



Estimating Cougar Predation Rates from GPS Location Clusters

Author(s): Charles R. Anderson, Jr. and Frederick G. Lindzey

Reviewed work(s):

Source: *The Journal of Wildlife Management*, Vol. 67, No. 2 (Apr., 2003), pp. 307-316

Published by: [Allen Press](#)

Stable URL: <http://www.jstor.org/stable/3802772>

Accessed: 29/12/2011 14:15

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Allen Press is collaborating with JSTOR to digitize, preserve and extend access to *The Journal of Wildlife Management*.

<http://www.jstor.org>

ESTIMATING COUGAR PREDATION RATES FROM GPS LOCATION CLUSTERS

CHARLES R. ANDERSON, JR.,¹ Zoology and Physiology Department, University of Wyoming, Box 3166, University Station, Laramie, WY 82071, USA

FREDERICK G. LINDZEY, U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Box 3166, University Station, Laramie, WY 82071, USA

Abstract: We examined cougar (*Puma concolor*) predation from Global Positioning System (GPS) location clusters (≥ 2 locations within 200 m on the same or consecutive nights) of 11 cougars during September–May, 1999–2001. Location success of GPS averaged 2.4–5.0 of 6 location attempts/night/cougar. We surveyed potential predation sites during summer–fall 2000 and summer 2001 to identify prey composition ($n = 74$; 3–388 days post predation) and record predation-site variables ($n = 97$; 3–270 days post predation). We developed a model to estimate probability that a cougar killed a large mammal from data collected at GPS location clusters where the probability of predation increased with number of nights (defined as locations at 2200, 0200, or 0500 hr) of cougar presence within a 200-m radius ($P < 0.001$). Mean estimated cougar predation rates for large mammals were 7.3 days/kill for subadult females (1–2.5 yr; $n = 3$, 90% CI: 6.3 to 9.9), 7.0 days/kill for adult females ($n = 2$, 90% CI: 5.8 to 10.8), 5.4 days/kill for family groups (females with young; $n = 3$, 90% CI: 4.5 to 8.4), 9.5 days/kill for a subadult male (1–2.5 yr; $n = 1$, 90% CI: 6.9 to 16.4), and 7.8 days/kill for adult males ($n = 2$, 90% CI: 6.8 to 10.7). We may have slightly overestimated cougar predation rates due to our inability to separate scavenging from predation. We detected 45 deer (*Odocoileus* spp.), 15 elk (*Cervus elaphus*), 6 pronghorn (*Antilocapra americana*), 2 livestock, 1 moose (*Alces alces*), and 6 small mammals at cougar predation sites. Comparisons between cougar sexes suggested that females selected mule deer and males selected elk ($P < 0.001$). Cougars averaged 3.0 nights on pronghorn carcasses, 3.4 nights on deer carcasses, and 6.0 nights on elk carcasses. Most cougar predation (81.7%) occurred between 1901–0500 hr and peaked from 2201–0200 hr (31.7%). Applying GPS technology to identify predation rates and prey selection will allow managers to efficiently estimate the ability of an area's prey base to sustain or be affected by cougar predation.

JOURNAL OF WILDLIFE MANAGEMENT 67(2):307–316

Key words: cougar, Global Positioning System, GPS, predation model, predation rate, prey composition, *Puma concolor*, Wyoming.

The influences of large carnivores on prey populations and ecosystem processes hinge on predation rates that may vary with prey species composition, by sex and age of prey, and by sex and age composition of the predator population. Cougar predation rates have been estimated by snowtracking (Connolly 1949), energetics models (Hornocker 1970, Ackerman et al. 1986), and via intensive radiotelemetry (Shaw 1977, Harrison 1990, Beier et al. 1995, Murphy 1998, Nowak 1999). Cougar predation studies generally have relied on small samples of cougars, because of the difficulty of snow- or radiotracking these wide-ranging, solitary animals in rugged terrain.

Although deer dominate cougar diets in most areas (Spalding and Lesowski 1971, Ackerman et al. 1984, Logan and Sweanor 2001), elk (Hornocker 1970, Williams et al. 1995, Murphy 1998, Nowak 1999), bighorn sheep (*Ovis canadensis*; Williams et al. 1995, Wehausen 1996, Ross et al. 1997), moose (Ross and Jalkotzy 1996), and livestock (Shaw

1981, Cunningham et al. 1999) can be important in others. Only 2 studies found that cougars selected 1 ungulate species over another, and in both studies, elk were taken over mule deer (*O. hemionus*; Hornocker 1970, Murphy 1998). Within a prey population, however, young and/or solitary animals appear most vulnerable to cougar predation (moose: Ross and Jalkotzy 1996; elk: Hornocker 1970, Murphy 1998, Nowak 1999; feral horses [*Equus caballus*]: Turner et al. 1992; bighorn sheep: Ross et al. 1997; mule deer: Hornocker 1970, Shaw 1977, Logan and Sweanor 2001). Ackerman et al.'s. (1986) predictions based on energetic needs for various sex, age, and reproductive classes of cougars suggested increased predation rates with cougar body mass and reproductive status and were supported by Murphy (1998), although the diets in these studies were primarily mule deer and elk, respectively.

Wildlife studies that have utilized GPS technology have primarily addressed GPS collar performance, reporting large data-storage capacity and high accuracy (Rempel et al. 1995, Moen et al. 1996, Bowman et al. 2000). Application of GPS

¹ E-mail: cander@uwyo.edu

technology to animal movement investigations provides a potential tool for studying predation rates and identifying prey-selection patterns. Our objectives were to determine whether cougar kills of large mammals could be detected from data records of store-on-board GPS collars and, if detectable, to develop a model to estimate probability of a predation event based on characteristics of GPS data records.

STUDY AREA

The Snowy Range, located in southeast Wyoming, USA, about 30 km west of Laramie, is a 2,120 km² portion of the Medicine Bow National Forest surrounded by private, Bureau of Land Management, and state-owned lands. The range is bounded by state highway 230 on the west, US Interstate 80 on the north, the Laramie River and Sand Creek drainages on the east, and the Wyoming–Colorado border on the south. Elevation ranges from about 2,100 m in the valleys to 3,652 m at Medicine Bow Peak. Vegetation communities are dominated by sagebrush (*Artemisia tridentata*) grasslands in the peripheral valleys, lodgepole pine (*Pinus contorta*) with interspersed quaking aspen (*Populus tremuloides*), Rocky Mountain juniper (*Juniperus scopulorum*), and limber pine (*Pinus flexilis*) at mid-elevations, and Engelmann spruce (*Picea engelmannii*)/subalpine fir (*Abies lasiocarpa*) forests with occasional limber pine (Alexander et al. 1986) at higher elevations. Understory dominants in the mid- and high-elevation communities include huckleberry (*Vaccinium scoparium*), buffaloberry (*Shepherdia canadensis*), serviceberry (*Amelanchier alnifolia*), snowberry (*Symphoricarpos* spp.), and common juniper (*J. communis*). Riparian areas are composed primarily of willow (*Salix* spp.) interspersed with narrowleaf cottonwood (*P. angustifolia*) at low elevations.

Mule deer and elk are the most common ungulates in the Snowy Range. Post-hunting season composition counts during winter 1999–2000 were 492 male, 1,704 female, and 1,161 young mule deer, and 416 male, 1,166 female, and 635 young elk (Wyoming Game and Fish Department 1999). Pronghorn and white-tailed deer (*O. virginianus*) are abundant in adjacent sagebrush–grassland habitats and lower-elevation riparian areas, respectively. Bighorn sheep and moose are present in low numbers. Small mammals common in the Snowy Range include porcupine (*Erethizon dorsatum*), pine squirrel (*Tamiasciurus hudsonicus*), cottontail (*Sylvilagus nuttallii*), and snowshoe hare (*Lepus americanus*) and occasionally

beaver (*Castor canadensis*) and yellow-bellied marmot (*Marmota flaviventris*). Other carnivores include coyote (*Canis latrans*), pine marten (*Martes americana*), bobcat (*Lynx rufus*), and black bear (*Ursus americanus*).

METHODS

We trailed cougars using hounds and immobilized them upon capture with a mixture of 5 mg/kg Telazol® (Aveco Company, Inc., Cherry Hill, New Jersey, USA) and 1 mg/kg xylazine hydrochloride delivered in hypodermic dart fired from a CO₂ pistol. Cougars (>1 yr old and self sufficient) were collared with GPS receivers (GPS2000; Lotek, Inc., Newmarket, Ontario, Canada). We programmed collars to attempt position acquisitions at 1600, 1900, 2200, 0200, 0500, and 0800 hr each day, targeting the nocturnal period when cougars are most likely pursuing prey or feeding (Ackerman 1982, Hopkins 1989, Beier et al. 1995). Age (subadult [1–2.5 yr] or adult [≥ 3 yr]) was estimated from tooth wear, canine ridge eruption, spotting progression, and evidence of lactation for females (Shaw 1979, Ashman et al. 1983, Lindzey et al. 1989). We estimated age of dependent cougars (young of collared females) by backdating to the time of localized denning activity of their mother.

Predation Site Surveys

We downloaded data from collars upon death of the cougar or when we recaptured the animals to remove collars (Apr–May 2000, 2001). Location data were plotted in ArcView® (Environmental Systems Research Institute 1999) and sequentially inspected with the Tracking Analyst extension to identify location clusters. We initially defined location clusters as ≥ 2 locations within 200 m during the same or consecutive 16-hr periods (i.e., 1600–0800 hr). We examined χ^2 goodness-of-fit to assess potential bias ($P < 0.05$) in time of successful GPS location attempts for each cougar. After we identified potential predation sites (location clusters) from GPS collar records, we located them on the ground using a handheld GPS receiver and searched for prey remains by walking 5–10-m-wide strip-transects within the area described by the outer point radius plus 10 m. The U.S. Department of Defense discontinued selective availability in spring 2000, between the period when most cougars were monitored and when potential predation sites were searched. Thus, error associated with cougar locations before spring 2000 was about 43 m (Moen et al.

1996) and that associated with searches was <5 m (Bowman et al. 2000). Variables recorded at potential predation sites included carcass presence or absence, portions of carcasses found, prey species sex/age (young-of-year/adult), cougar sign, and distance from the cluster center point to the carcass. We used exterior condition of bones (e.g., oily, dry, chalky), presence and condition of bone marrow, hair at cache sites, and vegetation growth under and around bones to determine whether remains were of an age consistent with the suspected predation event. Potential predation sites to be searched were initially selected to maximize sample size by choosing clusters close to one another. Other sites were searched as time permitted. We used the longest time period between the potential predation event and when a carcass was found at a 3-night cluster (high probability of predation) to define the period when large-mammal carcass detection may become inconsistent.

Predation Model Development

We used logistic regression analyses (Hosmer and Lemeshow 1989, SAS Institute 1990, Mehta and Patel 1993) to estimate the probability of a large-mammal predation event (carcass presence was coded as 1 and absence as 0) as a function of number of locations in a cluster, number of nights at a cluster (locations from 1600 hr 1 day to 0800 hr the next), presence/absence of daytime locations distant from the cluster (i.e., daybed), sex/age and reproductive class of the cougar, and all combinations of consecutive, nocturnal locations. We hypothesized that nocturnal presence at location clusters represented cougar predation and thus, the latter predictor variable was used to evaluate which combination of nocturnal locations best predicted cougar predation when examining number of locations and number of nights at a cluster. We based model selection on strength of variable significance (Wald χ^2 , $P < 0.05$). We used forward stepwise logistic regression for initial model development. To avoid potential inadequacies of stepwise analysis (James and McCulloch 1990), we compared the stepwise model to various models containing stepwise variables selected and each variable not included during stepwise analysis (included individually). All 2-way interactions also were investigated. We used the Hosmer-Lemeshow goodness-of-fit test (Hosmer and Lemeshow 1989) to assess adequate fit of our data to the logistic regression model, where significant results ($P < 0.05$) suggest lack-of-fit.

To evaluate the model, we applied it to the GPS location record of a cougar (subadult male) not included in the original analyses and searched sites that the model identified as potential predation sites (i.e., locations at 2200, 0200, or 0500 hr). We later included data from this cougar in the overall data set and refit the model to increase sample size.

We summed the predation probabilities associated with each cluster to estimate total number of predation events for each cougar and estimated individual predation rates by dividing total number of days monitored by estimated number of predation events. To construct 90% confidence intervals around individual cougar predation rates, we used the model coefficient standard error to obtain a 90% confidence interval for each estimated predation event, and summed the lower and upper bounds to get a confidence interval for total number of predation events. We then divided the total monitoring period by the lower bound estimate and upper bound estimate to get a predation-rate confidence interval for each cougar. We averaged the coefficients of variation across individuals to obtain predation-rate confidence intervals for sex/age and reproductive classes.

Prey Composition and Predation Characteristics

We identified species and sex-age class of prey carcasses from hair or skeletal remains following Moore (1974) and Adrian (1996). Remains of adults that could not be sexed in the field were sexed via gender polymerase chain reaction amplification of the zinc finger motif found on the x gene (ZFX) and the sex determining region found on the Y gene (SRY), where males exhibit 2 bands (ZFX = 425 base pairs, SRY = 225 base pairs) and females exhibit 1 band (SRY = 225 base pairs; Wyoming Game and Fish Laboratory, Laramie, Wyoming, USA). We examined diets of male and female cougars for differences ($P < 0.05$) using χ^2 contingency analyses (StatXact-Turbo; Mehta and Patel 1992). We tested for differences in number of nights cougars spent on carcasses of elk and mule deer and elk and pronghorn using 1-tailed *t*-tests for unequal variance ($P < 0.05$); data were not included if the collar ceased collecting GPS data while the cougar was at a kill. We examined data for patterns that would suggest cougars were more successful at killing prey at certain times of night by comparing the times cougars were first located at clusters with expected times using χ^2 goodness-of-fit analysis.

Using ArcView®, we examined distribution of daytime and early evening locations (0800, 1600, 1900 hr) associated with a kill (i.e., daybeds). Daybeds were defined as locations at 0800, 1600, or 1900 hr that were outside GPS location clusters and from which the cougar returned to the confirmed and predicted predation site. Predicted predation sites were defined by the predation model as location clusters with probability of predation >0.5 . We included early evening locations (1900 hr) because subsequent analysis suggested that cougars were not often associated with predation sites at this time. Differences in daybed distances outside location clusters ($P < 0.05$) between confirmed and predicted predation sites were examined using a 2-tailed *t*-test for equal variance. For sites with multiple daybeds (1/day) outside a single cluster, we used the mean distance to maintain independence.

RESULTS

We collared 11 cougars (2 adult males, 4 adult females with large young [3 litters 4–8 months old, 1 litter 14–17 months old], 2 adult females without young, and 3 subadult females) with GPS receivers between September 1999 and January 2000. Weight of GPS collars was 1.6–2.2% of cougar body mass. We recovered 6 GPS collars between November 1999 and March 2000 via harvest and 4 others via capture between April and May 2000; the remaining collar failed just prior to retrieval (adult female with 5–8 month-old young). We observed no injuries caused by the GPS collars, and movement patterns of each cougar were comparable to those previously obtained from VHF radiocollars (C. R. Anderson, unpublished data). Monitoring periods averaged 78 nights ($n = 10$, range = 28–188), and mean number of locations/night ranged from 2.4 to 5.0/cougar. Time of successful GPS location attempts did not differ from equality among cougars ($\chi^2_5 \leq 8.31$, $P \geq 0.140$), suggesting that successful locations were unbiased for time of location attempt. Nights without a GPS location occurred only 12 times (0–3/cougar, total monitoring = 784 nights for all 10 cougars). We identified 188 potential kill sites from GPS data records and searched 94 sites an average of 201 days after the potential predation event (mode = 105, range = 3–388). We found prey remains at 61 sites. Prey remains were not found at 5 of 17 sites with 3–7 consecutive nights of cougar presence that were searched >38 weeks (273 days) after clustering. However, we found remains at all 24 sites searched

≤ 38 weeks (270 days) after 3 or more nights of cougar presence. We used 66 sites in model development (removing those searched after 38 weeks) including GPS data from 2 subadult females ($n = 21$ sites), 2 females with young ($n = 19$), 1 adult female ($n = 14$), and 1 adult male ($n = 12$). Prey remains were found at 46 of these sites (32 deer, 8 elk, 3 pronghorn, 2 livestock, 1 porcupine). Because we suspected that small-prey (<15 kg) detection was inconsistent at GPS location clusters, and our objective was to identify large-mammal kills, we considered the single porcupine kill as a nonpredation event for model development.

Ninety-one percent of location clusters used in model development contained 3-dimensional GPS positions (signals from ≥ 4 satellites yielded *x*, *y* coordinates and elevation). Mean distance from kills to cluster centers was 42.6 m (range = 0.0–106.5). Mean number of times a cougar was located at the 45 sites with large mammal kills was 9.3 (range = 2–28), and mean number of subsequent nights spent at the kill was 3.5 (range = 1–8). At clusters where we did not find large prey remains ($n = 21$), cougars were located an average of 3.3 times (range = 2–5) and remained 1.9 nights (range = 1–6).

Cougar Predation Models

Logistic regression analyses suggested that the number of nights at a cluster best predicted a large-mammal predation event, where nights at a cluster was defined as cougar presence at 2200, 0200, or 0500 hr. Cluster duration exhibited the strongest relationship ($\chi^2_1 = 12.71$, $P < 0.001$) of all univariate models and was the only significant variable ($P < 0.05$) included among multivariate models compared (Fig. 1).

When we applied the initial model (Fig. 1) to the data collected from a single cougar (subadult male) monitored December 2000–May 2001, it predicted 38 potential predation sites (locations at 2200, 0200, or 0500 hr) from GPS records. We searched 36 of the 38 sites for evidence of kills, but precluded 5 sites because they were too densely vegetated to facilitate discovery of prey remains. We detected 9 large (5 elk, 3 mule deer, 1 moose) and 4 small-mammal predation events (3 porcupine, 1 coyote) at the 31 sites searched. Number of predation events estimated by the model from the GPS records for this subadult male was 13.4, an overestimate of large prey killed (13.4 vs. 9).

Data from this subadult male were then added to the original data set, and the model was refit to

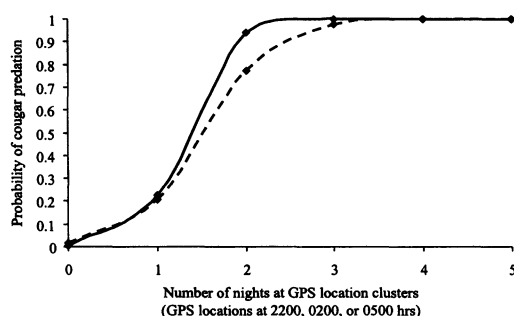


Fig. 1. Probability of cougar predation (p) at GPS location clusters where $p = \exp^u / (1 + \exp^u)$. Solid line represents cougar predation data from 66 observations collected in southeast Wyoming, USA, Sep 1999–Apr 2000, where $u = -5.2280 + 3.9922$ (number of nights), $SE_{\beta_0} = 1.4103$, and $SE_{\beta_1} = 1.1198$; the Hosmer-Lemeshow goodness-of-fit test suggested these data fit the logistic model ($\chi^2_1 = 0.98$, $P = 0.998$). Dashed line represents cougar predation data from 66 observations collected in southeast Wyoming, USA, Sep 1999–Apr 2000, and 31 observations collected from a single cougar, Dec 2000–May 2001 where $u = -3.8467 + 2.5287$ (number of nights), $SE_{\beta_0} = 0.8040$, and $SE_{\beta_1} = 0.5305$; these data appeared appropriate for the logistic regression model (Hosmer-Lemeshow $\chi^2_1 = 6.86$, $P = 0.144$). Number of nights from GPS locations at 2200, 0200, or 0500 hr.

the combined data. Location clusters where small mammals were detected ($n = 4$) were treated as nonpredation sites (i.e., coded as 0). Refitting the model with the 31 additional clusters from the subadult male resulted in a similar model. Again, number of nights at GPS location clusters, defined as presence at 2200, 0200, or 0500 hr, was the most significant predictor variable ($\chi^2_1 = 22.72$, $P < 0.001$) among all univariate models and the only significant variable ($P < 0.05$) included in multivariate models compared (Fig. 1).

Predicted predation probabilities with number of nights at GPS location clusters were similar for

both models (Fig. 1). One notable difference, however, was the predicted probability of predation with 2 nights recorded at the same location. The initial model (Fig. 1, solid line) suggested a predation probability of 0.94 with 2 nights of cougar presence recorded, whereas the latter model (Fig. 1, dashed line) predicted a 0.77 chance of a predation event with 2 nights of cougar presence.

Cougar Predation Rates

Monitoring periods for individual cougars ranged 28–188 days ($\bar{x} = 84.0$; Table 3). Estimated large-mammal predation events ranged 3.8–22.8/cougar ($\bar{x} = 12.1$). Mean estimated large-mammal predation rate for all cougars was 7.0 days/kill (90% CI: 5.8 to 10.4), but ranged from 5.4 days (90% CI: 4.5 to 8.4) for family groups to 9.5 days (90% CI: 6.9 to 16.4) for the subadult male. Percent of successful GPS location attempts ranged 39.3–82.7% ($\bar{x} = 60.5$) for individual cougars.

Prey Composition

We detected prey remains (9 species) at 74 clusters from 11 cougars (Table 1). This included all GPS location clusters searched during initial model development (Fig. 1, solid line; $n = 66$), those added for subsequent model development (Fig. 1, dashed line; $n = 31$), and those searched but not included in model development (>38 weeks post predation; $n = 28$). Cougars spent longer periods on elk carcasses ($\bar{x} = 6.0$ nights, $SD = 3.7$, $n = 14$) than deer ($\bar{x} = 3.4$ nights, $SD = 1.8$, $n = 43$; $t_{15} = 2.60$, $P = 0.010$) and pronghorn ($\bar{x} = 3.0$ nights, $SD = 1.3$, $n = 6$; $t_{18} = 2.70$, $P = 0.007$). Female cougars killed more mule deer than other species, and male cougars killed more elk than other species ($\chi^2_3 = 20.61$, $P < 0.001$; Table 1). Males killed proportionately more adult male elk

Table 1. Prey species (n , [%]) detected at GPS location clusters of cougars by sex, age, and reproductive class in the Snowy Range, southeast Wyoming, USA, Sep–May, 1999–2001.

Prey	Subadult female ($n = 19$)	Adult female ($n = 11$)	Family group ($n = 17$)	Subadult male ($n = 14$)	Adult male ($n = 14$)
Deer ^a	13 (68)	8 (73)	17 (100)	3 (21)	4 (29)
Elk	0	3 (27)	0	5 (36)	7 (50)
Pronghorn	4 (21)	0	0	0	2 (14)
Porcupine	0	0	0	4 (29) ^b	1 (7)
Livestock ^c	2 (11)	0	0	0	0
Moose	0	0	0	1 (7)	0
Coyote	0	0	0	1 (7)	0

^a Includes 44 mule deer and 1 white-tailed deer.

^b Two of 4 porcupines were detected at the same location.

^c Includes 1 domestic sheep and 1 domestic calf.

Table 2. Sex–age composition (%) of large prey detected at GPS location clusters ($n = 69$) of male ($n = 3$) and female ($n = 8$) cougars in the Snowy Range, southeast Wyoming, USA, Sep–May, 1999–2001.

Cougar sex	Total no. of prey	Deer ^a				Elk				Pronghorn			
		Males	Females	Young	Unk ^b	Males	Females	Young	Unk ^b	Males	Females	Young	Other
Male	22	5	9	5	14	27	9	14	5	5	0	5	5 ^c
Female	47	19	32	21	9 ^d	2	2	2	0	4	2	2	4 ^e
Total	69	14	25	16	10	10	4	6	1	4	1	3	4

^a Includes 44 mule deer and 1 white-tailed deer (female).^b Unk = unknown^c Moose calf.^d Includes 2 adults of unknown sex and 2 unknown sex/age.^e Includes 1 domestic sheep (female) and 1 domestic calf.

and females killed proportionately more adult female mule deer (Table 2). Three cougars from 2 sex–age classes killed pronghorn. Other prey items detected at GPS location clusters included a moose calf, 2 livestock (1 *Ovis aries*, 1 *Bos taurus*), and 6 small mammals (5 porcupines, 1 coyote; Table 1).

We pooled data from confirmed ($n = 40$) and probable predation sites (cougar presence ≥ 2 nights, predation probability ≥ 0.77 , $n = 42$) because arrival time at clusters was similar ($\chi^2_5 = 3.70$, $P = 0.594$; Fig. 2). Initial locations (presumed time period of kill) were not random across time intervals ($\chi^2_5 = 37.95$, $P < 0.001$), but did not differ among sex–age and reproductive classes ($\chi^2_5 \leq 8.31$, $P \geq 0.140$). Kills sharply increased from 1901–2200 hr, peaked at 2201–0200 hr, and gradually declined until 0801–1600 hr (Fig. 2).

We detected daybeds outside the predation cluster at 28 of 69 (40.6%) confirmed and 37 of 64 (57.8%) probable predation sites. Distances

from daybeds to confirmed and probable predation sites did not differ ($t_{63} = -0.25$, $P = 0.803$) and averaged 844 m (SD = 612, $n = 65$, range = 90–3380). Multiple daybeds associated with a single kill occurred at 31 of 65 sites ($\bar{x} = 2.68/\text{site}$, SD = 1.11, range = 2–6); cougar use of the same bed site occurred at only 3 of 31 sites.

DISCUSSION

Cougar Predation Models

Cougar predation rates estimated by the model generally agree with rates estimated from snow-tracking, radiotracking, and energetics models when size of primary prey is considered (Table 4). A lower rate estimated by Shaw (1977) may have resulted from undetected kills when a cougar stayed only 1 night. Both Beier et al. (1995) and our study documented kills where the cougar was present for a single night. Predation rates estimated by Hornocker (1970) also may have been underestimated because the cougar energy requirements were derived from captive cougars. Why Connolly's (1949; 9.7 days/kill) estimate, derived from snowtracking, reflected a wider interval than ours (7 days/kill) is unclear. Estimates of predation rate will reflect the sex and age of cougars in the sample, however. If cougars tracked by Connolly (1949) were primarily subadults or females without young, overall predation rate likely would be lower than the estimate derived from our more-inclusive sample.

Because we used store-on-board GPS collars, the period between recognizing a potential predation event (after the collar was retrieved and data downloaded and analyzed) and searching the site was often long, decreasing the chance of separating scavenging from predation. Scavenging, documented but infrequent in cougars (Ack-

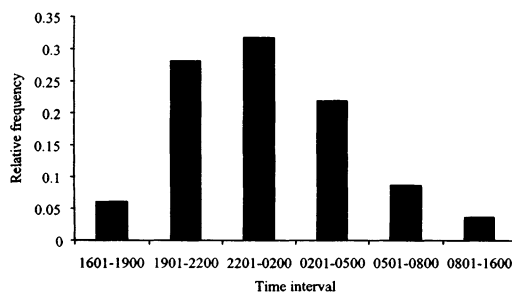


Fig. 2. Frequency distribution of time intervals cougars were first located at confirmed ($n = 40$) and probable ($n = 42$) predation sites combined identified from GPS location clusters collected Sep–May, 1999–2001, in the Snowy Range, southeast Wyoming, USA. Probable predation sites consist of ≥ 2 nights of cougar presence (presence at 2200, 0200, or 0500 hr) where cougar predation probability ≥ 0.77 .

Table 3. Length of monitoring period, percent GPS locations acquired (attempted at 1600, 1900, 2200, 0200, 0500, 0800 hr each day), number of estimated large mammal kills from number of nights (locations at 2200, 0200, or 0500 hr) at GPS location clusters ($n = 226$), and estimated cougar predation rates of large mammals (days/kill) from 11 cougars of 5 sex-age and reproductive classes Sep–May, 1999–2001 in the Snowy Range, southeast Wyoming, USA.

Cougar class Cougar ID	Monitoring period (days)	% GPS locations acquired	No. of estimated large mammal kills ^a	Estimated predation rate (90% CI) ^b
Subadult female				
619	64	81.3	10.9	5.9 (4.9 to 8.1)
620	95	61.9	14.1	6.7 (5.7 to 9.4)
632	32	39.3	3.4	9.4 (8.5 to 12.1)
Mean	63.7	60.8	9.5	7.3 (6.3 to 9.9)
Adult female				
628	86	67.1	10.4	8.3 (6.9 to 11.7)
645	42	42.2	7.4	5.7 (4.7 to 9.5)
Mean	64.0	54.7	8.9	7.0 (5.8 to 10.8)
Family group				
623 ^c	87	39.7	14.7	5.9 (5.0 to 9.6)
607 ^d	112	82.1	19.9	5.6 (4.8 to 8.3)
618 ^e	50	82.7	10.9	4.6 (3.7 to 7.3)
Mean	83.0	68.2	15.2	5.4 (4.5 to 8.4)
Subadult male				
635	141	44.0	14.9	9.5 (6.9 to 16.4)
Adult male				
626	188	59.4	22.8	8.2 (7.0 to 11.3)
644	28	66.1	3.8	7.4 (6.5 to 10.1)
Mean	108.0	62.8	13.3	7.8 (6.8 to 10.7)
Grand mean	84.0	60.5	12.1	7.0 (5.8 to 10.4)

^a Estimated number of large mammal kills = sum of predation probabilities (p) at GPS location clusters where $p = \exp^u / 1 + \exp^u$ and $u = -3.8467 + 2.5287$ (number of nights). Nights = GPS locations at 2200, 0200, or 0500 hr.

^b Predation rate = length of monitoring period / estimated number of predation events.

^c Litter size = 2, age = 4–7 months.

^d Litter size = 2, age = 4–8 months.

^e Litter size = 2, age = 15–17 months.

erman et al. 1984, Logan and Sweanor 2001, Murphy 1998, Nowak 1999), may have introduced an unknown, but likely small amount of bias into our predation rate estimates. We felt comfortable in separating bones from animals that had died during the previous fall and winter from those that had died earlier and been exposed to hot and dry summer conditions. The likelihood of finding bones of an animal that had died during the fall or winter of other causes at a location cluster where a cougar coincidentally exhibited sedentary behavior for reasons other than foraging (e.g., illness) seems small. Additionally, skeletal remains were found at only 1 of 11 clusters consisting of primarily daytime locations. Applying GPS collars that can be downloaded on demand (which were not available during our study) to identify cougar predation should further reduce these potential problems.

Application of the initial model to predict predation events in a subadult male cougar identified potential problems. The initial model did not include GPS records from subadult males,

and food habits and predation rates of this sex-age class may differ from others (Murphy 1998). Model predictions were similar to detected predation, but only when 1 coyote and 3 porcupine kills were included. The model was developed only from large mammals, however, and it overestimated large-mammal kills for this cougar (13 estimated and 9 detected). Inclusion of GPS records of this subadult male with kills of small mammals coded as no-kill into the original data set likely improves the model by making it more applicable to all cougar sex-age and reproductive classes. The model will profit from additional data sets to capture variation within and between cougar sex-age and reproductive classes.

Global positioning system locations appeared accurate enough that circumference of clusters, buffered by 10 m, enclosed predation sites. Global Positioning System error should have been minimal because all but 9 clusters without prey remains were based on 3-D locations (Moen et al. 1997, Bowman et al. 2000). Additionally, accuracy of 2-D locations is similar to 3-D locations if the

Table 4. Cougar predation rates (days/kill) of ungulates from North American cougar studies.

Location	Predation rate	Cougar sex-age ^a	Primary prey ^b	Technique	Source
Central Utah	9.7	US	MD	Snowtracking	Connolly (1949)
Central Idaho	18–26	AD	MD	Energetics model	Hornocker (1970)
	4.5 ^c	FG	MD	Snowtracking	
West central Arizona	6.8	FG	MD	Radiotracking	Shaw (1977)
	10.4	AF	MD		
Southern Utah	8.5	AM	MD	Energetics model	Ackerman et al. (1986)
	16.1	AF	MD		
	4.8 ^d	FG	MD		
	4.5 ^e	FG	MD	Radiotracking	
Central British Columbia	2.7–6.4	FG	BS, MD	Radiotracking	Harrison (1990)
Southern California	7.6	US	MD	Radiotracking	Beier et al. (1995)
Northwest Wyoming	7.5	M	Elk	Radiotracking	Murphy (1998)
	11.1	AF	Elk, MD		
	7.2	FG	Elk, MD		
	11.0	SM	Elk, MD		
	10.3	SF	MD, Elk		
Northeast Oregon	7.7	UF	MD, Elk	Radiotracking	Nowak (1999)
Southeast Wyoming	7.0	US	MD, Elk	GPS location clusters	This study
	7.8	AM	Elk, MD		
	7.0	AF	MD, Elk		
	5.4 ^f	FG	MD		
	9.5	SM	Elk, MD		
	7.3	SF	MD, PH		

^a AD = unspecified adult, FG = family group, AF = adult female, AM = adult male, US = unspecified sex/age, SM = subadult male, SF = subadult female, UF = adult females with and without young.

^b Primary prey listed if >20% of ungulate diet. Prey species listed in order of frequency. MD = mule deer, BS = bighorn sheep, PH = pronghorn.

^c Observed from snowtracking a female with 3 32-kg young (likely 6–8 months old).

^d Estimated from Ackerman et al. (1986:Fig. 2) for an adult female with 2 9-month-old young.

^e Observed from radiotracking females with 3 6–8-month-old young.

^f Estimated from 3 litters of 2 young each. Ages = 4–7 months, 4–8 months, and 15–17 months (mean age = 9 months).

elevation from the last 3-D position is similar to that of the 2-D (Moen et al. 1997). Furthermore, the mean distance from carcasses to cluster centers (43 m) matched the mean GPS error reported by Moen et al. (1996) for an earlier version of the GPS collar we used. We believe it is unlikely that the 9 2-D clusters biased the model because 6 of them represented only a single night of cougar presence and were probably not large-mammal kills.

Predation Rates

The lowest predation rates estimated were from subadults (1 male, 1 female) supporting Murphy's (1998) prediction that predation rates should be related to age and experience of cougars. Two other subadult females, however, killed prey as frequently as adult females. Predation rates also varied between the 2 adult females without young, but this may have been due to 1 being in the later stages of pregnancy when captured. The similarity of adult male predation rates and those of subadult and adult females likely reflected the

tendency for adult males to kill elk and female cougars to kill mule deer.

Prey Composition

Cougars in the Snowy Range may be partitioning prey as suggested by Murphy (1998). Subadult female cougars on the Snowy Range killed mostly mule deer and pronghorn, the subadult male killed mostly elk and small mammals, adult females killed predominantly mule deer and elk, females with young preyed on mule deer, and adult males killed more elk than other sex-age classes (Table 1). Although others have suggested that cougars kill more young and male mule deer (Hornocker 1970, Shaw 1977, Murphy 1998), the sex and age of mule deer killed by female cougars in our study area appeared similar to estimated composition in the mule deer population (Wyoming Game and Fish Department 1999). Our small sample size may have reduced our chances of detecting selection. Dispersion of collared cougars in relation to nonuniform dispersion of deer and elk over the range may have

resulted in the apparent selection of species we observed.

MANAGEMENT IMPLICATIONS

Modeling predation rates from GPS location records will significantly reduce the cost and effort of estimating this parameter by precluding the need for intensive ground or aerial monitoring. In a relatively simple system with a single large ungulate prey species, predation rates could be estimated simply from GPS records with no need to investigate kill sites. In more complex systems, where cougars can switch among prey species, kill-site investigations may be required. In either case, identifying predation rates and prey selection will allow managers to estimate the effect of cougar predation on the area's prey population(s) if prey abundance can be estimated.

The model we constructed to estimate predation events from GPS records of cougar movements may improve as more GPS records with verified kills by various sex and age cougars are added. As we collected 125 observations in 46 days, additional records could be generated quickly. Continuing advances in GPS collar technology will further enhance a model-based approach for estimating predation rates. For example, GPS data accuracy increased when selective availability was discontinued in 2000. The cost of GPS collars continues to decrease, potentially allowing purchase of more collars to increase sample size. Collars are becoming lighter and capable of collecting an increasing number of locations. Timed breakaway devices preclude the need to recapture collared cougars. And, improvements in the reliability of remote downloading systems will allow biologists more timely retrieval of data, improving estimates of prey species and their sex and age. The advancement of GPS technology provides opportunities to investigate more detailed hypotheses of predator-prey relationships and ecosystem processes.

ACKNOWLEDGMENTS

The Wyoming Game and Fish Department, Wyoming Animal Damage Management Board, and the Pope and Young Club funded this project. We are indebted to D. Wroe for the intense effort required to capture and handle cougars. Field assistance from H. Cruickshank, L. Johnson, and T. Chapman was appreciated. We thank D. France of France Flying Service, Saratoga, Wyoming, for aerial telemetry, and K. Sargent and D. Hawk of the Wyoming Game and Fish Laboratory, Laramie,

Wyoming, for gender assays of cougar prey remains. We thank P. Beier and D. Maher for suggestions on improving the manuscript. Capture protocols were reviewed and approved under the University of Wyoming Animal Care and Use Committee form number A-3216-01.

LITERATURE CITED

- ACKERMAN, B. B. 1982. Cougar predation and ecological energetics in southern Utah. Thesis, Utah State University, Logan, Utah, USA.
- , F. G. LINDZEY, AND T. P. HEMKER. 1984. Cougar food habitats in southern Utah. *Journal of Wildlife Management* 48:147–155.
- , ———, AND ———. 1986. Predictive energetics model of cougars. Pages 333–352 in S. D. Miller and D. Everetts, editors. *Proceedings of the International Cat Symposium*, Kingsville, Texas, USA.
- ADRIAN, W. J., editor. 1996. *Wildlife forensic field manual*. Second edition. Colorado Division of Wildlife, Fort Collins, Colorado, USA.
- ALEXANDER, R. R., G. R. HOFFMAN, AND J. M. WIRSING. 1986. Forest vegetation of the Medicine Bow National Forest in southeastern Wyoming: a habitat type classification. U.S. Forest Service Research Paper RM-271. U.S. Forest Service, Rocky Mountain Range Experiment Station, Fort Collins, Colorado, USA.
- ASHMAN, D. L., G. C. CHRISTENSEN, M. L. HESS, G. K. TSUKAMOTO, AND M. S. WICKERSHAM. 1983. The mountain lion in Nevada. *Federal Aid in Wildlife Restoration Project W-48-15, Final Report*. Nevada Department of Wildlife.
- BEIER, P., D. CHOATE, AND R. H. BARRETT. 1995. Movement patterns of mountain lions during different behaviors. *Journal of Mammalogy* 76:1056–1070.
- BOWMAN, J. L., C. O. KOCHANNY, S. DEMARIS, AND B. D. LEOPOLD. 2000. Evaluation of a GPS collar for white-tailed deer. *Wildlife Society Bulletin* 28:141–145.
- CONNOLLY, E. J. 1949. Food habits and life history of the mountain lion. Thesis, University of Utah, Salt Lake City, Utah, USA.
- CUNNINGHAM, S. C., C. R. GUSTAVSON, AND W. B. BALLARD. 1999. Diet selection of mountain lions in southeast Arizona. *Journal of Range Management* 52:202–207.
- ENVIRONMENTAL SYSTEMS RESEARCH INSTITUTE. 1999. *Introduction to ArcView® GIS, version 3.2*. ESRI, Redlands, California, USA.
- HARRISON, S. 1990. Cougar predation on bighorn sheep in the Junction Wildlife Management Area, British Columbia. Thesis, University of British Columbia, Vancouver, British Columbia, Canada.
- HOPKINS, R. A. 1989. Ecology of the puma in the Diablo Range, California. Dissertation, University of California, Berkeley, California, USA.
- HORNOCKER, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho primitive area. *Wildlife Monographs* 21.
- HOSMER, D. W., AND S. LEMESHOW. 1989. *Applied logistic regression*. John Wiley & Sons, New York, New York, USA.
- JAMES, C. F., AND C. E. MCCULLOCH. 1990. Multivariate analysis in ecology and systematics: panacea or Pandora's box? *Annual Review of Ecology and Systematics* 21:129–166.

- LINDZEY, F. G., B. B. ACKERMAN, D. BARNHURST, T. BECKER, T. P. HEMKER, S. P. LAING, C. MECHAM, W. D. VAN SICKLE. 1989. Boulder-Escalante cougar project. Final Report. Utah Division of Wildlife Research, Salt Lake City, Utah, USA.
- LOGAN, K. A., AND L. L. SWEANOR. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, D.C., USA.
- MEHTA, C., AND N. PATEL. 1992. StatXact-Turbo: statistical software for exact nonparametric inference. Cytel Software, Cambridge, Massachusetts, USA.
- , AND ———. 1993. LogXact—Turbo: logistic regression software featuring exact methods. Cytel Software, Cambridge, Massachusetts, USA.
- MOEN, R., J. PASTOR, AND Y. COHEN. 1997. Accuracy of GPS telemetry collar locations with differential correction. *Journal of Wildlife Management* 61:530–539.
- , ———, ———, AND C. C. SCHWARTZ. 1996. Effects of moose movement and habitat use on GPS collar performance. *Journal of Wildlife Management* 60:659–668.
- MOORE, T. D., L. E. SPENCE, AND C. E. DUGNOLLE. 1974. Identification of the dorsal guard hairs of some mammals of Wyoming. Bulletin No. 14. Wyoming Game and Fish Department, Cheyenne, Wyoming, 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, Idaho, USA.
- NOWAK, M. C. 1999. Predation rates and foraging ecology of adult female mountain lions in northeast Oregon. Thesis, Washington State University, Pullman, Washington, USA.
- REMPEL, R. S., A. R. RODGERS, AND K. F. ABRAHAM. 1995. Performance of a GPS animal location system under boreal forest canopy. *Journal of Wildlife Management* 59:543–551.
- ROSS, I. P., AND M. G. JALKOTZY. 1996. Cougar predation on moose in southwestern Alberta. *Alces* 32:1–8.
- , ———, AND M. FESTA-BIANCHET. 1997. Cougar predation on bighorn sheep in southwestern Alberta during winter. *Canadian Journal of Zoology* 74:771–775.
- SAS INSTITUTE. 1990. SAS technical report P-200. Release 6.04 edition. SAS Institute, Cary, North Carolina, USA.
- SHAW, H. G. 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*. University of Montana, Missoula, Montana, USA.
- . 1979. A mountain lion field guide. Special Report No. 9. Arizona Game and Fish Department Phoenix, Arizona, USA.
- . 1981. Comparison of mountain lion predation on cattle on two study areas in Arizona. Pages 306–316 in L. Nelson and J. M. Peek, editors. *Proceedings of the Wildlife Livestock Relationships Symposium*. University of Idaho, Forest, Wildlife, and Range Experiment Station, Moscow, Idaho, USA.
- SPALDING, D. J., AND J. LESOWSKI. 1971. Winter food of the cougar in south-central British Columbia. *Journal of Wildlife Management* 35:378–381.
- TURNER, J. W., M. L. WOLFE, AND J. F. KIRKPATRICK. 1992. Seasonal mountain lion predation on a feral horse population. *Canadian Journal of Zoology* 70:929–934.
- WEHAUSEN, J. D. 1996. Effects of mountain lion predation on bighorn sheep in the Sierra Nevada and Granite Mountains of California. *Wildlife Society Bulletin* 24:471–479.
- WILLIAMS, J. S., J. J. MCCARTHY, AND H. D. PICTON. 1995. Cougar habitat use and food habits on the Montana Rocky Mountain Front. *Intermountain Journal of Sciences* 1:16–28.
- WYOMING GAME AND FISH DEPARTMENT. 1999. Annual big game herd unit reports: Laramie Region. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.

Received 31 December 2001.

Accepted 8 December 2002.

Associate Editor: White, Jr.