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Evaluating Global Positioning System Telemetry Techniques for Estimating Cougar Predation Parameters

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ABSTRACT Using clusters of locations obtained from Global Positioning System (GPS) telemetry collars to identify predation events may allow more efficient estimation of behavioral predation parameters for the study and management of large carnivore predator–prey systems. Applications of field- and model-based GPS telemetry cluster techniques, however, have met with mixed success. To further evaluate and refine these techniques for cougars (*Puma concolor*), we used data from visits to 1,735 GPS telemetry clusters, 637 of which were locations where cougars killed prey >8 kg in a multi-prey system in west-central Alberta. We tested 1) whether clusters were reliably created at kill locations, 2) the ability of logistic regression models to identify kill occurrence (prey >8 kg) and multinomial regression models to identify the prey species at a kill cluster, and 3) the duration of monitoring required to accurately estimate kill rate and prey composition. We found that GPS collars programmed to attempt location fixes every 3 hours consistently identified locations where prey >8 kg were handled, and cluster creation was robust to GPS location acquisition failures (poor collar fix success). The logistic regression model was capable of estimating cougar kill rate with a mean 5-fold cross validation error of <10%, provided the appropriate probability cutoff distinguishing kill clusters from non-kill clusters was selected. Logistic models also can be used to direct visits to clusters, reducing field efforts by as much as 25%, while still locating >95% of all kills. The multinomial model overpredicted occurrence of primary prey (deer) in the diet and underpredicted consumption of alternate prey (e.g., elk and moose) by as much as 100%. We conclude that a purely model-based approach should be used cautiously and that field visitation is required to obtain reliable information on species, sex, age, or condition of prey. Ultimately, we recommend a combined approach that involves using models to direct field visitation when estimating behavioral predation parameters. Regardless of the monitoring approach, long continuous monitoring periods (i.e., >100 days of a 180-day period) were necessary to reduce bias and imprecision in kill rate and prey composition estimates. (JOURNAL OF WILDLIFE MANAGEMENT 73(4):586–597; 2009)

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Predation is simultaneously one of the most important, most controversial, and least understood aspects of large carnivore ecology and management. Even after decades of study, the form of many of the underlying mechanisms driving predation rates continues to be a subject of debate (Abrams and Ginsburg 2000, Skalski and Gilliam 2001, Vucetich et al. 2002, Eberhardt et al. 2003), and data often are insufficient to test fundamental hypotheses regarding the effects large carnivores have on their prey (Boutin 1992). One prerequisite for resolving controversy, testing hypotheses, and developing useful models for management is to accurately estimate parameter values for behavioral components of predation. Estimates of the rate at which prey are killed (Sand et al. 2008), the selection of prey species in multi-prey systems (Robinson et al. 2002, Knopff and Boyce 2007), the age–sex structure of prey (Mills and Shenk 1992), the physical condition of prey (Husseman et al. 2003), and the spatial distribution of predation risk (Hebblewhite et al. 2005, Kauffman et al. 2007, Creel 2008) are fundamental to understanding the effects large carnivores have on prey populations and ecosystem structure. Estimating these parameters accurately is an important challenge for ecologists and wildlife managers.

To date, snow-tracking and radiotracking have been the primary techniques used to intensively monitor large carnivores for estimating behavioral parameters of predation. Snow-tracking can provide a detailed record of predation events but is labor intensive and can be employed only when snow conditions permit. Radiotracking is not limited by snow cover but also requires intense efforts in the field (e.g., Beier et al. 1995). Even when snow is available and intensive monitoring possible, sample sizes (no. of individuals or groups monitored) tend to be small and continuous monitoring intervals short. Small sample sizes can undermine inferences about the basic mechanisms of predation (Marshal and Boutin 1999), and short monitoring periods can lead to prohibitively wide confidence intervals around parameter estimates (Hebblewhite et al. 2004). Despite the importance of estimating behavioral parameters of predation for understanding predator–prey dynamics, therefore, the onerous nature of available methods has meant that quality estimates (based on appropriate sample size and sampling intensity) are rarely obtained for large carnivores.

Global Positioning System (GPS) radiotelemetry has created new possibilities to efficiently survey large carnivore predation, permitting increased sample size and monitoring duration. Because prey takes time to consume (i.e., handling time), large carnivores wearing GPS radiocollars set to an appropriate location-fix interval should produce multiple location fixes in places where prey are handled. Anderson and Lindzey (2003) pioneered a technique for identifying and visiting these clusters of GPS telemetry locations to

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locate prey killed by cougars (*Puma concolor*) and used it to estimate kill rate and prey composition in the Snowy Range, Wyoming, USA. Similar field-based techniques have since been developed for wolves (*Canis lupus*) in both Scandinavia (Sand et al. 2005) and North America (Webb et al. 2008). Models parameterized using initial results from field data collected during visits to clusters also have been proposed as a means to estimate parameters of predation indirectly using GPS telemetry data alone (i.e., no additional field visitation), further improving efficiency and reducing total costs of research (Anderson and Lindzey 2003, Webb et al. 2008). Models designed to estimate kill rate have been developed (Anderson and Lindzey 2003, Franke et al. 2006, Zimmermann et al. 2007, Webb et al. 2008) and models designed to estimate prey composition at the species level in multi-prey systems have been suggested (Anderson and Lindzey 2003, Webb et al. 2008) but not attempted.

Field-based techniques are generally considered useful, but correction factors might need to be employed to adjust for bias introduced when kills are not identified by GPS location clusters (Sand et al. 2005). Detection failure has not been assessed for cougars, but can be extensive for wolves, particularly for prey smaller than deer, and can occur even when the time interval between GPS location fixes is short (Webb et al. 2008). Moreover, using models to estimate kill rate has been variously considered by researchers to be useful (Anderson and Lindzey 2003, Franke et al. 2006), somewhat useful (Webb et al. 2008), and not useful (Zimmermann et al. 2007). Consequently, additional evaluation and refinement of GPS telemetry techniques for estimating large carnivore predation parameters is required to more fully assess their utility and improve upon it where possible.

We employed a large data set of field visits to cougar GPS telemetry clusters to evaluate, refine, and expand upon both field- and model-based techniques for estimating parameters of predation. Our primary objectives were 3-fold. The first was to assess the importance for cougars of several potential sources of bias that have been explicitly or implicitly identified in recent studies of wolf kill rate. These sources of bias include the potential lack of cluster creation at kill sites (Sand et al. 2005), the effect of the number of location fixes obtained by GPS collars on parameter estimation (Sand et al. 2005, Webb et al. 2008), the size of prey that can be reliably detected using GPS location clusters (Webb et al. 2008), and the selection of an appropriate probability cutoff level for logistic regression models used to identify kills from GPS data (Zimmermann et al. 2007, Webb et al. 2008). Second, we endeavored to expand on available model-based techniques by developing and assessing models capable of predicting not only kill locations (kill rate) but also species killed at that location (prey composition) without field visitation. Third, because sampling duration can have an important influence on the confidence placed in predation parameter estimates (Hebblewhite et al. 2004), we focused on identifying the sampling duration required to accurately estimate seasonal kill rate and prey composition for individual cougars in a multi-prey system.

STUDY AREA

We studied cougar predatory behavior in a 16,900-km^2 study area located along the central eastern slopes of Alberta's Rocky Mountains (centered approx. at 52°18′N, 115°48′W). The study area was bordered by Banff and Jasper national parks to the west and extended east to the towns of Rocky Mountain House, Alberta, Canada, and Caroline, Alberta, Canada. Rugged mountains in the west gave way to rolling foothills and eventually to flat agricultural land in the east. The region's climate was characterized by warm, dry summers and cold, snowy winters. Chinook winds provided sporadic warming during winter, often resulting in complete removal of the snowpack from south-facing slopes. The study area was mostly public land with an increasing proportion of private lands in the east. It was primarily forested (63%), but rock, ice, and bare ground (14%—primarily in the mountains), and cut-blocks of various ages (8%) also were important land-cover classes. Conifer forests dominated the region and were composed primarily of lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*). Black spruce (*Picea mariana*) and tamarack (*Larix laricina*) were common in low-lying areas, and aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) were patchily distributed throughout the region. Typical understory species were green alder (*Alunus crispa*), willow (*Salix* spp.), and rose (*Rosa acicularis*). Human recreational activity was common, especially during summer, and Alberta's oil, gas, and forestry industries were active on the landscape. Cougars in the area were managed as a big-game animal and were hunted according to a strict quota system during winter (Ross et al. 1996).

Numerous species of ungulates were potential prey for cougars, including large numbers of elk (*Cervus elaphus*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), and feral horses (*Equus caballus*). Smaller numbers of bighorn sheep (*Ovis canadensis*), woodland caribou (*Rangifer tarandus*), and mountain goats (*Oreamnos americanus*) were patchily distributed in the western portion of the study area. Large domestic ungulates (e.g., cattle and llama) were available also, primarily on private lands in the eastern portion of the study area. Non-ungulate prey were abundant and included ruffed grouse (*Bonasa umbellus*), spruce grouse (*Falcipennis canadensis*), snowshoe hare (*Lepus americanus*), beaver (*Castor canadensis*), porcupine (*Erethizon dorsatum*), coyote (*Canis latrans*), and red fox (*Vulpes vulpes*).

METHODS

We used data from 24 cougars (15 ad F, 5 ad M, 3 sub-ad F, and 1 sub-ad M) captured during winters 2005–2006 and 2006–2007. We accomplished capture by using trained hounds to track and tree cougars and then administering 3 mg/kg Telazol and 2 mg/kg xylazine via remote injection (University of Alberta Animal Care Protocol no. 479505). At capture we weighed, measured, sexed, and assigned to cougars one of 3 age classes (kitten, sub-ad, or ad). We estimated age using a combination of pelage spotting progression (Shaw 1986), tooth color and wear characteristics (Ashman et al. 1983, Shaw 1986), and gum-line recession (Laundré et al. 2000). We obtained photographs of dentition at each capture and made post-hoc comparisons to ensure consistency among estimated ages. Exact ageing (e.g., by month) was not possible, and we considered cougars kittens if they still traveled with their mothers, subadults from dispersal until approximately 2.5 years, and adults if >2.5–3 years. We fitted all cougars with Lotek 4400S GPS collars (Lotek Engineering, Newmarket, ON, Canada), programmed to obtain a GPS location every 3 hours, from which we could download data remotely on demand. We monitored cougars closely between 1 December 2005 and 18 August 2007 using a combination of ground and aerial telemetry for as long as each collar remained active. During the monitoring period individual cougars wore active GPS collars for 25–495 consecutive days ($\bar{x} = 191$, SD = 138), resulting in 130–2,617 location points per individual ($\bar{x} = 895$, SD = 659). We downloaded location data remotely from active GPS collars every 2–3 weeks, usually from the ground but occasionally during aerial telemetry flights.

We used Python™ programming language (Python Software Foundation, Hampton, NH) to develop a rule-based algorithm capable of identifying GPS location clusters from collar data (program available from the authors). Following Anderson and Lindzey (2003), we defined a cluster spatially as $\geq$2 points located within 200 m of each other. The algorithm initially searched within the 200-m limit and also used a temporal screen of 6 days when identifying associated points. Two initial points fitting these space–time restrictions formed a seed cluster and the geometric center of the cluster was calculated. The program then added additional points occurring within 200 m of the geometric center and within the temporal window of 6 days to the cluster, one at a time. It adjusted the geometric center with each additional point and repeated the process until no more points could be added. We allowed clusters to persist beyond the initial 6-day temporal screen provided that the difference between the last point and the next new point at a cluster was always $\leq$6 days. After completing these calculations, the program output a number of descriptive variables for each identified cluster. These variables included the geometric center of the cluster, the largest distance from the geometric center to a point (cluster radius), the number of location fixes occurring within 200 m of the geometric center, the number of fixes obtained while the cluster persisted, and number of 24-hour periods where $\geq$1 fix was obtained at the cluster.

We programmed geometric centers into handheld GPS units and used these to locate clusters in the field. Ground crews of $\geq$2 people conducted systematic searches at each cluster location. We searched clusters with a radius of $\leq$50 m by walking 8 transect lines along cardinal compass bearings (e.g., N, NE, E) out to 50 m, walking 20 m to the right, and then zig-zagging back to the cluster center. For clusters with a radius of >50 m we employed the same 8-line technique out to 50 m and then made concentric circles varying between 5 m and 10 m apart (depending on visibility) out to the full extent of the cluster radius (up to 200 m). We assigned a kill to a GPS location cluster if we found prey remains that closely matched the dates over which the cluster was created and we also found evidence of cougar feeding behavior (e.g., carcass had been buried, hair mat at cache site, multiple cougar scats). We assigned cougar scavenging to clusters where the carcass clearly had been killed by something other than a cougar (e.g., remains from a wolf-killed, hunter-killed, or road-killed animal) or if the carcass age differed greatly from the dates the cougar spent at the cluster. Using this classification scheme, instances of scavenging on fresh carcasses that were not obviously killed by something other than a cougar could be misclassified as a kill. We closely examined all found remains (scavenging or kills) to determine species, age, sex, and condition (marrow fat).

In their pioneering work, Anderson and Lindzey (2003) failed to address the potential that clusters might not form at some cougar kill locations. To evaluate the ability of GPS collars with a 3-hour fix interval to identify locations where cougar-killed prey by creating clusters, we snow-tracked collared cougars prior to downloading GPS data and subsequently compared kills found during snow-tracking sessions to GPS data to determine whether clusters were consistently created at kill sites.

Model Development

We used logistic regression (Hosmer and Lemeshow 2000) to model presence or absence of a kill at a GPS cluster. We were primarily interested in producing a model capable of predicting ungulate kill rate without resorting to field visitation, but because we wanted a general model for all cougars in all seasons and did not want to miss ungulate neonates in spring, we coded all kills of prey weighing >8 kg as kills (1) and all clusters where we found either nothing or prey <8 kg as non-kills (0). Unlike other attempts to develop logistic regression kill-rate estimators for large carnivores using GPS location data (i.e., Anderson and Lindzey 2003, Zimmermann et al. 2007, Webb et al. 2008), therefore, we incorporated moderate-sized non-ungulate prey (e.g., beaver, porcupine, coyote) into model development. We did not use data from clusters truncated by initial collaring or collar removal or failure in model development. In addition, we removed clusters created at nursery sites where females had kittens. Nursery clusters can be easily screened from a data set, even without on-the-ground visitation, because of the distinctive pattern of prolonged use (often >1 month) and creation of subsidiary clusters of shorter duration (often kills) with repeated movement between these clusters and the nursery site (Beier et al. 1995, Benson et al. 2008).

We developed a candidate set of predictive models based solely on cougar movement behavior at clusters. Although there is evidence that habitats at large carnivore kill sites differ from habitats at locations associated with other behavioral states (Kauffman et al. 2007), we wanted the model to be as broadly applicable as possible and so did not include site-specific habitat covariates in model development. We used 5 potential explanatory variables output by our clustering program: 1) duration of cluster (hr); 2) number of points at the cluster (corrected to account for variation in fix success by dividing by the proportion of successful fixes obtained while the cluster persisted); 3) fidelity to the cluster site (points at cluster minus points away over the duration of the cluster); 4) number of 24-hour periods during which we recorded $\geq$1 location point at the cluster; and 5) a binary variable dividing clusters into those with points spanning more than one 24-hour period and those with all points occurring within 24 hours. We developed candidate models using various combinations of the predictor variables. To avoid multi-collinearity we did not use highly correlated predictor variables (i.e., $|r| > 0.7$) in the same model. Because the small sample size correction for Akaike's Information Criterion (AIC_c) converges to the AIC at large sample sizes, it can be applied for model selection regardless of sample size, and we used it to identify a top model from our candidate set (Burnham and Anderson 2002).

The probability output from the logistic regression model at which a cluster is assigned kill or non-kill status can be set arbitrarily, most commonly at 0.5 (e.g., Zimmermann et al. 2007), or it can be defined by using sensitivity and specificity curves to obtain an optimal output (e.g., Webb et al. 2008). Cutoff selection can determine whether the model performs well or poorly at prediction (Hosmer and Lemeshow 2000) and might affect kill rate estimation. We investigated the effect of using 4 different cutoff levels (0.5, 0.4, 0.3, and the optimum derived from the data) on kill rate estimation. We evaluated model classification using receiver–operator characteristic (ROC) curves. We assessed the ability of the model to predict kill rate at the various cutoff levels using *k*-fold cross-validation with 5 data partitions (Boyce et al. 2002). Other studies test the generality of kill rate models within a study area by withholding data (usually from an individual or a small subset of individuals), testing the ability of the model to predict kill rate for the withheld data, and then either refitting the model by incorporating withheld data (Anderson and Lindzey 2003) or leaving testing data out of final model parameterization entirely (Webb et al. 2008). The *k*-fold technique may be more appropriate because prediction is evaluated based on a representative sample of the population instead of a potentially unrepresentative single animal or small subset of animals and because the *k*-fold technique permits use of all available data for initial model selection (i.e., data are withheld only when assessing prediction, not when identifying a top model).

We also explored the possibility that prey composition might be estimated using model-based (indirect) methods. We assigned all prey >8 kg located at clusters to one of 5 prey types: deer (white-tailed and mule deer combined), elk, moose, feral horses, and other (all other prey). We developed multinomial logistic regression models (Hosmer and Lemeshow 2000) to assign a probability that a given kill cluster fell into one of these categories. For model development we used only data from clusters where we found a kill and could unambiguously assign it to one of these prey categories. We developed a candidate set of models based primarily on cluster variables associated with duration and intensity of use (no. of points, fidelity, and binary day periods), reasoning that larger prey would result in longer handling times for cougars (Anderson and Lindzey 2003). We also used information about individual cougars because cougar age (sub-ad vs. ad) and especially sex (M vs. F) have been suggested to contribute to prey selection (Ross and Jalkotzy 1996, Murphy 1998, Anderson and Lindzey 2003). Finally, we risked reducing broader model applicability by incorporating site-specific habitat covariates extracted from a Geographical Information System under the assumption that different habitat selection patterns of ungulate prey types might be a critical component of effective discrimination between kill types. We used deer as the reference category in model development and we selected a top model using AIC_c. The multinomial model output a set of probabilities, one for each possible category of kill (Hosmer and Lemeshow 2000). The category with the highest probability was the predicted category. Just as with the logistic models, we used 5-fold cross-validation to assess the predictive capacity of the top multinomial prey composition model.

Assessing the Influence of Fix Success and Improving Efficiency in the Field

Low and variable GPS location acquisition rates are common problems encountered in GPS radiocollar studies of cougars (Anderson and Lindzey 2003, Land et al. 2008). Lower than average GPS acquisition might reduce the probability of cluster creation at some kills, biasing estimates of kill rate and prey composition. Webb et al. (2008) examined the effect of reducing the time between GPS location attempts (fix interval) on the probability of locating wolf-killed prey and found that kill rate for small prey was underestimated at longer fix intervals. Variation in fix acquisition, however, presents a different problem. Reductions in fix success are more likely to approximate a random loss of data, as opposed to the strictly systematic data reduction as the fix interval is lengthened. This type of fix loss can contain runs of missed points, a pattern that may be even more likely to result in detection failure. To assess the extent to which reduced fix success biases cougar kill rate and prey composition, we used data from 4 collars that obtained above average fix success (>60%; see results) and were deployed on cougars for $\geq$11 months. We randomly removed fixes to simulate reduced GPS acquisition at 3 levels (45%, 30%, and 15%). We then reran the clustering algorithm at each reduced level to determine how many clusters were lost and the number of kill clusters lost. We also used the logistic regression model at the optimal cutoff level to identify changes in the number of kills predicted by the model as fix success declined. Finally, we examined the composition of prey lost at each level of GPS acquisition reduction.

In cases where detailed information is required about large carnivore predation events, there may be no substitute for field visitation. Hence, we assessed the potential for statistical models to help guide cluster visitation and improve the efficiency of field-based parameter estimation for cougars. We used the top logistic regression model to output the probability that each cluster we visited represented a kill. We then simulated various cutoff probabilities below which we would not have visited a cluster in the field. We assessed amount of effort saved and proportion and type of kills missed at each probability cutoff. Because availability of smaller prey (e.g., ungulate neonates, beaver) was reduced in winter and we expected that handling times might be longer in winter due to slower meat spoilage, we also examined the effect of season on cutoff selection for cluster visits.

Next, we explored the effect that sampling duration had on estimates of kill rate and prey composition. Our goal was to identify the minimum duration of intensive monitoring required to provide estimates of cougar kill rate and prey composition close to the true values obtained from long-term monitoring of individuals. Because inferences about kill rate and prey composition often pertain to either summer or winter in seasonal environments, we investigated the sampling intensity required to provide estimates for one season (180-day period). We used resampling procedures to simulate various sampling intensities from the first 180 days for each of 10 cougars that we continuously monitored for ≥180 days. We randomly generated 10 samples for each cougar at each of 10 sampling intensities, increasing at intervals of 10% up to 180 days (e.g., 18 days, 36 days, 54 days, …, 180 days). Thus, we generated 1,000 simulated monitoring periods. We obtained percentage of error in kill rate (KR_{kj}) for simulations at the kth sampling intensity for the jth cougar using the following:

$$KR_{kj} = \frac{\left(\sum_{i=1}^{n} |\hat{x}_i - X_j|\right)/n}{X_j} \tag{1}$$

where $\hat{x}_i$ = kill rate of the ith simulated monitoring period at the kth sampling intensity for the jth cougar, X_j = kill rate for the jth cougar obtained over the full 180-day intensive monitoring period, and n = number of simulated monitoring intervals generated at the kth sampling intensity. We calculated mean error in prey composition (PC_{kj}) using the following equation:

$$PC_{kj} = \frac{\sum_{i=1}^{n}\left(\frac{\sum_{l=1}^{m} |\hat{y}_l - Y_{lj}|}{2}\right)}{n} \tag{2}$$

where $\hat{y}_l$ = estimated percentage of the lth prey type in the ith simulated monitoring period at the kth sampling intensity for the jth cougar, Y_{lj} = percentage of the lth prey item in the diet of the jth cougar obtained over the full 180-day intensive monitoring period, m = number of prey items in the jth cougar's diet, and n = number of simulated monitoring intervals generated at the kth sampling intensity. We then calculated the mean error and confidence limits for kill rate and prey composition at each sampling intensity using KR_{kj} and PC_{kj} of all 10 cougars. We tested the hypothesis that the relationship between sampling intensity and mean error would be nonlinear (i.e., error would decline rapidly over initial increases in sampling intensity and then deliver diminishing returns at higher sampling intensities) by using 1-tailed t-tests to compare residuals of the best-fit linear and quadratic curves.

RESULTS

We visited 1,735 GPS location clusters identified using the rule-based clustering algorithm for 24 instrumented cougars (mean clusters/cougar = 72.3, SD = 53.5). On average, we visited clusters 21 days after they were made (SD = 14.9) and the maximum time between cluster creation and cluster visitation was 144 days. In total, we spent 1,508 hours searching at cluster locations. If kills were present we usually found them quickly, in many cases before we implemented systematic search. On average, 0.6 hours of searching were required to locate a kill and 1.0 hours to conclude absence of a kill at a cluster. We found cache sites (location where a cougar buried and consumed prey), on average, within 27.1 m (SD = 24.7) of the geometric center of the cluster. Most time invested in obtaining data was spent getting to the cluster location.

We found 637 prey >8 kg, 30 prey <8 kg, and 37 instances of scavenging at cluster sites. Clusters where prey >8 kg were present averaged 12 locations (SD = 9.6) and spanned 71.5 hours (SD = 60.6). Even when we considered only clusters associated with non-ungulate prey <40 kg but >8 kg (n = 90), clusters maintained an average of 8 locations (SD = 6.0) and 52.8 hours (SD = 88.6). Once a cougar killed an animal >8 kg, it displayed high fidelity to the location where it cached the prey, with an average of 87.9% (SD = 19.7%) of GPS fixes obtained over the cluster duration occurring within 200 m of the cache site. Five species of wild ungulate (elk, moose, feral horse, mule deer, and white-tailed deer) comprised most (85.9%) prey we found at cluster locations. Beaver (4.5%) and coyote (1.5%) were the most common non-ungulate prey represented at clusters. At 14 (2.2%) clusters where predation occurred, we found >1 prey item. Most often this consisted of female ungulates and their young offspring. However, on several occasions, an ungulate and a mesocarnivore (coyote or fox that likely was scavenging from the ungulate carcass) were both killed at a cluster. We rarely (n = 2) recorded kills of >1 large ungulate (e.g., >1 ad). The largest number of cougar kills located at one cluster was 4 (1 ad F deer, 2 deer fawns, and 1 coyote). We probably underestimated the number of multiple kills occurring at cougar GPS clusters, however, because we usually stopped searching at clusters once we found a kill.

To assess the efficacy of using collars with a 3-hour fix rate to locate prey killed by cougars, we conducted 29 snow-

Table 1. The 5 top-ranked logistic regression models for discriminating kills (>8 kg) from non-kills at 1,735 cougar Global Positioning System location clusters along the central east slopes of Alberta's Rocky Mountains, December 2005 to August 2007. Model log-likelihood (LL), number of estimated parameters (K), small sample size corrected Akaike's Information Criterion (AIC$_c$), AIC$_c$ difference (ΔAIC$_c$), and Akaike weight (w_i) are displayed.

Rank	Variables	LL	K	AIC$_c$	ΔAIC$_c$	w_i
1	COR_AT,[a] FIDELITY,[b] BIDAY1,[c] AVERAGE_DI[d]	−582.180	4	1,173.254	0.00	0.82
2	COR_AT, FIDELITY, BIDAY1	−584.953	3	1,176.495	3.24	0.16
3	COR_AT, FIDELITY, AVERAGE_DI	−587.608	3	1,181.741	8.49	0.12
4	COR_AT, FIDELITY	−589.831	2	1,183.920	10.67	0.04
5	COR_AT	−635.227	1	1,272.538	99.28	0.00

[a] No. of location fixes divided by the proportion of successful fixes over the duration of the cluster.
[b] No. of fixes away from the cluster subtracted from the no. of fixes at the cluster over the duration of the cluster.
[c] Binary variable indicating 1-day or >1-day period spent at the cluster.
[d] Average distance of all points at the cluster from the geometric center of the cluster.

tracking sessions of collared cougars spanning >351 cougar hours of activity. During our tracking sessions we found 5 prey items killed by cougars. Four of the kills were deer (2 of which were fawns aged 5 months and 9 months), each of which had a cluster of ≥11 location fixes associated with it. The fifth kill we found was a snowshoe hare that did not have an associated cluster.

Model Performance

The top model predicting presence or absence of a kill of prey >8 kg at a cluster included covariates for the number of points at a cluster (corrected for fix success), number of day periods, fidelity to the cluster, and average distance of points from geometric center (Table 1). Kills were more likely to be present at clusters that had higher numbers of corrected points, at clusters where the cougar was present >1 day, at clusters for which the cougar showed high fidelity, and at clusters where the average distance from the geometric center of the cluster was smaller (Table 2). The optimal probability cutoff above which we considered a cluster a kill >8 kg was 0.22. The top model fit the data well with a ROC area under the curve of 0.93 (i.e., outstanding discrimination between kills and non-kills; Hosmer and Lemeshow 2000).

Assessing model predictive capacity using k-fold cross-validation at the 0.22 cutoff demonstrated that the model had high classification success (86%) and provided estimates of cougar kill rates averaging within 8.7% of the true value (Table 3). Conducting the k-fold procedure for the same model at 3 arbitrarily selected cutoff levels (0.3, 0.4, 0.5) demonstrated that choice of cutoff level had a large effect on kill-rate estimation (Table 3). Both the optimal cutoff (0.22) and the 0.3 cutoff provided reasonable estimates of kill rate (on average within 10% of the true value), whereas the 0.4 and 0.5 cutoffs underestimated kill rate by >16% (Table 3). Because clusters were more often non-kill than kill sites, errors of false positive (incorrectly identifying a non-kill cluster as a kill) and false negative (incorrectly identifying a kill cluster as a non-kill) canceled each other out to produce better estimates of kill rate at lower cutoff levels, despite slight increases in overall classification success at higher cutoff levels (Table 3).

Of the 637 kills >8 kg that we found at GPS location clusters, 468 (73.3%) were deer, 47 (7.4%) moose, 38 (6.0%) elk, 21 (3.3%) feral horses, and 63 (9.9%) other prey (primarily non-ungulate). Several candidate models in the multinomial set were statistically indistinguishable in their ability to discriminate between these categories (Table 4). These models represent slight variations on a theme and we selected the model with the most variables (the second-ranked model) for prediction because this model explained the most total variation (i.e., it had the lowest log likelihood). The selected model included behavioral variables (no. of points at a cluster, no. of day periods spent at the cluster, and average distance of points from geometric center), individual cougar characteristics (cougar age and sex), and environmental covariates (season, wet openings, dry openings, mixed forest, clear-cuts, and terrain ruggedness within a radius of 500 m from the cache site) to predict the type of kill (Table 5). The 5-fold cross-validation we used to assess the predictive capacity of the model revealed a mean percentage correctly classified of 74.8%. The model overpredicted deer (Table 6), which were the most abundant prey. Other prey were underrepresented by the model and also were burdened with more variation in the predicted level of dietary importance (Table 6).

Table 2. Coefficients for the highest-ranking logistic regression model used to predict presence or absence of a kill at a Global Positioning System location cluster for cougar along the central east slopes of Alberta's Rocky Mountains, December 2005 to August 2007.

Variable	Coeff.	SE	95% CI
COR_AT[a]	0.188	0.202	0.149 to 0.229
FIDELITY[b]	0.112	0.014	0.085 to 0.140
BIDAY1[c]	1.071	0.219	0.643 to 1.500
AVERAGE_DI[d]	−0.007	0.003	−0.012 to −0.001
Constant	−2.722	0.152	−3.020 to −2.424

[a] No. of location fixes divided by the proportion of successful fixes over the duration of the cluster.
[b] No. of fixes away from the cluster subtracted from the no. of fixes at the cluster over the duration of the cluster.
[c] Binary variable indicating 1-day or >1-day period spent at the cluster.
[d] Average distance of all points at the cluster from the geometric center of the cluster.

Assessing the Influence of Fix Success and Improving Efficiency in the Field

The Lotek GPS collars we employed averaged 60% fix success, ranging from 45% to 83% for individual cougar.

Table 3. Mean and standard deviation of 5-fold cross-validation for percentage of correctly classified, rates of misclassification, and deviation from known cougar kill rate for predictions at 4 probability cutoff levels derived from logistic regression models distinguishing kill locations from non-kill locations for cougar along the central east slopes of Alberta's Rocky Mountains, December 2005 to August 2007.

	Correctly classified		Rate of false positive[a]		Rate of false negative[b]		Deviation from known kill rate	
Cutoff	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
0.22	86.08	3.1	21.51	4.63	8.76	2.41	+8.67	5.56
0.3	87.58	1.76	14.79	1.91	11.06	2.35	−6.58	7.57
0.4	87.89	1.15	11.17	2.00	12.44	2.14	−16.11	10.21
0.5	87.60	1.6	9.37	2.90	13.58	2.12	−22.69	10.51

[a] Rate of false positive is the no. of clusters incorrectly considered kills by the model divided by the true no. of kill clusters.
[b] Rate of false negative is the no. of clusters incorrectly considered non-kills by the model divided by the true no. of non-kills.

Simulated fix success reduction by random removal of GPS locations revealed that the number of clusters created dropped rapidly as we reduced fix success (Fig. 1). However, clusters where kills were present were more resistant to fix success reductions than were non-kill clusters (Fig. 1). Indeed, reducing fix success to 45% resulted in only a slight underestimate of kill rate ($\bar{x} = 3.8\%$). Reductions to 30% resulted in more substantial underestimates ($\bar{x} = 11.4\%$), and by the time we reduced fix success to 15% we lost a substantial proportion of cougar kill clusters ($\bar{x} = 34.1\%$) and most non-kill clusters ($\bar{x} = 85.9\%$). The top logistic regression model using the optimal cutoff of 0.22 further underestimated the number of kill clusters by approximately 15%, regardless of the level to which we reduced fix success (Fig. 1). We first lost clusters associated with smaller prey such as beaver and deer as we reduced fix success, whereas we lost no large ungulates such as elk, moose, or feral horses from the kill sample until we reduced fix success to 15%.

Applying the top logistic regression model to our entire cluster dataset ($n = 1{,}735$) revealed that visiting only those kills with a probability above the optimal cutoff of 0.22 would have reduced our efforts in the field by 60% but also would have eliminated 14% ($n = 88$) of cougar-killed prey from our sample. Over 80% of these eliminated prey were either ungulate young of the year (most of them in summer) or smaller non-ungulate prey such as beaver and coyote, resulting in a strong sampling bias against smaller prey if we used this cutoff. By using the more conservative probability cutoff level of 0.1 to direct field visitation, on the other hand, it would still have been possible to eliminate 23% of the field effort while maintaining almost perfect documentation of kills >8 kg (98%). When we examined the kill probability output by the model at a kill cluster by season, we found that more clusters with low model probabilities were associated with kills >8 kg in summer ($\bar{x} = 0.686$, 15 Apr–14 Oct) than in winter ($\bar{x} = 0.801$, 15 Oct–14 Apr; 2-tailed t-test, $P < 0.001$). Consequently, in summer close to 1.5 times as many clusters must be visited (model probability cutoff = 0.1) to locate ≥95% of cougar prey >8

Table 4. The 5 top-ranked models for discriminating prey type (deer, elk, moose, feral horse, other) at 637 cougar kills along the central east slopes of Alberta's Rocky Mountains, December 2005 to August 2007. Model log-likelihood (LL), number of estimated parameters (K), small sample size corrected Akaike's Information Criterion (AIC_c), AIC_c difference (ΔAIC_c), and Akaike weight (w_i) are displayed.

Rank	Variables	LL	K	AIC_c	ΔAIC_c	w_i
1	C_SEX,[a] C_AGE,[b] SEASON,[c] COR_AT,[d] BIDAY1,[e] DNWETOP,[f] DNDECMI,[g] TER_RUG,[h] DNNATOP,[i] DNALLCU[j]	−441.097	10	907.823	0.000	0.261
2	C_SEX, C_AGE, SEASON, COR_AT, BIDAY1, AVERAGE_DI,[k] DNWETOP, DNDECMI, TER_RUG, DNNATOP, DNALLCU,	−439.515	11	907.953	0.129	0.244
3	C_SEX, C_AGE, SEASON, COR_AT, BIDAY1, DNWETOP, DNDECMI, TER_RUG, DNNATOP	−442.820	9	908.135	0.312	0.223
4	C_SEX, C_AGE, SEASON, COR_AT, DNWETOP, DNDECMI, TER_RUG, DNNATOP	−444.534	8	908.581	0.758	0.178
5	C_SEX, C_AGE, SEASON, COR_AT, BIDAY1, AVERAGE_DI, DNWETOP, DNDECMI, DNCONIF,[l] TER_RUG, DISTWAT	−441.277	11	911.476	3.653	0.042

[a] Cougar sex.
[b] Cougar age.
[c] Season.
[d] No. of location fixes divided by the proportion of successful fixes over the duration of the cluster.
[e] Binary day period.
[f] Wet openings.
[g] Mixed forest (deciduous and conifer).
[h] Terrain ruggedness.
[i] Natural openings.
[j] Clear-cuts.
[k] Average distance of all points at the cluster from the geometric center of the cluster.
[l] Conifer forest.

Table 5. Coefficients for the highest-ranked multinomial regression model used to predict the species of kill at a cougar kill cluster along the central east slopes of Alberta's Rocky Mountains, December 2005 to August 2007. All coefficients are in relation to deer, which is the reference category.

Variable	Coeff.			
	Moose	Elk	Horse	Other
C_SEX[a]	3.019	1.999	4.516	1.884
C_AGE[b]	1.053	1.936	16.220	−0.191
COR_AT[c]	0.026	0.013	0.003	−0.054
BIDAY1[d]	−0.466	−0.033	0.341	−0.684
AVERAGE_DI[e]	0.008	0.007	−0.004	0.008
SEASON[f]	−2.98	−0.925	−1.309	−0.351
TER_RUG[g]	−0.03	−0.010	−0.021	−0.028
DNWETOP[h]	−0.03	−0.023	−0.041	0.003
DNDECMI[i]	−0.002	0.002	0.003	−0.001
DNNATOP[j]	0.001	0.007	−0.027	0.005
DNALLCU[k]	−0.000	0.001	−0.003	−0.001
Constant	−6.67	−7.528	−40.193	−2.497

[a] Cougar sex (1 = F, 2 = M).
[b] Cougar age (1 = sub-ad, 2 = ad).
[c] No. of location fixes divided by the proportion of successful fixes over the duration of the cluster.
[d] Binary day period (0 = <1-day period, 1 = >1-day period spent at the cluster).
[e] Average distance of all points at the cluster from the geometric center of the cluster.
[f] Season (0 = summer, 1 = winter).
[g] Terrain ruggedness.
[h] Wet openings.
[i] Mixed forest (deciduous and conifer).
[j] Natural openings.
[k] Clear-cuts.

kg than must be visited to locate the same percentage of prey >8 kg in winter (model probability cutoff = 0.15).

We found no obvious optimal level of effort that should be employed to estimate kill rate and prey composition for a season (180-day period). The relationship between mean error in kill rate and sampling intensity was linear (i.e., the best-fit quadratic equation did not differ from the best fit straight line; t-test, $P = 0.13$), indicating that each investment in time yields an approximately equal return in improved accuracy. The relationship between mean error in prey composition and sampling intensity, on the other hand, was quadratic (t-test, $P = 0.02$), but the curve was shallow and returns on time invested in the field did not diminish rapidly (Fig. 2). Despite the lack of a clearly defined optimal level of effort that allowed accurate estimation of both parameters, it is clear that short monitoring periods produce estimates of kill rate and prey composition that are both biased and imprecise. Indeed, 108 consecutive days of monitoring were required before the upper bound of a 95% confidence interval surrounding the mean error of both kill rate and prey composition dropped below 20% (Fig. 2).

Table 6. Proportion of the true composition of each prey species predicted by the top multinomial model distinguishing prey species at cougar kill locations along the central east slopes of Alberta's Rocky Mountains, December 2005 to August 2007, for each of 5 randomly assigned partitions of the data. A value of 1.00 represents correct prediction.

Species	Partition 1	Partition 2	Partition 3	Partition 4	Partition 5	$\bar{x}$	SD
Deer	1.12	1.20	1.24	1.20	1.20	1.19	0.04
Elk	0.44	0.00	0.00	0.00	0.37	0.16	0.22
Moose	1.50	0.71	0.58	0.85	0.92	0.91	0.35
Horse	1.00	0.33	0.50	0.00	0.25	0.41	0.37
Other	0.08	0.30	0.33	0.36	0.40	0.29	0.12

DISCUSSION

Our rule-based clustering algorithm proved effective for identifying locations where cougars killed prey >8 kg. Webb et al. (2008) promote the use of statistical clustering programs (e.g., Kulldorff et al. 2005) for kill-site identification. However, to use these programs effectively, biologically reasonable constraints (rules) must be applied to the spatial and temporal extent of clusters they identify. In practice, therefore, statistical programs only improve on a rule-based algorithm if the statistical probability associated with the cluster output will be used in subsequent models for kill site identification. If subsequent modeling will be based on parameters not derived from the statistical program (e.g.,

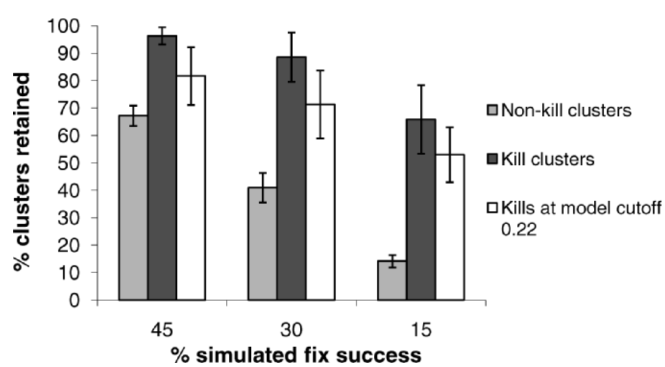

Figure 1. Percentage of non-kill clusters, kill clusters, and model-predicted kill clusters retained at 3 levels of simulated fix success for 680 non-kill clusters and 260 kill clusters generated by 4 cougars with >60% initial fix success in west-central Alberta, December 2005 to August 2007.

Webb et al. 2008), then rule-based algorithms such as the one we have developed for identifying clusters serve equally well and have the advantage of outputting user-defined descriptive variables associated with the cluster (e.g., geometric center of cluster, no. of 24-hr periods at a cluster) in one step.

Although the total number of kills we located during snow-tracking sessions of GPS-radiocollared cougars was small, it was encouraging to find that detection rates were high (100% of the ungulate prey had GPS location clusters associated with them). Moreover, simulated fix success reduction demonstrated that clusters at locations where prey >8 kg were found were exceptionally robust to fix loss (because of the large number of fixes originally obtained), indicating that a cluster is likely to form at locations where prey >8 kg were handled. However, our small sample of snow-tracking data for GPS-collared cougar in winter and our lack of an independent evaluation technique for detection rates in summer imply that further tests of this conclusion are warranted. In general, success of GPS clusters for locating cougar-killed prey, even when fix success is low, is likely due to this predator's long handling times (even for prey 8–40 kg) and high fidelity to kill locations. Differences in handling behavior between solitary predators such as cougar and group-hunting predators such as wolves may partially explain why recent applications of GPS telemetry for estimating wolf kill rate report much lower detection rates than we found (Sand et al. 2005, Zimmermann et al. 2007, Webb et al. 2008). We suspect that future applications of GPS cluster techniques will work best for large carnivores that, like cougar, display high fidelity to kill locations and have long handling times.

The generally low and variable fix success observed in our study is consistent with other deployments of various types of GPS collars on cougars (Anderson and Lindzey 2003, Land et al. 2008). Surprisingly, fix success did not bias kill rate or prey composition estimates until it was reduced below 45% and the bias did not become severe until it fell below 30%. Although fix success on cougar GPS collars may generally be high enough for bias to be avoided when prey are handled, it would still be possible to fail to detect cougar predation events (prey >8 kg) if prey were killed but not consumed. In Scandinavia, GPS-collared wolves occasionally failed to produce location clusters at kills when human disturbance truncated prey handling (Zimmermann et al. 2007). Similar situations are possible for cougars, especially in multi-predator systems where encounter competition occurs between cougars and other large carnivores (Murphy et al. 1998, Ruth 2003). We documented several instances of wolf and bear visits to cougar kill sites, including a number of usurpations of cougar kills by dominant predators (K. Knopff, University of Alberta, unpublished data); however, most cougar displacements occurred after cougars had begun handling prey, and in only 6 cases (<1% of kills we visited) was the carcass usurped after collars obtained only 2–4 location fixes. Therefore, it is probably rare for cougars to handle prey >8 kg for such a short duration that clusters fail to be produced.

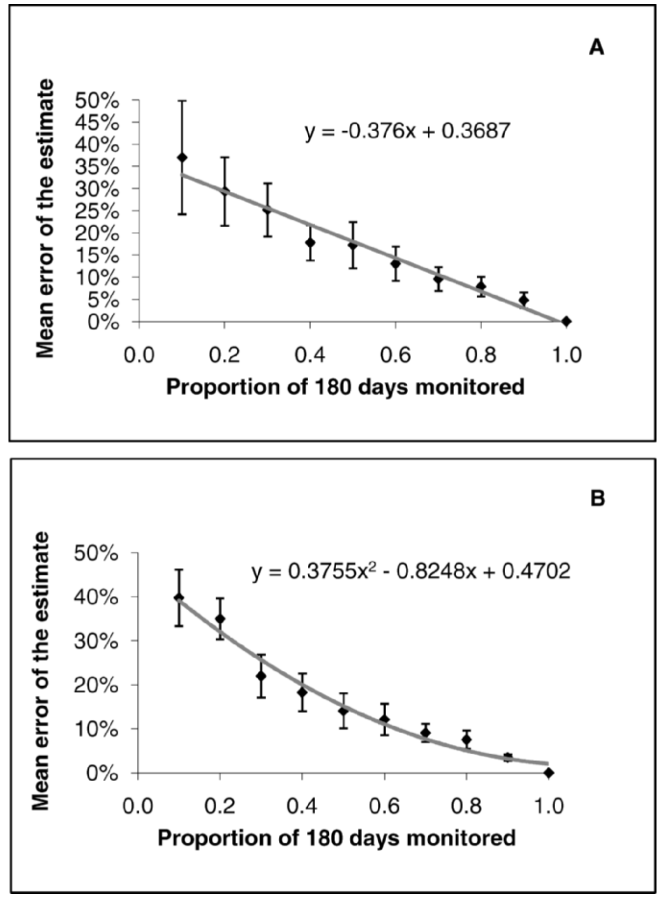

Figure 2. Relationship between the proportion of a 180-day period monitored and (A) mean absolute error (%) in kill rate estimates and (B) mean absolute error (%) in prey composition estimates obtained using 1,000 simulated sample periods drawn from continuous 180-day monitoring sessions for 10 cougars in west-central Alberta, December 2005 to August 2007. Ninety-five–percent confidence intervals bracket each error estimate. The best fit (linear or quadratic) curve and their equations are displayed.

Estimates of behavioral parameters of predation also can be biased if cougars consume carcasses of animals they did not kill, creating GPS telemetry location clusters at scavenging sites that are misclassified as kills. Anderson and Lindzey (2003) were unable to address the influence of scavenging on cougar kill-rate estimation because of technological limitations but suggested the influence would be minor because cougars were believed to scavenge infrequently. However, this potential bias can be addressed directly by employing collars from which GPS data can be downloaded regularly to ensure the interval between cluster creation and field visitation is sufficiently short that cause of death can be identified. Using downloadable collars, we were able to identify 37 clear instances of scavenging (approx. 5% of all clusters where we found carcasses) and remove these from our kill sample, diminishing the effect of this form of bias.

Finally, the simple act of measuring or marking has been shown to affect the quality of inference that can be made in certain ecological studies (Cahill et al. 2001, Jackson and Wilson 2002). The GPS collars we used were not especially heavy (<2% of cougar bodyweight) but were bulky. If wearing a collar did affect cougar predatory behavior, it introduced an unknown bias into our estimates of predation parameters. Future studies capable of assessing this potential source of bias would be valuable.

Although we demonstrate that GPS cluster techniques can be expanded beyond Anderson and Lindzey's (2003) application to ungulates and used to identify other prey >8 kg killed and consumed by cougars wearing collars with a 3-hour fix rate, prey <8 kg (e.g., snowshoe hare) are likely to be underestimated by this technique. Such small prey are easily consumed by a cougar in one feeding session spanning <3 hours (K. Knopff, unpublished data), resulting in the lack of cluster creation. Moreover, small prey are often entirely consumed (K. Knopff, unpublished data) and little evidence of the predation event may be available, making the kill difficult to find even if a cluster is created. Neonatal deer might fall into this category if they are killed in the first few weeks of life. Increasing fix rates to detect a greater proportion of smaller prey is possible (Webb et al. 2008), but creation of additional clusters to be visited in the field may be prohibitively labor intensive.

An important finding of our study is that monitoring periods must be long if accurate and precise estimates of cougar kill rate and prey composition are required (Fig. 2). Because handling time, search time, and species killed are all variable, and because cougar predatory events occur infrequently, long intervals of monitoring are required to accumulate a sufficient number of inter-kill intervals and prey types to encompass this variation. For a cougar with a known 180-day kill rate of 0.7 prey >8 kg/week and a prey composition consisting of 72.2% deer, for instance, 36-day subsampling yielded kill rates between 0.38 and 1.55 prey >8 kg/week and a diet of between 25% and 100% deer. Consequently, prey selection or kill rate estimates derived from large-carnivore sample units (i.e., individuals or groups) monitored for short periods could lead to inappropriate conclusions about predator–prey dynamics and about differences in predatory behavior (e.g., between regions, seasons, time periods, or age–sex classes). Most studies of large carnivore predation to date have not addressed this potentially important issue. The duration of monitoring required for quality parameter estimation will depend on the variability and average length of inter-kill intervals and on dietary diversity. Predators with shorter or less variable inter-kill intervals and lower dietary diversity will require shorter monitoring periods.

Where models can be employed for parameter estimation, they may greatly reduce cost and effort associated with monitoring over the duration necessary to generate quality estimates. *K*-fold validation of our top logistic regression model supports the assertion of Anderson and Lindzey (2003) that such models can be used effectively to predict cougar kill rates. Our best model, however, proved to be quite different from the univariate number of nights at a cluster model adopted by Anderson and Lindzey (2003). Because cougars in our study displayed high fidelity to kill locations, commonly produced non-kill (bed-site) clusters at night, and occasionally produced clusters at predation events with only diurnal locations associated with them, we used the number of 24-hour periods to approximate Anderson and Lindzey's (2003) number-of-nights model. This univariate model, however, did not perform well when compared with other models in our candidate set (Akaike wt = 0.00). Our much larger sample size, inclusion of non-ungulate prey, and incorporation of a wider variety of explanatory variables may account for the difference in performance between studies. In addition, cougars in west-central Alberta did not consistently use day beds >200 m from the kill as they did in Wyoming (Anderson and Lindzey 2003) and in California (Beier et al. 1995). In regions where remote day beds are common, a covariate or interaction term incorporating the proportion of nocturnal fixes at a cluster may be an important addition to our model. Although we suspect that our more comprehensive top model might improve on the univariate model outside our study area, we caution against its unguarded application. External validation using a representative sample of age–sex classes of cougars from several study areas will be required to fully assess the model's broader applicability. Such broad-scale meta-analyses should be possible in the near future given the prevalence of GPS collar use in contemporary studies of cougar ecology.

An essential caveat for the predictive success of our logistic regression models was the appropriate selection of the probability cutoff used to distinguish kills from non-kills (Table 3). A probability cutoff of 0.5 is automatically applied by most statistical software packages, and there may be some statistical benefits associated with its use (Hosmer and Lemeshow 2000). However, if prediction is the primary goal, cutoff selection using sensitivity–specificity analysis is preferred (Hosmer and Lemeshow 2000). Use of a 0.5 cutoff in the wolf kill rate model of Zimmermann et al. (2007), therefore, may have resulted in the inappropriate conclusion that the model was of little predictive use. We would have concluded similarly if we applied only a 0.5 cutoff when evaluating our kill model (Table 3). However, the blind application of sensitivity–specificity–defined optimal cutoffs also should be avoided (Fielding and Bell 1997). Estimating the spatial distribution of predation risk, for instance, requires that kill locations are identified on a landscape and related to habitat characteristics (e.g., Hebblewhite et al. 2005, Kauffman et al. 2007). Using the optimal cutoff of 0.22 to identify kill locations would result in the incorporation of many non-kill locations (false positives) into the sample, resulting in substantial model contamination, which could be reduced by selecting a more conservative cutoff (e.g., 0.5 or higher). Conversely, when using the logistic model to improve field efficiency by eliminating some non-kill clusters from the visited sample while retaining most kills, a cutoff well below the optimum should be employed. The appropriate probability cutoff level, therefore, must be selected for each intended application of the logistic model.

Unfortunately, the multinomial models we used to predict cougar prey composition were not nearly as useful. The reasonable classification success we experienced was an artifact of the large number of deer in the sample and the propensity for the model to predict deer. Webb et al. (2008) obtained an equivalent result when using multinomial models to separate rare events (large or small prey) from each other and from a common event (no prey) at wolf GPS telemetry clusters. Webb et al. (2008) reported high model classification success (88%), but the ability to predict rare events (kills) was poor and the model misclassified 82% of small prey and 40% of large prey as non-kills. Precise estimates of prey composition are critical for certain management and conservation scenarios such as identifying disproportionate population-level prey selection, which can lead to asymmetrical apparent competition (Chaneton and Bonsall 2000, Cooley et al. 2008), or detecting predators specializing in small populations of alternate prey (Knopff and Boyce 2007). For such applications, the underrepresentation of non-deer prey in our model predictions is unacceptable. The failure of multinomial models to effectively predict cougar prey species composition in west-central Alberta, however, does not preclude the use of such models to predict prey composition for other predators or for cougars in other places, especially where prey exhibit strong spatial segregation.

MANAGEMENT IMPLICATIONS

Studies of cougar predatory behavior conducted prior to the advent of GPS collar technology were constrained by available sampling techniques, resulting in estimates of behavioral parameters of predation that were generally derived from small sample sizes and short monitoring periods. Thus, the scope of appropriate inference and hypothesis-testing regarding cougar predation has been limited. Global Positioning System telemetry cluster techniques offer a substantial improvement in efficiency for estimating these parameters, allowing detailed monitoring of predation histories over long periods for large numbers of cougars simultaneously. Although we found that we could estimate cougar kill rate using models alone, field visitation yields far better data and is a superior alternative when resources permit. We therefore recommend that researchers and managers wishing to understand and quantify the effects cougars have on populations of prey use logistic model probability to direct field visitation when estimating parameter values. Field visitation is especially crucial in multi-prey systems where apparent competition or individual cougar specialization is suspected and their identification is important for effective ungulate management. Proper application of GPS cluster techniques over sufficient monitoring periods will promptly remedy the current paucity of detailed predation histories for individual cougar, improving the quality of parameter estimates and providing opportunities to enhance hypothesis testing and perhaps to resolve some of the controversy surrounding the effects cougars and other large carnivores have on their prey.

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