



Comparing Ground Telemetry and Global Positioning System Methods to Determine Cougar Kill Rates

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ABSTRACT We assessed whether use of 2 methods, intensive very high frequency (VHF) radiotelemetry and Global Positioning System (GPS) cluster sampling, yielded similar estimates of cougar (*Puma concolor*) kill rates in Yellowstone National Park, 1998–2005. We additionally determined biases (underestimation or overestimation of rates) resulting from each method. We used modeling to evaluate what characteristics of clusters best predicted a kill versus no kill and further evaluated which predictor(s) minimized effort and the number of missed kills. We conducted 16 VHF ground predation sequences resulting in 37 kill intervals (KIs) and 21 GPS sequences resulting in 84 KIs on 6 solitary adult females, 4 maternal females, and 5 adult males. Kill rates (days/kill and biomass [kg] killed/day) did not differ between VHF and GPS predation sampling methods for maternal females, solitary adult females, and adult males. Sixteen of 142 (11.3%) kills detected via GPS clusters were missed through VHF ground-based sampling, and the kill rate was underestimated by an average of 5.2 (95% CI = 3.8–6.6) days/kill over all cougar social classes. Five of 142 (3.5%) kills identified by GPS cluster sampling were incorrectly identified as the focal individual's kill from scavenging, and the kill rate was overestimated within the adult male social class by an average of 5.8 (95% CI = 3.0–8.5) days/ungulate kill. The number of nights (locations between 2000 hours and 0500 hours) a cougar spent at a cluster was the most efficient variable at predicting predation, minimizing the missed kills, and minimizing number of extra clusters that needed to be searched. In Yellowstone National Park, where competing carnivores displaced cougars from their kills, it was necessary to search extra sites where a kill may not have been present to ensure we did not miss small, ungulate prey kills or kills with displacement. Using predictions from models to assign unvisited clusters as no kill, small prey kill, or large prey kill can bias downward the number of kills a cougar made and bias upward kills made by competitors that displace cougars or scavenge cougar kills. Our findings emphasize that field visitation is crucial in determining displacement and scavenging events that can result in biases when using GPS cluster methods in multicarnivore systems.

KEY WORDS bias, cluster sampling, cougar, Global Positioning System (GPS), kill rate, multicarnivore, *Puma concolor*, scavenging, very high frequency (VHF), Yellowstone National Park.

Predation can directly influence characteristics and dynamics of prey, including sex–age composition, distribution, and grouping behavior, sometimes limiting population size and growth rates (Ballard et al. 2001, Creel et al. 2005, Hernández and Laundré 2005, Mao et al. 2005). Understanding the frequency at which large carnivores kill ungulate prey per unit of time, termed the kill rate, is an important component of determining carnivore influences on prey species, from year to year, across state management units and regions, and of understanding ecosystem processes. The objectives in estimating kill rates can vary from determining the number of kills/individual predator per unit time, the proportion of prey killed each year (total predation response), or the variation in kill rate, to determining factors that influence kill rates or comparing the kill rates of different carnivore species. Kill rates may differ with prey species' composition, vulnerability, and biomass, as influenced by sex and age of the prey and by sex and age of the predator population (Murphy 1998, Anderson and Lindzey 2003, Mattson et al. 2007).

Locating kills of large carnivores, such as cougars (*Puma concolor*) and wolves (*Canis lupus*), is difficult because carnivores range over wide areas, can consume prey quickly

(e.g., wolf packs), or are secretive and conceal their kills to reduce detection by competitors and scavengers (e.g., cougars; Connolly 1949, Beier et al. 1995). Such behaviors generally result in high cost per effort, limit sample sizes (no. of individuals monitored and length of time monitored), and potentially undermine statistical and biological inferences related to predation (Anderson and Lindzey 2003, Hebblewhite et al. 2003, Knopff et al. 2009). Before Global Positioning System (GPS) technology, kill rates of cougars and wolves were variously estimated using snow tracking (Connolly 1949, Huggard 1993, Hebblewhite et al. 2003), daily aerial tracking (Peterson 1977), ground observations (Murie 1944), energetic models (Ackerman et al. 1986, Laundré 2005), intensively monitoring radio-collared individuals (Shaw 1977, Beier et al. 1995, Murphy 1998), and a combination of methods (Smith et al. 2004). These methods have advanced understanding of predation rates but also have limitations. Aerial and ground methods can miss kills of small prey for which handling times are generally short (Smith et al. 2004, Sand et al. 2005, Webb et al. 2008). Hazards to human safety (e.g., from grizzly bears [*Ursus arctos*] and avalanches) and limited road access in remote areas generally limit ground very high frequency (VHF) methods to daytime locations, potentially resulting in missed kills. Thus, more recently, GPS collars have enabled increased duration of sampling intervals and sample sizes, resulting in decreased bias and increased precision

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when sampling large carnivore predation (Anderson and Lindzey 2003, Sand et al. 2005, Matson et al. 2007, Webb et al. 2008, Knopff et al. 2009). Global Positioning System radiocollars provide the opportunity to locate kill sites from clusters of locations without the need for intensive aerial and ground telemetry monitoring or tracking in snow (Anderson and Lindzey 2003, Sand et al. 2005, Webb et al. 2008, Knopff et al. 2009).

Various approaches to defining clusters of GPS locations, followed by field searches of cluster sites, have been employed to model the probability of a cluster containing no kill, a large prey kill, or a small prey item (Anderson and Lindzey 2003, Mattson et al. 2007, Webb et al. 2008, Knopff et al. 2009). To further enhance sampling efficiency, probabilities have been extended to classify unvisited clusters as no kill or large or small prey kill and used to calculate kill rate (Mattson et al. 2007, Webb et al. 2008). Although these methods have proven promising, various challenges remain, and results for approaches on one carnivore species at one study site may be limited in application at another site (Webb et al. 2008). Distinguishing nonkill sites from kill sites of small prey is an acknowledged challenge (Sand et al. 2005, Franke et al. 2006, Webb et al. 2008), potentially complicated by scavenging (Fuller 1991, Huggard 1993, Murphy 1998, Logan and Sweanor 2001, Bauer et al. 2005) and displacements by competing carnivores (Murphy 1998, Anderson and Lindzey 2003, Ruth 2004), which may introduce error into kill rate estimates if not accurately detected. In multicarnivore systems, kill rates of dominant species may appear lower if displacement events are missed or, alternatively, may appear higher when kills made by a subordinate carnivore are incorrectly assigned to the dominant carnivore. Ultimately, it is important to determine and avoid biases when estimating kill rates for any of the various purposes.

Ongoing research by the Yellowstone Cougar Project seeks to quantify interference competition between cougars, wolves, and bears at cougar kills and to determine whether such competition increased cougar kill rates after wolf reintroduction (Ruth 2004). During a prewolf study on cougars, GPS technologies were not available, and Murphy (1998) developed an intensive VHF ground-telemetry sampling procedure to estimate cougar kill rates. Our postwolf reintroduction study initially employed these VHF methods, but we additionally used GPS technology to increase sample sizes and to quantify bias associated with daytime-limited VHF predation sequences. As part of this larger project, our objectives were to 1) determine whether kill-rate estimates from intensive VHF ground sampling and GPS sampling corroborate each other, 2) evaluate factors that best predicted the probability of a kill from GPS clusters yet minimized effort and number of missed kills, and 3) assess sources of bias in both methods in a multicarnivore system. Kill rates presented here are for comparisons of sampling methods and should not be cited as final cougar kill rates for our study area. Those rates will be presented in future publications.

STUDY AREA

We studied cougar predation on a 3,779-km² area across the northern range (NR) of Yellowstone National Park (YNP) and adjacent national forest and private land. Cougars used elevations from 1,500 m along the Yellowstone River near Gardiner, Montana, USA, up to 2,900 m near Cooke City, Montana, USA. Vegetation was primarily grassland and sagebrush steppe at lower elevations, dominated by Idaho fescue (*Festuca idahoensis*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and big sagebrush (*Artemisia tridentata*). At higher elevations, a conifer forest of Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) covered about 41% of the northern range (Houston 1982, Wright et al. 2006). Mean annual precipitation varied from 24 cm in the Gardiner basin to 35 cm in the upper Lamar River valley, with average monthly temperatures ranging from -12° C to 13° C (Coughenour and Singer 1996). Vegetation, climate, and geology of the area were described in detail by Houston (1982) and Despain (1990).

Elk (*Cervus elaphus*; 9,500–19,000 animals) and mule deer (*Odocoileus hemionus*; numbering 1,600–2,500) were the most abundant ungulates and served as primary cougar prey during 1987 to 2005 (Lemke et al. 1998, Smith et al. 2004, White and Garrott 2005, Cross 2009, Hamlin and Cunningham 2009). Also present on the study area were 175–225 bighorn sheep (*Ovis canadensis*), 700–1,000 pronghorn antelope (*Antilocapra americana*), <200 moose (*Alces alces*), 100 mountain goats (*Oreamnos americanus*), and small numbers of white-tailed deer (*Odocoileus virginianus*), all of which were occasionally killed by cougars (Murphy 1998, Smith et al. 2004). Bison (*Bison bison*) numbered 2,000–4,000 but were not cougar prey (Murphy 1998). The NR wolf population grew from approximately 48 wolves to 106 wolves in 3–7 wolf packs between 1998 and 2005 (Smith et al. 2005, 2006). Wolves, grizzly bears (about 60–70 animals), and black bears (*Ursus americanus*; unknown abundance) displaced cougars from their kills and, along with coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*), also scavenged kills.

METHODS

We captured adult cougars using hounds and immobilized those cougars with an average (SD) of 8.8 mg/kg (2.59) ketamine in the tree and an additional 2.07 mg/kg (2.10) ketamine and 0.63 mg/kg (0.11) xylazine after we lowered them to the ground. Cougar capture and handling procedures followed Kreeger (1996) and Quigley (2000) and were approved by the Hornocker Wildlife Institute/Wildlife Conservation Society Animal Care and Use Committee (no. 1998-YCW-502) and YNP (research permit no. YELL-SCI-0039). We estimated ages of cougars with unknown birthdays and >9 weeks of age by tooth wear (Ashman et al. 1983, Anderson and Lindzey 2000), body weight, neck measurements, pelage characteristics (Murphy 1998, Anderson and Lindzey 2000), gum-line recession (Anderson and Lindzey 2000, Laundré et al. 2000), and by evidence of lactation or previous suckling for females

(Anderson and Lindzey 2000). We fitted adults (>30 months), independent subadults (14–30 months), and dependent kittens (4.5 weeks to 18 months) with VHF transmitter collars (MOD 125, 225, 400, 500; Telonics®, Inc., Mesa, AZ). We affixed each VHF collar with a treated-canvas expansion splice (subadults), durable seatbelt splice (resident adults), or an elastic expansion collar that we designed and affixed to kitten transmitters (MOD 125 and 225). All canvas splices expanded. Some canvas splices were torn halfway through in 10.5–36 months, whereas other canvas splices rotted and broke away within 18–35 months. A durable seatbelt splice rotted and broke within 5 years for one adult that eluded recapture. We replaced most collars and eventually removed them from adults through recapture.

We fitted a subsample of adult cougars with store-on-board or query-on-demand GPS collars (Telonics, Inc. and Televilt®, Inc., Lindesberg, Sweden). As with VHF transmitter packages, we were concerned about the size of the transmitter box for collaring a hypercarnivorous species reliant on head mobility to kill prey. Transmitter box dimensions ranged from $6.9 \times 5.1 \times 3.6$ cm (length \times ht \times depth) for the largest Telonics VHF collar (MOD 500), $10.9 \times 6.9 \times 5.8$ cm for Telonics store-on-board collars, $8.6 \times 9.8 \times 8.0$ cm for Televilt Simplex, and $8.5 \times 6.1 \times 6.4$ cm for Televilt Tellus models. Therefore, we only placed Telonics store-on-board collars on adult male cougars (average neck circumference = 47.5 cm), whereas we placed other GPS collars on adult females (neck circumference, \bar{x} = 38.9 cm) as well as males. Weight of GPS collars was 0.95–2.2% of cougar body mass. Because each collared individual was part of a long-term population-monitoring program, we did not use remote-release mechanisms on GPS collars until the final year of the study.

We either randomly selected a radiocollared cougar from 1 of 3 social classes (ad M, ad F, maternal F) before initiating a predation sequence, or we sampled a radiocollared cougar and GPS predation sampling simultaneously. An estimated 68% and 88% of adult cougars present on the study area were radiomarked by winters 2000–2001 and 2001–2002, respectively. The adult study population remained stable during our sampling; thus, we sampled with replacement, although individuals were only available for resampling in different seasons and different social classes. For example, if we conducted a predation sequence on a solitary, adult female cougar during winter, she was only available for resampling as a maternal female or in summer. Because of GPS collar malfunctions, we were only able to sample one maternal female with GPS methods. Otherwise, we sampled 3–5 individuals with VHF and 3–5 individuals with GPS methods within each social class. We sampled 80% of the average, estimated, adult population during our study.

During a VHF predation sampling sequence, our goal was to locate the focal cougars 1–3 times each day, search every prior location site, and continue the sequence until we documented ≥ 2 ungulate prey (elk, deer, bighorn sheep, antelope; Murphy 1998). Because access was limited to one road on our study area, we obtained all ground locations by

hiking in an arc around the cougar to triangulate its location. We obtained ≥ 3 compass bearings and triangulated the location of the focal cougar without disturbing the individual or family group. On average, we intensively searched location sites within 2 days (range = 0–18) after cougars left the area to locate prey carcasses.

For GPS predation sampling, we used 3 types of GPS collars as different models of collars became available and were deployed (Table 1). We first used Telonics store-on-board collars programmed to attempt 8 location fixes, primarily during night and crepuscular hours at 0100 hours, 0700 hours, 1400 hours, 1600 hours, 1800 hours, 1900 hours, 2100 hours, and 2300 hours. After March 2003, we used only Televilt-brand collars and programmed them to attempt 8 fixes at 3-hour intervals between 0200 hours and 2300 hours. We retrieved data from collars through preprogrammed (Televilt Simplex collars) or query-on-demand (Televilt Tellus collars) downloads or when we retrieved the collar through remote collar release, recapture, or death of the cougar. We plotted location data in Arc8.0 and sequentially inspected it to identify location clusters. We identified clusters of ≥ 2 GPS locations < 200 m apart as candidates for ground investigation (Anderson and Lindzey 2003, Mattson et al. 2007). We included locations separated by ≥ 1 day in the cluster because such events can occur when females depart kills to retrieve kittens from hiding spots. On average, we investigated location clusters within 196 days (range = 1–460) for store-on-board data and 11 days (range = 0–79) for data from remote downloads. Because location clusters may not form at some cougar kill locations (Knopff et al. 2009), we evaluated if, and how many, kills we missed through cluster-only sampling by searching every GPS location ($n = 392$) downloaded during 3 time frames on 3 individual cougars we located for a range of 10–43 days. We searched locations within an average of 8 days (range = 1–27) from time of fix.

To further evaluate proportion of kills missed by each method, we employed simultaneous VHF and GPS sampling during 4 predation sequences; that is, we searched clusters of locations ($n = 3$ sequences) or every location ($n = 1$ sequence) from GPS downloads during the same time frame as the VHF ground sampling. Field personnel conducted VHF ground sampling, as described above, independent of knowledge from GPS downloads. We coded kills as to whether we located them through VHF ground sampling, GPS sampling, or through both methods.

We obtained 95% of ground locations between 0800 hours and 1600 hours. We used this time frame to determine whether we would have missed any GPS kill clusters during VHF sampling outside of simultaneous sampling periods.

We searched all location sites of cougars that we obtained through focal, individual VHF sampling and 2,733 of 13,987 (19.5%) GPS locations. For focal, individual VHF sampling, we intensively searched location sites by following compass bearings, determining a site center and error (\bar{x} = 33 m, SD = 81, $n = 641$), and walking 5–10-m-wide strip-transects in all directions out to the boundary of compass bearings, generally all < 200 m. If we located no kill or other

Table 1. Global Positioning System (GPS) collars and fix success for adult cougars on the northern range of Yellowstone National Park, 1998–2005.

Cougar no.	Social class	GPS model ^a	Range of dates	No. of days monitored	No. of possible fixes	No. of successful fixes	Successful fixes (%)	Comments
M127	Ad M	Gen II store-on-board	Feb–May 2001	63	504	370	73.4	GPS unit damaged
M137	Ad M	Gen II store-on-board	Feb–Jun 2001	117	944	710	75.2	GPS unit damaged
M148	Ad M	Gen II store-on-board	Mar 2002–Feb 2003	329	1,650	1,296	78.5	
F125	Maternal F	Simplex programmed download	Mar 2003	14	112	59	52.7	No predation
F107	Maternal F	Simplex programmed download	Mar–Jul 2003	121	968	571	58.4	No predation
M148	Ad M	Simplex programmed download	Mar–Nov 2003	253	2,024	1,201	59.3	
F111	Ad F, maternal F	Simplex programmed download	Apr–Jul 2003	92	744	358	48.1 ^b	Dennded 30 May
F112	Ad F, maternal F	Simplex programmed download	Apr–Oct 2003	180	1,440	906	62.9 ^c	Dennded 6 Sep
M131	Ad M	Simplex remote download	Jan–Mar 2004	76	196	152	77.6	
F107	Ad F, maternal F	Simplex remote download	Feb–Sep 2004	221	1,544	356	20.2 ^d	Dennded 4 Jun
M127	Ad M	Simplex programmed download	Mar–Apr 2004	59	382	311	81.4	
F125	Maternal F	Simplex programmed download	Jan–Nov 2004	295	2,010	1,259	62.6	
F125	Ad F, maternal F	Tellus remote download	Feb–Dec 2005	320	2,560	2,179	85.1 ^e	Dennded 25 Jun
M192	Ad M	Tellus remote download	Feb 2005	9	64	61	95.3	Dropped collar
F47	Ad F	Tellus remote download	Jan–Jun 2005	138	1,112	1,108	99.6	Mortality 11 Jun

^a The GPS manufacturers were Telonics, Inc. (Mesa, AZ) for GenII store-on-board and Televilt, Inc. (Lindesberg, Sweden) for Simplex–programmed download and Simplex and Tellus remote download systems.

^b Predenning = 64.2%; postdenning = 27.6%.

^c Predenning = 67.7%; postdenning = 37.5%.

^d Predenning = 21.5%; postdenning = 19.0%.

^e Predenning = 87.9%; postdenning = 83.2%.

sign (tracks, bed sites, scrapes), we continued searching in larger transects in all directions up to 400 m (distance cougars may bed from a kill; Beier et al. 1995) from the site center. We located GPS cluster sites using a hand-held GPS receiver and visited every location identified in the entire cluster, even if we found a kill at a previous GPS location. If we found no kill at cluster locations, we walked 5–10-m-wide strip-transects within the area described by the outer points of the cluster (Anderson and Lindzey 2003). If we still located no kill or other sign, we continued searching up to 400 m beyond the cluster center.

Variables we recorded at each site included presence or absence of a carcass, cougar sign, number of bed sites and toilets, distance to nearest bed site from the kill or location center, slope, aspect, predominant vegetation type (Despain 1990), estimated percentage of carcass consumption, injuries or arthritic bones of the prey, and scavenger sign. We additionally identified species and sex–age class (young of yr, yearling, or ad) of prey carcasses from skeletal or hair remains. Remains of adults or calves that we could not sex in the field were sexed by technicians via gender polymerase chain reaction amplification at Wyoming Game and Fish Laboratory (Laramie, WY; Anderson and Lindzey 2003). We used exterior condition of bones (e.g., oily, dry, chalky), presence and condition of bone marrow, and vegetation growth under and around bones to determine whether remains were of an age consistent with the suspected

predation event (following Anderson and Lindzey 2003). In some cases, we located multiple kills of similar time-since-death at cluster sites. Because these cases were typically associated with delayed site investigations from store-on-board collars, we were unsure whether the focal cougar made all the kills. Consequently, we removed these kills and the kill interval from analyses.

We used a categorization chart with increasing supporting evidence to categorize kills as possible, probable, or positive cougar kills (Kunkel et al. 1999, Ruth and Buotte 2007). Evidence that provided support of a probable or positive cougar kill included hemorrhaging or bites to the throat or base of skull, no hemorrhaging or bites along the legs, caching or burial of the kill, and presence of bed sites (with cougar hair present) and toilets, which suggested a cougar had spent enough time at the kill to eat and defecate (Connolly 1949, Beier et al. 1995, Bank and Franklin 1998). We used only probable and positive kills in analyses.

Kill Rate Calculations

Various methods have been used to locate kill sites and estimate kill rates of wolves and cougars (Anderson and Lindsey 2003, Hebblewhite et al. 2003, Smith et al. 2004, Sand et al. 2005, Knopff et al. 2009). Our objectives were not a presentation of cougar kill rate per se, but a comparison of methods and potential sources of error. We

used the kill interval as our sampling unit rather than number of kills per sampling interval as suggested by Hebblewhite et al. (2003). We calculated the kill interval (KI) as the number of days from the day one kill was made to the day before the next kill (also see Murphy 1998), and therefore, KI included the time a cougar spent at a kill (handling time) and time associated with other behaviors (e.g., bedded, traveling, hunting, mating) before the next kill. Thus defined, each KI was determined by the study animal, not by sampling interval length. We did not include in any KIs kills we documented on the first day of initiating a VHF predation sequence and times we lost VHF telemetry contact with a cougar during the predation sequence. That is, for comparison of VHF telemetry and GPS methods, we did not estimate KIs and kill rates over a larger time frame (e.g., winter, annual).

We averaged KIs for all individuals within a social class (solitary ad F, ad M, and maternal F) for each of the VHF and GPS sampling methods. We standardized kill rates for comparison by converting daily kill rates to biomass (kg) of ungulate killed per day (Murphy 1988). We estimated weights of elk and deer by using sex-specific growth models constructed by Murphy (1998) from empirical data on live and field-dressed weights (Johnson 1951, Quimby and Johnson 1951, Greer and Howe 1964, Robinette et al. 1973, Anderson et al. 1974). We estimated weights of other ungulate prey from the literature (O'Gara 1968, Festa-Bianchet et al. 1996). We compared VHF to GPS kill rates for the 3 cougar social classes using days/ungulate kill and biomass (kg) of ungulate/day with Mann-Whitney U tests.

GPS Clusters and Model Development

Using chi-square tests, we tested whether distribution of times (i.e., successful GPS locations) we first located cougars at clusters differed for large kills (i.e., >80 kg), small kills, or where no kill was present. We used modeling to evaluate what characteristics of clusters best defined a kill versus no kill (see also Anderson and Lindzey 2003, Webb et al. 2008, Knopff et al. 2009), yet our goal was to evaluate which predictor(s) minimized effort and number of missed kills. We used logistic regression analyses (Hosmer and Lemshow 2000, Anderson and Lindzey 2003) and multimodel inference (Burnham and Anderson 2002) to assess predictive models on the odds of a cluster containing a kill (we coded a kill as 1 and absence of a kill as 0) as a function of 1) number of nights (from 2000 hours to 0500 hours) at a cluster, 2) duration (hr) at a cluster, 3) minimum distance (m) between consecutive cluster locations, 4) number of nighttime locations in a cluster, 5) proportion of cluster locations occurring at night, and 6) search delay, that is, days between cluster initialization (first day in a cluster) and the date field crews visited the cluster to search for prey remains (Webb et al. 2008). We also explored the same factors in predicting prey size (we coded large prey >80 kg as 1, small prey \leq 80 kg as 0) and whether a cougar had been displaced from its kill (we coded displacement as 1, no displacement as 0). Duration and number of nights at a cluster were highly correlated ($R = 0.95$, $P = 0.00$), thus we did not include

them in the same model. We used model-averaged estimates (Burnham and Anderson 2002) to calculate 95% confidence intervals and evaluated efficiency of predictors with 95% confidence intervals that did not bound zero for models that were highly supported (change in Akaike's Information Criterion adjusted for small sample size [ΔAIC_c] < 2.0) and those that were plausible ($2.0 < \Delta AIC_c < 7.0$) in the model set. We evaluated each predictor's efficiency by plotting the proportion of kill clusters that would be missed and the proportion of empty clusters that would need to be searched at varying cutoffs for each predictor.

We ranked models based on their ΔAIC_c values (Burnham & Anderson 2002) and assessed model fit with receiver operating characteristic (ROC) curves (Boyce et al. 2002). Receiver operating characteristic curves are a plot of the true-positive fraction versus the false-positive fraction obtained by varying the probability cutoff for classifying an observation. The area under the ROC curve (AUC) for a model with no predictive capacity (a straight line) would equal 0.5, whereas a perfect model would have an AUC of 1.0. Models with an AUC of 0.7–0.9 are considered to have useful application, and those with AUC values >0.9 to be highly accurate (Swets 1988, Manel et al. 2001).

RESULTS

We collared 83 cougars (6 ad M, 13 ad F, 9 subadult M, 3 subadult F, 28 M kittens, 24 F kittens) with VHF transmitters from March 1998 through March 2005. We fitted a subsample of 10 adult cougars (5 M, 5 F) with GPS collars of various makes and models between February 2001 and November 2006 (Table 1). We monitored GPS-collared cougars for periods that averaged 152.5 days (range = 9–329 days) for a total of 76 radiomonths.

Between 16 November 1998 and 25 June 2005, we conducted 16 VHF predation sequences, resulting in 37 KIs, and 21 GPS sequences, resulting in 84 KIs on 6 solitary adult females, 4 maternal females, and 5 adult males. The VHF ground predation sequences averaged 30.4 days (range = 17–68 days), and continuous GPS sampling averaged 38.1 days (range = 5–194 days). Kill intervals ranged from 1 day to 21 days for VHF predation sequences and from 1 day to 24 days for GPS sequences. We searched 382 ground predation locations, which included 165 locations associated with 53 kills (12 large prey, 41 small prey), 152 bed sites, and 65 locations with other sign (e.g., tracks) or with no obvious cougar sign. We visited 196 GPS location clusters ($\bar{x} = 10$ locations/cluster, $SD = 10.5$), at which we documented 142 kills (58 large prey, 80 small prey, 4 undetermined prey size), 32 bed sites, and 22 sites with other sign or with no obvious cougar sign. Ninety-four percent of GPS locations were searched within 2 weeks of fix time. Of the remaining 24 locations searched between 2 and 67 weeks of fix time, 6 (25%) were bed sites, and 18 (75%) had no identifiable cougar sign. Location sites were searched for 10 minutes to 11 hours ($\bar{x} = 1.5$ hr, $SD = 1.4$ hr), with cluster sites searched the longest and on multiple days.

Kill rates (days/kill) did not differ between VHF and GPS predation sampling methods for maternal females, solitary adult females, adult males, or all adults combined (Table 2). We also found no difference (Table 2) between VHF and GPS methods for the 3 social classes when standardizing kill rate to kilograms of biomass killed per day.

Four VHF predation sequences were conducted simultaneously with GPS predation sequences on 1 maternal female, 1 adult female, and 2 adult males and resulted in 8 VHF KIs and 12 GPS KIs. Median kill rate (days/kill) did not differ ($T = 82.0$, $P = 0.907$) between simultaneous VHF (median = 7.5) and GPS (median = 7.5) sampling methods. Kilograms of biomass killed per day also did not differ ($T = 79.5$, $P = 0.757$) between simultaneous VHF (median = 20.1) and GPS (median = 21.8) sampling methods.

Errors Detected in Sampling Methods

Although we detected no difference in cougar kill rates (days/kill or kg/day) using VHF ground-based and GPS cluster sampling methods, we did identify 2 errors that occurred: missed kills (omissions) and incorrectly associating a kill with the focal individual. Sixteen of 142 (11.3%) kills detected via GPS clusters were missed through VHF-based sampling because only night locations were associated with the cluster. Omission of kills through VHF sampling resulted in an underestimate of kill rate (i.e., overestimated the no. of days in KIs) by an average of 5.2 (95% CI = 3.8–6.6) days per kill for all cougar social classes. For example, a kill rate estimate of 12.2 days/kill (i.e., lower kill rate) resulting from VHF sampling may actually be 7.0 days/kill (i.e., higher kill rate) when GPS sampling methods are used.

Kills missed with VHF sampling included small prey items ($n = 10$); prey with displacement ($n = 6$) by wolves, bears, or cougars; and instances where cougars bedded >1 km from a kill ($n = 1$). We missed one kill of an adult female cougar during VHF predation sampling because she fed on the kill only at night and bedded 2 km away from the kill during the day, as revealed through simultaneous GPS sampling.

No kills found by VHF ground sampling were missed by GPS cluster sampling. However, 5 of 142 (3.5%) kills that were identified by GPS cluster sampling were incorrectly identified as the focal individual's kill. In all 5 cases, GPS-sampled adult male cougars scavenged from other cougar ($n = 1$) or wolf kills ($n = 1$) or displaced other cougars from their kills ($n = 3$). We determined misidentification errors from our simultaneous VHF predation sampling (2 times) or by overlaying GPS location data from other cougars (2 times). In one case, we identified wolf sign at a cougar GPS cluster site. Subsequent overlay of VHF wolf location data indicated wolves made the kill. Male cougar M131 scavenged from the kill 5 days after wolves were observed feeding on the kill and spent a minimum of 29 hours at the kill as determined from GPS location data. Through VHF predation sampling, we documented 3 other cases of cougars scavenging: in 2 cases, a male displaced adult females from their kills, whereas the third case was a subadult female that scavenged discarded parts from a hunter-killed elk. Incorrectly associating a kill with the focal cougar through GPS

Table 2. Very high frequency (VHF) ground and Global Positioning System (GPS)-sampled kill rates of cougars on the northern range of Yellowstone National Park, 1998–2005.

Kill rate by social class	VHF		GPS		P-value ^b
	<i>n</i> ^a	Median	<i>n</i> ^a	Median	
Days/kill					
Maternal F	18	5.0	45	4.0	0.207
Ad F	10	8.5	18	8.5	0.772
Ad M	9	8.0	21	7.0	0.524
Biomass (kg)/day					
Maternal F	18	12.2	40	19.0	0.063
Ad F	8	9.2	17	14.9	0.244
Ad M	9	13.7	20	21.8	0.203

^a The *n* is the kill interval (KI).

^b P-values are from Mann–Whitney tests.

cluster sampling overestimated the kill rate within the adult male social class by an average of 5.8 (95% CI = 3.0–8.5) days/ungulate kill. That is, the kill rate of adult males is probably lower (i.e., more days in KIs because fewer kills actually occurred) than the estimate of 10.0 days/kill determined through GPS sampling. In addition to scavenging, cougars were displaced from 27.5% (24 large and 15 small ungulate prey) of 142 kills, at minimum. Because 73% of displacements were detected during simultaneous VHF sampling and when GPS sites were searched ≤14 days after the kill was made, displacements were probably missed at some clusters investigated >14 days after the kill was made.

GPS Clusters and Models

Times we first located cougars at GPS clusters of kills of large prey ($n = 49$) and small prey ($n = 73$) exhibited a similar distribution ($\chi^2_6 = 5.0$, $P = 0.550$). Seventy-three percent of large kills and 64% of small kills occurred between 2000 hours and 0500 hours (Fig. 1). Kills of large prey peaked at 0200 hours (27%), whereas kills of small prey peaked at 2300 hours and 0200 hours (40% total). By contrast, times we first located cougars at kill clusters, and at locations associated with bed sites or other sign, exhibited different distributions ($\chi^2_7 = 29.2$, $P = 0.000$). The GPS locations not associated with kills but limited to bed sites, scrapes, or tracks were commonly (23%) initiated at approximately 0800 hours with 69% occurring in time intervals from 0800 hours to 1700 hours.

Five of 26 models were strongly to somewhat supported ($\Delta AIC_c < 7.0$) in discriminating kills from nonkill clusters (Table 3). The best model ($\Delta AIC_c \leq 2$) predicting presence or absence of a cougar kill contained the number of hours at a cluster of locations (duration) and the proportion of cluster locations occurring between 2000 hours and 0500 hours. Model-averaged duration ($\beta = 0.13$, 95% CI = 0.07–0.18) and the proportion of nighttime locations ($\beta = 2.61$, 95% CI = 1.28–3.94) indicated that kills were more likely to be present at clusters the longer a cougar was located at a kill and as the proportion of night locations to daytime locations at a cluster increased. Although this model was statistically very useful in predicting a predation event (AUC = 0.93), it carried most of the model weight because of the extended

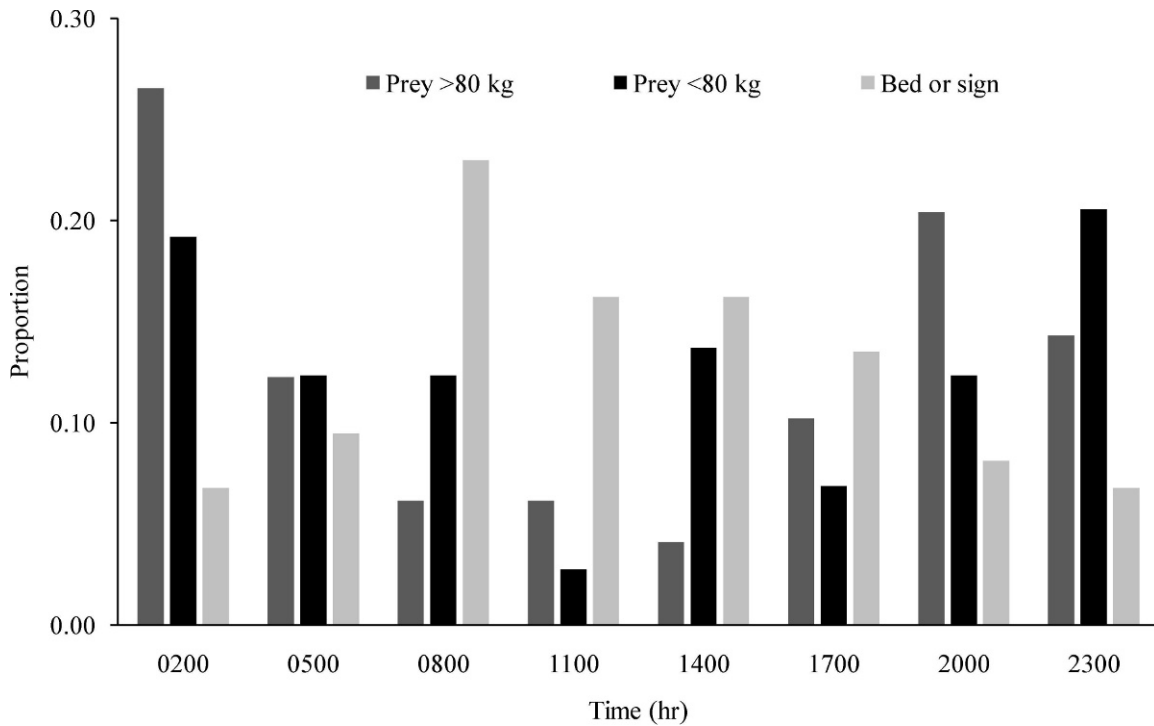


Figure 1. Distribution of time periods we first located cougars at Global Positioning System (GPS) clusters of large prey ($n = 49$) and small prey ($n = 73$), and GPS locations where we confirmed day beds, tracks, or scrapes ($n = 74$) on the northern range of Yellowstone National Park, 1998–2005.

duration (250 hr) cougars occasionally remained at kills. The second-best model added search delay, and the third-best model contained minimum distance between consecutive cluster locations, duration, and proportion of night locations. Search delay (by each 10 days; $\beta = -0.004$; 95% CI = -0.02 to 0.01) and minimum distance between consecutive cluster locations (by 100 m; $\beta = -0.11$; 95% CI = -0.52 to 0.30) had 95% confidence intervals for model-averaged beta estimates that bounded zero. Number of nights (locations between 2000 hours and 0500 hours) at the cluster was included in the fifth model ($\Delta AIC_c = 6.60$) and proved useful in predicting a predation event (AUC = 0.91). The model-averaged beta for number of nights ($\beta = 0.08$, 95% CI = 0.08 – 0.08) did not bound zero, indicating that the odds a kill was present at a cluster increased as the number of nights a

cougar was present increased. Running our models to predict displacement versus no displacement from a kill and predicting a large-prey versus small-prey kill had little useful application based on AUC. The top model for displacement included number of nights in a cluster, with an AUC of 0.669. The top model for prey size was number of nighttime locations in a cluster, with an AUC of 0.669.

Although statistically important, duration at a cluster and proportion of nighttime locations in a cluster were not efficient variables for minimizing missed kills while also minimizing numbers of extra clusters that we needed to search. Using the 3-hour minimum duration between location attempts that our GPS collars were programmed for, a location had a 0.52 probability of predicting cougar predation, but included 53 clusters where no kill was present.

Table 3. Top 5 of 26 logistic regression models with a difference in Akaike's Information Criterion adjusted for small sample size (ΔAIC_c) < 7.0 for discriminating cougar kills from nonkills at 196 Global Positioning System (GPS) location clusters on the northern range of Yellowstone National Park, 1998–2005.

Models ^a	K^b	AIC_c	ΔAIC_c	w_i	ROC AUC ^c
1. Int + duration + proppnight	4	115.56	0.00	0.48	0.93
2. Int + duration + proppnight + search delay	5	117.24	1.68	0.21	0.93
3. Int + duration + proppnight + least	5	117.41	1.85	0.19	0.93
4. Int + duration + proppnight + least + search delay	6	119.09	3.53	0.08	0.93
5. Int + numnights	3	122.15	6.60	0.02	0.91

^a Models are shown in decreasing rank with covariate structure and information theoretic model selection diagnostics AIC_c , ΔAIC_c , and Akaike wt (w_i). Abbreviations: int = intercept; duration = no. of hr at cluster; proppnight = proportion of cluster locations occurring at 2000 hours, 2300 hours, 0200 hours, and 0500 hours; least = min. distance (m) between consecutive cluster locations; numnights = no. of nights (locations at 2000 hours, 2300 hours, 0200 hours, and 0500 hours) at the cluster; search delay = days between cluster initialization (first day in a cluster) and the date field crews visited the cluster to search for prey remains (Webb et al. 2008).

^b K = no. of parameters.

^c We used receiver operating characteristics (ROC) to assess model fit (Boyce et al. 2002). Area under the ROC curve (AUC) for a model with no predictive capacity (a straight line) would equal 0.5, whereas a perfect model would have an AUC of 1.0.

Thus, although we detected all kills with 3-hour durations, we needed to search 53 extra sites where no kill was present. Increasing the duration of time at a cluster to predict a kill decreased the number of extra clusters that we needed to search but increased the number of kills that we would have missed (Fig. 2A). The proportion of nighttime locations in a cluster also did not perform well in the trade-off between kills missed and searching extra clusters (Fig. 2B).

Number of nights at a cluster increased efficiency by minimizing kills that would be missed while also minimizing the number of extra clusters that we needed to search (Fig. 2C). Using ≥ 2 nights at a cluster had a high probability (0.93) of predicting a cougar kill (Fig. 3; Anderson and Lindzey 2003), but we missed 38 of 142 kills (27%), and we needed to search 4 extra sites (no kill). Using ≥ 1 night to define a kill had a lower probability (0.56) of predicting a kill (included more sites where there was no kill), but we missed only one kill (0.7%) and needed to search 24 (45%) extra sites (no kill). The one missed kill resulted from an adult male cougar displacing another adult male cougar and no nighttime locations were associated with the cluster. All adult cougar social classes (solitary F, M, maternal F) exhibited kill clusters with ≥ 1 night. We also evaluated whether missed GPS location fixes resulted in misclassification of 1-night clusters and found only 1 of 55 clusters (1.8%) had the potential of being classified as a 2-night instead of a 1-night cluster.

DISCUSSION

Ground telemetry and GPS methods yielded similar estimates of cougar kill rates for each adult social class, but each method introduced different sources of bias. In our multicarnivore study area, VHF sampling was restricted to primarily daytime locations because we had limited road access in the study area; grizzly bears were active during spring, summer, and fall; and avalanche hazards were high in winter. These conditions made it unsafe and unrealistic to monitor VHF signals via foot travel throughout the night. Detection rates of cougar kills were lower with VHF monitoring 1) when cougars occasionally bedded far from a kill during the day, only visiting the kill at night; and 2) when displacement by other carnivores occurred within a few hours of the kill being made. Kills missed through VHF sampling biased kill rates lower (i.e., increased the KI length because we erroneously excluded kills) than the true kill rate. Thus, calculations of annual prey offtake by cougars (i.e., total predation response) would potentially be underestimated. However, because we were locating cougars ≥ 1 times a day during VHF sampling, with most of the cougar population radiocollared, we were able to scan for other collared cougars and note the presence of competitors as well as avian and mammalian scavenger activity as the days since kill progressed. In addition, we field-searched locations as soon as the cougar left the area, allowing for detection and interpretation of fresh sign, hence, more accurate classification of cause of death at kill sites.

The GPS sampling and cluster techniques provide substantial improvement in efficiency and sample size over VHF

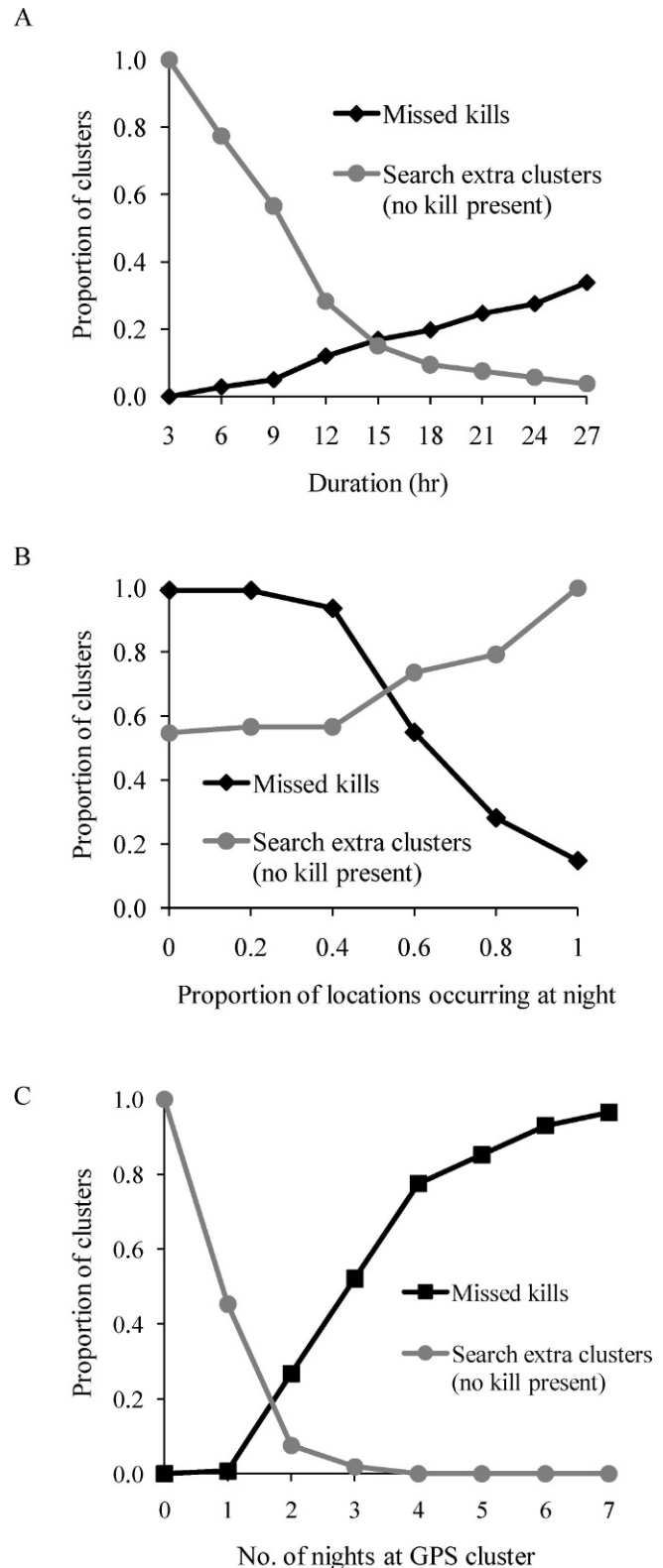


Figure 2. Trade-off in proportion of Global Positioning System (GPS) clusters where we missed cougar kills and searched additional GPS clusters where no kill was present when we defined clusters by (A) 3-hour intervals of duration at a cluster, (B) proportion of locations occurring at night (2000 hr, 2300 hr, 0200 hr, and 0500 hr), and (C) number of nights a cougar was located at a GPS cluster. We sampled cougars on the northern range of Yellowstone National Park, 1998–2005.

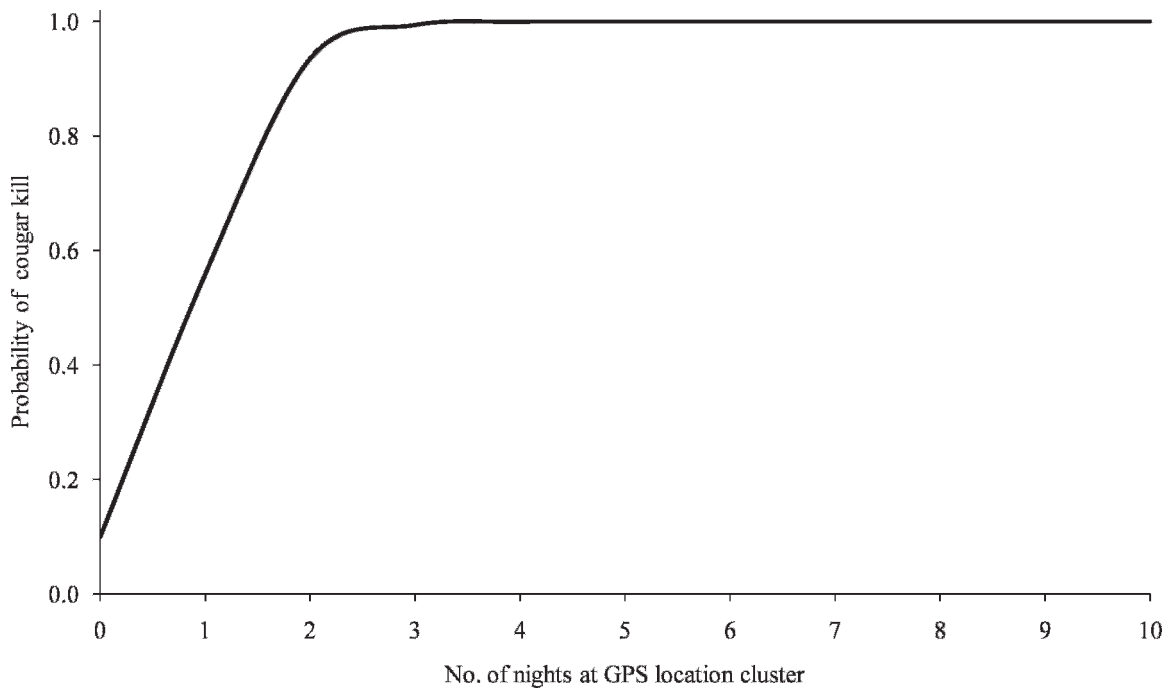


Figure 3. Probability of a cougar kill as number of nights (2000 hr, 2300 hr, 0200 hr, and 0500 hr) at a Global Positioning System (GPS) cluster increased for cougar kills documented with GPS sampling methods on the northern range of Yellowstone National Park, 1998–2005.

sampling techniques, thus improving inferences regarding carnivore predation (Anderson and Lindzey 2003, Hebblewhite et al. 2003, Webb et al. 2008, Knopff et al. 2009). Identifying clusters where kills are present with GPS locations is a robust method, even with low fix success, because cougars generally display high fidelity to kill sites and have long handling times (Knopff et al. 2009). In addition, because GPS collars can be programmed to collect diurnal and nocturnal locations, GPS sampling resulted in detection of nighttime-only kills, which we missed with our VHF methods. However, failing to detect a cluster when prey-handling time is reduced because of human disturbance or displacement by other carnivores or attributing a kill to the focal cougar when it was actually scavenging introduces biases in kill-rate estimations (Murphy et al. 1998, Ruth 2004, Zimmerman et al. 2007). Distinguishing nonkill cluster sites from small-kill and large-kill cluster sites may be particularly challenging in multicarnivore systems (Webb et al. 2008). In our data set, with limited sample sizes, predicting clusters as large prey, small prey, and no kill clusters was confounded by displacement from other carnivores. We identified displacement of cougars from 27.5% of kills within our GPS predation samples through a combination of simultaneous VHF sampling where we observed scavengers approach a kill, searching all clusters of ≤ 2 locations, and quick investigation of field sites. Large kills can erroneously be predicted as small prey, and small ungulate kills can be underrepresented in kill predictions, thus biasing kill rate lower for the subordinate species when calculating biomass (kg) of ungulate per day. Alternatively, kill rates of dominant species, such as wolves, may be reduced if carcasses generated by cougars or other

sources (e.g., winterkill) are frequently encountered and scavenged (Huggard 1993).

Wolf or bear displacement within 1 day can obscure any sign that the kill was made by a cougar, potentially resulting in the kill being classified as cougar scavenging or in the failure of a cluster of cougar locations to have formed at the carcass. Cougar kill rate estimates will be biased higher if clusters that formed at a carcass where cougars were scavenging are classified as cougar kills. Assigning cougar scavenging to clusters where the prey was clearly killed by something other than a cougar is highly dependent on how quickly a cluster is visited (Knopff et al. 2009), and cougar scavenging on another cougar kill could easily go undetected. The high variability in scavenging documented for various study areas, ranging from infrequent (this study, Murphy 1998, Anderson and Lindzey 2003) up to 43% reported in southern California, USA (Bauer et al. 2005), suggest that the influence of scavenging on cougar kill-rate estimation could be minor in some systems and significant in others.

Although predictors in our best model differed from the number of nights at a cluster model adopted by Anderson and Lindzey (2003), our assessment of field efficiency in reducing number of missed kills and sites to be searched supported this predictor in our multicarnivore system. Certainly, various predictors may be evaluated to successfully define clusters from GPS locations (see Anderson and Lindzey 2003, Webb et al. 2008, Knopf et al. 2009). Yet, using predictions from models to assign unvisited GPS clusters as no kill, small-prey kill, or large-prey kill should only occur after thorough field investigation of system-

specific biases. Although standardization of methods across study areas should be a goal, there is benefit to establishing site-specific cluster and kill-discrimination rules from the many options now available (Webb et al. 2008). Predictors included in the best model may have high predictive capabilities yet vary in efficiency of trade-off between missing kills and including searches of clusters where no kill may be present. Assessing efficiency of individual variables, such as we did, or through selection of a probability cutoff, such as Knopff et al. (2009), at an early stage of GPS cluster sampling will improve field efficiency and predictive capabilities of cluster modeling. In YNP, the duration cougars remained at large-prey and small-prey kills was similar, but duration was less when cougars were displaced by a dominant carnivore than when they were not displaced; thus, it was necessary to search extra sites where no kill may have been present. Protocols that increase field visitation of a greater number of clusters to maximize detection of small prey during summer or displacements and scavenging will depend on the questions addressed within the study system (Knopff et al. 2009).

Several options may reduce biases when using GPS locations to determine kill rates of carnivores, many discussed previously by Sand et al. (2005). Increasing the fix rate to help detect displacement events is possible but will reduce the life span of the GPS transmitters, and creation of additional clusters to be visited in the field will increase labor intensity (Sand et al. 2005, Webb et al. 2008, Knopff et al. 2009). Although also costly, placing GPS collars on all competing carnivores would aid in detecting displacement and in reducing biases introduced by scavenging. Scavenging and displacement errors can be minimized by cross-checking for duplicate clusters of all GPS-collared individuals during a certain time frame and through overlay of VHF and GPS locations of other collared cougars and competing carnivores. When monetary resources are limited, biologists might consider an early pilot study using daily VHF sampling simultaneously with GPS sampling to determine displacement and scavenging biases, then using the data to develop a cluster-modeling approach with testing on the new data as proposed by Webb et al. (2008). Using query-on-demand download schedules to reduce time between kill and field-site searches would enhance GPS methods because the freshest evidence of predator and scavenger activity is the easiest to detect and interpret. Field personnel need to be well trained to determine cause of death and to recognize signs of predators and scavengers in the system. Biases may need to be reassessed if prey availability or carnivore density changes during the study. For example, as our study progressed, the elk calf:female ratio declined (Cross 2009), the ratio of females to calf elk increased in the cougar-kill sample, and the wolf population increased (Smith et al. 2005, 2006). The odds a cougar was displaced from a kill by wolves and bears was greater for large ungulate prey and also greater as wolf use increased (T. Ruth, Selway Institute, unpublished data). Once site-specific biases are addressed, using standardized methods of estimating kill rates and

variance will facilitate comparison across studies (Hebblewhite et al. 2003).

MANAGEMENT IMPLICATIONS

Although methods to predict kills from clusters and to identify small prey versus large prey continue to improve (Hebblewhite et al. 2003, Webb et al. 2008, Knopff et al. 2009), documenting displacements and scavenging influences on predation rate in multicarnivore–multiprey systems requires field visitation soon after the kill is made. In systems where competing carnivores displace subordinate carnivores from their kills, it may be necessary to increase the number of GPS collars deployed in a given time frame, the frequency at which locations are acquired, and the number of cluster sites searched where no kill may be present to ensure displacements and scavenging are not missed. Employing these recommendations and determining other ecosystem-specific biases will further enhance the estimating of kill rates and the determining factors influencing kill rate, thus, providing greater understanding of the role of predation in multicarnivore–multiprey systems.

ACKNOWLEDGMENTS

We thank M. Hornocker for initiating and providing support to our research. This research would not have been possible without funding support provided by the Richard King Mellon Foundation, the Laura Moore Cunningham Foundation, the Charles Engelhard Foundation, Mr. L. Westbrook, the Michael Cline Foundation, Mr. R. Comegys, the Argosy Foundation, the Summerlee Foundation, the Tim and Karen Hixon Foundation, the National Geographic Society, M. and A. Manship, and the Yellowstone Park Foundation. We thank K. Gunther, K. Murphy, and D. Smith of YNP for unending assistance with field methods and logistical support. R. Stradley (Gallatin Flying Service), S. Monger (Mustang Aviation), and D. Chapman (Montana Aircraft Inc.) provided excellent flying services and aerial support to ground crews. We thank J. Newby, M. Maples, M. Sawaya, E. Shanahan, C. Whitman, and numerous other cougar project technicians for valuable assistance collecting cougar predation data. Veterinarian K. Quigley assisted with cougar capture and handling training and veterinary support. Logistical and research permit support was provided by YNP, Gardiner Office of the U.S. Forest Service, and Montana Department of Fish, Wildlife and Parks. C. Anderson, Jr. and J. Newby provided helpful comments and suggestions on an early draft of this article.

LITERATURE CITED

- Ackerman, B. B., F. G. Lindzey, and T. P. Hemker. 1986. Predictive energetics model for cougars. Pages 333–352 in S. D. Miller and D. D. Everett, editors. *Cats of the world: biology, conservation, and management*. National Wildlife Federation, Washington, D.C., USA.
- Anderson, A. E., D. E. Medin, and D. C. Bowden. 1974. Growth and morphometry of the carcass, selected bones, organs, and glands of mule deer. *Wildlife Monograph* 39.
- Anderson, C. R., Jr., and F. G. Lindzey. 2000. A photographic guide to estimating mountain lion age classes. Wyoming Cooperative Fish & Wildlife Research Unit, Laramie, USA.

- Anderson, C. R., Jr., and F. G. Lindzey. 2003. Estimating cougar predation rates from GPS location clusters. *Journal of Wildlife Management* 67:307–316.
- Ashman, D. L., G. C. Christensen, M. L. Hess, G. K. Tsukamoto, and M. S. Wickersham. 1983. The mountain lion in Nevada. U.S. Fish and Wildlife Service Federal Aid in Wildlife Restoration Project W-48-15, final report, Washington, D.C., and Nevada Department of Wildlife, Reno, USA.
- Ballard, W. B., D. Lutz, T. W. Keegan, L. H. Carpenter, and J. C. deVos, Jr. 2001. Deer–predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer. *Wildlife Society Bulletin* 29:99–115.
- Bank, M. S., and W. L. Franklin. 1998. Puma (*Puma concolor patagonica*) feeding observations and attacks on guanacos (*Lama guanicoe*). *Mammalia* 62:599–605.
- Bauer, J. W., K. A. Logan, L. L. Sweanor, and W. M. Boyce. 2005. Scavenging behavior in puma. *Southwestern Naturalist* 50:466–471.
- Beier, P., D. Choate, and R. H. Barrett. 1995. Movement patterns of mountain lions during different behaviors. *Journal of Mammalogy* 76:1056–1070.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modeling* 157:281–300.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Connolly, E. J. 1949. Food habits and life history of the mountain lion. Thesis, University of Utah, Salt Lake City, USA.
- Coughenour, M. B., and F. J. Singer. 1996. Elk population processes in Yellowstone National Park under the policy of natural regulation. *Ecological Applications* 6:573–593.
- Creel, S., J. Winnie, Jr., B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86:3387–3397.
- Cross, P. C. 2009. Northern Yellowstone Cooperative Wildlife Working Group 2008 annual report. U.S. Geological Survey, Bozeman, Montana, USA.
- Despain, D. 1990. Yellowstone vegetation: consequences of environment and history in a natural setting. Roberts Rinehart, Boulder, Colorado, USA.
- Festa-Bianchet, M., W. J. King, J. T. Jorgenson, K. G. Smith, and W. D. Wishart. 1996. The development of sexual dimorphism: seasonal and lifetime mass changes in bighorn sheep. *Canadian Journal of Zoology* 74:330–342.
- Franke, K. A., T. Caelli, G. Kuzyk, and R. J. Hudson. 2006. Prediction of wolf (*Canis lupus*) kill sites using hidden Markov models. *Ecological Modeling* 197:237–246.
- Fuller, T. K. 1991. Effect of snow depth on wolf activity and prey selection in north central Minnesota. *Canadian Journal of Zoology* 69:283–287.
- Greer, K. R., and R. E. Howe. 1964. Winter weights of northern Yellowstone elk, 1961–62. *Transactions of the North American Wildlife Conference* 29:237–248.
- Hamlin, K. L., and J. A. Cunningham. 2009. Monitoring and assessment of wolf–ungulate interactions and population trends within the Greater Yellowstone Area, southwestern Montana, and Montana statewide: final report. Montana Department of Fish, Wildlife, and Parks, Wildlife Division, Helena, USA.
- Hebblewhite, M., P. C. Paquet, D. H. Pletscher, R. B. Lessard, and C. J. Callaghan. 2003. Development and application of a ratio estimator to estimate wolf kill rates and variance in a multiple-prey system. *Wildlife Society Bulletin* 31:993–946.
- Hernández, L., and J. W. Laundré. 2005. Foraging in the “landscape of fear” and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. *Wildlife Biology* 11:215–220.
- Hosmer, D. W., and S. Lemshow. 2000. Applied logistic regression. Second edition. John Wiley & Sons, New York, New York, USA.
- Houston, D. B. 1982. The northern Yellowstone elk: ecology and management. Macmillan, New York, New York, USA.
- Huggard, D. J. 1993. Effect of snow depth on predation and scavenging by gray wolves. *Journal of Wildlife Management* 57:382–388.
- Johnson, D. E. 1951. Biology of the elk calf, *Cervus canadensis nelsoni*. *Journal of Wildlife Management* 15:396–410.
- Knopff, K. H., A. A. Knopff, M. B. Warren, and M. S. Boyce. 2009. Evaluating Global Positioning System telemetry techniques for estimating cougar predation parameters. *Journal of Wildlife Management* 73:586–597.
- Kreeger, T. J. 1996. Handbook of wildlife chemical immobilization. International Wildlife Veterinary Services, Laramie, Wyoming, USA.
- Kunkel, K. E., T. K. Ruth, D. H. Pletscher, and M. G. Hornocker. 1999. Winter prey selection by wolves and cougars in and near Glacier National Park, Montana. *Journal of Wildlife Management* 63:901–910.
- Laundré, J. W. 2005. Puma energetics: a recalculation. *Journal of Wildlife Management* 69:723–732.
- Laundré, J. W., L. Hernández, D. Struebel, K. Altendorf, and C. López-González. 2000. Aging mountain lions using gum-line recession. *Wildlife Society Bulletin* 28:963–966.
- Lemke, T. O., J. A. Mack, and D. B. Houston. 1998. Winter range expansion by the northern Yellowstone elk herd. *Intermountain Journal of Sciences* 4:1–9.
- Logan, K. A., and L. L. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, D.C., USA.
- Manel, S., H. Ceri Williams, and S. J. Ormerod. 2001. Evaluating presence–absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* 38:921–931.
- Mao, J. S., M. S. Boyce, D. W. Smith, F. J. Singer, D. J. Vales, J. M. Vore, and E. H. Merrill. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. *Journal of Wildlife Management* 69:1691–1707.
- Mattson, D. J., J. Hart, M. Miller, and D. Miller. 2007. Predation and other behaviors of mountain lions in the Flagstaff Uplands. Pages 31–42 in D. J. Mattson, editor. Mountain lions of the Flagstaff Uplands; 2003–2006 Progress Report. U.S. Geological Survey Pen-File Report 2007–1050. <<http://pubs.usgs.gov/of/2007/1062/>>. Accessed 20 Mar 2008.
- Murie, A. 1944. The wolves of Mt. McKinley. United States Government Printing Office, Washington, D.C., USA.
- Murphy, K. M. 1998. The ecology of the cougar (*Puma concolor*) in the northern Yellowstone Ecosystem: interactions with prey, bears, and humans. Dissertation, University of Idaho, Moscow, USA.
- O’Gara, B. W. 1968. A study of the reproductive cycle of the female pronghorn (*Antilocapra americana Ord*). Dissertation, University of Montana, Missoula, USA.
- Peterson, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. United States National Park Service Science Monograph Series 11:1–210.
- Quigley, K. 2000. Immobilization and biological sampling protocols. Hornocker Wildlife Institute/Wildlife Conservation Society, Bozeman, Montana, USA.
- Quimby, D. C., and D. E. Johnson. 1951. Weights and measurements of Rocky Mountain elk. *Journal of Wildlife Management* 15:57–62.
- Robinette, L. W., C. H. Baer, R. E. Pillmore, and C. E. Knittle. 1973. Effects of nutritional change on captive mule deer. *Journal of Wildlife Management* 37:312–326.
- Ruth, T. K. 2004. Ghost of the Rockies: the Yellowstone cougar project. *Yellowstone Science* 12:13–24.
- Ruth, T. K., and P. C. Buotte. 2007. Cougar ecology and cougar–carnivore interactions in Yellowstone National Park; final technical report. Hornocker Wildlife Institute/Wildlife Conservation Society, Bozeman, Montana, USA.
- Sand, H., B. Zimmermann, P. Wabakken, H. Andrèn, and H. C. Pederson. 2005. Using GPS technology and GIS cluster analyses to estimate kill rates in wolf–ungulate ecosystems. *Wildlife Society Bulletin* 33:914–925.
- Shaw, H. 1977. Impact of mountain lion on mule deer and cattle in northwestern Arizona. Pages 17–32 in R. L. Phillips and C. Jonkel, editors. Proceedings of the 1975 Predator Symposium, 16–19 June 1975, University of Montana, Missoula, USA.
- Smith, D. W., T. D. Drummer, K. M. Murphy, D. S. Guernsey, and S. B. Evans. 2004. Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. *Journal of Wildlife Management* 68:153–166.
- Smith, D. W., D. R. Stahler, and D. S. Guernsey. 2005. Yellowstone wolf project: annual report, 2004. Yellowstone Center for Resources, Yellowstone National Park YCR-2005-02, Mammoth, Wyoming, USA.

- Smith, D. W., D. R. Stahler, and D. S. Guernsey. 2006. Yellowstone wolf project: annual report, 2005. Yellowstone Center for Resources, Yellowstone National Park YCR-2006-04, Mammoth, Wyoming, USA.
- Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. *Science* 240:1285–1293.
- Webb, N. F., M. Hebblewhite, and E. H. Merrill. 2008. Statistical methods for identifying wolf kill sites using Global Positioning System locations. *Journal of Wildlife Management* 72:798–807.
- White, P. J., and R. A. Garrott. 2005. Yellowstone's ungulates after wolves—expectations, realizations, and predictions. *Biological Conservation* 125:141–152.
- Wright, G. J., R. O. Peterson, D. W. Smith, T. O. Lemke. 2006. Selection of northern Yellowstone elk by gray wolves. *Journal of Wildlife Management* 70:1070–1078.
- Zimmerman, B., P. Wabakken, H. Sand, H. C. Pedersen, and O. Liberg. 2007. Wolf movement patterns: a key to the estimation of kill rate? *Journal of Wildlife Management* 33:1177–1182.

Associate Editor: Gese.