

Efficacy of GPS cluster analysis for predicting carnivory sites of a wide-ranging omnivore: the American black bear

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Abstract. The capacity to describe and quantify predation by large carnivores expanded considerably with the advent of GPS technology. Analyzing clusters of GPS locations formed by carnivores facilitates the detection of predation events by identifying characteristics which distinguish predation sites. We present a performance assessment of GPS cluster analysis as applied to the predation and scavenging of an omnivore, the American black bear (*Ursus americanus*), on ungulate prey and carrion. Through field investigations of 6854 GPS locations from 24 individual bears, we identified 54 sites where black bears formed a cluster of locations while predating or scavenging elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), or cattle (*Bos* spp.). We developed models for three data sets to predict whether a GPS cluster was formed at a carnivory site vs. a non-carnivory site (e.g., bed sites or non-ungulate foraging sites). Two full-season data sets contained GPS locations logged at either 3-h or 30-min intervals from April to November, and a third data set contained 30-min interval data from April through July corresponding to the calving period for elk. Longer fix intervals resulted in the detection of fewer carnivory sites. Clusters were more likely to be carnivory sites if they occurred in open or edge habitats, if they occurred in the early season, if the mean distance between all pairs of GPS locations within the cluster was less, and if the cluster endured for a longer period of time. Clusters were less likely to be carnivory sites if they were initiated in the morning or night compared to the day. The top models for each data set performed well and successfully predicted 71–96% of field-verified carnivory events, 55–75% of non-carnivory events, and 58–76% of clusters overall. Refinement of this method will benefit from further application across species and ecological systems.

Key words: black bear carnivory; GPS location cluster; kill site; predator–prey interactions; prey composition; telemetry; ungulate; *Ursus americanus*.

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INTRODUCTION

In-depth knowledge of predator–prey dynamics has been limited due to a paucity of suitable methods for identifying predation events.

Although cause-specific mortality studies of prey species can quantify the impact carnivores have on prey populations (e.g., Ballard et al. 2001), inferences about carnivore behavior and ecology including predation rates, carnivore diet

composition, and individual variation or variation across demographic classes are limited by this method. Recently, the analysis of carnivore movements via location data from GPS collars has provided a novel approach to predation research. Analysis of spatiotemporal clustering of carnivore GPS locations enables remote identification of predation events by selecting characteristics of clusters that distinguish predation clusters from non-predation clusters including metrics of time spent at the site, movement within the site, or habitat characteristics at the site among others. First developed by Anderson and Lindzey (2003), GPS cluster analysis has been used to identify predation events from obligate carnivores including cougars (*Puma concolor*, Anderson and Lindzey 2003, Knopff et al. 2009, Ruth et al. 2010, Elbroch and Wittmer 2013), wolves (*Canis lupus*, Sand et al. 2005, Franke et al. 2006, Demma et al. 2007, Webb et al. 2008, Lake et al. 2013), lions (*Panthera leo*, Tambling et al. 2010), leopards (*Panthera pardus*, Martins et al. 2010, Pitman et al. 2012), jaguars (*Panthera onca*, Cavalcanti and Gese 2010), Eurasian lynx (*Lynx lynx*, Mattisson et al. 2011, Krofel et al. 2013), and bobcats (*Lynx rufus*, Svoboda et al. 2013).

Cluster analysis has been validated when compared to several traditional methods of investigating predation. Tracking predator movements via VHF radiotelemetry resulted in an underestimation of kill rates compared to cluster analysis (Ruth et al. 2010). Cluster analysis detected 100% of predation events identified via snow-tracking (Knopff et al. 2009) and provides an opportunity to monitor predation year round without limitations due to snow conditions. While smaller prey items were underestimated by cluster analysis compared to scat analysis, both methods resulted in nearly equivalent prey composition in large carnivore diets due to the low biomass from small prey in predator diets and high success in locating large prey with GPS clusters (Martins et al. 2010, Bacon et al. 2011, Pitman et al. 2013). Tracking predation with movement data from GPS collars has the advantage of providing continuous data year round across wide-ranging habitats and affords opportunities to collect more detailed information on prey characteristics (e.g., species, sex, age, and condition) and monitoring individual variation in predatory behavior of carnivores.

Cluster models developed for one species may not be directly applicable to other species due to variable movement patterns and feeding behavior among carnivore species (Webb et al. 2008). Predator and prey body size impact how long a carnivore spends at a predation site, while dietary plasticity in facultative carnivores can affect how often clusters are formed at non-carnivorous feeding sites. Furthermore, prey density and availability, availability of non-prey food sources (e.g., vegetation, mast), and competition with other carnivores may affect applicability of cluster models across populations within a species. Therefore, the utility of this method needs strengthening by continued refinement through application in a variety of predator-prey systems.

The first application of cluster analysis to a facultative carnivore investigated grizzly bear (*Ursus arctos*) predation of moose calves (Rauset et al. 2012). This was followed by two more general (i.e., varying ungulate species and ages) applications to grizzly bear consumption of ungulates (Cristescu et al. 2015, Ebinger et al. 2016). As of yet, the accuracy of cluster analysis has not been assessed for predicting predation and scavenging (hereafter collectively referred to as carnivory) events by American black bears (*Ursus americanus*). As omnivores, black bears exhibit movement patterns and feeding behaviors that provide an interesting challenge for the application of cluster analysis to this species. Movements associated with scavenging behavior as well as cluster formation at non-carnivorous feeding sites may lead to less distinguishable clustering of GPS locations than those of obligate carnivores. Black bear predation is an important proximate cause of ungulate neonate mortality (e.g., Zager and Beecham 2006, White et al. 2010, Yarkovich et al. 2011), and scavenging by black bears can impact cougar kill rates (Elbroch et al. 2015) and access to carrion by other scavengers (Allen et al. 2014). However, rigorous methods of quantifying black bear carnivory are lacking. Few studies have quantified black bear carnivory of ungulates through monitoring of black bear movements and behavior (Ballard 1992, Fortin et al. 2013a), which could provide a more complete assessment of the impacts of carnivory on black bears, prey species, and competing carnivore population dynamics.



Fig. 1. Core study area in the southwest Jemez Mountains, New Mexico, where GPS location clusters formed by black bears were field-investigated to assess performance of GPS cluster analysis in predicting carnivory events, 2012–2014.

Thus, our objective was to test whether ungulate (i.e., elk, *Cervus elaphus*, mule deer, *Odocoileus hemionus*, and cattle, *Bos* spp.) carnivory events can be accurately predicted based on the characteristics of black bear GPS location clusters and to develop a model that maximizes detectability of carnivory events. We identified a cluster definition that maximizes efficiency of field investigations and selected a fix interval for GPS collar data collection that maximizes efficiency of battery life for GPS collars. By determining the accuracy of GPS cluster analysis in predicting black bear carnivory events, we provide a basis for improving techniques for assessing trophic

relationships of omnivorous species and contribute to broader understanding of black bear ecology and interrelationships with ungulates.

Study area

The southwest Jemez Mountains, located in north-central New Mexico's Rio Arriba and Sandoval counties, lie within the southernmost boundary of the Southern Rockies Ecoregion. The core study area of approximately 85,000 ha (Fig. 1) centered around the town of Jemez Springs (35°46' N, 106°41' W) and comprised the Valles Caldera National Preserve (VCNP) and Santa Fe National Forest (SFNF), with a small

portion (<10%) of private, Pueblo of Jemez, and New Mexico State Trust lands. Elevations ranged from 1670 to 3431 m with steep canyons and mesas descending from a volcanic caldera that encompassed montane grassland valleys and forested resurgent domes. Vegetation communities transitioned with increasing elevation from pinyon–juniper woodlands (*Pinus edulis* and *Juniperus* spp.) and ponderosa pine (*Pinus ponderosa*) forests to spruce (*Picea* spp.) and fir (*Pseudotsuga* spp.) forests interspersed with aspen (*Populus tremuloides*) stands. With a semi-arid continental climate, the mean daily temperature in January was -2°C and in July was 18°C in Jemez Springs (Western Regional Climate Center, 2012–2014), with variation across elevations. Annual precipitation averaged 642 mm (SD = 72.6; VCNP Valle Grande meteorological station, elevation 2644 m, 2003–2011), with the majority falling in heavy summer rainstorms and winter snowstorms.

Large mammals in the study area included elk, mule deer, black bears, and cougars. Common black bear vegetative food sources comprised acorns (*Quercus gambelii*), piñon nuts, juniper berries, currants and gooseberries (*Ribes* spp.), prickly pear (*Opuntia* spp.), and abundant graminoids. Social insects (e.g., ants, *formicidae*) and abundant small mammal species provided additional food sources.

METHODS

Animal capture and handling

Between June 2012 and July 2014, we captured black bears using baited culvert traps or leg snares. We administered 4.4 mg/kg ketamine and 2 mg/kg xylazine to chemically immobilize bears for processing. We fitted each adult black bear with a GPS collar (Advanced Telemetry Systems G2110E Iridium/GPS location collar, Isanti, Minnesota, USA or Northstar NSG-LD2 GPS collar with Globalstar Satellite Tracking System, King George, Virginia, USA) programmed to record locations at either 3-h or 30-min intervals and to transmit location data via satellite every 48 h between 1 April and 30 November each year. Following processing, we administered either 0.15 mg/kg yohimbine or 2 mg/kg tolazoline as an antagonist. All capture and handling procedures followed acceptable methods (Sikes

et al. 2016) and were approved by the New Mexico State University Institutional Animal Care and Use Committee (Protocol #2011-038).

Cluster identification and selection for field investigation

Based on earlier work by Knopff et al. (2009) and Svoboda et al. (2013), we developed a rule-based algorithm which relied on spatial and temporal restrictions to identify clusters of point locations within the GPS collar data using Program R (version 3.1.2; R Core Team 2015; Appendix S1). Our algorithm checked each GPS location against only the locations that occurred within the defined time period (i.e., 12 h or 24 h) to determine whether any of those locations occurred within the defined distance (i.e., 30, 50, 100, or 200 m) of the given location. If two locations fell within the time and distance criteria, those locations were assigned a cluster identification number. Rather than identifying a geometric center to be adjusted as each new location is added to a cluster and then adding locations to the cluster if they occur within the designated time and distance criteria, our algorithm added locations to a cluster if a location fell within the designated time and distance constraints of any location within a cluster. In order to test a range of definitions for applicability to black bear carnivory of elk, mule deer, and livestock, we applied a broad cluster definition to GPS locations to guide field investigation. This definition joined any ≥ 2 locations that occurred within 200 m or 100 m of each other into a cluster for 3-h and 30-min collar data, respectively, and excluded locations recorded outside the time constraint from the core cluster locations (Anderson and Lindzey 2003, Knopff et al. 2009, Rauset et al. 2012).

Field investigation of clusters

During field investigations, we used a handheld GPS unit to locate each cluster. We searched for evidence of carnivory by walking concentric transects 5 m apart up to a 30 m radius around each GPS location (Rauset et al. 2012) that composed each cluster. Ungulate carcass remains with matted or trampled feeding areas indicated a carnivory event, which could include either predated or scavenged ungulates. When sufficient evidence was present, we identified the

species, age, and sex of ungulate prey and carrion based on morphological measurements, hair samples, and tooth condition (Moore et al. 1974, Heffelfinger 2010). Scat containing ungulate remains was not considered sufficient evidence to classify a cluster as a carnivory event. We investigated clusters within 2 weeks of cluster formation (up to 1 month if the bear was active in the area for an extended period of time). We investigated clusters after cessation of bear activity at the site for researcher safety and to minimize disturbance which could impact the distribution of GPS locations within the cluster. A subsample of clusters was searched while the sites were still in use when field personnel were available to increase crew size to ≥ 2 .

Cluster definition and fix interval

For analysis, we utilized data downloaded directly from retrieved collars when available rather than data received via satellite transmission to increase the number of successful location fixes available in the data. All analyses were performed in the R programming language (R Core Team 2015; Appendix S2). To determine how locations were to be grouped into clusters for analysis, we evaluated a range of cluster definitions and fix intervals for greatest efficiency. The most efficient fix interval was one that maximized the likelihood of cluster formation at an ungulate carnivory site while maximizing battery life. The most efficient cluster definition was one that maximized the likelihood of cluster formation at an ungulate carnivory site while creating the fewest clusters to minimize wasted search effort. To determine which fix interval and cluster definition best met these objectives, we subsampled the 30-min fix interval data into 30 min, 1, 2, and 3 h (combined with 3-h collar data) fix intervals. We used the cluster detection algorithm to group locations into clusters using eight cluster definitions (i.e., each combination of spatial restrictions of 30, 50, 100, and 200 m and temporal restrictions of 12 and 24 h between any given location and at least one other location in the cluster). Each resulting data set was associated with one of the eight cluster definitions and contained all GPS locations from all study animals within the monitoring period (1 April to 30 November each year), including both field-investigated and non-investigated locations. All

locations that occurred within 30 m (the maximum search radius) of an ungulate carcass were marked so that any cluster that contained a marked location was considered an ungulate carnivory cluster.

For each data set, we then summarized the number of ungulate carcasses included in at least one cluster (to account for how often carcasses were lost if a definition was too broad to form a cluster at each carcass), the number of field-investigated carnivory clusters (to account for duplicate clusters forming at a single carcass), the total number of clusters formed, and the proportion of all locations that were isolated from clusters. We selected the longest fix interval (maximized battery life) from the subsampled 30-min collar data that retained enough locations to form clusters at all of the field-investigated ungulate carnivory sites. Using this fix interval for the 30-min collar data and the 3-h fix interval for combined data from the 30-min and 3-h collars, we then determined which definitions (one for each of the two data sets) met the following criteria: (1) maximized the number of field-investigated ungulate carnivory events where clusters were formed, (2) minimized the number of ungulate carnivory events where multiple clusters formed at a single event, (3) maximized the number of isolated locations (i.e., not grouped into clusters), and (4) minimized the number of clusters formed.

Model development

We developed cluster analysis models for each of three data sets after applying the selected fix intervals and cluster definitions. The first data set included locations from all study animals, but only including GPS locations that occurred at 3-h fix intervals (hereafter, 3-h interval data). The second data set included locations only from animals fitted with collars with a 30-min fix interval (hereafter, 30-min interval data). These 30-min interval data were included to account for carnivory of ungulate neonates that might be consumed in < 3 h. The final data set was a subset of the 30-min interval data, truncated to May–July of each year and including only elk calf carnivory events (hereafter, calving season data). This data set was intended to refine a cluster model that specifically identified black bear carnivory events targeting elk calves.

We performed mixed-effects logistic regression to model the probability of an ungulate carnivory event for each GPS cluster in each data set as a function of seven possible predictor variables (Table 1). The predictors Fixes (Knopff et al. 2009) and Duration (Anderson and Lindzey 2003, Tambling et al. 2010) were calculated as either the number of GPS fixes (corrected for the fix success rate) or total time duration of the cluster. Spread is an index for how much movement occurred within the cluster, calculated as the mean distance between every possible pair of locations within the cluster. Travel away from and returning to the cluster was measured by Fidelity (Knopff et al. 2009). The time of day a cluster began was indicated by Initiation (modification of Ruth et al. 2010, Rauset et al. 2012, and Svoboda et al. 2013), grouped into four activity periods: morning, day, evening, and night based on results from Lewis and Rachlow (2011) and adjusted for local photoperiod. Habitat type and Season indicate where and when the cluster was formed; Season was excluded as a covariate in the calving season data models.

Individual black bears were the experimental units so Bear ID served as a random factor within which clusters were nested. Hereafter, a field-investigated cluster of GPS locations will be referred to as an observation, an observation where an ungulate carnivory event occurred will be an event, and an observation where no ungulate carnivory occurred will be a non-event. We assigned each event one of four prey classes (elk calf, adult mule deer, adult elk, or cattle) to determine whether multinomial logistic regression could be used to estimate prey and carrion composition in black bear diets; however, models failed to converge due to small sample sizes within some of the ungulate classifications. Consequently, we conducted a logistic regression with observations simply classified as events vs. non-events.

We screened for collinearity among predictor variables by calculating variance inflation factors (VIF, Fox and Monette 1992) to identify highly related variables, which we avoided including in the same model. We included a model in the top model set if all variables in the model were significant ($P < 0.1$). To identify these models for each data set, we ran a logistic regression (Bates 2010) first on the global model that included all variables then removed the least significant variable,

Table 1. Descriptions of logistic regression model covariates assessed for significance in predicting back bear carnivory events from GPS location clusters in the Jemez Mountains, New Mexico, 2012–2014.

Covariate	Description
Duration	Total time span (h) of the cluster: $Time_{(last\ GPS\ fix)} - Time_{(first\ GPS\ fix)}$
Fixes	Number of GPS locations (i.e., GPS fixes) in the cluster, corrected for variation in GPS fix success: $Number\ of\ GPS\ fixes\ in\ the\ cluster / proportion\ of\ successful\ GPS\ fixes\ within\ the\ duration\ of\ the\ cluster$
Spread	Mean of distances (m) among every possible pair of GPS fixes within the cluster
Fidelity	Proportion of the duration that a bear spent at the cluster vs away from the cluster: $(Number\ of\ GPS\ fixes\ in\ the\ cluster - Number\ of\ GPS\ fixes\ away\ from\ the\ cluster\ within\ the\ cluster\ duration) / Total\ number\ of\ GPS\ fixes\ within\ the\ duration\ of\ the\ cluster$
Initiation	Time of day of first GPS fix in the cluster, classed into four activity periods: morning and evening active periods (400–930 and 1700–2230 h) and day and night inactive periods (1000–1630 and 2300–330 h)
Habitat	Habitat structure: Cover (shrub or tree canopy) and Open (edge habitats, open meadow, and human development)
Season	Early (April–July) and Late (August–November)
Bear ID	Individual black bear (experimental unit)

repeating the process until all variables in the model presented P -values of < 0.1 (Hosmer and Lemeshow 2000). Rotating through excluding the various subsets of variables involved in a multicollinearity gave rise to multiple possible models which became our top model set. We identified the best model for each data set out of the top model set based on its ability to predict events, as assessed by generalized cross-validation. We did not use an information theoretic approach because our goal was to predict ungulate carnivory events rather than testing a set of a priori hypotheses; therefore, we focused our model selection approach on the predictive performance of the models. By performing a generalized cross-validation on each logistic regression in the top model sets, we obtained a probability estimate for whether each observation was an event. Rather than excluding data during model development and then using the withheld data for model validation, k -fold cross-validation divides the data into k partitions, using one of the partitions for the test data and the remaining $k - 1$ partitions as

the training data set. It then rotates through each of the k partitions using each partition, in turn, as the test data set. Hence, all k subsets of the data are eventually used in model development and assessment (Knopff et al. 2009). Generalized cross-validation is the extreme of this where every observation is cycled through as an individual test data set, using the remaining $n - 1$ observations as the training data set. This can be useful given the small sample numbers of observations classified as events.

The cutoff point of the probability value ($\hat{\pi}$) at which an observation is predicted to be an event or non-event can be set arbitrarily and can impact the prediction performance of the model (Hosmer and Lemeshow 2000). The probability threshold that returns the highest correct classification rate for all observations (i.e., overall correct classification rate) may not be the best probability threshold for correct classification of events (e.g., Svoboda et al. 2013), particularly where a data set contains considerably more non-events than events. To investigate probability thresholds for prediction that would give improved classification rates for events while limiting degradation of the overall correct classification rate, we calculated sensitivity (correct classification rate of events) and specificity (correct classification rate of non-events) for each model using each probability value output during cross-validation as the probability threshold. We then selected the probability threshold that maximized the sum of sensitivity and specificity (i.e., combined correct classification rate) for each model. The combined correct classification rate is not a true rate (may be >1) but gives equal weight to both sensitivity and specificity, as opposed to the overall correct classification rate which is heavily influenced by the proportion of non-events to events. We selected the best model from each top model set by its ability to accurately predict events when using the probability threshold that maximizes combined correct classification rate. By maximizing sensitivity this way, we minimized the false-negative rate, thereby reducing the risk of incorrectly classifying events as non-events.

RESULTS

We included data from 24 collared individuals (9 F, 15 M) for analysis, of which 18 wore collars

with a 3-h fix interval and seven wore collars with a 30-min fix interval. One individual wore each collar type in different years due to recapture (therefore $n = 25$). Within the monitoring seasons between June 2012 and November 2014, individual bears wore active GPS collars 18–519 d ($\bar{x} = 184$, $SD = 119$), for a combined total of 50,685 locations. Average collar fix success rate was $78.5\% \pm 3.9\%$ ($\bar{x} \pm SE$, $n = 25$). Across all fix interval and cluster definitions, 35–80% of locations occurred within a cluster (Table 2). We investigated 6854 GPS locations in the field (35.7% recorded by 3-h collars, 64.3% recorded by 30-min collars) and found 56 ungulate carnivory events. Of the 24 individual black bears monitored (25 GPS collars), we found no evidence of ungulate carnivory by nine individuals (4 F, 5 M). The prey items at carnivory events were elk calves ($n = 39$), adult mule deer ($n = 7$), adult elk ($n = 6$), and cattle ($n = 4$). One mother–young of year pair of each species was identified; each of these cases was counted as one carnivory event. We censored one elk calf carnivory event from cluster analysis due to human disturbance that impacted cluster formation, and classified one elk calf carnivory event as a non-event due to evidence that the calf was killed and consumed by an uncollared bear and merely visited by the collared bear. We identified small prey (e.g., rabbits, *Sylvilagus nuttallii*, woodrats, *Neotoma cinerea*, and passerines) at 17 clusters, although these were not classified as carnivory events for cluster analysis. Clusters formed by 3-h collars indicated 30 ungulate carnivory events, and clusters formed by 30-min collars indicated 24 ungulate carnivory events.

Fix interval and cluster definition

The 3-h interval data formed clusters at ≤ 44 ungulate carnivory events (Table 2). All cluster definitions with a 12-h time restriction created duplicate clusters at carnivory events; therefore, the 24-h restriction was optimal. The smallest spatial restriction (30 m) best met the criteria to minimize wasted search effort in the field; however, this spatial restriction failed to include five ungulate carnivory events in clusters. The most efficient cluster definition for the 3-h interval data was therefore ≥ 2 locations within 50 m and within 24 h of one another. This definition created 617 clusters from

Table 2. Metrics for selecting a fix interval and cluster definition to structure the GPS location data used in cluster analysis to predict black bear carnivory in the Jemez Mountains, New Mexico, 2012–2014.

Fix interval	Cluster definition		Ungulate Carcasses (n)¶	Clusters (n)†			GPS locations‡			Bears (n)§
	Distance	Time		Events	Non-events	Total	Clustered (%)	Isolated (%)	Total (n)	
3 h	30 m	12 h	38	52	548	3082	35	65	25,087	25
		24 h	39	40	540	3145	38	62		
	50 m	12 h	42	56	606	3519	42	58		
		24 h	44	44	573	3564	45	55		
	100 m	12 h	43	57	653	4021	52	48		
		24 h	44	45	568	3930	56	44		
200 m	12 h	44	55	579	4211	64	36			
	24 h	44	45	474	3911	68	32			
2 h	30 m	12 h	15	18	171	885	38	62	7090	7
		24 h	15	15	167	901	41	59		
	50 m	12 h	15	17	175	980	46	54		
		24 h	15	15	161	973	49	51		
	100 m	12 h	17	18	170	1065	56	44		
		24 h	17	17	152	1020	60	40		
1 h	30 m	12 h	19	23	271	1610	51	49	14,749	7
		24 h	19	22	253	1593	53	47		
	50 m	12 h	20	24	259	1733	59	41		
		24 h	20	23	240	1673	61	39		
	100 m	12 h	20	24	227	1740	69	31		
		24 h	20	22	194	1613	72	28		
30 min	30 m	12 h	24	30	363	2799	62	38	30,680	7
		24 h	24	26	329	2686	64	36		
	50 m	12 h	24	29	337	2838	69	31		
		24 h	24	26	293	2650	71	29		
	100 m	12 h	24	29	280	2568	78	22		
		24 h	24	27	250	2353	80	20		

† Number of field-investigated clusters identified as Events (ungulate carnivory occurred at the cluster) or Non-Events (no evidence of ungulate carnivory at the cluster), and total number of clusters formed (includes investigated and not investigated clusters) within the monitoring period.

‡ Proportion of GPS locations that occur as part of a cluster or in isolation and total number of locations in the data set.

§ Number of black bear collars included in the data set.

¶ Number of ungulate carcasses identified during field investigations that occur within 30 m of a GPS location that is grouped in a cluster.

field-investigated GPS locations, 7.1% ($n = 44$) of which were ungulate carnivory events used in model development.

When the 30-min interval data were transformed into lower resolution fix intervals, clusters formed at fewer carnivory events. Doubling the fix interval from 30 min to 1 h resulted in the omission of 17.7% of carnivory events from clusters. Increasing the fix interval to 2 and 3 h omitted 29.2% and 41.7% of carnivory events, respectively. The 30-min fix interval was therefore retained for analysis of these data to preserve carnivory events. With this fix interval, all cluster definitions formed duplicate clusters at ungulate carnivory events. However, the 24-h time restriction minimized the number

of duplicate carnivory clusters (24 h: ≤ 2 ; 12 h: 3–6); therefore, this was the most efficient time restriction. All of the spatial restrictions formed clusters at 24 carnivory sites. The most efficient spatial restriction in terms of minimizing wasted search effort was 30 m; therefore, the cluster definition for the 30-min interval data was defined as ≥ 2 locations within 30 m and within 24 h of one another. This definition created 355 clusters, 7.3% ($n = 26$) of which were ungulate carnivory events used in model development. The calving season data were grouped into clusters according to the same fix interval and cluster definition as the 30-min interval data. These data formed 247 clusters, 7.3% ($n = 18$) of which were elk calf carnivory events.

Model performance

Duration and Fixes were the only highly collinear covariates, each with a VIF in excess of 10 in all three data sets when included in the same model. When either of these predictors was used without the other, all VIF were below 2. Due to their high correlation ($r \geq 0.8$) in all three data sets, resulting models were similar with either of these two predictors substituted for the other in the model. For each data set, we compared predictive ability of the top models to determine whether Duration or Fixes exhibited superior prediction performance.

Duration, Fixes, Habitat, Spread, Season, and Initiation were each significant predictor variables in the top model set ($P < 0.1$; Table 3). Clusters were more likely to be carnivory events if they exhibited longer duration or contained more fixes, if they occurred in open habitats, if they were in the early season, and if they exhibited reduced spread (Table 3). Clusters were less likely to be carnivory events if they were initiated in the morning or night compared to the day (Table 3). All top models included either the Duration or Fixes covariate (Table 3). Total handling times (Duration) at ungulate carnivory clusters ranged from 30 min (elk calves) to 409 h (bull elk). Despite the fact that 66% of the ungulates at carnivory events were elk calves, bears spent 181% and 100% more time overall feeding on adult ungulates than elk calves based on the 3-h and 30-min interval data sets, respectively.

Habitat was a significant predictor in all top models ($P < 0.005$, Table 3). Of the Open Habitat clusters, 18.6% and 20.3% were ungulate carnivory events, while only 4.8% and 4.2% of clusters in Cover habitat were ungulate carnivory events in the 3-h and 30-min interval data, respectively. Season was a significant predictor for both data sets in which it was included as a covariate ($P < 0.09$, Table 3). Ungulate carnivory events comprised 11.9% and 9.1% of Early Season clusters, but only 3.2% and 2.9% of Late Season clusters in the 3-h and 30-min interval data, respectively. Black bears consumed 69% of elk calves in May and June (peak calving season) and only 10% between August and November. Spread varied widely among clusters, with the mean distance between all pairs of locations in a cluster ranging from 0 to 64.5 m (0.8 to 44.5 m at events). Spread was only significant in the top

models for the 30-min data sets ($P < 0.02$, Table 3). Initiation was significant in two of the models for the 3-h interval data ($P < 0.09$). Fidelity was not a significant predictor in any models ($P > 0.1$).

Using the usual probability decision point of $\hat{\pi} = 0.5$ to predict whether an observation was an event or non-event resulted in very low overall correct classification rates (<8% for each data set, Table 4). Sensitivity improved at the expense of specificity and the overall correct classification rate when the probability threshold was adjusted to the point at which the maximum combined correct classification rate occurred for each logistic regression (Table 4, Fig. 2). For example, the maximum combined classification rate for Model A was 1.58, which occurred when any observation with a $\hat{\pi} \geq 0.0614$ was classified as an event. With this adjusted probability threshold, Model A presented 88% sensitivity and 70% specificity, with a correct classification of 70% of events and non-events combined.

Logistic regression of the 3-h interval data resulted in four top models with Habitat, Season, and either Fixes or Duration as the best predictors (Models A and B, respectively), two of which also included Initiation (Models C and D, Table 3). With the adjusted probability threshold ($\hat{\pi} = 0.0596$), Model C exhibited the best predictive ability, with highest sensitivity, highest specificity, and highest overall correct classification within this data set (Table 4). Initiation was significant in this model ($P = 0.07$ overall), with morning and night initiation periods significantly different than day ($P < 0.05$), although the evening period was not significantly different than day ($P > 0.1$, Table 3). Therefore, we retained this model as the best predictor of carnivory events for the 3-h interval data set. Compared to the next best performing model that excludes Initiation (Model A), Model C showed 5.3% higher sensitivity, 7.5% higher specificity, and 8.3% higher overall accuracy (Table 4).

There were two top models for the calving season data with Habitat, Spread, and either Fixes or Duration as the best predictors (Models I and J, respectively, Table 3). Both models predicted events with identical accuracy; however, Model I exhibited marginally superior performance in non-event prediction (4.3% higher specificity), combined accuracy (2.1% more accurate), and overall accuracy (4.0% more accurate, Table 4).

Table 3. Estimated coefficients, standard errors, *P*-values, and odds ratios with 90% confidence intervals for the top logistic regression models predicting black bear carnivory events in the Jemez Mountains, New Mexico, 2012–2014.

Data	Model	Covariate	Class	Estimate	SE	<i>P</i>	Odds ratio	90% CI		
								Upper	Lower	
3 h 50 m 24 h	A	Intercept		-2.898	0.330	0.000				
		Habitat	Open	1.198	0.405	0.003	3.314	1.705	6.441	
		Season	Late	-1.522	0.419	0.000	0.218	0.110	0.434	
		Fixes		0.086	0.020	0.000	1.090	1.054	1.127	
	B	Intercept		-2.803	0.321	0.000				
		Habitat	Open	1.157	0.407	0.005	3.179	1.631	6.198	
		Season	Late	-1.681	0.430	0.000	0.186	0.092	0.377	
	C	Duration		0.024	0.005	0.000	1.024	1.016	1.033	
		Intercept		-2.151	0.412	0.000				
		Habitat	Open	1.382	0.423	0.001	3.982	1.989	7.972	
		Season	Late	-1.615	0.431	0.000	0.199	0.098	0.403	
		Initiation	Evening	-0.708	0.505	0.161	0.493	0.215	1.127	
			Morning	-1.385	0.701	0.048	0.250	0.079	0.790	
			Night	-1.092	0.450	0.015	0.336	0.160	0.702	
		Fixes		0.084	0.021	0.000	1.087	1.050	1.126	
		D	Intercept		-2.089	0.409	0.000			
			Habitat	Open	1.322	0.424	0.002	3.751	1.870	7.523
	Season		Late	-1.767	0.440	0.000	0.171	0.083	0.352	
Initiation	Evening		-0.670	0.503	0.183	0.512	0.224	1.168		
	Morning		-1.356	0.702	0.054	0.258	0.082	0.815		
	Night		-1.028	0.451	0.023	0.358	0.171	0.749		
30 min 30 m 24 h	E	Duration		0.023	0.006	0.000	1.023	1.014	1.033	
		Intercept		-2.244	0.548	0.000				
		Habitat	Open	1.982	0.458	0.000	7.255	3.422	15.381	
		Spread		-0.090	0.034	0.007	0.914	0.865	0.966	
	F	Fixes		0.033	0.009	0.000	1.034	1.019	1.049	
		Intercept		-2.292	0.569	0.000				
		Habitat	Open	1.929	0.470	0.000	6.884	3.187	14.866	
	G	Spread		-0.086	0.033	0.009	0.918	0.870	0.968	
		Duration		0.044	0.012	0.000	1.045	1.026	1.065	
		Intercept		-1.911	0.585	0.001				
		Habitat	Open	1.846	0.460	0.000	6.336	2.980	13.474	
		Spread		-0.096	0.034	0.005	0.909	0.859	0.962	
	H	Season	Late	-1.216	0.727	0.094	0.297	0.090	0.977	
		Fixes		0.035	0.009	0.000	1.035	1.020	1.051	
		Intercept		-1.716	0.590	0.004				
		Habitat	Open	1.799	0.455	0.000	6.040	2.863	12.742	
	Calving season 30 min 30 m 24 h	I	Spread		-0.106	0.035	0.003	0.900	0.849	0.953
			Season	Late	-1.669	0.756	0.027	0.188	0.055	0.651
Duration				0.054	0.014	0.000	1.056	1.031	1.080	
J		Intercept		-1.839	0.767	0.017				
		Habitat	Open	1.696	0.543	0.002	5.450	2.236	13.286	
		Spread		-0.111	0.045	0.014	0.895	0.831	0.964	
		Fixes		0.034	0.012	0.005	1.034	1.014	1.055	
J		Intercept		-1.797	0.761	0.018				
		Habitat	Open	1.616	0.533	0.002	5.031	2.101	12.048	
		Spread		-0.102	0.044	0.020	0.903	0.840	0.971	
	Duration		0.040	0.017	0.020	1.041	1.012	1.071		

Table 4. Correct classification rates of each logistic regression model predicting black bear carnivory in the Jemez Mountains, New Mexico (2012–2014), using a probability cutoff of $\hat{\pi} = 0.5$ or an adjusted probability cutoff.

Model	$\hat{\pi} = 0.5$	Maximized combined correct classification rate (CCR)				
	Overall CCR	$\hat{\pi}$	Sensitivity (Event CCR)	Specificity (Non-event CCR)	Combined CCR	Overall CCR
A	0.0681	0.0614	0.8837	0.6981	1.5818	0.7050
B	0.0681	0.0698	0.8372	0.7452	1.5824	0.7455
C	0.0697	0.0596	0.9302	0.7504	1.6807	0.7634
D	0.0713	0.0612	0.9302	0.7435	1.6737	0.7585
E	0.0704	0.0617	0.7600	0.7356	1.4956	0.7380
F	0.0704	0.1248	0.5600	0.8511	1.4111	0.8338
G	0.0704	0.0395	0.9600	0.5532	1.5132	0.5803
H	0.0704	0.0915	0.6800	0.8328	1.5128	0.8169
I	0.0769	0.0723	0.7059	0.7467	1.4526	0.7409
J	0.0769	0.0661	0.7059	0.7162	1.4220	0.7126

For both of these data sets, predictive capacity of the models did not differ dramatically between models that included Fixes vs. models that included Duration.

Analysis of the 30-min interval data resulted in four top models, all of which included Habitat and Spread as significant predictors (Table 3). Two of the models included Season as a covariate (Models G and H with Fixes and Duration, respectively) and two excluded Season (Models E and F with Fixes and Duration, respectively, Table 3). The models that included Season as a covariate both exhibited superior prediction of events and greater combined accuracy (though lower overall accuracy) than their counterparts that excluded Season (Model E vs G and Model F vs H, Table 4). The most accurate event prediction (96.0%) was achieved by Model G (26.3% higher sensitivity than the next best model, Model E, Table 3). Overall highest accuracy occurred with Model F, marginally higher than the next best model (2.1% more accurate than Model H, Table 4). However, overall accuracy is strongly associated with prediction of non-events due to the disproportion of non-events vs. events in the sample sizes for each data set.

The models that best predicted events at the probability threshold where combined correct classification rate was maximized were Models C, G, and I. For the 3-h interval data, the best model (Model C) included the covariates Fixes, Habitat, Season, and Initiation as predictors of ungulate carnivory clusters and resulted in the following log odds regression equation ($\hat{\pi}$ = estimated probability that an observation is an event):

$$\log\left(\frac{\hat{\pi}}{1-\hat{\pi}}\right) = -2.151 + 0.084 \text{ fixes} \\ + 1.382 I_{\text{other}}(\text{Habitat}) \\ - 1.615 I_{\text{late}}(\text{Season}) \\ - 0.708 I_{\text{evening}}(\text{Initiation}) \\ - 1.385 I_{\text{morning}}(\text{Initiation}) \\ - 1.092 I_{\text{night}}(\text{Initiation}) \quad (1)$$

This model presented 93% sensitivity and 75% specificity, with an overall correct classification rate of 76% using a probability threshold of 0.0596 (Table 4). The false-negative rate was 7%, and the false-positive rate was 25%. Odds ratios for this model estimate that a cluster was 3.9 times more likely to be a carnivory site if it occurred in open or edge habitats than in closed-canopy areas, and 9% more likely with each additional GPS fix in the cluster (Table 3). A cluster was 80% less likely to be an ungulate carnivory event if it occurred in the late season, 75% less likely if it was initiated in the morning than during the day, and 76% less likely to be a carnivory event if it was initiated in the night than during the day (Table 3).

The best model for the 30-min interval data included the predictors Fixes, Habitat, Season, and Spread. This model (Model G) presented 96% sensitivity and 55% specificity, with an overall correct classification rate of 58% using a probability threshold of 0.0395 (Table 4). The false-negative rate was 4% and the false-positive rate was 45%. The log odds regression equation for Model G was as follows:

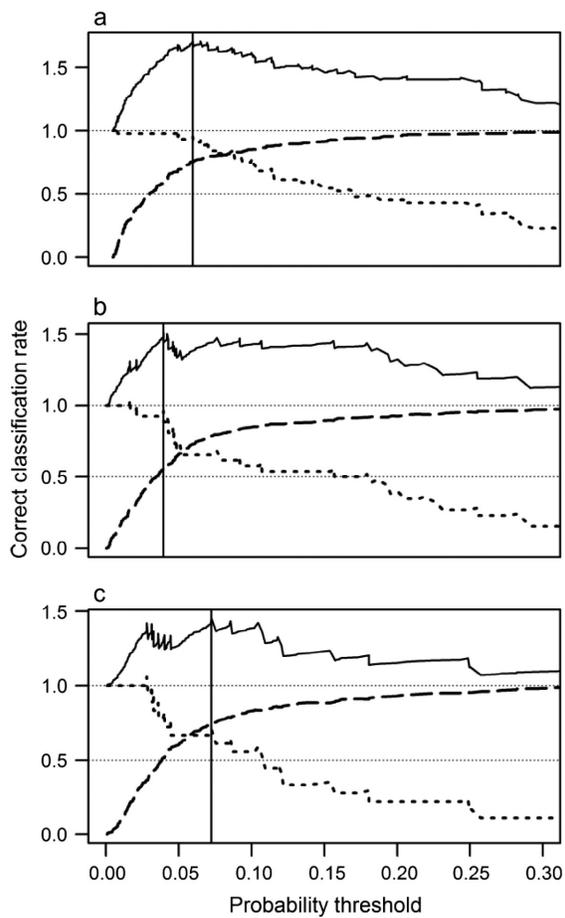


Fig. 2. Maximized combined correct classification rates for Models C (a), G (b), and I (c) predicting black bear carnivory in the Jemez Mountains, New Mexico, 2012–2014. The dotted line shows sensitivity (correct classification rate of events), the dashed line shows specificity (correct classification rate of non-events), and the solid line shows the combined correct classification rate. The vertical line occurs at the probability threshold where the combined correct classification rate is maximized.

$$\log\left(\frac{\hat{\pi}}{1-\hat{\pi}}\right) = -1.911 + 0.035 \text{ fixes} \\ + 1.846 I_{\text{other}}(\text{habitat}) \\ - 1.216 I_{\text{late}}(\text{season}) - 0.096 \text{ spread} \quad (2)$$

Odds ratios for this model estimate that a cluster was 6.3 times more likely to be a carnivory site if it occurred in open habitats. Odds of a cluster being a carnivory site increased 4% with each additional GPS fix in the cluster (Table 3).

A cluster was 9% less likely to be a carnivory event for each additional meter in the mean spread between locations within the cluster, and 70% less likely to be a carnivory event if it occurred in the late season (Table 3).

The best model for the calving season data (Model I) included the predictors Fixes, Habitat, and Spread. The log odds regression equation for Model I was as follows:

$$\log\left(\frac{\hat{\pi}}{1-\hat{\pi}}\right) = -1.839 + 0.034 \text{ fixes} \\ + 1.696 I_{\text{other}}(\text{habitat}) - 0.111 (\text{spread}) \quad (3)$$

Compared to the full-season data sets, this model exhibited poorest sensitivity (71%) but high specificity (75%) and a high overall correct classification rate of 74% using a probability threshold of 0.0723 (Table 4). The false-negative rate was 29%, and the false-positive rate was 25%. This model estimates that a cluster is 5.4 times more likely to be a carnivory site if it occurs in open habitats and 3% more likely for each additional GPS fix in the cluster (Table 3). A cluster is 11% less likely to be a carnivory site for each additional meter of mean spread between locations within the cluster (Table 3).

DISCUSSION

Our analysis suggests that GPS cluster models are useful for predicting black bear carnivory sites and perform well compared to models developed for other carnivore species. Our models correctly classified 71–96% of carnivory events with overall accuracy of 58–76%. While some cougar predation models performed with as high as 86% overall accuracy (21.5% of clusters misclassified as kills, Knopff et al. 2009), others overestimated kill rates by 49% (Anderson and Lindzey 2003). Wolf predation models demonstrated up to 100% accuracy for large-bodied prey species, although 40% of small-bodied prey were misclassified (Webb et al. 2008). When modeling grizzly bear predation of moose calves, 22 of 23 verified kills were predicted (Rauset et al. 2012), but when modeling grizzly bear consumption of ungulates more generally (i.e., varying ungulate species and age), 48% ± 1% of carnivory sites were accurately predicted (Cristescu et al. 2015). Ebinger et al. (2016)

achieved 78–88% correct classification of large-biomass carcasses and 30% of small-bodied carcasses used by grizzly bears. Bobcat predation of white-tailed deer fawns was particularly difficult to model, with 34.1% of kill sites correctly classified and overall accuracy of 67.1% (Svoboda et al. 2013).

Knopff et al. (2009) noted that prediction of predation events via GPS cluster analysis will likely be most successful for large carnivores that have long handling times and display high fidelity to the kill locations. GPS cluster analysis may be less appropriate for modeling predation of small-bodied prey (Knopff et al. 2009, Palacios and Mech 2010) due to short handling times, observational error during field investigations, or misclassifying a small-prey carnivory event as a non-event. Our models indicate that fidelity to a cluster site was not a significant predictor of black bear carnivory events, contrasting with results from Cristescu et al. (2015) who found that grizzly bear fidelity to carnivory sites was lower than fidelity to bedding sites, yet served as a significant predictor. The ungulate remains at 68% of the carnivory events we identified were elk calves, which can range in mass from approximately 15 kg at birth (Barber-Meyer et al. 2008) to 90–145 kg in November (Cook et al. 2010). Our results show that black bears primarily consumed elk calves as neonates in May and June (peak calving season), when body size was relatively small. We did not identify deer fawn scavenging or predation with the exception of one doe–fawn pair. Mule deer populations in our study area are unknown but substantially lower than elk populations (New Mexico Department of Game and Fish, *unpublished data*). Low mule deer density may have provided black bears too few opportunities to prey on mule deer neonates. It is also possible that fawns were consumed too completely or removed from the site by scavengers so that remains could not be detected during field investigations. Alternatively, the fix interval resolution may have been too coarse for clusters to form at fawn predation sites due to short handling times.

Fix intervals determine the level of detail with which GPS data loggers record animal movements. More frequent fix intervals provide finer scale data, but this must be balanced with the restraints of battery life and associated collar and

capture costs. Fix intervals employed in GPS cluster analysis studies have varied from 10 to 30 min on wolves (Sand et al. 2005, Demma et al. 2007, Webb et al. 2008), 30 min to 1 h on grizzly bears (Rauset et al. 2012, Cristescu et al. 2015), and 3 h on cougars (Anderson and Lindzey 2003, Knopff et al. 2009, Ruth et al. 2010), depending on the size of prey researchers sought to detect and other factors. When compared to scat analysis for diet composition, GPS cluster analysis was found to underestimate small prey items although it proves reliable for larger prey items (Bacon et al. 2011, Tambling et al. 2012). More frequent GPS fix intervals can improve detection of smaller prey items such as ungulate neonates (Sand et al. 2005). When fix intervals were increased from 1 to 2 h, 80% of grizzly bear carnivory sites were retained, while an increase to 12 h retained 50% of carnivory sites (Cristescu et al. 2015). However, we found an increase even from 30-min to 3-h fix intervals omitted almost half of carnivory sites. By field-investigating isolated locations in addition to clusters, it is possible to determine whether carnivory events occur with very short handling times (i.e., less than the fix interval). For example, Ruth et al. (2010) identified 53 kills associated with 165 locations of 382 field-investigated cougar locations with 3-h fix intervals.

Both of the higher resolution data sets showed mean distance between locations within a cluster was a significant predictor of black bear ungulate carnivory events, although it was not significant in the 3-h interval data. Because the mean distance between locations within a cluster is limited by the spatial restriction used to define the cluster, the influence of this predictor in a GPS cluster model will vary depending on the cluster definition used. A within-cluster movement variable had not been included in cluster analyses for other carnivores until Cristescu et al. (2015) included two similar covariates in grizzly bear carnivory models. For most obligate carnivores, clusters will form at predation sites and at resting sites, so it is critical for models to distinguish between these two activities. The average distance from each location in a cluster to the cluster's centroid was significant in predicting grizzly bear carnivory, with lower distance values at carnivory sites than at non-carnivory foraging sites (Cristescu et al. 2015). However, for omnivores, a cluster model must distinguish between

carnivory sites, resting sites, and non-carnivory foraging sites. Depending on the food item, foraging sites may exhibit greater distances between locations (e.g., grazing for graminoids) or lesser distances (e.g., foraging in a tree for acorns) than carnivory sites. This issue is confounded by clusters where black bears both rest and feed at the same site. In several cases, GPS collars on black bears during this study went into mortality (4 or 6 h mortality switch) at resting sites, carnivory sites, and vegetation foraging sites due to inactivity of the bear.

Our models showed that clusters are more likely to be ungulate carnivory events when formed in spring and early summer or in habitats without tree or shrub cover. Similarly, grizzly bear clusters occurring in spring were more likely to be carnivory events than those in summer or fall (Cristescu et al. 2015). Scavenging opportunities can peak in early spring due to winter die-off of ungulates and in the fall as a result of the rut and hunter harvest (Green et al. 1997, Milakovic and Parker 2012); however, the majority of spring carnivory events observed in our study were ungulate neonates. We also observed that a higher proportion of carnivory events that occurred in open habitats were ungulate neonates. Black bear diets are dominated by graminoids and neonate ungulates in the spring, while summer diets shift toward mast and social insects (Raine and Kansas 1990, Bull et al. 2001). While black bears prefer structural cover, Bastille-Rousseau et al. (2011) demonstrated that black bears selected for areas with higher vegetation abundance during spring and early summer, which opportunistically increased their chances of encountering ungulates. Seasonal variation in diet composition may be increased for facultative carnivores compared to obligate carnivores.

The day period in which a cluster was initiated was significant in predicting black bear carnivory for only one of the three data sets, although time of initiation has been shown to be important for other carnivore species. The majority of clusters formed at predation events by cougars were initialized between 2000 and 0500 h, while non-predation clusters were initialized between 0800 and 1700 h (Ruth et al. 2010). At clusters formed by leopards, kills were more likely to be present when clusters began during diurnal or crepuscular hours (Pitman et al. 2012). Grizzly

bear clusters were more likely to be carnivory events when initiated in crepuscular and nocturnal periods than diurnal periods (Cristescu et al. 2015). Number of active periods and number of locations that occur within active periods were both significant predictors of grizzly bear predation of moose calves (Rauset et al. 2012). While optimal hunting conditions drive many large carnivores to exhibit nocturnal activity patterns, black bear carnivory is often less a result of hunting than opportunistic predation of neonates (Kunkel and Mech 1994, Bastille-Rousseau et al. 2011) and scavenging. Black bears exhibit high plasticity in diel activity patterns, with variation across seasons (e.g., Bridges et al. 2004) and demographic classes (e.g., Lewis and Rachlow 2011) and variation in response to human disturbance (e.g., Matthews et al. 2006) and foraging opportunities (e.g., Reimchen 1998). Most commonly, however, black bear activity peaks during the day (Fortin et al. 2013b). Time of initiation of carnivory events by black bears likely reflects the opportunistic nature of black bear carnivory and is therefore less distinct from time of initiation of bedsites and non-carnivory foraging sites.

Further research, management, and conservation implications

Our results evince factors that are important in selecting clusters before field investigation to increase likelihood of locating black bear carnivory events. Black bear predation of ungulate neonates and scavenging of ungulates killed by cougars, human hunters, or other causes have important implications throughout the ecological community. Although black bears rarely kill adult ungulates (Zager and Beecham 2006), consumption of ungulates may be supplemented by livestock mortalities that are not retrieved by ranchers, ungulates wounded but not recovered during hunts, and gut piles or carrion left behind after successful hunter harvest. Kleptoparasitism by black bears can force cougars to increase predation frequencies to compensate for lost prey (Elbroch et al. 2015). As dominant scavengers, black bears can also limit consumption of carrion by other scavengers, potentially influencing scavenger survival and population dynamics (Allen et al. 2014).

Future research could consider the implications of black bear sex and age, competing

predators, and composition of ungulate populations as cluster analysis is implemented across ecological systems. Where ungulate populations are below desired levels, predator control is often considered as a management tool. When a carnivore species exhibits high variability in carnivory rates among individuals, however, predator control will only be effective when particular individuals are targeted. The impacts of black bear scavenging behavior on cougar predation rates and on behavior and fitness of other scavengers are poorly understood. Likewise, the impacts of ungulate biomass availability on black bear fitness and population dynamics are largely unknown, although increased consumption of ungulate neonates has been linked to increased vigor (i.e., larger body size and increased reproductive success) in some black bear populations (Schwartz and Franzmann 1991). Black bear use of ungulates as food can vary depending on the availability of prey, carrion, and other food sources (Ballard 1992, Zager and Beecham 2006, Fortin et al. 2013a). Therefore, predation rates and quantity of ungulate biomass in black bear diets in one population may be dramatically different from another. Monitoring black bear carnivory events can provide a more complete assessment of the extent to which ungulate biomass contributes to black bear fitness and impacts the ecological community.

Increased sample sizes resulting from greater field efficiency will contribute to the development of more robust cluster models just as increased field investigation of these events will improve understanding of black bear carnivorous behaviors. Selection of a cluster definition will depend in part on the fix interval employed and resources available for field investigations. Our results indicate that a 30 m maximum distance between locations within a cluster will allow for the detection of carnivory events with a 30-min fix interval; however, a 50 m distance is necessary with a 3-h fix interval. Larger maximum distances between locations may decrease the risk of omitting carnivory events; however, field investigations of clusters will require more time and search effort if larger distances are employed. We found that a maximum of 24 h between locations was appropriate for clusters with a 3-h fix interval; however, this temporal screen resulted in duplicate clusters forming at carnivory events

with a 30-min fix interval. To decrease the overestimation of carnivory rates in cluster models, a longer temporal screen between locations should be incorporated into a cluster definition with fix intervals <3 h. Again this will result in increased search time per cluster.

Our models provide a mechanism for associating animal behavior with GPS location data by identifying locations of ungulate carnivory by black bears. We accepted a tradeoff between sensitivity and false-positive rates because we were not attempting to estimate carnivory rates. Our objective of maximizing the number of carnivory events detected by the models was met by minimizing the false-negative rate. While highly specific cluster models will improve accuracy within a population and may be suitable for estimating carnivory rates, more general models provide a basis for application across populations. Variations in prey composition and density or competition with other carnivores can affect handling times, site fidelity, movements within a cluster, time of day of cluster initiation or activity, and other predictors in a cluster model. Refinement of a cluster model to estimate black bear carnivory rates should entail field investigations of isolated locations in addition to clusters or should employ GPS collars with a shorter fix interval in order to detect carnivory of small ungulate prey.

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