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Discriminating grey wolf kill sites using GPS clusters

Courtney C. Irvine¹ | Seth G. Cherry² | Brent R. Patterson^{1,3}

¹Trent University, 1600 W Bank Drive,
Peterborough, ON K9L 0G2, Canada

²Parks Canada Agency, Box 220, Radium Hot
Springs, BC V0A 1M0, Canada

³Ontario Ministry of Natural Resources and
Forestry, 2140 East Bank Drive,
Peterborough, ON K9L 1Z8, Canada

Correspondence

Courtney C. Irvine, Parks Canada Agency, PO
Box 212, Heron Bay, ON P0T 2E0, Canada.
Email: courtney.irvine@pc.gc.ca

Present address

Courtney C. Irvine, Parks Canada Agency, PO
Box 212, Heron Bay, ON P0T1R0, Canada.

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Abstract

Characteristics of spatio-temporal clusters of locations from global positioning system (GPS)-collars have been used to distinguish kill sites of various predators. We deployed GPS collars on 9 grey wolves (*Canis lupus*) in the southwest area of Prince Albert National Park in central Saskatchewan, Canada, and used a GPS location clustering algorithm to identify kill sites of ungulate and other large-bodied prey during winter, December 2013–March 2017. We used logistic regression in a model-selection framework to determine if spatio-temporal and habitat characteristics of grey wolf GPS clusters could be used to reliably identify sites where wolves had killed prey. Global positioning system clusters were more likely to be wolf kill sites when they had a higher number of location fixes, did not begin within 300 m and 30 days of a previous cluster, did not begin within 1 km and 4 days of a previous cluster, began in the evening, had a high percentage of fixes occurring during the day, occurred farther from open habitat, and had both a high number of location fixes and a high percentage of fixes occurring during the day. Our results highlight the limits of using spatio-temporal clusters with a fix rate of 1/hour to discriminate wolf kill sites in systems dominated by deer (*Odocoileus* spp.) because of the associated short handling time with these prey.

KEYWORDS

Canis lupus, grey wolf, GPS cluster, kill site, Saskatchewan, spatio-temporal cluster



The advent of animal-borne sensors (e.g., geolocator tags, global positioning system [GPS]-collars) has yielded new advances and opportunities for basic and applied research in the field of animal behavior and ecology (Wilmers et al. 2015, Wittemyer et al. 2019). High-resolution spatio-temporal animal relocation data enables analysis of wildlife movement and its interactions with the ecosystem (Bar-David et al. 2009, Wittemyer et al. 2019). Identifying regions of positive spatial autocorrelation of relocation data provides an indication of where and when animals restrict their movement (Ebinger et al. 2016). Areas of recursion are usually sites of ecological significance in the life history of individuals across taxa (Bracis et al. 2018, Picardi et al. 2020). Identifying regions of recursive movement can identify the location of ecological events, such that changes in space-use can be associated with behavioral states (Picardi et al. 2020). This approach has been applied to a variety of animal ecology phenomena, such as foraging and responses to resource dynamics (Bar-David et al. 2009, Seidel and Boyce 2015), identifying breeding locations, measuring site fidelity, estimating breeding success (Picardi et al. 2020), and identifying predation events (Anderson and Lindzey 2003).

Predation events have ecological, economic, and social consequences (Terborgh et al. 2001, Treves and Karanth 2003, Bacon et al. 2011), are directly related to the conservation of species involved in these interactions (Dale et al. 1994, Sinclair et al. 1998, Peckarsky et al. 2008, McPhee et al. 2012a), and have important cascading effects in ecosystems (Schaller 1972, Beschta and Ripple 2009). Quantification of predation events and kill rates can provide insight into the functional responses of predators to prey availability, prey regulation via predator control, and prey switching in multi-prey systems (Merrill et al. 2010). Because of the secretive nature and wide-ranging behavior of many large carnivores, and the long temporal scale over which observations are required, predation events and their consequences are difficult to study.

Anderson and Lindzey (2003) first developed a method to evaluate if spatio-temporal clustered GPS locations were associated with kill sites of cougars (*Puma concolor*). Since then, the use of spatio-temporal GPS clusters to identify kill sites has been refined for cougars (Knopff et al. 2009, Ruth et al. 2010, Elbroch and Wittmer 2013, Wilckens et al. 2015), and applied to other predators including lions (*Panthera leo*; Tambling et al. 2010, 2012), leopards (*Panthera pardus*; Martins et al. 2010, Pitman et al. 2012), jaguars (*Panthera onca*; Cavalcanti and Gese 2010, Gese et al. 2016), Eurasian lynx (*Lynx lynx*; Mattisson et al. 2011, Krofel et al. 2013), bobcats (*Lynx rufus*; Svoboda et al. 2013), grizzly bears (*Ursus arctos*; Rauset et al. 2012, Cristescu et al. 2015, Ebinger et al. 2016, Kermish-Wells et al. 2017), black bears (*Ursus americanus*; Kindschuh et al. 2016), wolverines (*Gulo gulo*; Scrafford and Boyce 2018), and wolves (*Canis lupus*; Zimmerman et al. 2007, Webb et al. 2008, DeCesare 2012, Lake et al. 2013).

Spatio-temporal patterns of recursion are important in distinguishing kill sites from non-kill sites. For example, cougar kill sites were distinguished by the number of nights an individual was detected at a cluster (Anderson and Lindzey 2003), the corrected number of location fixes in the cluster, the fidelity of the individual to the cluster, a binary indicator of 1-day or >1-day period spent at the cluster, and the average distance of points from the geometric center (centroid) of the cluster (Knopff et al. 2009). Characteristics of recursion represent biological components of predation events such as handling time, diel variation, and space-use around a prey carcass. Cluster duration variables indicating handling time have been characteristic in distinguishing predation events among predator species (Ruth et al. 2010, Svoboda et al. 2013, Kermish-Wells et al. 2017, Scrafford and Boyce 2018).

Cluster duration is an important metric to discriminate GPS clusters that are wolf kill sites. For example, wolf kill sites have been distinguished by the number of days an individual spent within 100 m of the cluster center and the number of GPS locations within 100 m of the center during the continuous time span of the cluster (Webb et al. 2008); by the number of positions and the number of visits to the GPS cluster (Zimmerman et al. 2007); by consecutive time spent at a GPS cluster and fidelity to the GPS cluster (DeCesare 2012); and by the number of location fixes in a GPS cluster (Lake et al. 2013). As wolves may capture prey that exceed their physiological limits of consumption in a single feeding event, these metrics may provide complete representations of handling time and carcass use.

Other characteristics of GPS clusters have also been included in discriminatory models for wolf kill sites, such as diel variation, spatio-temporal proximity to other clusters, and unique identifiers of wolf packs. The number of location fixes during the afternoon (Zimmerman et al. 2007) and the proportion of midday locations (DeCesare 2012) have been negatively associated with wolf kill sites, while the proportion of fixes during the night



has been positively associated with kill sites (Sand et al. 2005). This suggests that wolves exhibit diel variation in handling killed prey. Wolf movement rates have a high impact on predation rates (McPhee et al. 2012a), and are not uniform throughout the 24-hour period (Vander Vennen et al. 2016). Rather, wolf movement rates were highest in the early evening in Northern Ontario, Canada, corresponding to higher rates of wolf predation during that time (Vander Vennen et al. 2016). Start-time of GPS clusters was not discriminatory for wolf kill sites in Scandinavia (Zimmerman et al. 2007). Other researchers observed GPS clusters where wolves rest for long periods adjacent to kill sites, and reported that spatio-temporal proximity (within 1 km and 4 days of a previous cluster with consecutive time >8 hr) was negatively associated with wolf kill sites (DeCesare 2012). Lastly, handling time and correspondingly, cluster duration, may vary with wolf pack size, and age, sex, and social structure of members, and considering these variables was discriminatory for wolf kill sites compared to other variables tested in Alaska, USA (Lake et al. 2013).

Physical features of landscapes can affect occurrence or outcomes of predator-prey encounters, and manifest as differences in habitat at kill sites compared to non-kill sites (Kauffman et al. 2007, MCPhee et al. 2012b). Thus, inclusion of spatial attributes may improve models that distinguish kill sites. Slope and seismic line density improved the fit of the top-ranking model discriminating between kill sites and non-kill site for grey wolves in the Rocky Mountains of Canada, but it did not change omission and commission errors of the model (Webb et al. 2008). Habitat variables were seemingly unimportant in distinguishing kill sites from non-kill sites of jaguars in southern Pantanal, Brazil (Gese et al. 2016), while environmental covariates (season, wet openings, dry openings, mixed forest, clear-cuts, and terrain ruggedness) were useful in discriminating prey species of cougar kill sites in west-central Alberta, Canada (Knopff et al. 2009), suggesting that the usefulness of habitat variables to elucidate kill sites may reflect differences in predator behavior.

Previous models have been successful in discriminating wolf kill sites from non-kill sites (Webb et al. 2008, DeCesare 2012, Lake et al. 2013), but those that were tested with reserved or novel data had variable rates of commission and omission errors (24% and 4% [Webb et al. 2008]; 49% and 43% [Zimmerman et al. 2007]). Palacios and Mech (2011) reported that cluster duration was similar between wolf GPS clusters that were feeding sites of small prey (e.g., white-tailed deer [*Odocoileus virginianus*], beaver [*Castor canadensis*]) and those that were rest sites. This suggests that cluster duration characteristics alone may be insufficient to discriminate wolf kill sites if small prey items are common components of the diet. Several authors have stated that field visitation is still required to obtain reliable information on species, age, sex, and condition of prey and that without independent validation, models from previous studies should be applied cautiously (Webb et al. 2008, Knopff et al. 2009, Elbroch et al. 2018). The applicability of spatio-temporal clustered GPS locations is likely to improve with continued use to distinguish predation events across a wide range of predators and ecosystems.

Grey wolves are well-studied organisms and are important predators in the boreal forest (Mech et al. 2015). The objectives of this study were to apply a previously developed clustering algorithm to novel GPS position data of grey wolves collected in central Saskatchewan, Canada, during winter to identify spatial clusters and develop a system-specific model for identifying spatial clusters that were kill sites. We predicted that we would be able to reliably discriminate wolf kill sites using a combination of spatio-temporal characteristics and habitat characteristics of the position clusters previously found to be indicative of wolf kill sites in other ecosystems.

STUDY AREA

This study occurred in the southwest corner of Prince Albert National Park and vicinity in central Saskatchewan, within the range of the Sturgeon River plains bison (*Bison bison bison*) population (53° 44'N, 106° 40'W; ~960 km²; Merkle et al. 2015), during winter between December 2013–March 2014, November 2014–March 2015, November 2015–March 2016, and November 2016–March 2017. The study area was within the Boreal Plains Ecozone, dominated by aspen (*Populus* spp.) parkland in the south, boreal forest in the north and agricultural



land outside of the national park to the west. Land uses were agricultural (cropland, permanent pasture), rural development, and protected area. Land cover classes included deciduous (38%) and coniferous forest (37%), water bodies (5%), shrub (5%), and meadows (3%; Merkle et al. 2015). Wetlands, bare ground, and urban (roads, trails, infrastructure) land cover classes also occurred. Terrain was mostly flat (0° to 13° slope) and occurred 450 m to 700 m above sea level. Climate was continental, with long cold winters (Jan temp \bar{x} = -18°C) and short warm summers (Jul temp \bar{x} = 16°C); average annual precipitation was 430 mm and the majority fell as rain (50%) during June, July, and August (Evans et al. 2009). Snow accumulated to an average depth of 30.8 cm in February, with an extreme value of 55 cm recorded during the study. Forest communities were dominated by aspen, spruce (*Picea* spp.), and jack pine (*Pinus banksiana*), while meadow communities were composed of grasses, sedges, and rushes (Courant and Fortin 2012). Ungulate prey species included an at-risk population of free-ranging plains bison (Cherry et al. 2019, Simon and Fortin 2019), moose (*Alces alces*), elk (*Cervus canadensis*), white-tailed deer, and mule deer (*O. hemionus*). Carnivorous mammal species included grey wolves, cougars, Canada lynx (*Lynx canadensis*), black bears, weasels and their allies (Mustelidae), coyotes (*Canis latrans*), and red foxes (*Vulpes vulpes*).

METHODS

We deployed GPS-enabled collars (Telonics Iridium Model TGW-4570-3; Telonics, Mesa, AZ, USA) on grey wolves captured within the range of the Sturgeon River plains bison population in Prince Albert National Park beginning in December 2013; we removed all GPS collars by the end of March 2017. We located and physically restrained wolves via nets deployed from helicopters to complete collaring; we did not use chemical immobilization. The GPS-collars recorded Universal Transverse Mercator (UTM) location via satellite once per hour, on the hour. We estimated the horizontal error of the GPS collars by calculating the average displacement of 11 collars deployed in open-canopy test locations prior to deployment on wolves (Horne et al. 2007). We estimated wolf pack size each year by the number of wolves observed in each pack during capture for collar deployment, opportunistic aerial observations of wolf packs, and by the number of observed wolves on remote wildlife camera image sequences deployed within pack territories.

We identified GPS clusters using a location data clustering algorithm in Python (Python version 2.7.8, www.python.org, accessed 4 Nov 2014) originally written for cougar data (Knopff et al. 2009) and modified for wolf kill sites (Webb et al. 2008). The GPS clusters were identified when a wolf was relocated within 300 m and 4 days of a previous location and continued to build as long as this qualification was met (Webb et al. 2008, DeCesare 2012). We combined GPS clusters from individual wolves within the same pack by visual verification in ArcGIS 10.5.1 (Esri, Redlands, CA, USA).

We visited GPS clusters for field verification 3 January 2014–28 March 2014, 25 November 2014–25 March 2015, 30 November 2015–18 March 2016, and 24 January 2017–28 March 2017 using teams of 2 observers. We traveled to GPS clusters via snow machine on the nearest trail, and then on foot or snowshoe; we used a helicopter infrequently to access remote areas. We prioritized visiting GPS clusters with >5 location fixes that had occurred 1–4 weeks beforehand. At each GPS cluster, we searched a 300-m radius around each wolf cluster centroid for signs of wolf activity (bedsites, scat, scent marking) and prey carcass remains (bones, hair, blood, rumen; Webb et al. 2008). We also searched the area around each satellite fix location in the cluster. Searches of GPS clusters took, on average, 34 minutes to complete (kill site: \bar{x} = 42 min, range = 2–170 min, n = 212; non-kill site: \bar{x} = 31 min, range = 5–140 min, n = 710).

We designated each visited GPS cluster as a kill site, a non-kill site, a return visit, a true scavenging event, or inconclusive. We confirmed kill sites by the presence of rumen, a large amount of blood and hair, or skeletal remains corresponding to the time of the cluster. Non-kill sites had no evidence of prey remains, and usually some evidence of resting (bed sites). A return visit was a GPS cluster within 300 m of a GPS cluster that was a previously visited kill site. A true scavenging event was a GPS cluster in which we found prey remains, but we suspected or knew the



prey individual had died before wolves were present (e.g., anthropogenic hunting event, frozen carcass in stream with large amounts of biomass remaining). We classified GPS clusters as inconclusive if field observations were inadequate to determine whether one of the events described had occurred. We removed non-kill sites associated with rendezvous locations from the dataset ($n = 3$; DeCesare 2012). If we identified a kill site, we determined prey species in the field based on hair and skeletal remains and categorized prey into young-of-the-year, yearling, or adult age classes based on presence of antlers, and patterns of tooth eruption (Stelfox 1993). To distinguish between white-tailed deer and mule deer prey, we collected hair or tissue samples in the field, and performed genetic evaluation of cytochrome B and control region mitochondrial DNA markers (Appendix A).

We extracted the number of GPS location fixes in the cluster (1 fix rate/hr) using the GPS data clustering algorithm in Python (Knopff et al. 2009) to indicate the magnitude of wolf recursion at the cluster site. We calculated all other spatio-temporal variables in R (R Core Team 2017). We assigned 2 binary indicators to clusters based on their spatio-temporal relativity to other clusters. First, we determined whether each cluster was within 1 km and 4 days of a previous cluster to identify resting sites in proximity to kill site locations (DeCesare 2012). Second, we determined whether each cluster was within 300 m and 30 days of a previous cluster to identify clusters that represented return visits to previously made kills because we often observed repeated use of kill sites in our dataset. We assigned 2 indicators of cluster timing to account for diel variation in wolf predation events. First, we calculated the percentage of location fixes of the cluster that occurred during the day (1000–1559), previously found to be a predictive variable of wolf kill sites (Zimmerman et al. 2007, DeCesare 2012). Second, we assessed whether the cluster started in the evening (1600–2059), corresponding to the highest rates of wolf movement and predation rates in Northern Ontario (Vander Vennen et al. 2016). We assigned a value of pack-year (unique to each wolf pack, each year of data collection) to each cluster to address how differences in pack size and structure among wolf packs and among years may affect cluster duration (DeCesare 2012, Lake et al. 2013).

We extracted habitat characteristics of the clusters in ArcGIS version 10.5.1. We combined a supervised classification of a SPOT5 multispectral image (Aug 2008; 10×10 -m pixel resolution, 89% accuracy; Dancose et al. 2011), which contained 95% of visited GPS clusters, with the Agriculture and Agri-Food Canada Crop Inventories map (2016; 30×30 -m pixel resolution, 92% accuracy of agricultural land classes, 69% accuracy of other land cover classes; Agriculture and Agri-food Canada 2017). We accepted raster values from the supervised classification where both values existed during combination. We assigned values for 2 habitat characteristics that have been associated with wolf kill sites in the past. Linear features are used as travel corridors by wolves to increase prey encounter rates (Kunkel and Pletscher 2000, Kauffman et al. 2007). We combined anthropogenic and natural linear features because wolves selected for these features at approximately the same rate during winter in Northern Ontario (Newton et al. 2017). We extracted linear features (trail or road, river) of the land cover classification and determined the distance between the centroid of each GPS cluster and the nearest linear feature (m). We took a similar approach to determine the distance (m) of the centroid of each GPS cluster to open land cover classes: water, meadow, wetland, agriculture, and barren. Open areas facilitated prey detection by wolves (Kunkel and Pletscher 2000, Creel et al. 2005) but decreased predation success, given an encounter, in a wolf-elk system in Alberta (Hebblewhite et al. 2005). In cases where the centroid occurred within the open land cover polygon, we assigned a distance of zero. Centroid locations were, on average, 75.0 m ($SE = 4.9$, $n = 210$) from the rumen or major evidence of the killed prey.

We used logistic regression in a model selection framework to determine if spatio-temporal and habitat characteristics of grey wolf GPS clusters could be used to reliably identify sites where wolves had killed prey. We performed all statistical analysis in R 3.4.3. We removed inconclusive events ($n = 32$) and true scavenging events ($n = 2$) from the dataset. We considered return visits to known kill sites ($n = 29$) as non-kill sites (DeCesare 2012). When multiple collared wolves were present at the same cluster, we chose an individual wolf's GPS cluster to represent the pack because the number of location fixes by individuals at the same GPS cluster were not different ($F_{7,559} = 1.307$, $P = 0.24$). We chose the individual wolf that had the earliest fix at the cluster, or if multiple wolves arrived at the same time, we selected the breeding male or female to represent the pack if known; otherwise, we

selected an individual randomly (Mech 2011). We removed GPS clusters of Wolf 42 (Figure 1) during the fourth year of the study (Nov 2016–Mar 2017; $n = 24$) from analysis because the movement behavior of this wolf was not consistent with the pack; a former member of the Amyot pack, this wolf occupied space at the edge and within Amyot territory, but its movements were temporally distinct from other wolves in this pack.

We standardized all variables to improve model convergence and checked for collinearity ($|r| > 0.6$) among variables. We stratified the data by prey species, then randomly selected 75% of the clusters as training data. We created 16 candidate models and compared them using Akaike's Information Criterion corrected for small sample sizes (AIC_c ; Burnham and Anderson 2004). Then, we tested if removing non-informing parameters ($P > 0.05$) of the top model improved the parsimony of the model (i.e., decreased $\Delta AIC_c > 2$). We examined the fit of the top-ranking model via the receiver-operator characteristic (ROC) area under the curve (Boyce et al. 2002), and its predictive performance using the withheld 25% of the data. Lastly, we compared cluster duration characteristics among prey species and prey ages at kill sites to identify the effect these categories had on model variables.

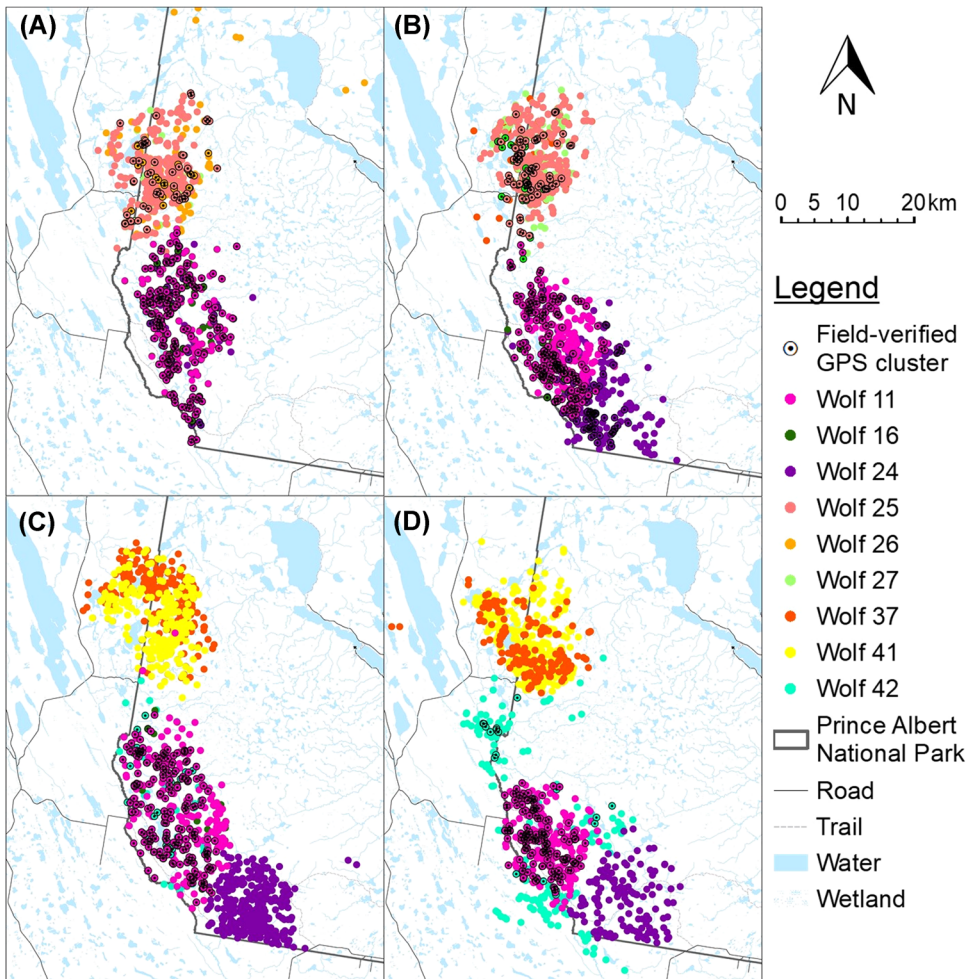


FIGURE 1 Global positioning system (GPS) clusters of 9 grey wolves created and field-verified between A) 17 December 2013–28 March 2014, B) 31 October 2014–25 March 2015, C) 31 October 2015–18 March 2016, and D) 31 October 2016–9 March 2017 in central Saskatchewan, Canada



RESULTS

We collared 9 individual grey wolves among 3 wolf packs over the course of this study. Individuals were re-collared through multiple years of the study when possible. We recorded 56,562 locations of wolves over 4 winter seasons. Average GPS collar fix success rate was 96.4% (range = 72.90–99.97%). The estimated horizontal error of the collars was 5.4 m. These data resulted in 6,191 individual wolf GPS clusters, of which we visited 1,727 for field verification (Figure 1). Accounting for cases where multiple wolves from the same pack each created a GPS cluster, we visited 989 unique GPS clusters. Between November 2015 to March 2016, and January 2017 to March 2017, we visited Amyot pack GPS clusters preferentially (Figure 1). Wolf 11 (breeding female of Amyot pack) was collared during all years of the study and thus had the highest proportion of GPS location data collected, while wolf 16 (breeding male of Amyot pack) had the highest number of GPS clusters visited relative to data collected of all collared wolves.

We found non-kill sites most frequently ($n = 710$); we found kill sites at 212 GPS clusters, 32 GPS clusters were inconclusive, 29 GPS clusters were return visits to kill sites of the same pack, and 2 GPS clusters were true scavenging events (i.e., death of prey unrelated to the wolf pack in question). Of the kill sites, 57.2% ($n = 123$) were white-tailed deer, 18.2% ($n = 39$) were moose, 8.4% ($n = 17$) were deer for which genetic testing was inconclusive, 7.9% ($n = 15$) were mule deer, 5.1% were bison ($n = 11$), 1.9% were black bears ($n = 4$), and 1.4% ($n = 3$) were elk.

Using training data ($n = 697$), we identified the most parsimonious model (Table 1) whereby variables of duration, spatio-temporal proximity to other GPS clusters, diel variation, and habitat predicted which GPS clusters of grey wolves were more likely to be kill sites. Removing non-informing parameters (distance to linear feature, and the interactions of the number of location fixes with distance to open habitat, distance to linear feature, and starting during the evening) further improved the parsimony of the model ($\Delta AIC_c = 3.90$). The GPS clusters were more likely to be kill sites when they had a higher number of location fixes, did not begin within 300 m and 30 days of a previous cluster, did not begin within 1 km and 4 days of a previous cluster, began in the evening, had a high percentage of fixes occurring during the day, occurred farther from open habitat, and had both a high number of location fixes and a high percentage of fixes occurring during the day. Wolf pack size estimates were different among years and territories (Table 2) but including a variable for pack-year and its interaction with the number of fixes in the cluster decreased the parsimony of the model ($\Delta AIC_c = 8.56$).

The top model (Table 3) fit the data (Hosmer and Lemeshow goodness-of-fit test: $\chi^2_8 = 6.14$, $P = 0.63$). When we tested the model with the reserved 25% of data ($n = 230$), the ROC area under the curve was moderate (0.86), and the accuracy was 0.84, significantly better than a no information rate ($P = 0.001$). Out of 30 predicted kill sites, field visits confirmed 25 were kill sites and 5 were non-kill sites. Out of 200 predicted non-kill sites, 169 were confirmed non-kill sites and 31 were kill sites. While the model was sensitive to non-kill sites (97.1% classified correctly), it was not specific to kill sites (44.6% classified correctly), and the balanced accuracy reflected this discrepancy (0.71).

The number of location fixes at kill sites was different among prey species, and more variable among prey age classes of large-bodied prey species such as bison and moose than small-bodied prey like white-tailed deer; across prey species, the number of location fixes was similar among young-of-the-year prey individuals (Figure 2). Clusters that were not kill sites and within 300 m and 30 days of a previous cluster were more often return visits to kills of large-bodied prey species than small-bodied prey.

DISCUSSION

We used an algorithm with decision rules previously shown to predict grey wolf kill sites in the Rocky Mountains of Canada (Webb et al. 2008, DeCesare 2012) and in Alaska, USA (Lake et al. 2013) to identify GPS clusters as the basis of the design and execution of this study. Consistent decision rules to classify GPS clusters could enhance reliability of such models and facilitate comparisons of results among studies from different areas



TABLE 1 Candidate models, number of parameters (K), Akaike's Information Criterion corrected for small sample sizes (AIC_c), change in AIC_c (ΔAIC_c), and model weights (ω) of logistic regression for whether global positioning system (GPS) clusters were kill sites of grey wolves collared in central Saskatchewan, Canada, December 2013–March 2017

Candidate model	K	AIC_c	ΔAIC_c	ω
Duration ^a + proximity ^b + diel ^c + habitat ^d	12	614.43	0.00	0.76
Duration + proximity + diel	8	617.62	3.19	0.15
Duration + proximity + habitat	8	619.40	4.97	0.06
Duration + proximity + diel + habitat + pack ^e	22	622.99	8.56	0.01
Duration + proximity + diel + pack	18	623.61	9.18	<0.01
Duration + proximity	4	625.18	10.75	<0.01
Duration + proximity + habitat + pack	18	626.80	12.38	<0.01
Duration + habitat + diel	10	627.20	12.77	<0.01
Duration + proximity + pack	14	628.75	14.32	<0.01
Duration + diel	6	632.12	17.69	<0.01
Duration + habitat	6	633.76	19.33	<0.01
Duration + diel + habitat + pack	20	638.16	23.73	<0.01
Duration + diel + pack	16	640.38	25.95	<0.01
Duration	2	640.90	26.48	<0.01
Duration + habitat + pack	16	642.96	28.53	<0.01
Duration + pack	12	646.23	31.80	<0.01

^aDuration = number of location fixes.

^bProximity = within 300 m and 30 days of a previous cluster, within 4 days and 1 km of a previous cluster.

^cDiel = cluster starts during the evening (1600–2059), the percentages of location fixes during the day (1000–1559), and the interaction of each of those characteristics with the number of location fixes.

^dHabitat = distance to open habitat, distance to linear feature, and the interaction of each of those characteristics with the number of location fixes.

^ePack = unique qualifier for each pack of each year of the study.

TABLE 2 Size estimates for Amyot and Nesslin wolf packs during winters December 2013–March 2017, central Saskatchewan, Canada

Wolf pack	Winter season	Estimated number of wolves in pack
Amyot	2013–2014	15 ^a
	2014–2015	12 ^{a,b}
	2015–2016	6 ^b
	2016–2017	4 ^b
Nesslin	2013–2014	12 ^a
	2014–2015	Unknown

^aObserved number of wolves in pack during capture for collar deployment.

^bObserved number of wolves in pack on remote wildlife camera images.



TABLE 3 Coefficient estimate, standard error, Wald statistic (Z), and P value of parameters included in the top-ranked logistic regression model of whether global positioning system (GPS) clusters of grey wolves in central Saskatchewan, Canada, December 2013–March 2017 were kill sites

Parameter	Coefficient estimate	Standard error	Z	P
Intercept	−1.71	0.16	−10.56	≤0.001
Fixes ^a	0.69	0.14	5.01	≤0.001
300 m 30 days ^b	−1.28	0.34	−3.79	≤0.001
1 km 4 days ^c	−0.61	0.24	−2.51	0.012
Start evening ^d	0.71	0.23	3.10	0.002
Open ^e	0.34	0.08	4.03	≤0.001
Percent day ^f	0.01	0.00	2.16	0.031
Fixes × percent day	0.02	0.01	3.13	0.002

^aNumber of location fixes in the cluster.

^bIs the cluster within 300 m and 30 days of a previous cluster?

^cIs the cluster within 1 km and 4 days of a previous cluster?

^dDoes the cluster begin within the hours of 1600–2059?

^eDistance from cluster centroid to nearest open land cover type (agriculture, meadow, lake, wetland, barren ground).

^fThe percentage of location fixes that occur within the hours of 1000–1559.

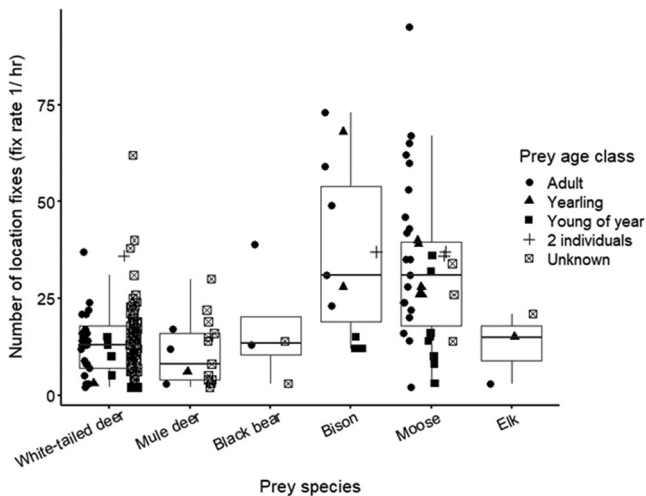


FIGURE 2 Number of global positioning system (GPS) location fixes (fix rate = 1/hr) at grey wolf kill sites in winter among prey species and prey age classes in central Saskatchewan, Canada, December 2013–March 2017

(Webb et al. 2008). Having multiple individual wolves collared in the same pack was sometimes redundant when multiple wolves attended the same kill site; however, it provided reliability as collars failed and individuals perished and dispersed from the study area. Further, there were kill sites where only 1 collared pack member was present, even though there were multiple collared wolves in the pack (25% of kills, $n = 34$). Thus, we were able to capture more predation events, especially of small prey, by having >1 individual collared in each wolf pack.

Our top-ranking model performed moderately in classifying testing data into kill sites and non-kill sites; other studies have reported similar or higher ROC values for models discriminating kill sites of grey wolves



(0.85 [Webb et al. 2008], 0.91 [DeCesare 2012], 0.97 [Lake et al. 2013]), higher errors of commission errors (49% [Zimmerman et al. 2007], 24% [Webb et al. 2008]), and lower rates of omission errors (43% [Zimmerman et al. 2007], 4% [Webb et al. 2008]). The number of location fixes was a discriminating variable in the top distinguishing model of kill sites and non-kill sites; this is consistent with other studies of grey wolves (Zimmerman et al. 2007, Lake et al. 2013). In applying this technique to future studies of wolves, the number of location fixes could be used to filter GPS clusters visited for field verification to lessen the burden of field work and reduce the number of non-kill sites visited. Researchers should be aware that this technique would omit predation events of small prey (Sand et al. 2005, Franke et al. 2006, Webb et al. 2008, Bacon et al. 2011), a result supported by the high number of kill sites misclassified as non-kill sites in the testing data of this study.

The kill site omission errors in our testing data resulted from GPS clusters with a low number of location fixes in the cluster, with the majority linked to predation events of deer (29/31 misclassified predation events). Our omission error was higher than previous studies, potentially because of the prevalence of deer in wolf diet in our study system (77% of kills) compared to previous studies in Scandinavia (2% of kills; Zimmerman et al. 2007) and in Alberta (59–68% of kills; Webb et al. 2008). There were numerous predation events on deer with a low number of location fixes in our complete dataset (29 kill sites with <5 fixes in the GPS cluster); thus, we expect if the top-ranking model was applied to novel data in this system, a large number of deer kill sites would not be detected. Degree of pack-splitting may have important implications for the ability of research to detect all kills made by a wolf pack, particularly when deer are a primary prey item and handling times are correspondingly short (Webb et al. 2008, Metz et al. 2011). In addition, smaller prey such as beaver, grouse, and hares can be killed and consumed in very short intervals by wolves (Palacios and Mech 2011, Gable et al. 2016). Very fine GPS collar fix intervals, or alternative methods may be necessary to reliably detect all wolf predation events of deer and smaller prey. Activity sensors have increased the predictability of GPS clusters (Blecha and Alldredge 2015), and audio-video recorders on GPS collars (Brockman et al. 2017, Studd et al. 2021) will likely enhance methods of distinguishing predation events, especially of small prey with low handling times. Using this model to identify predation events would reduce the amount of field verification required to estimate kill rates of large-bodied prey species. As such, it could provide a method for land managers to verify the number of adult bison predation events per winter to contribute to population estimates and viability models for this threatened species (Committee on the Status of Endangered Wildlife in Canada 2013).

Our study supports using metrics to classify clusters relative to previously formed clusters; for example, clusters that occur within 4 days and 1 km of a previous cluster are likely locations where wolves rest nearby while consuming carcasses, and clusters that occur within 300 m and 30 days of a previous clusters are likely locations where wolves returned to previously killed carcasses. Including these variables of spatio-temporal proximity reduced our commission error compared to previous studies because using cluster duration alone would confuse these events as kill sites. These secondary clusters occurred more frequently following predation events of large-bodied prey (e.g., adult moose carcasses) than smaller-bodied prey (e.g., adult deer).

Our study also supports using metrics associated with diel variation in wolf behavior to distinguish kill sites. The GPS clusters that were kill sites were likely to begin during the evening (1600–2059), consistent with high rates of wolf movement, and corresponding rates of predation in Northern Ontario (Vander Vennen et al. 2016). Zimmerman et al. (2007), however, reported that GPS cluster start time (morning, afternoon, night) was not an important distinguishing characteristic of kill sites but that GPS clusters with a low proportion of fixes in the afternoon indicated a moose kill site in Scandinavia. A low percentage of fixes during midday was also associated with wolf kill sites in the Rocky Mountains of Canada (DeCesare 2012). In our study, the percentage of fixes that occurred during the day (1000–1559) and its interaction with the number of location fixes in the cluster were positively associated with wolf kill sites in our top model. Further metrics of diel variation in wolf predation behavior could be useful in distinguishing kill sites of smaller prey, as hunting behavior may be characteristic of kill sites, even if corresponding prey handling time (cluster duration) is short.



Habitat variables were also included in the top-ranking model. Distance to open habitat was an important distinguishing characteristic of whether a GPS cluster was a kill site or a non-kill site in our data, while distance to linear features was not an informing parameter and removed from the final model. Wolf kill sites in our study system were typically farther from open areas than non-kill sites because closed canopies may increase hunting success. For example, grasslands and open conifer forests reduced the risk of elk being killed after encounter by grey wolves, while dense cover in forests rendered elk more vulnerable in Banff National Park (Kunkel and Pletscher 2000, Hebblewhite et al. 2005). Closed land cover types may increase predation risk due to decreased detection distance or reduced ability to escape (Kunkel and Pletscher 2000, Hebblewhite et al. 2005). This finding supports arguments for inclusion of habitat variables for discriminating models of kill sites (Pitman et al. 2012).

Handling time at kill sites is generally thought to decrease with increasing wolf pack size (Messier and Cr  t   1985, Metz et al. 2011). In our data, including a variable representing each pack each winter decreased the parsimony of the predictive model, suggesting limited variation among wolf packs and years despite differences in size. This aligns with other research where wolf pack size did not influence handling time at wolf kill sites (Hayes et al. 2000, Wikenros 2001, Johnson et al. 2017). We did not identify the age, sex, or social structure among members in packs in this study, but these demographic features affect predation behavior, including time spent at kill sites (Sand et al. 2006, MacNulty et al. 2009, Lake et al. 2013). Pack attendance at carcasses decreases with pack size (J  drzejewski et al. 2002, Metz et al. 2011), which may explain the lack of correlation between pack size and handling time. It is also likely that scavengers, such as ravens (*Corvus corax*), play a large role in mediating the difference in time spent at carcasses among wolf pack sizes (Hayes et al. 2000, Peterson and Ciucci 2003, Vucetich et al. 2012).

The number of location fixes at kill sites was different among prey species and prey age classes (Figure 2). Generally, there were more location fixes at kills of large-bodied prey species than small-bodied prey species; this distinction was especially prevalent among adult prey. Kill sites of young-of-the-year prey had similar numbers of location fixes among prey species. These patterns result from biomass available from different prey individuals, which overlaps among age classes of different species (Webb et al. 2008). Habitat variables at kill sites may clarify patterns among prey species unrelated to biomass because habitat can govern the occupancy and vulnerability of species to predation. In our dataset, bison kill sites were closer to open cover types than non-kill sites, while kill sites of all other prey species were farther from open cover types. Habitat attributes of GPS clusters correctly classified 74.8% of kills by cougars into prey species categories (Knopff et al. 2009). Other researchers have grouped prey into size classes to accommodate small sample sizes of individual prey species and age classes (Webb et al. 2008, McPhee et al. 2012b, Wilckens et al. 2015, Ebinger et al. 2016). Identifying kills in specific, non-overlapping prey biomass categories rather than prey species may be more successful at distinguishing among GPS clusters (Webb et al. 2008). A model that accurately distinguishes all prey species would be useful for characterizing kill rates in a multi-prey system, but space-time characteristics of GPS clusters may not provide enough information to do so successfully.

MANAGEMENT IMPLICATIONS

Our study suggests that wolf kill sites are not always as easily detected using GPS cluster methodology as previously suggested especially when small prey (e.g., deer and young bison and moose) are prevalent. This reinforces the notion that distinguishing models are system-specific, and emphasizes the importance of conducting field visits to GPS clusters to determine predictive models. Further, our research highlights the importance of testing predictive models with novel or withheld data, as even our top-ranking model selected from parameters previously reported to be predictive of wolf kill sites performed only moderately. Our model was successful in distinguishing non-kill sites (a low number of non-kill sites were identified as kill sites in the testing data) so this technique could be useful for reducing field efforts of visiting potential kill sites but would be prone to missing predation events of



small prey (a high number of kill sites were mis-classified as non-kill sites in the testing data). Our results indicate spatio-temporal characteristics associated with wolf kill sites are highly variable in multi-prey systems; GPS clusters can reliably detect kills sites of large-bodied prey, such as adult bison or moose, but detecting kill sites of smaller prey is less reliable.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

ETHICS STATEMENT

Capture, collar deployment, and subsequent behavioral tracking adhered to Parks Canada Agency Animal Care standards (permit PANP-2013a).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from Parks Canada Agency. Restrictions apply to the availability of these data, which were used under license for this study.

ORCID

Courtney C. Irvine  <https://orcid.org/0000-0002-5375-9024>

Seth G. Cherry  <https://orcid.org/0000-0003-4242-3629>

Brent R. Patterson  <https://orcid.org/0000-0002-0252-0654>

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APPENDIX A: MOLECULAR METHODS FOR SPECIES DETERMINATION OF DEER (*ODOCOILEUS* SPP.) PREY IN CENTRAL SASKATCHEWAN

Species determination of deer (*Odocoileus* spp.) prey was difficult at wolf kill sites because wolves consume most or all of a deer carcass after killing it (Ballard et al. 2003). Patches of hair or hide, bone fragments, blood-stained snow, and rumen identified a predation event but not prey species reliably. Thus, we used molecular techniques for discriminating deer prey. We expected white-tailed deer (*O. virginianus*) to be more prominent than mule deer (*O. hemionus*) in this system.

We collected 103 tissue and 61 hair samples at deer kills made by grey wolves during December 2013–March 2014, October 2014–March 2015, October 2015–March 2016, and October 2016–March 2017. We stored samples frozen in plastic bags. We subsampled tissue to a 0.5-cm² section and placed into 1x lysis buffer for transport. We transported hair in paper envelopes. We placed samples into 250 µL of 1x lysis buffer and 50 µL total of proteinase K and incubated at 56°C for 1 hour and 37°C overnight to release DNA into solution (Walker 2018).

We extracted DNA using the Wizard® SV 96 Genomic DNA Purification System (Promega, Madison, WI, USA) and eluted it in 80 µL 1xTE (Walker 2018). We amplified mitochondrial DNA samples at the cytochrome b region using a primer pair developed by the Ontario Ministry of Natural Resources and Forestry (OMNRF): forward primer, UngGludg 5'TGATATGAAAAAYCATCGTTG3'; reverse primer, UngCBR1 5'CCAGCAGACGCAGACAAAAT3' (Walker 2018).

We amplified the product using the following polymerase chain reaction (PCR) parameters: 1xPCR Buffer, 0.2 mM dNTPs, 1.5 mM MgCl₂, 0.2 µg/ml BSA, 0.4 µM of each primer, 0.5U of Taq and a total of 5 ng of DNA (Walker 2018). We incubated the product for 5 minutes at 94°C, 30 cycles of 30 seconds at 94°C, 30 seconds at 51°C, 30 seconds at 72°C, and finally 8 minutes at 72°C (Walker 2018). We cleaned the PCR product using the ExoSAP protocol (Walker 2018).

We sequenced 468 base pairs at the cytochrome b region in the mitochondrial genome using the Big Dye™ Terminators v3.1 cycle sequencing kit (Applied Biosystems, Waltham, MA, USA) with the forward UngGludg primer LGL283 5'-TACACTGGTCTTGTAAC-3' located within tRNAThr (Bickham et al. 1996) and the reverse primer ISM015 5'-ATGGCCCTGTAGAAAGAAC-3' (R. Purdue, Illinois State Museum, personal communication). We sequenced tissue samples from 4 individuals of known species as cytochrome b reference samples. We acquired 1 white-tailed deer sample from Texas and 1 mule deer sample from Wyoming for the United States Fish and Wildlife Society for Wildlife Forensic Science proficiency testing, and 1 elk (*Cervus canadensis*) sample from eastern Ontario and 1 moose (*Alces alces*) sample from northwestern Ontario from the Natural Resources DNA Profiling and Forensic Centre.

We sequenced 517 base pairs within the control region of the mitochondrial genome to increase resolution (Walker 2018). We acquired reference samples of this region of mule deer and white-tailed deer from an existing Saskatchewan reference database provided by the Wildlife Forensic DNA Laboratory at Trent University. We used maximum likelihood phylogenetic analysis to create haplotype trees of the reference species at each region of the mitochondrial genome then compared the sequences of each unknown sample to the haplotypes and determined species at each region (Walker 2018).

We sequenced mitochondrial DNA only; thus, these results do not provide any information on paternal genetic contribution. Hybridization between white-tailed deer and mule deer has been documented in sympatric regions of these 2 species (Carr et al. 1986, Bradley et al. 2003, Russell et al. 2019). We refer to the species determination of each individual, but it is possible hybrid individuals exist in our dataset. More conclusive identification is not possible without microsatellite genotyping analysis and a robust reference database from the study area.

Nine haplotypes emerged via maximum likelihood phylogenetic analysis at the cytochrome b region corresponding to reference samples for this region; we successfully sequenced and identified 149 unknown samples to species at this region (Walker 2018). Thirteen haplotypes emerged via maximum likelihood phylogenetic analysis at the control region corresponding to reference samples from the Saskatchewan database; we successfully sequenced and identified 76 unknown samples at this region (Walker 2018).

Cytochrome b and control region sequencing of the mitochondrial genome yielded identical results for species determination. We identified 135 samples as white-tailed deer, 17 samples as mule deer, and 1 sample as elk. Eleven samples failed to provide enough data to determine species.