8)	Behavior (eq 9)	Site-specific (eq 10)	Behavior (eq 11)	Site-specific (eq 12)
$LOCS_{100}$[a]	0.284	0.325	0.055	0.106	0.297	0.331	0.329	0.422
$DAYS_{NC-100}$[b]	0.735							
$DAYS_{C-100}$[c]		0.766						
$DAYS_{NC-1K}$[d]			0.847					
$DAYS_{C-1K}$[e]				0.791	0.358	0.095	1.363	0.576
SLP[f]		−0.111		−0.240		−0.083		−0.252
DNSEIS[g]		−0.768						
DNWELL[h]						−8.675		−0.473
Constant	−4.596	−3.465	−3.102	−2.511	−4.468	−3.698	−7.418	−5.912

[a] No. of 1-hr locations within 100 m of the cluster center during the continuous handling interval.
[b] No. of noncontinuous days spent within 100 m of the cluster center.
[c] No. of continuous days spent within 100 m of the cluster center.
[d] No. of noncontinuous days spent within 1 km of the cluster center.
[e] No. of continuous days spent within 1 km of the cluster center.
[f] Slope (°).
[g] Density of seismic lines within 5 km^2 of the cluster center.
[h] Density of well sites within 5 km^2 of the cluster center.

areas where wolves rely primarily on deer, for example, would likely be lower than in our system. In addition, because we located some (11 of 25) kills in the sample used to evaluate the STPSS via aerial telemetry, they may not be completely representative of all wolf kills in our system due to a handling time–detection bias. However, if we had visited all clusters identified by the STPSS, our rate of locating kill sites of large-bodied prey would be higher than the 45% detection rate reported for aerial monitoring of radiocollared wolves in Yellowstone National Park (Smith et al. 2004), as well as the 87% detection rate reported by Sand et al. (2005), who identified kill sites of moose using the criterion of ≥2 sequential 1-hour wolf GPS locations within 100 m. Although Franke et al. (2006) reported 100% detection of wolf kills, the dataset consisted of only 7 total kill events, all of which had been previously located by aerial observations, and therefore may not consist of a representative sample of kill sites (e.g., bias towards kills with longer handling time). In our study, in all cases where kills were missed with GPS collar sampling intervals ≥2 hours, only one wolf GPS location was present at the kill site (within 200 m). Sand et al. (2005) suggested that where kill sites consisted of only one location, wolves may have been disturbed by humans and, therefore, abandoned the prey item. Alternatively, because we had other animals collared in each pack, we found that at kill sites where only one GPS

Table 3. Comparison of the top-ranked multinomial logistic regression models for predicting whether an identified cluster of wolf Global Positioning System (GPS) locations is a non–kill site, a kill site of small-bodied prey species (deer, sheep), or a kill site of a large-bodied prey species (moose, elk, feral horse, domestic cow) from data on collared wolves in the central east slopes of the Rocky Mountains in Alberta, Canada, 2005–2006. Models are shown in order of decreasing rank with model log-likelihood (LL), number of estimated parameters (K), Akaike's Information Criterion (AIC), AIC difference (Δ_i), and AIC weight (w_i).

Rank	Variables	LL	K	AIC	Δ_i	w_i
Behavior						
1	$LOCS_{100}$[a], $DAYS_{C-1K}$[b]	−110.81	2	225.88	0.00	0.58
2	$LOCS_{100}$, $DAYS_{C-1K}$, PKSIZE[c]	−110.77	3	225.08	2.17	0.20
3	$LOCS_{100}$, $DAYS_{NC-1K}$[d]	−112.18	2	228.61	2.74	0.15
Site-specific						
1	$LOCS_{100}$, $DAYS_{C-1K}$, PKSIZE, SLP[e]	−104.92	4	218.72	0.00	0.26
2	$LOCS_{100}$, $DAYS_{NC-1K}$, SLP, DNWELL[f]	−105.34	4	219.55	0.83	0.17
3	$LOCS_{100}$, $DAYS_{C-1K}$, PKSIZE, SLP, DNWELL, DROAD[g]	−101.48	6	219.57	0.85	0.17

[a] No. of 1-hr locations within 100 m of the cluster center during the continuous handling interval.
[b] No. of continuous days spent within 1 km of the cluster center.
[c] Pack size.
[d] No. of noncontinuous days spent within 1 km of the cluster center.
[e] Slope (°).
[f] Density of well sites with 5 km^2 of the cluster center.
[g] Density of roads with 5 km^2 of the cluster center.

Table 4. Classification accuracy of 2-step binomial logistic regressions and multinomial logistic regressions for classifying 221 clusters derived using the space–time permutation scan statistic of wolf Global Positioning System locations collected in March 2006 in the central east slopes of the Rocky Mountains of Alberta, Canada (Kulldorff et al. 2005). We searched identified clusters for prey remains, which included 22 small-bodied prey (deer), 10 large-bodied prey (elk, moose, horse), and 189 nonkills.

	Obs no.								Non–kill sites vs. kill sites			
	Behavior				Site-specific				Eq 5; eqs 9 and 11[a]		Eq 6; eqs 10 and 12[b]	
Classified no.	Nonkill	Small	Large	Total	Nonkill	Small	Large	Total	No.	%	No.	%
Binomial regression												
Nonkill	137	9	0	146	141	12	1	154				
Small	44	9	3	56	36	7	1	44				
Large	8	4	7	19	12	3	8	23				
Total	189	22	10	221	189	22	10	221				
Error												
Correct									160	72	160	72
Omission									9	4	13	6
Commission									52	24	48	22
Multinomial regression												
Nonkill	185	18	4	207	178	18	3	199				
Small	2	2	1	5	8	2	2	12				
Large	2	2	5	9	3	2	5	10				
Total	189	22	10	221	189	22	10	221				
Error												
Correct									195	88	189	86
Omission									22	10	21	9
Commission									4	2	11	5

[a]For binomial regression, error rates are based on results of eq 5 only; for multinomial regression, error rates are based on results from eqs 9 and 11 (see Table 2).

[b]For binomial regression, error rates are based on results of eq 6 only; for multinomial regression, error rates are based on results from eqs 10 and 12 (see Table 2).

location occurred the packs were split into ≥ 2 groups, and the GPS collared wolf was not present at the kill site for the entire time required to handle the prey. Degree of pack-splitting may have important implications for the ability of researchers to detect all wolf kills made by a pack, particularly when deer are a primary prey item and handling times are correspondingly short as compared to larger prey.

Although visiting all clusters in the field to determine whether they are kill sites will provide the most accurate measure of kill rates, this requires extensive field effort and associated cost. As a result, modeling the probability of each cluster being a kill site provides 2 distinct advantages. First, where field visits are not possible, we have demonstrated that kill sites can be distinguished from non–kill sites with 72–88% accuracy depending on the modeling approach. In our example, using multinomial regression to distinguish kill sites omitted more kills, including both small- and large-bodied prey, and would give a more conservative estimate of kill rates. In contrast, using the 2-step binomial regression omitted fewer kill sites and identified 100% of the kill sites of the large-bodied prey, with 70% of these classified correctly as large prey. We suspect that differences between the approaches might occur, in part, because optimal cut-off values for classifying clusters based on the ROC plot are not readily available in most statistical software packages for multinominal regression where ≥ 3 classes are simultaneously distinguished.

Second, when resources for field inspections are available but limited, our approach can help guide these efforts. For example, if we had visited only the 75 clusters that were classified as kill sites (Table 4), we would have detected 100% of the large-bodied prey and 60% of small-bodied prey that were identified as potential kills by the cluster scan technique. In a system where wolves feed primarily on large-bodied prey species, this level of field effort may be sufficient to characterize kill rates of these prey. Alternatively, as resources become available to extend field verification, predicting the probability that a cluster represents a kill allows prioritization of sites to visit. Finally, although we found that sex and age of GPS collared wolves and the number of wolves in monitored packs were not important in distinguishing among cluster types, we likely lacked sufficient sample sizes of individual wolves and packs to thoroughly test the importance of these factors, which may ultimately improve classification success as well.

In the end, our models were more successful at distinguishing kill sites of large-bodied prey species (moose, elk, feral horses, domestic cattle) from non–kill sites than from small-bodied prey species (deer and sheep), which is consistent with previous studies (Sand et al. 2005, Franke et al. 2006). Because number of hourly GPS locations at kill sites during the continuous handling interval was the most consistent variable in distinguishing among prey types, the higher relative variability in time wolves remained feeding on small-bodied prey than large prey was most likely responsible for these results. For example, handling time of large-bodied prey (20.4 ± 13.5 hourly locations) overlapped less with non–kill sites (4.8 ± 3.7 hourly locations) than did small-bodied prey (10.6 ± 8.0 hourly locations). Franke et al. (2006) also suspected that deer kills were not detected by hidden Markov models but could not verify this without intensive ground-tracking. Although Sand et al. (2005) detected roe deer (*Capreolus capreolus*), they also did not assess how many kills of this species might have been missed. Extensive scavenging by wolves also might complicate distinction of non–kill sites from kill sites of either body size class. However, we detected only 14 occurrences of scavenging across the combined 547 clusters visited in our study area, and there was an average of only 5.5 ± 3.8 hourly GPS locations at these sites. Therefore, in our system we believe that scavenging played only a minor role in distinguishing among cluster types.

We suspect distinguishing non–kill sites from sites where small-bodied prey species are killed will remain a challenge when using remotely sensed locations to find kills. Nevertheless, several possible refinements exist to improve the approach. First, increasing the frequency of sampling animal locations, for example to 5 minutes, or using other movement measures might reveal alternative predator behaviors with lower variability and less overlap that could be used to distinguish among cluster types. Alternatively, incorporating variables into the models that reflect prey encounter rates, such as prey densities or probability of prey use, temporal measures (i.e., time of day), or factors that reflect prey vulnerability also might improve our ability to identify kill sites of different prey species from non–kill sites (see Kunkel and Pletscher 2000, Hebblewhite et al. 2005, Sand et al. 2005). To date, our work and that of others indicates the potential for using clusters of wolf GPS locations to identify kill sites of large-bodied prey species, which may be adequate to document predation rates in a system consisting of only large prey species like moose or where small prey species are not of primary interest (Sand et al. 2005, Franke et al. 2006).

MANAGEMENT IMPLICATIONS

Our approach presents several options for using clusters of wolf GPS locations to identify kill sites and develop subsequent estimates of kill rates. However, we caution that our results may be site-specific and are dependent on the distribution of prey body sizes found in our study. The direct use of our models should be undertaken only with the understanding that variation in wolf handling time of prey items will likely have substantial implications for both the cluster scan and logistic regression components of this technique. In applying this technique to new areas, we recommend that researchers use a random sample of previously identified wolf kills to evaluate the ability of the STPSS to identify potential kill sites, and potentially reconstrain handling time and cluster spread parameters if the scan performs poorly. In addition, we recommend refitting our top logistic regression models based on data collected from visiting a random sample of identified clusters, and reevaluating the ability of the models to correctly classify clusters as kills or nonkills.

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