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Identifying bobcat *Lynx rufus* kill sites using a global positioning system

Nathan J. Svoboda, Jerrold L. Belant, Dean E. Beyer, Jared F. Duquette & James A. Martin

The role of predation in ecological systems has received considerable attention in scientific literature and is one of the most important, yet least understood aspects of carnivore ecology. Knowledge of factors that improve our ability to detect predation events using animal telemetry data could be used to develop strategies to reduce time and resources required to obtain reliable kill estimates. Using Global Positioning System telemetry-collars, we investigated 246 bobcat *Lynx rufus* location clusters to identify white-tailed deer *Odocoileus virginianus* kill sites in the Upper Peninsula of Michigan, USA, during May–August, 2009–2011. We documented kills of white-tailed deer at 42 location clusters. We used logistic regression and Akaike Information Criterion for small samples to identify factors (i.e. number of locations in cluster, time from cluster formation to investigation, time of day and land cover) that may influence bobcat behaviour and our ability to detect white-tailed deer kill sites. Clusters with more locations and the search of clusters within 14 days after cluster formation increased odds of detecting bobcat kill sites. The best-performing model was 67% accurate overall and identified 34% of kill sites and 75% of non-kill sites. Applying our best-performing model with the optimal cut-off value would result in a twofold increase in the identification of white-tailed deer kill sites reducing time and effort to find a similar number of kill sites without models by half. Identifying factors that improve our ability to identify bobcat kill sites can reduce field effort and search time.

Key words: bobcat, GPS locations, *Lynx rufus*, Michigan, *Odocoileus virginianus*, predation, white-tailed deer

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Predator-prey interactions represent an important ecological process that can influence species abundance and community structure (Shastri & Diwekar 2006). Improving our knowledge of predator-prey dynamics includes an understanding of types of prey killed, rates of kills and associated ecological influences (Merrill et al. 2010). Earlier research assessing carnivore kill sites were often limited to circumstances that allowed direct observation of predations such as cheetah *Acinonyx jubatus* kills of ungulates (Bissett & Bernard 2007) or indirect observations of predation events (e.g. following tracks of European lynx

Lynx lynx in snow; Odden et al. 2006). Thus, identification of kill sites has generally been restricted to species that inhabit relatively open areas where researchers can observe predation events, or limited to locations or seasons with suitable tracking conditions. Many carnivore species occur in forests or other vegetation types where tracking or direct observations are impractical or not possible, requiring alternate methods to locate kill sites. In addition, identification of kill sites is needed throughout the year, including periods with potentially unsuitable tracking conditions. Difficulty in locating kill sites is

exacerbated as most carnivores traverse large areas, and some carnivores may hide kills or consume prey rapidly (Ruth et al. 2010, Tambling et al. 2010).

Capturing and fitting carnivores with Global Positioning System (GPS) radio-transmitters allows for frequent relocations, which can facilitate location of kill sites (Knopff et al. 2009), den locations (Olson et al. 2011), day beds (Anderson & Lindzey 2003) and rendezvous sites (Merrill & Mech 2003). Recently, several studies have used GPS technology to better understand prey selection and investigate kill sites of carnivores (Anderson & Lindsey 2003, Cavalcanti & Gese 2010, Ruth et al. 2010). This technology has been used to document kills by large carnivores including jaguars *Panthera onca* (Cavalcanti & Gese 2010), cougars *Puma concolor* (Anderson & Lindsey 2003, Knopff et al. 2009) African lions *Panthera leo* (Tambling et al. 2010), leopards *Panthera pardus* (Martin et al. 2011) and gray wolves *Canis lupus* (Sand et al. 2005, Demma et al. 2007, Zimmerman et al. 2007). However, we are unaware of any study assessing the effectiveness of this technique on medium-sized carnivores. Medium-sized carnivores have different diets, consumption rates and handling times (Leopold & Krausman 1986, Labisky & Boulay 1998, Arjo et al. 2002) than large carnivores indicating a need to develop models specific to their predatory behaviour.

Though previous studies have characterized metrics that influenced whether a grouping of relocations (i.e. a cluster) was a kill site (Knopff et al. 2009), fewer have attempted to develop models that researchers can use to increase efficacy of detecting kill sites (e.g. Webb et al. 2008, Tambling et al. 2010). Metrics used in previous studies include biological factors that may affect predator kill success (habitat type, time of day; Anderson & Lindzey 2003, Webb et al. 2008), predator movement characteristics (rate of movement, site fidelity; Knopff et al. 2009) and factors that may affect the probability of detecting prey at the kill site (number of locations at cluster, elapsed time from cluster formation to investigation; Sand et al. 2005, Zimmerman et al. 2007, Knopff et al. 2009). Including multiple metrics in model development provides biologists with a comprehensive approach to efficiently identify potential kill sites based on the biological characteristics and movements of the predator while maximizing the probability of detecting a kill site in the field.

Success in detecting carnivore kill sites using models developed from GPS data has varied among species; however, common metrics include number

of locations in a cluster and time from cluster formation to investigation (Knopff et al. 2009, Tambling et al. 2010). Additionally, whether GPS clusters are associated with kill sites may vary among land cover and time of day (e.g. day or night) a cluster is formed (Anderson & Lindzey 2003, Webb et al. 2008). To our knowledge, no study has yet assessed the efficacy of using GPS telemetry-collars to locate kill sites of bobcats *Lynx rufus*. We were interested in detection of bobcat kill sites of white-tailed deer *Odocoileus virginianus* as part of a larger study of predator-prey relationships.

Specifically, we assessed potential factors that could influence the probability of white-tailed deer kill site detection before investigators conducted site searches. We included biological factors that may affect predator kill success as well as factors affecting the probability of detecting prey remains. Our objectives were to determine: 1) if GPS locations from telemetered bobcats could be used to locate kill sites of white-tailed deer, and 2) evaluate a model to assess the predictive ability of several biological influences and movement characteristics at cluster locations to discriminate between kill sites and non-kill sites. This would reduce time spent searching clusters of locations representing non-kill sites. Because larger prey items require longer handling time and bobcats are primarily nocturnal or crepuscular (Hall & Newsom 1978, Anderson & Lovallo 2003) we hypothesized that bobcat kill sites of white-tailed deer would have a greater number of locations than non-kill sites and predation events would occur at night. In addition, given that increased elapsed time since cluster formation to investigation increases the likelihood that prey will be entirely consumed (e.g. DeVault et al. 2011) or degraded by insects (DeVault et al. 2004, Burkepile et al. 2006), we hypothesized that the probability of detecting kill sites would increase with reduced time from cluster formation (i.e. presumed time of predation) to investigation.

Material and methods

Study area

We conducted our study during May-August, 2009-2011, in Menominee County, Upper Peninsula of Michigan, USA (45°34'14"N, 87°20'47"W). The 900-km² area is bordered on the east by Lake Michigan, on the north by US Highway 2, on the west by US Highway 41 and on the south by the town of

Stephenson. The area is mostly forested, but includes some agricultural land and residential units. Conifer forests dominate the area and consist primarily of hemlock *Tsuga canadensis*, pine *Pinus* spp., white cedar *Thuja occidentalis*, spruce *Picea* spp., tamarack *Larix laricina* and balsam fir *Abies balsamea*. Deciduous forests include birch *Betula* spp., aspen *Populus* spp. and maple *Acer* spp. Lowland areas are comprised of tag alder *Alnus rugosa*, willow *Salix* spp. and other species consistent with boreal coniferous wetlands. Agricultural crops include corn, soybeans and hay. Climate varies due to lake-effect weather patterns, but typical May-August temperatures range from 3-25°C with extremes reaching 32°C; rainfall during this period is typically 12.2-14.5 cm (National Oceanic and Atmospheric Administration 2010). Bobcat density in our study area is about 3 individuals/100 km² (Stricker et al. 2012).

Data collection and analysis

We captured bobcats during April-May, 2009-2011, using modified No. 3 Oneida Victor Soft-Catch® padded foothold traps (Oneida Victor, Euclid, Ohio, USA; Powell & Proulx 2003) with commercial lures, urine and visual attractants. We restrained bobcats using a noose pole and intramuscularly injected each with a combination of ketamine and xylazine (Kreeger 1999) using a pole syringe. After induction we weighed, sexed and extracted a lower first premolar or upper incisor for age estimation using *cementum annuli* techniques (Crowe 1972). We fitted bobcats with Lotek 7000SU GPS collars (Lotek Wireless, Newmarket, Ontario, Canada), programmed to obtain a location every 15 minutes from capture to 31 August in the year of capture. We downloaded location data remotely from fixed-winged aircraft every 3-4 days. We calculated the fix success rate for each radio-collar by dividing the number of successful fixes by the number of attempted fixes. Capture and handling procedures followed Mississippi State University Institutional Animal Care and Use Committee protocol # 09-004.

We used program R (version 2.15.0; R Development Core Team 2010) to develop a rule-based algorithm to identify GPS location clusters from location data. Because of similar predatory behaviour between cougars and bobcats (e.g. cache prey and solitary predators), we defined clusters, following Knopff et al. (2009), as ≥ 8 locations within 50 m of each other within a 24-hour period. The cluster algorithm initially searched within 50 m of the first chronological location and used an initial 24-hour

temporal screen to identify associated points. The first two points meeting the time-space constraints produced a seed cluster from which the geometric center was calculated. The program then sequentially added points occurring within space and time constraints of the geometric center. The program recalculated the geometric center after each additional point and the process was repeated until no more points were added. Clusters were allowed to persist beyond the temporal screen provided that the difference between the last point and the next new point at a cluster was ≤ 24 hours. After calculations were completed, we determined the geometric center, number of locations and time and date of the first and last location of each cluster. We mapped cluster locations in ArcMap 9.2 (Environmental Systems Research Institute, Redmond, California, USA) to facilitate field searches.

We used the geometric center of each cluster to locate clusters in the field with handheld GPS units. We used 2-5 trained observers to conduct systematic searches at each cluster to determine whether it was a kill site. We searched clusters by walking eight transect lines in each cardinal and intercardinal direction (e.g. N, NE, E and SE) 50 m from the geometric center, then walking 38 m to the right before zigzagging back to the geometric center (Fig. 1; Knopff et al. 2009). We searched the entire defined search pattern of each cluster irrespective of the number of individuals searching or whether a kill site was identified. We assigned a cluster as a white-tailed deer kill site if prey remains were found that closely matched the dates over which the cluster occurred (e.g. decomposition characteristics, presence of insects or larvae), and evidence of bobcat feeding was observed on prey (e.g. cached remains, scratch marks or hemorrhaging). If evidence of a recent deer predation was not observed, if the deer was considered killed by a species other than bobcat, or if decomposition of the deer did not match the dates the bobcat was at the location, the cluster was classified as a scavenge site. We documented and confirmed bobcat bed sites at kill sites using physical (e.g. bobcat hair at bedsite; Podgorski et al. 2008) and visible evidence (e.g. depression in vegetation or soil; Akenson et al. 2003). To avoid possible effects of capture on bobcats (i.e. atypical behaviour due to capture stress), we did not investigate clusters formed within three days of capture.

We used mixed effects logistic regression (Hosmer & Lemeshow 2000) with individual bobcat as a random effect using the LMER function and Laplace

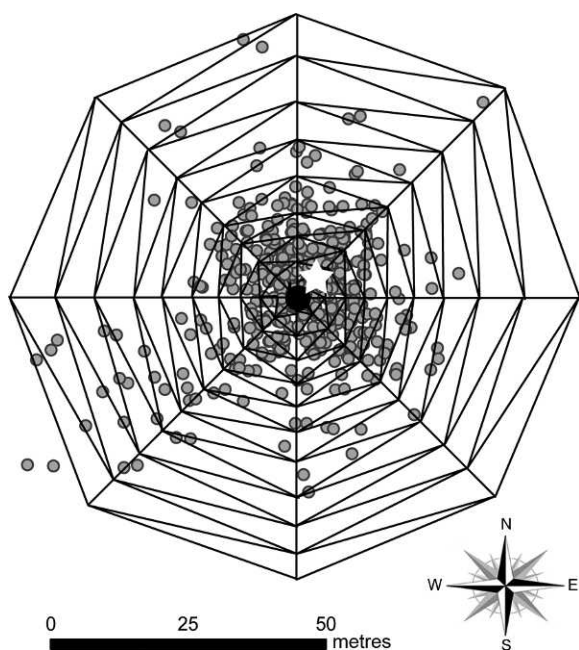


Figure 1. Search area (50-m radius) and search pattern surveyed by 2-5 trained observers during investigation of bobcat cluster locations ($N = 246$) in Michigan's Upper Peninsula, during May-August, 2009-2011. Black circle indicates cluster center, gray circles indicate bobcat locations and white star indicates kill location.

approximation to estimate likelihood in program R (version 2.15.0, R Development Core Team 2010) to model presence of a deer kill at each cluster location. We coded all clusters where we identified evidence of a deer kill as 1, while remaining sites (e.g. bed sites, loafing sites and scavenging sites) were coded as non-kills (0). For each cluster, we recorded four potential fixed-effect explanatory variables: number of locations comprising cluster, elapsed time in minutes from cluster formation to investigation, land-cover type where cluster was located and time of day. We categorized land-cover type as upland forest, lowland forest, non-forested wetland, agriculture or developed (e.g. roads or buildings). Time of day was determined by using time of the first location comprising the cluster and was categorized as day (1; 06:32-21:06) or night (0; 21:06-06:32) based on mean sunrise and sunset times during May-August.

To increase the efficacy of identifying bobcat kill sites of white-tailed deer, we selected a set of *a priori* explanatory variables previously identified in the literature as important factors for identifying kill site locations, and then developed a set of candidate models based on all combinations of variables excluding interaction terms. We randomly selected 70% of all cluster locations searched (white-tailed

deer kill sites and non-kill sites) proportionally by individual bobcat for model development and used the remaining 30% for model validation. We evaluated variable normality using the Shapiro-Wilk statistic and used the Spearman-rank correlation method to test for collinearity before model fitting and did not use highly correlated ($|r| > 0.7$) predictor variables in the same model (Zar 1996). We used Akaike Information Criterion adjusted for small sample size (AIC_c) to determine model ranks (Burnham & Anderson 2002). We calculated Akaike weights to measure model support and model selection uncertainty, and calculated relative importance of model parameters and determined parameter estimates using model-averaged weighting (Burnham & Anderson 2002). We then calculated unconditional standard errors (SE) and 95% confidence limits for each parameter. We determined best supported models by examining AIC_c scores and individual model weights, selecting models within four AIC_c units of the best supported model ($\Delta AIC_c = 0$). We used receiving operator characteristic (ROC) curves to calculate sensitivity (error of omission; identifying a kill site as a non-kill site) and specificity (error of commission; identifying a non-kill site as a kill site; Webb et al. 2008) for the best supported models.

Whether a cluster is classified as a kill site or a non-kill site in a logistic regression model is determined by the probability output and can be set arbitrarily, commonly at 0.5 (e.g. Zimmerman et al. 2007), or it can be defined by using ROC curves to obtain optimal output (e.g. Webb et al. 2008, Knopff et al. 2009). Predictive success of the model can be maximized by changes in cut-off values (Hosmer & Lemeshow 2000). We investigated the effect of using seven cut-off values (i.e. 0.50, 0.53, 0.55, 0.56, 0.57, 0.58 and 0.60) on best supported models. We selected these cut-off values based on preliminary analyses that suggested these values encompassed the potential range of maximum model accuracy. To assess model accuracy, we ran 1,000 iterations of each model at each cut-off value, randomly selecting 70% of the data at each run. We then calculated means and 95% confidence intervals for sensitivity and specificity similarly for all cut-off levels for each candidate model. We used ROC curves to assess the optimal cut-off value and model predictive success, and then selected the best predictive model and applied the optimal cut-off value to develop a final composite model using 100% of cluster locations. We report means other than model parameter estimates with ± 1 standard deviation.

Table 1. Model results for factors influencing detection of bobcat kill sites of white-tailed deer, Upper Peninsula, Michigan, USA, during May-August, 2009-2011. Model terms are number of locations comprising a cluster (LOCS), elapsed time from cluster formation to investigation (ELAPSED), time of day (day or night) cluster was initiated (TIME) and land-cover type predation occurred (COVER). K = number of parameters in model. ΔAIC_c = the difference between the AIC_c value of the best supported model and successive models. All models with ΔAIC_c scores ≤ 4 are included. w_i = Akaike model weight.

Model	K	AIC_c	ΔAIC_c	w_i
LOCS + ELAPSED	3	128.247	0.000	0.614
TIME + LOCS + ELAPSED	4	130.347	2.100	0.215
COVER + LOCS + ELAPSED	7	130.804	2.557	0.171

Results

We captured seven bobcats (one adult female, one juvenile female and five adult males) and searched 246 clusters (mean = 35.1 ± 18.1 clusters/bobcat). GPS collars averaged 96.8% fix success, ranging from 94.8% to 97.7% per bobcat. We searched clusters 6.2 ± 3.4 days after formation (range: 1.5-24.6 days) and identified kill sites 1.5-13.2 days (mean = 5.1 ± 2.6) after cluster formation. Most (82%) kill sites were detected < 7 days after cluster formation. Clusters consisted of 8-546 locations (mean = 57 ± 77) and kill sites were comprised of 11-464 locations (mean = 114 ± 5) with most (71%) kill sites exceeding 50 locations. We found white-tailed deer remains (37 fawns and five adults) at 17.1% of cluster sites. Scavenging activity on white-tailed deer was identified at 2% ($N = 6$) of cluster sites and bobcat bed sites were identified at 19% ($N = 8$) of kill sites.

We developed models for deer kill sites using 172 clusters (mean = 24.6 ± 12.7 clusters/bobcat) of which we detected kills at 17.4% ($N = 30$). On average, we visited these 172 clusters 6.4 ± 3.6 days after formation. Mean number of locations at these clusters was 52.5 ± 66.0 and bobcats initiated slightly more clusters (55.3%) during the day. We found no

evidence of multicollinearity between pairwise combinations of predictor variables.

The best-supported model included number of locations in cluster and time from cluster formation to investigation (Table 1). We were more likely to detect deer kill sites at clusters with more locations investigated soon after cluster formation (Table 2). More specifically, with an increase of 50 locations per cluster, clusters were 2.1 times more likely to be deer kill sites. With an increase of one day from cluster formation to investigation, clusters were 1.4 times less likely to be deer kill sites. Relative importance was greatest for number of locations per cluster and time from cluster formation to investigation. The optimal probability cut-off value above which we considered a cluster a white-tailed deer predation was 0.56 (Table 3). Assessing model predictive capacity by resampling model validation demonstrated that the top model had intermediate overall accuracy (67.1%) and was capable of identifying 34.1% of kill sites and 74.5% of non-kill sites. Resampling model validation for the same model at other cut-off values (e.g. 0.53, 0.55 and 0.57) demonstrated that choice of cut-off value had a large effect on deer kill site accuracy (see Table 3).

After applying cluster validation data, the simplest model with greatest accuracy was: kill site = $-0.68 + 0.01 \times \text{LOCS} - 0.35 \times \text{ELAPSED}$. Models with greater

Table 2. Model averaged parameter estimates of bobcat kill sites for white-tailed deer, Upper Peninsula, Michigan, USA, during May-August, 2009-2011. Model terms are number of locations comprising a cluster (LOCS), elapsed time from cluster formation to investigation (ELAPSED), time of day (day or night) cluster was initiated (TIME) and land-cover type predation occurred (COVER). Land-cover types are agriculture (COVER(3)), upland forest (COVER(4)), lowland forest (COVER(5)) and non-forested wetland (COVER(6)).

Model term	Parameter estimate	Standard error	95% Confidence limit		Relative importance
			Upper	Lower	
LOCS	0.020	0.004	0.028	0.012	1.000
ELAPSED	-0.365	0.120	-0.132	-0.598	1.000
TIME	0.024	0.137	0.292	-0.244	0.215
COVER (3)	-0.035	0.288	0.527	-0.597	0.171
COVER (4)	0.045	0.247	0.525	-0.436	0.171
COVER (5)	-0.258	0.313	0.353	-0.869	0.171
COVER (6)	-0.046	0.289	0.517	-0.609	0.171

Table 3. Model estimates for overall accuracy, sensitivity and specificity for predictions at seven cut-off values derived from 1,000 iterations of logistic regression models distinguishing bobcat kill locations from non-kill locations of white-tailed deer, Upper Peninsula, Michigan, USA, during May-August, 2009-2011. Iterations were performed by randomly sampling 70% of data and validating models using the remaining 30% of data. Model terms are number of locations comprising a cluster (LOCS), elapsed time from cluster formation to investigation (ELAPSED), time of day (day or night) cluster was initiated (TIME) and land-cover type predation occurred (COVER). Overall accuracy is the mean percentage of kill sites and non-kill sites correctly identified by the model. Mean sensitivity is the mean percentage of kill sites correctly identified by the model. Mean specificity is the mean percentage of non-kill sites correctly identified by the model.

Model	Cut-off	Overall accuracy			Sensitivity			Specificity		
		Mean	95% CI		Mean	95% CI		Mean	95% CI	
			Lower	Upper		Lower	Upper		Lower	Upper
LOCS + ELAPSED	0.50	23.43	18.02	29.07	93.70	81.25	100.00	7.45	2.94	13.79
	0.53	44.03	34.88	55.23	67.31	46.43	87.88	38.53	26.12	53.79
	0.55	62.03	51.74	72.67	42.26	22.22	65.71	66.18	54.07	77.30
	0.56	67.11	57.56	77.33	34.08	13.79	58.06	74.50	64.49	84.14
	0.57	70.98	62.21	79.65	26.96	7.41	50.00	80.64	71.74	89.04
	0.58	73.23	65.70	81.98	22.53	6.67	41.94	84.77	77.14	92.36
	0.60	76.76	69.77	83.72	13.88	0.00	30.77	91.03	83.45	96.55
TIME + LOCS + ELAPSED	0.50	23.54	19.19	29.07	93.25	81.82	100.00	7.96	2.92	15.97
	0.53	44.43	34.88	55.81	67.27	44.83	87.50	39.05	26.47	52.48
	0.55	61.90	51.74	72.67	42.54	20.83	65.71	65.98	53.24	77.93
	0.56	66.89	56.98	76.74	34.59	13.79	58.33	73.99	64.71	84.03
	0.57	70.91	62.21	79.65	27.69	10.00	50.00	80.06	71.32	88.19
	0.58	73.62	65.70	81.98	22.37	6.45	43.75	84.60	76.26	92.20
	0.60	76.55	69.77	83.14	14.63	0.00	33.33	90.57	83.46	96.58
COVER + LOCS + ELAPSED	0.50	25.32	19.77	31.98	91.41	78.12	100.00	10.31	4.90	17.99
	0.53	47.04	37.79	56.40	63.66	43.75	83.33	42.84	31.39	54.61
	0.55	60.61	51.16	70.93	44.14	24.24	67.74	64.19	54.48	74.83
	0.56	65.59	56.40	75.58	37.33	16.67	62.50	71.70	62.22	81.38
	0.57	69.44	61.05	78.49	30.38	12.12	55.88	77.75	68.66	86.21
	0.58	72.28	63.95	81.40	25.22	8.00	50.00	82.34	74.10	90.28
	0.60	75.99	68.60	83.14	16.90	3.23	35.29	89.19	82.96	94.93

complexity did not improve overall accuracy (see Table 3). Using all cluster data ($N = 246$), the top composite model was: $\text{kill site} = -0.78 + 0.02 \times \text{LOCS} - 0.37 \times \text{ELAPSED}$.

Discussion

We were able to identify bobcat cluster locations which included kill sites of white-tailed deer. Using our top model with a cut-off value of 0.56, we could have detected a twofold increase in white-tailed deer kill sites and reduced total search effort by half compared to searching cluster sites at random. Similar to other studies (Webb et al. 2008, Knopff et al. 2009), the effectiveness of our model algorithm increased efficiency of identifying kill sites of large prey. Previous models for other carnivores suggest reduced success in identifying kill sites of small prey (Knopff et al. 2009). For example, estimates of the

number of prey < 8 kg killed by cougars are probably biased low relative to estimates of the number of larger prey killed using GPS cluster techniques (Knopff et al. 2009). Because we were interested in identifying bobcat predation of white-tailed deer, our model would be an improvement for future studies, eliminating most non-kill sites and predicting 34% of white-tailed deer kill sites.

Our models were less successful in predicting kill sites than studies of larger carnivores (Sand et al. 2005, Webb et al. 2008, Knopff et al. 2009). We attributed this in part to the typically smaller prey (i.e. fawns < 5 kg) identified in our study. Smaller-bodied prey take less time to consume and typically result in less evidence at kill sites (Knopff et al. 2009), making positive identification more difficult. Predators can also move smaller-bodied prey to avoid disturbance by humans (Sand et al. 2005, Zimmerman et al. 2007) or competing carnivores (Knopff et al. 2009, Ruth et al. 2010), further reducing the ability

to detect kill sites. Bobcats often cache prey (Anderson & Lovallo 2003) which might reduce kill site identification, particularly regarding small prey that is easier to conceal. Finally, differences in handling time between comparatively smaller-bodied prey in our study and larger prey in other studies (e.g. moose *Alces alces*; Knopff et al. 2010 and elk *Cervus elaphus*; Anderson & Lindzey 2003) may partially explain our lower detection rates.

Odds of detecting a kill site increased with the number of locations forming a cluster. We did not locate kill sites at clusters with < 11 locations and most (71%) kill sites exceeded 50 locations, likely a result of longer handling times associated with solitary predators (Knopff et al. 2010, Merrill et al. 2010). An increase in time spent at a kill site may result in additional evidence left by the predator at the predation location (e.g. increased tracks and scat or disturbed vegetation) facilitating kill site identification. We documented rest sites at kill sites, which would increase the number of locations in clusters. This is consistent with Kirby et al. (2010) who suggested that areas used for bobcat foraging were also suitable loafing areas.

We did not expect deer kill sites to be more likely to occur at clusters initiated during the day. Bobcat activity is not typically diurnal (Hall & Newsom 1978, Anderson & Lovallo 2003) although they may alter activity to coincide with periods of the greatest prey activity (Buie et al. 1979). However, white-tailed deer fawns are typically more active during the day and likely more vulnerable to predation during this time when does are feeding away from fawns (Halls 1984). Thus, bobcats may have altered their foraging activity to coincide with peak activity and vulnerability of deer fawns.

As expected, we found that increasing time from cluster formation to investigation decreased the odds of detecting a kill site. Increased time before cluster investigation increases the likelihood of prey being entirely consumed or scavenged by other predators (e.g. DeVault et al. 2011). In addition, increased time allows for carcass degradation by insects or microbes (DeVault et al. 2004, Burkepile et al. 2006), reducing the ability to distinguish prey that was killed vs scavenged. Maximum time from cluster formation to investigation in our study was 24.6 days. However, no kill sites were detected at clusters investigated > 13.2 days after cluster formation and most (82%) kill sites were detected < 7 days after cluster formation. In contrast, maximum times between cluster formation and investigation in previous studies of large

carnivores ranged from 45-671 days (Webb et al. 2006, Knopff et al. 2009, Ruth et al. 2010, Tambling et al. 2010). We recognize that remains of prey, particularly in dry climates, may be detectable for longer periods. However, caution must be exercised when classifying prey remains as kills. If study objectives require differentiating predation from scavenging events or determining predation rates among sympatric carnivore species, we recommend searching clusters as soon as practical after formation (see also Ruth et al. 2010).

An important consideration in determining the predictive success of our model is the appropriate selection of the probability cut-off value used to distinguish kills from non-kills (see Table 3). The probability cut-off value is commonly set at 0.5 (e.g. Zimmerman et al. 2007) which may have some statistical benefits (Hosmer & Lemeshow 2000). However, if the primary objective of the model is prediction, determining the cut-off value using sensitivity-selectivity analysis is recommended (Hosmer & Lemeshow 2000). Similar to Zimmerman et al. (2007) and Knopff et al. (2009), applying only a 0.5 cut-off value would have resulted in us concluding that our model had little predictive benefit. Applying this model would have unnecessarily inflated the number of false positives (i.e. overestimated the number of clusters classified as kill sites) and reduced the model's ability to reduce field effort and improve overall efficacy. We selected the cut-off value that provided the optimal output between sensitivity and specificity for detecting white-tailed deer kill sites. An appropriate cut-off value should be selected and evaluated for each intended application of the logistic model (Knopff et al. 2009).

We identified factors that can improve researchers' ability to detect bobcat kill sites before field investigation, and thereby reduce the overall field effort. When using cluster data to identify bobcat kill sites of white-tailed deer, we recommend investigating clusters when predator presence exceeds 50 locations. Further, we suggest that researchers should investigate clusters as soon as practical after cluster formation, if possible within seven days following cluster initiation. When applying this approach to other study areas, we recommend that researchers select a random sample of identified kill sites and evaluate the ability of the model to identify these kill sites. We further recommend refitting our top model using this data and reevaluating the ability of the model to correctly distinguish between kill sites and non-kill sites.

To further improve model performance, we recommend that future research investigate the use of other model parameters that may improve the model's predictive success (e.g. site fidelity and number of days/nights at cluster). Site fidelity is an important factor when investigating predation events of solitary predators (Knopff et al. 2009), presumably due to longer handling times and a tendency to revisit kill sites (Merrill et al. 2010). Anderson & Lindzey (2003) found that the number of nights a cougar spends at a cluster is important when identifying predation sites, and suggest that this parameter is useful when investigating predation of nocturnal predators. Researchers should also consider including model parameters such as age and sex as these have been suggested to influence prey selection (Ross & Jalkotzy 1996, Anderson & Lindzey 2003) and predatory behaviour (Anderson & Lindzey 2003, Knopff et al. 2009). Researchers developing and applying location-based models to identify kill sites must recognize that variability in factors influencing predator behaviour are likely species- and system-specific.

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References

- Akenon, J.J., Nowak, M.C., Henjum, M.G. & Witmer, G.W. 2003: Characteristics of mountain lion bed, cache and kill sites in northeastern Oregon. - In: Becker, S., Bjornlie, D., Linzey, F. & Moody, D. (Eds.); Proceedings of the Seventh Mountain Lion Workshop. Wyoming Game and Fish Department, Lander, Wyoming, USA. pp. 111-118.
- Anderson, C.R., Jr. & Lindzey, F.G. 2003: Estimating cougar predation rates from GPS location clusters. - *Journal of Wildlife Management* 67: 307-316.
- Anderson, E.M. & Lovallo, M.J. 2003: Bobcat and lynx. - In: Feldhamer, G.A., Thompson, B.C. & Chapman, J.A. (Eds.); *Wild Mammals of North America: biology, management, and conservation*. The Johns Hopkins University Press, Baltimore, Maryland, USA, pp. 758-786.
- Arjo, W.M., Pletscher, D.H. & Ream, R.R. 2002: Dietary overlap between wolves and coyotes in northwestern Montana. - *Journal of Mammalogy* 83: 754-766.
- Bissett, C. & Bernard, R.T.F. 2007: Habitat selection and feeding ecology of the cheetah (*Acinonyx jubatus*) in the thicket vegetation: is the cheetah a savanna specialist? - *Journal of Zoology (London)* 271: 310-317.
- Buie, D.E., Fendley, T.T. & McNab, H. 1979: Fall and winter home ranges of adult bobcats on the Savannah River Plant, South Carolina. - In: Escherich, P.C. & Blum, L. (Eds.); *Proceedings of the 1979 bobcat research conference*. National Wildlife Federation, Washington D.C., USA. Scientific Technical Series 6: 42-46.
- Burkpile, D.E., Parker, J.D., Woodson, C.B., Mills, H.J., Kubanek, J., Sobecky, P.A. & Hay, M.E. 2006: Chemically mediated competition between microbes and animals: Microbes as consumers in food webs. - *Ecology* 87: 2821-2831.
- Burnham, K.P. & Anderson, D.R. 2002: Model selection and multimodel inference: a practical information-theoretic approach. - Springer, New York, New York, USA, 496 pp.
- Cavalcanti, S.M.C. & Gese, E.M. 2010: Kill rates and predation patterns of jaguars (*Panthera onca*) in the southern Pantanal, Brazil. - *Journal of Mammalogy* 91: 722-736.
- Crowe, D.M. 1972: The presence of annuli in bobcat tooth cementum layers. - *Journal of Wildlife Management* 36: 1330-1332.
- Demma, D.J., Barber-Meyer, S.M. & Mech, L.D. 2007: Testing global positioning system telemetry to study wolf predation on deer fawns. - *Journal of Wildlife Management* 71: 2767-2775.
- DeVault, T.L., Brisbin, I.L. & Rhodes, O.E., Jr. 2004: Factors influencing the acquisition of rodent carrion by vertebrate scavengers and decomposers. - *Canadian Journal of Zoology* 82: 502-509.
- DeVault, T.L., Olson, Z.H., Beasley, J.C. & Rhodes, O.E., Jr. 2011: Mesopredators dominate competition for carrion in an agricultural landscape. - *Basic and Applied Ecology* 12: 268-274.
- Hall, H.T. & Newsom, J.D. 1978: Summer home ranges and movement of bobcats in bottomland hardwoods of southern Louisiana. - *Proceedings of the Annual Conference of the Southeastern Associations of Fish and Wildlife Agencies* 30: 427-436.
- Halls, L.K. 1984: White-tailed deer: ecology and management. - Wildlife Management Institute, Washington D.C., USA, 870 pp.
- Hosmer, D.W. & Lemenshow, S. 2000: Applied logistic regression. - John Wiley & Sons, New York, New York, USA, 373 pp.
- Kirby, J.D., Rutledge, J.C., Jones, I.G., Conner, M.L. & Warren, R.J. 2010: Effects of time of day and activity status

- on bobcat (*Lynx rufus*) cover-type selection in southwestern Georgia. - *Southeastern Naturalist* 9: 317-326.
- Knopff, K.H., Knopff, A.A., Kortello, A. & Boyce, M.S. 2010: Cougar kill rate and prey composition in a multiprey system. - *Journal of Wildlife Management* 74: 1435-1447.
- Knopff, K.H., Knopff, A.A., Warren, M.B. & Boyce, M.S. 2009: Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. - *Journal of Wildlife Management* 73: 586-597.
- Kreeger, T.J. 1999: Handbook of wildlife chemical immobilization. 3rd edition. - Wildlife Pharmaceuticals, Fort Collins, Colorado, USA, 342 pp.
- Labisky, R.F. & Boulay, M.C. 1998: Behavior of bobcats preying on white-tailed deer in the Everglades. - *The American Midland Naturalist* 139: 275-281.
- Leopold, B.D. & Krausman, P.R. 1986: Diets of 3 predators in Big Bend National Park. - *Journal of Wildlife Management* 50: 290-295.
- Martin, Q., Horsnell, W.G.C., Titus, W., Rautenbach, T. & Harris, S. 2011: Diet determination of the Cape Mountain leopards using global positioning system location clusters and scat analysis. - *Journal of Zoology (London)* 283: 81-87.
- Merrill, E., Sand, H., Zimmerman, B., McPhee, H., Webb, N., Hebblewhite, M., Wabakken, P. & Frair, J.L. 2010: Building a mechanistic understanding of predation with GPS-based movement data. - *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 2279-2288.
- Merrill, S.B. & Mech, D.L. 2003: The usefulness of GPS telemetry to study wolf circadian and social activity. - *Wildlife Society Bulletin* 31: 947-960.
- National Oceanic and Atmospheric Administration 2010: National Climatic Data Center monthly data for Escanaba, Michigan. - Available at: <http://www.ncdc.noaa.gov/oa/ncdc.html> (Last accessed on 4 August 2011).
- Odden, J., Linnell, J.D.C. & Andersen, R. 2006: Diet of Eurasian lynx, *Lynx lynx*, in the boreal forest of south-eastern Norway: the relative importance of livestock and hares at low roe deer density. - *European Journal of Wildlife Research* 52: 237-244.
- Olson, L.E., Squires, J.R., DeCesare, N.J. & Kolbe, J.A. 2011: Den use and activity patterns in female Canada lynx in the northern Rocky Mountains. - *Northwest Science* 85: 455-462.
- Podgorski, T., Schmidt, K., Kowalczyk, R. & Gulczynska, A. 2008: Microhabitat selection by Eurasian lynx and its implications for species conservation. - *Acta Theriologica* 53: 97-110.
- Powell, R.A. & Proulx, G. 2003: Trapping and marking terrestrial mammals for research: integrating ethics, performance criteria, techniques, and common sense. - *ILAR Journal* 44: 259-276.
- R Development Core Team 2010: R: A language and environment for statistical computing. - R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.r-project.org> (Last accessed on 6 October 2011).
- Ross, P.I. & Jalkotzy, M.G. 1996: Cougar predation on moose in southwestern Alberta. - *Alces* 32: 1-8.
- Ruth, T.K., Buotte, P.C. & Quigley, H.B. 2010: Comparing ground telemetry and global positioning system methods to determine cougar kill rates. - *Journal of Wildlife Management* 74: 1122-1133.
- Sand, H., Zimmerman, B., Wabakken, P., Andr  n, H. & Pedersen, J.C. 2005: Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. - *Wildlife Society Bulletin* 33: 914-925.
- Shastri, Y. & Diwekar, U. 2006: Sustainable ecosystem management using optimal control theory: Part 2 (stochastic systems). - *Journal of Theoretical Biology* 241: 522-532.
- Stricker, H.K., Belant, J.L., Beyer, D.E., Jr., Kanefsky, J., Scribner, K.T., Etter, D.E. & Fierke, J. 2012: Use of modified snares to estimate bobcat abundance. - *Wildlife Society Bulletin* 36: 257-263.
- Tambling, C.J., Cameron, E.Z., du Toit, J.T. & Getz, W.M. 2010: Methods for locating African lion kills using global positioning system movement data. - *Journal of Wildlife Management* 74: 549-556.
- Webb, N.F., Hebblewhite, M. & Merrill, E.H. 2008: Statistical methods for identifying wolf kill sites using global positioning system locations. - *Journal of Wildlife Management* 72: 798-807.
- Zar, J.H. 1999: Biostatistical analysis. 4th edition. - Prentice-Hall, Englewood Cliffs, New Jersey, USA, 564 pp.
- Zimmerman, B., Wabakken, P., Sand, H., Pederson, H.C. & Liberg, O. 2007: Wolf movement patterns: a key to estimation of kill rate? - *Journal of Wildlife Management* 71: 1177-1182.