

Original Article

Do GPS Clusters Really Work? Carnivore Diet From Scat Analysis and GPS Telemetry Methods

MICHELLE M. BACON,¹ *Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada T6G 2E9*

GREG M. BECIC, *Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada T6G 2E9*

MARK T. EPP, *Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada T6G 2E9*

MARK S. BOYCE, *Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada T6G 2E9*

ABSTRACT Global Positioning System (GPS) data collected using radiocollars have allowed researchers to identify sites where predators have killed prey, but this method has yet to be compared with scat analysis, a more traditional method of determining diet composition. We analyzed 211 scat samples and compared composition of prey items with 266 kill sites found using GPS radiotelemetry data on cougars (*Puma concolor*) in the Cypress Hills of southeast Alberta and southwest Saskatchewan, Canada. Scat and kill site results showed significantly different occurrences of prey items; scat samples were better able to detect small mammals. However, larger prey made up >90% of the biomass of cougar diets, and when restricting the comparison to ungulate prey, both methods estimated nearly identical biomass consumed. As expected, GPS telemetry is biased against small prey but the method provides results comparable to scat analysis for larger prey that make up the majority of biomass consumed. © 2011 The Wildlife Society.

KEY WORDS Alberta, cougar, diet composition, Global Positioning System (GPS) radiocollars, *Puma concolor*, Saskatchewan, scat.

Documenting prey composition is one of the most common objectives of research studies involving large predators. Because predation can influence prey abundance, managers may be faced with making decisions on the management of both predator and prey (Hayes et al. 2000, Rominger et al. 2004). There are ecological, economic, and social consequences of the interaction between predator and prey; consequently, collecting data that give the best representation of diet consumed by a carnivore is essential (Kellert et al. 1996, Treves and Karanth 2003, Musiani and Paquet 2004).

Several methods have been used to characterize animal diets. The most commonly used method is fecal analysis, in which the researcher identifies hairs in scat to quantify prey consumed by a carnivore (Reynolds and Aebischer 1991, Ciucci et al. 1996, Klare et al. 2011). Other methods include fatty acid analysis, which identifies prey consumed by identifying unique patterns of carbon chains deposited in adipose tissue (Iverson et al. 2004), and stable isotope analysis, which uses carbon and nitrogen ratios found in metabolically inactive tissues to estimate the relative composition of the diet (Hobson and Wassenaar 1999, Kelly 2000, Phillips et al. 2005, Thompson et al. 2005).

In the field, very high frequency radiocollars on predators have long been used to locate kill sites and identify diet (Beier

et al. 1995). Recent advances in Global Positioning System (GPS) radiocollars fitted on carnivores have revolutionized researchers' ability to locate kill sites, increasing our knowledge about predation and decreasing time spent searching for kills (Sand et al. 2005, Franke et al. 2006, Zimmermann et al. 2007, Webb et al. 2008, Knopff et al. 2009). The identification of a grouping, or cluster, of GPS location points, and the subsequent field investigation of that site, allows researchers and managers to gather fine-scale information about prey, including species type, age, and sex (Anderson and Lindzey 2003). Models developed using GPS locations, such as those created for wolves (*Canis lupus*; Sand et al. 2005, Webb et al. 2008), and for cougars (*Puma concolor*; Knopff et al. 2009), have predicted the probability of a GPS cluster correctly identifying a predation event as well as estimating prey biomass at that kill site. Models developed to date have been tested in the field and, although effective, have been biased toward larger prey that required long handling times (Webb et al. 2008, Knopff et al. 2009). Previous studies identified other problems associated with GPS radiocollars, specifically missing fix locations altogether as well as missing fix locations in certain cover types (Frair et al. 2004, Hebblewhite et al. 2007).

Given these problems with GPS telemetry, and recognizing that kill sites located using GPS clusters are biased toward large prey, we questioned whether this new technology provided adequate data for characterizing large-carnivore diet composition. The GPS cluster technique has yet to

Received: 6 September 2010; Accepted: 8 September 2011;
Published: 21 November 2011

¹E-mail: mmbacon@ualberta.ca

be compared with analysis of prey detected from scat, which is a traditional and noninvasive method for analyzing wildlife diets that is not reliant on field investigators to locate and identify carcasses (Reynolds and Aebischer 1991, Litvaitis 2000). Hence, our objective was to compare prey composition of cougars from kill sites found using GPS clusters and hair samples identified from scats to verify whether the kill site method is reliable for the estimation of cougar prey selection.

STUDY AREA

We studied cougars in Cypress Hills Interprovincial Park, a 400-km² protected area in southeast Alberta and southwest Saskatchewan, Canada (49°40'N, 110°15'W). Having escaped glaciation in the last ice age, this island of forest habitat rose over 500 m above the surrounding prairie land, which was dominated by private livestock ranches. Four natural cover types made up the park ecosystem: montane (*Pinus contorta*, *Picea glauca*, *Populus tremuloides*, *Crataegus* spp., *Salix* spp.), fescue grassland (*Festuca* spp., *Danthonia* spp., *Agropyron* spp.), mixed-grass (*Agropyron* spp., *Stipa* spp.), and wetlands (Newsome and Dix 1968). A diversity of mammal species existed in the Cypress Hills, including white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), elk (*Cervus elaphus*), moose (*Alces alces*), pronghorn antelope (*Antilocapra americana*), coyote (*Canis latrans*), marten (*Martes americana*), beaver (*Castor canadensis*), porcupine (*Erethizon dorsatum*), and Richardson's ground squirrel (*Uroditellus richardsonii*). Cattle grazing occurred inside the park from June to October, and year-round on adjacent private ranches. A limited elk management hunt occurred each autumn on both the Alberta and Saskatchewan sides of the park; deer hunting was prohibited inside park boundaries, although they were hunted in adjacent wildlife management units. Mean annual precipitation during 1987–2007 was 561.6 mm and mean January and July temperatures were –9.0° C and 15.9° C (Environment Canada 2009).

Cougars, wolves, and bears (*Ursus* spp.) were eradicated from the region in the early 1900s (Alberta Fish and Wildlife Division 1992). Sightings of cougars have occurred sporadically since the mid-1990s, and increased substantially since the early 2000s, although none were confirmed until 2004 when a cougar kitten was struck and killed by a vehicle on an adjacent highway. In 2006 a wildlife camera captured a photo of a family of 3 cougars, and 3 other cougars were snared incidentally outside the park boundary. As of 2009, the population was estimated to be 15–20 adults. Including kittens located with family groups, population density was between 6.75 and 8.5 cougars/100 km², among the highest ever reported (Bacon et al. 2009, Quigley and Hornocker 2010).

METHODS

Kill Sites

We captured 6 cougars (2 ad M, 4 ad F) during winters 2008 and 2009 using trained hounds to track and tree cougars, and then administered a combination of either 2 mg/kg xylazine

and 3 mg/kg Telazol or 75 µg/kg medetomidine and 2 mg/kg ketamine via remote injection. All capture and monitoring efforts were conducted according to University of Alberta Animal Care Protocol number 568802, in compliance with guidelines approved by the Canadian Council on Animal Care (CCAC 2003). We fitted cougars with Lotek 4400S remote-downloadable GPS collars (Lotek Engineering, Newmarket, ON, Canada), programmed to take GPS locations every 3 hr. We collected 761–2,381 GPS locations per cougar and telemetry transmitters remained active on the animals for 106–358 days. Collars had an average 83% fix success rate. We monitored cougars from 25 April 2008 to 9 December 2009, downloading location data from active collars about every 3 weeks from the ground. Data were then transferred into ArcGIS 9.2. Following methods developed by Anderson and Lindzey (2003) and refined by Knopff et al. (2009), we identified GPS location clusters where ≥2 relocations were obtained within 200 m in a 6-day time frame. After identifying the geometric center of each cluster, we programmed these points into handheld GPS units and field crews conducted ground searches within a 200-m radius of the cluster locations. When prey remains were found at the cluster, we looked for evidence of cougar predation behavior including a buried carcass, a bed of hair at the cache, and scat piles. We examined all remains to identify species; when bones remained, we attempted to identify the age and sex of prey.

Scat Collection and Laboratory Analysis

We located cougar scat several ways: at kill sites and nonkill clusters found using the cluster method from the 6 radio-collared cougars ($n = 135$), at kill sites found opportunistically from uncollared cougars ($n = 5$), and opportunistically along trails in the park as well as on adjacent private land ($n = 71$). Scat collection began in May 2008 and continued until December 2009. Scats deposited by cougar were identified based on the shape, size, and distinctive untapered ends. We collected every cougar scat that we encountered, and each sample was bagged and labeled with a GPS coordinate, date, and cougar ID (9999 for unknown cougar), then stored in a –20° C freezer until processing.

Following lab procedures described by Ackerman et al. (1984), scat samples were autoclaved for 90 min to kill parasites, and then washed under warm water using a 0.455-mm metal sieve to remove excess fecal material. Remaining contents such as teeth, hooves, claws, and hair were air dried under a fume hood. Once dried, we randomly selected 20 hairs from each sample and placed them on slides, which were examined under a compound microscope. We identified hair based on the cuticular scales and medulla pattern (Moore et al. 1974), as well as size and color of the hair from reference specimens in the Zoology Museum at the University of Alberta. We pooled white-tailed deer and mule deer due to difficulties in distinguishing the species. We pooled hairs from sciurids smaller than marmots with pocket gophers (Geomyidae) and grouped them as “ground squirrels.” We pooled mice (*Mus*), shrews (*Sorex*), and voles (*Microtus*) as “small rodents.” We did not group badgers (*Taxidea taxus*)

with other mustelids because their larger body size would have affected biomass calculations.

Analysis of Hair From Scat

Numerous methods of scat analysis have been used to investigate diet composition of carnivores, including frequency analysis, dry and wet weights, relative volume, and biomass, all of which have their own biases but result in similar rankings of primary food items (Ciucci et al. 1996, van Dijk et al. 2007). To analyze the frequency of prey in scat, we calculated the occurrence of prey relative to the total prey items identified in scat (Reed et al. 2006). We used this method to account for instances when >1 prey item was found in a scat.

Although all sampling protocols for scat analysis have inherent biases, our sampling was designed to minimize these biases. For example, at kill sites we would encounter a number of scats, so to minimize pseudo-replication of these nonindependent scats we analyzed only one scat sample per location, be it a kill site, GPS cluster, or a random location (Marucco et al. 2008). In addition, carnivores consume fewer hairs for a given biomass of larger prey, creating a bias against large mammalian prey in scat methods (Weaver 1993). Therefore, we applied Ackerman et al.'s (1984) correction factor to the occurrence data, $y = 1.98 + 0.035x$, where y is the weight of prey consumed per collectable scat (kg/scat) and x is the mean prey body weight (kg). Prey items <2 kg did not have the correction factor applied to them because of the assumption that one small prey item would not comprise a total scat (Ackerman et al. 1984). Biomass consumed of each prey was calculated by multiplying the correction factor for that prey item by the occurrence of the given prey item relative to all prey items. Then, the relative biomass consumed of each prey was calculated by dividing the biomass consumed per prey item by the total biomass consumed.

Statistical Analysis

We used chi-square tests to compare the frequency of prey items in scat and at kill sites. We had insufficient sample sizes of some prey species for statistical analysis; so, we pooled cougar and coyote as "carnivores" and any prey <10 kg plus beaver as "small prey species."

To evaluate whether the 2 methods showed seasonal differences, we compared prey found in scat and at kill sites during summer and winter. This was a relevant comparison because snow cover occurred in our study area for >5 months/yr, occasionally creating difficulties in locating kills (especially small prey) and scat. We assigned prey identified in scat to summer or winter by the date when collected, because the majority of scat samples were <1 month old. Of 409 prey items, 259 were identified in scat from summer (May–Sep) and 150 were from winter (Oct–Apr). Kill sites were assigned to a season based on the date the GPS cluster was formed (assuming the date of cluster creation was the date of prey mortality); we located 141 kill sites in summer (May–Sep) and 125 kill sites in winter (Oct–Apr). For seasonal analysis, we eliminated moose and carnivores from statistical analysis due to small sample size.

Because ungulates were the predominant prey, we compared ungulate prey occurrence at kill sites and in scat using a chi-square test. To evaluate possible bias associated with retrieving scat samples at kill sites identified by the GPS cluster method, we compared occurrence of prey in scat found at kill sites with scat found incidentally, again using chi-square analysis.

RESULTS

Kill Sites Located With GPS Clusters

We identified 668 clusters between 25 April 2008 and 9 December 2009 using the GPS cluster method. Logistics and time prevented us from visiting all clusters; of the 668 identified, we visited 534 of these clusters (80%). Of the cluster sites that we visited, 266 were kill sites. In this sample of kills, 9 species (8 prey types) were found (Table 1). Deer accounted for 76% and elk accounted for 15% of all located kills.

Occurrence of Prey in Scat

In total, we collected 233 scat samples, but included only 211 in the analysis due to lack of sufficient hair, failure to precisely record the collection location, or pseudo-replication caused by collecting more than one sample per site. Scat from radiocollared and unknown cougars did not differ significantly in prey composition ($\chi^2 = 4.579$, $df = 3$, $P = 0.205$); thus, our analysis included samples from both radiocollared (known) cougars and unknown cougars, allowing us to increase sample size from a broader population.

We identified 4,220 hairs and detected 409 prey items in 211 scat samples analyzed, with a wider array of species represented in the scats than among kill sites. We found that 138 of 211 scat samples (65%) had >1 prey item. Deer represented 55% of all hairs identified and comprised 37% of the prey items identified. Elk represented 16% of the hairs identified and comprised 11% of the prey species. Sciurids (mostly ground squirrels) and geomyids (pocket gophers) combined represented 11% of hairs identified and comprised 24% of the prey items. Cougar hair represented 1% of all hairs identified in the scat (Table 1).

Distribution of Prey Items: Kills Versus Scat

We found a significant difference between the occurrence of prey items found at kill sites and those found in scat samples ($\chi^2 = 143.4$, $df = 4$, $P < 0.001$). We also observed a difference in prey composition between the 2 methods both in summer ($\chi^2 = 78.92$, $df = 2$, $P < 0.001$) and in winter ($\chi^2 = 48.05$, $df = 2$, $P < 0.001$; Fig. 1). These differences were largely attributable to the greater occurrence of smaller prey in scat samples. When we restricted our analysis to ungulate prey, we found no significant difference in the frequency of ungulate prey estimated by the 2 methods ($\chi^2 = 3.108$, $df = 2$, $P = 0.211$).

Biomass Consumed: Kills Versus Scat

We estimated the biomass that each species contributed to diet, for both methods, by including estimated weights of prey (Table 2). Based on nearly equal numbers of young of the year and adult prey found at kill sites, we used average

Table 1. Composition of cougar diet in Cypress Hills Interprovincial Park, Alberta and Saskatchewan, Canada, May 2008–December 2009. Kills located using Global Positioning System cluster methods. Scats analyzed by occurrence of prey items relative to total prey items, occurrence of prey items relative to total scats, and occurrence of prey items relative to total hairs.

Prey	Kills		Scats				
	No. of kills (<i>n</i> = 266)	% of kills	No. of prey items ^a (<i>n</i> = 409)	Prey items occur ^b (<i>n</i> = 409)	Scats occur ^c (<i>n</i> = 211)	No. of hairs ^d (<i>n</i> = 4,220)	Hairs occur ^e (<i>n</i> = 4,220)
Deer	202	75.9	152	37.2	72.0	2,338	55.4
Elk	41	15.4	46	11.2	21.8	660	15.6
Moose	4	1.5	3	0.7	1.4	34	0.8
Cougar	0	0.0	15	3.7	7.1	42	1.0
Coyote	5	1.9	0	0.0	0.0	0.0	0.0
Domestic cat	1	0.4	0	0.0	0.0	0.0	0.0
Porcupine	9	3.4	8	2.0	3.8	122	2.9
Beaver	1	0.4	10	2.4	4.7	83	2.0
Lagomorphs	0	0.0	3	0.7	1.4	21	0.5
Marmot	0	0.0	9	2.2	4.3	44	1.0
Badger	0	0.0	1	0.2	0.5	6	0.1
Muskrat	0	0.0	5	1.2	2.4	22	0.5
Skunk	0	0.0	3	0.7	1.4	17	0.4
Mustelid	0	0.0	10	2.4	4.7	122	2.9
Sciuridae	0	0.0	96	23.5	45.5	465	11.0
Small rodents	0	0.0	47	11.5	22.3	224	5.3
Wild turkey	3	1.1	1	0.2	0.5	20	0.5
Total	266	100	409	99.8	193.8	4,220.0	99.9

^a 211 scats, containing 409 prey items.

^b % occurrence of prey items relative to total prey items.

^c % occurrence of prey items relative to total no. of scats.

^d 211 scats, containing 4,220 hairs.

^e % occurrence of prey items relative to total no. of hairs.

estimated weight for adult and juvenile ungulates, and average weights for small mammals (data from Pattie and Fisher 1999). Both GPS clusters and scat analysis indicated that the majority of biomass consumed was from ungulates. Small mammals found in scats contributed <8% of biomass consumed. When we compared biomass of just the 3 ungulate prey species, we estimated nearly identical consumption of biomass using both the kill-site and scat methods (Table 3).

Lastly, to detect biases in scat biomass resulting from collecting samples at kill sites, we compared prey items and biomass of scat found at kill sites to scat found either incidentally or at clusters without kills. We included scat found inside the protected park and on adjacent private land. Again, there was no significant difference in the frequency of prey items between locations where scat were collected ($\chi^2 = 1.89$, *df* = 3, *P* = 0.59).

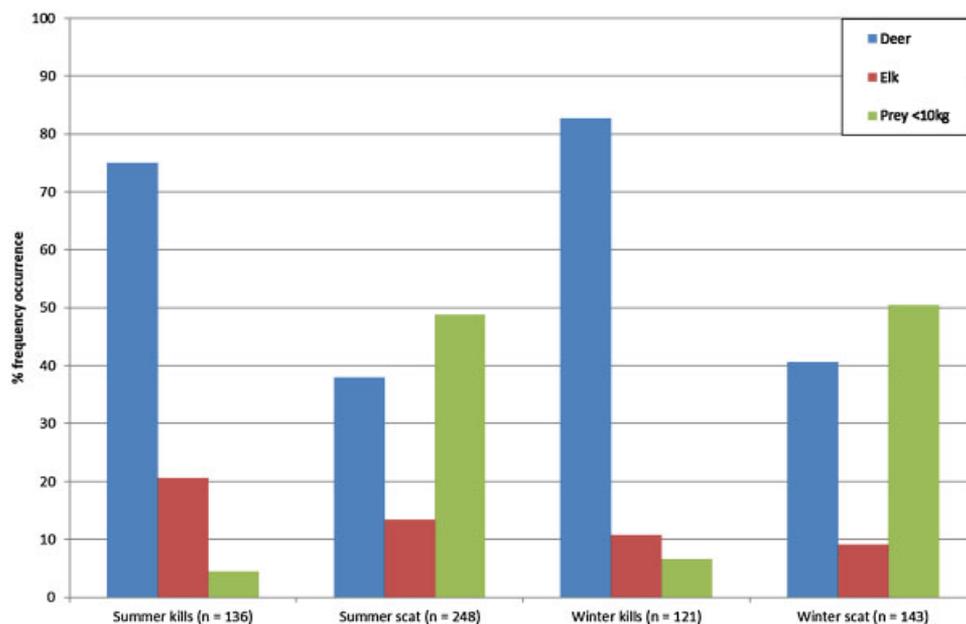


Figure 1. Occurrence of cougar prey items found at kill sites, and occurrence of prey items relative to all prey items in scat samples in summer (May–Sep) and in winter (Oct–Apr), Cypress Hills Interprovincial Park, of southeast Alberta and southwest Saskatchewan, Canada, May 2008–December 2009.

Table 2. Calculation of relative biomass consumed by cougars in Cypress Hills Interprovincial Park, Alberta and Saskatchewan, Canada, May 2008–December 2009. Kill sites located using Global Positioning System (GPS) cluster methods, and scat samples analyzed based on occurrence of prey items relative to all prey items identified.

Prey	Est. wt of prey (kg) ^a	Kill sites from GPS clusters (<i>n</i> = 266)			Prey items from scats (<i>n</i> = 409 items)			
		No. of kills	Biomass consumed (kg) ^b	Biomass consumed as % of all kill sites ^c	Prey items occur ^d	Correction factor (kg/scat) ^e	Total biomass consumed (kg) ^f	Relative biomass consumed (kg) ^g
Deer	40.50	202	8,181	49.1	37.2	3.4	126.3	46.8
Elk	180.00	41	7,380	44.3	11.2	8.3	93.1	34.5
Moose	227.00	4	908	5.5	0.7	9.9	7.3	2.7
Cougar	57.00	0	0	0.0	3.7	4.0	14.6	5.4
Coyote	16	5	80	0.5	0.0	2.5	0.0	0.0
Domestic cat	4	1	4	0.0	0.0	2.1	0.0	0.0
Porcupine	6.00	9	54	0.3	2.0	2.2	4.3	1.6
Beaver	26.50	1	26.5	0.2	2.4	2.9	7.1	2.6
Lagomorphs	2.73	0	0	0.0	0.7	2.1	1.5	0.6
Marmot	3.40	0	0	0.0	2.2	2.1	4.6	1.7
Badger	7.50	0	0	0.0	0.2	2.2	0.5	0.2
Muskrat	1.20	0	0	0.0	1.2	1.2	1.5	0.5
Skunk	3.05	0	0	0.0	0.7	2.1	1.5	0.6
Mustelid	0.56	0	0	0.0	2.4	0.6	1.4	0.5
Sciuridae	0.23	0	0	0.0	23.5	0.2	5.4	2.0
Small rodents	0.04	0	0	0.0	11.5	0.0	0.5	0.2
Wild turkey	7.40	3	22.2	0.1	0.2	2.2	0.5	0.2
Total		266	16,655.7	100.0	99.8	48.0	270.1	100.1

^a Lowest estimated live wt (kg) for large mammals, estimated mean live wt (kg) for small mammals, Pattie and Fisher (1999).

^b Estimated wt × no. of kills.

^c (Estimated wt × no. of kills)/total biomass consumed.

^d From Table 1; occurrence of prey items relative to total prey items.

^e From Ackerman et al. (1984) $y = 1.98 + 0.035x$; not for prey <2 kg.

^f Occurrence of prey items × correction factor.

^g Biomass consumed/prey item/total biomass consumed.

DISCUSSION

The frequency of prey differed significantly between scat and GPS telemetry methods. Scat samples revealed greater diversity of prey and a more complete picture of diet, whereas kill sites were biased toward large ungulate prey. However, when converted to biomass, it is evident that all nonungulate prey weighing <10 kg, along with beaver, contribute <8% to the total biomass consumed. Although some smaller prey will not be detected with data based on kill-site investiga-

tions, the GPS cluster method still provides reliable information about large-bodied prey that contribute most to cougar diets.

For most large terrestrial carnivores, ungulates make up the majority of their diets (Ross et al. 1997, Biswas and Sankar 2002, Gau et al. 2002, Husseman et al. 2003, Kortello et al. 2007). Using both kill site and scat analysis, we found that deer and elk contributed the highest proportion of biomass consumed by cougars in the Cypress Hills. Although small mammals were detected at high frequencies,

Table 3. Calculation of relative ungulate biomass consumed by cougars in Cypress Hills Interprovincial Park, Alberta and Saskatchewan, Canada, May 2008–December 2009. Kill sites located using Global Positioning System (GPS) cluster methods, and scat samples collected and analyzed based on occurrence of ungulate prey items relative to all ungulate prey items identified.

Prey	Est. wt of prey (kg) ^a	Kill sites from GPS clusters (<i>n</i> = 266)				Ungulate prey from scats (<i>n</i> = 201 items)				
		No. of kills	% of kills	Biomass consumed (kg) ^b	Biomass consumed as % of all kill sites ^c	No. of prey items ^d	Prey items occur ^e	Correction factor (kg/scat) ^f	Total biomass consumed (kg) ^g	Relative biomass consumed (kg) ^h
Deer	40.5	202	81.8	8,181	49.7	152	75.6	3.4	256.9	55.7
Elk	180.0	41	16.6	7,380	44.8	46	22.9	8.3	189.5	41.1
Moose	227.0	4	1.6	908	5.5	3	1.5	9.9	14.8	3.2
Total		247	100	16,469	100	201	100	21.6	461.2	100.0

^a Lowest estimated live wt (kg) for large mammals, Pattie and Fisher (1999).

^b Estimated wt × no. of kills.

^c (Estimated wt × no. of kills)/total biomass consumed.

^d Occurrence of prey items relative to all prey items.

^e From Table 1; occurrence of prey items relative to total prey items.

^f From Ackerman et al. (1984) $y = 1.98 + 0.035x$; not for prey <2 kg.

^g Occurrence of prey items × correction factor.

^h Biomass consumed/prey item/total biomass consumed.

they had minimal contribution to overall biomass. Small prey might be more abundant, but the caloric benefits are much lower than for deer or elk (Carbone et al. 2007).

A potential bias associated with diet composition from kill sites relates to the amount of meat consumed by other cougars and scavengers. Previous studies in California (USA) and Alberta have indicated that cougars are opportunistic scavengers (Bauer et al. 2005, Knopff et al. 2010). Using wildlife cameras in our study area, we found multiple cougars (as well as coyotes, small mammals, and birds) scavenging on a large elk carcass (Bacon and Boyce 2010). Murphy and Ruth (2010) report that consumption at a kill site by a single cougar varies significantly by study and location. Thus, estimates of deer and elk biomass consumed at kill sites might be biased high because some of the biomass is consumed by scavengers. Although we have not estimated the extent of bias caused by scavengers, our analysis of scat adjusted for some of the bias against larger prey because we applied the correction factor of Ackerman et al. (1984), and also because we used only a single scat found in the vicinity of a GPS cluster (Marucco et al. 2008). Our comparison between scat collected at kill sites and scat collected incidentally showed no significant difference in the frequency of prey, demonstrating that our methods largely eliminated the bias of large-bodied prey. This bias remains an issue with kill-site investigations and GPS cluster techniques (Ciucci et al. 1996).

MANAGEMENT IMPLICATIONS

Over the past few decades, large carnivores have re-established populations in former and new ranges (Fritts et al. 1997, Anderson et al. 2010). Data on prey composition are important for management of these predators because of concerns over perceived and real threats for human safety, the extent of livestock depredation losses, and effects on wild ungulate populations (Kellert et al. 1996, Woodroffe 2000, Graham et al. 2005, Laundré and Hernández 2010). Different methods for determining diet composition can yield varying results, which could in turn influence conservation and management actions.

The benefits and challenges of various diet-composition methods must be considered when deciding which to employ to characterize predation. Scat analysis is noninvasive and the associated financial costs are lower, but sample size is dependent on the biology and behavior of the species being studied (e.g., wolf rendezvous sites allow for high sample size whereas cougars cover their scat so that they are much more difficult to find incidentally). The identification of the carnivore depositing the scat could be a challenge, depending on the number of sympatric carnivores and domestic species that reside in the study area (Marucco et al. 2008). There are also errors associated with lab technicians' abilities to correctly identify prey from scat samples (Foran et al. 1997).

Global Positioning System radiocollars provide fine-scale information about habitat, movements, and predation events. Kill sites located using GPS cluster data allow researchers to get more precise species-specific kill-rate information in areas with closely related prey species (e.g., both

white-tailed and mule deer), as well as provide more detailed information about sex and age of prey (Merrill et al. 2010). However, GPS telemetry studies are costly and require handling the animal. Telemetry technology is not foolproof, and radiocollars often miss locations, have location errors, drop-off too early, or stop transmitting altogether (Frair et al. 2004, Hebblewhite et al. 2007). Models created from GPS data points show that sampling intervals and fix rate can influence the probability of locating a kill site, especially for small-bodied prey (Webb et al. 2008, Ruth et al. 2010). We have shown that GPS clusters under-represent prey diversity by missing small prey, but nevertheless provide accurate representation of the prey items most relevant to their diet. Recognizing this, researchers and managers must choose the method that will best fit their objectives, budget, and time available for field work.

ACKNOWLEDGMENTS

We are grateful for the assistance of volunteer technicians in the field, M. Landau and P. Jones in the scat lab, L. Hindbo, K. Knopff, A. Knopff, and N. Webb in captures, A. Morehouse for feedback on data analysis, and S. Ciuti for comments on the manuscript. We thank Cypress Hills Interprovincial Park for in-kind and logistic support during field work. Thanks also to local landowners for access to their lands. Funding was provided by Alberta Parks Tourism and Recreation, Saskatchewan Environment, Alberta Conservation Association, Alberta Sport Recreation Parks and Wildlife Foundation, Medicine Hat Fish and Game, Canadian Wildlife Federation, TD Friends of Environment, Heritage Association of Cypress Hills, Safari Club-Northern Alberta Chapter and the Richmond, Saskatchewan and Medicine Hat, Alberta chapters of The Lions Club. Laboratory space was provided by Alberta Cooperative Conservation Research Unit at the University of Alberta.

LITERATURE CITED

- Ackerman, B. B., F. G. Lindzey, and T. P. Hemker. 1984. Cougar food habits in southern Utah. *Journal of Wildlife Management* 48:147–155.
- Alberta Fish and Wildlife Division. 1992. Management plan for cougars in Alberta. Wildlife Management Planning Series no. 5, Edmonton, Alberta, Canada.
- Anderson, C. R., Jr., and F. G. Lindzey. 2003. Estimating cougar predation rates from GPS location clusters. *Journal of Wildlife Management* 67: 307–316.
- Anderson, C. R., Jr., F. Lindzey, K. H. Knopff, M. G. Jalkotzy, and M. S. Boyce. 2010. Cougar management in North America. Pages 41–54 in M. Hornocker and S. Negri, editors. *Cougar ecology and conservation*. University of Chicago Press, Illinois, USA.
- Bacon, M. M., and M. S. Boyce. 2010. Scavenging of an elk, *Cervus elaphus*, carcass by multiple cougars, *Puma concolor*, in southeastern Alberta. *Canadian Field Naturalist* 124:242–245.
- Bacon, M., K. Knopff, and M. S. Boyce. 2009. Eastward movement of cougars in Canada: an update from Cypress Hills Interprovincial Park. *Wild Felid Monitor* 2:19.
- Bauer, J. W., K. A. Logan, L. L. Swenor, and W. M. Boyce. 2005. Scavenging behaviour 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.

- Biswas, S., and K. Sankar. 2002. Prey abundance and food habits of tigers (*Panthera tigris tigris*) in Pench National Park, Madhya Pradesh, India. *Journal of Zoology* 256:411–420.
- Canadian Council on Animal Care [CCAC]. 2003. The CCAC Guidelines on the care and use of wildlife. <<http://www.ccac.ca/Documents/Standards/Guidelines/Wildlife.pdf>>. Accessed 20 Aug 2011.
- Carbone, C., A. Teacher, and J. M. Rowcliffe. 2007. The costs of carnivory. *PLoS Biology* 5:363–368.
- Ciucci, P., L. Boitani, E. R. Pelliccioni, M. Rocco, and I. Guy. 1996. A comparison of scat-analysis methods to assess the diet of the wolf *Canis lupus*. *Wildlife Biology* 2:37–48.
- Environment Canada. 2009. National climate data and information archive. <http://climate.weatheroffice.ec.gc.ca/climateData/monthlydata_e.html>. Accessed 17 Nov 2009.
- Foran, D. R., K. R. Crooks, and S. C. Minta. 1997. Species identification from scat: an unambiguous genetic method. *Wildlife Society Bulletin* 25:835–839.
- Frair, J. L., S. E. Nielsen, E. H. Merrill, S. R. Lele, M. S. Boyce, R. H. M. Munro, G. B. Stenhouse, and H. L. Beyer. 2004. Removing GPS collar bias in habitat selection studies. *Journal of Applied Ecology* 41:201–212.
- Franke, K. A., T. Caelli, G. Kuzyk, and R. J. Hudson. 2006. Prediction of wolf (*Canis lupus*) kill sites using hidden Markov models. *Ecological Modelling* 197:237–246.
- Fritts, S. H., E. E. Bangs, J. A. Fontaine, M. R. Johnson, M. K. Phillips, E. D. Koch, and J. R. Gunson. 1997. Planning and implementing a reintroduction of wolves to Yellowstone National Park and central Idaho. *Restoration Ecology* 5:7–27.
- Gau, R. J., R. Case, D. F. Penner, and P. D. McLoughlin. 2002. Feeding patterns of barren ground grizzly bears in the central Canadian Arctic. *Arctic* 55:339–344.
- Graham, K., A. P. Beckerman, and S. Thirgood. 2005. Human–predator–prey conflicts: ecological correlates, prey losses and patterns of management. *Biological Conservation* 122:150–171.
- Hayes, C. L., E. S. Rubin, M. C. Jorgensen, R. A. Botta, and W. M. Boyce. 2000. Mountain lion predation of bighorn sheep in the Peninsular Ranges, California. *Journal of Wildlife Management* 64:954–959.
- Hebblewhite, M., M. Percy, and E. H. Merrill. 2007. Are all Global Positioning System collars created equal? Correcting habitat-induced bias using three brands in the central Canadian Rockies. *Journal of Wildlife Management* 71:2026–2033.
- Hobson, K., and L. I. Wassenaar. 1999. Stable isotope ecology: an introduction. *Oecologia* 120:312–313.
- Hussemann, J. S., D. L. Murray, G. Power, C. Mack, C. R. Wenger, and H. Quigley. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. *Oikos* 101:591–601.
- Iverson, S. J., C. Field, W. D. Bowen, and W. Blanchard. 2004. Quantitative fatty acid signature analysis: a new method of estimating predator diets. *Ecological Monographs* 74:211–235.
- Kellert, S. R., M. Black, C. Reid Rush, and A. J. Bath. 1996. Human culture and large carnivore conservation in North America. *Conservation Biology* 10:977–990.
- Kelly, J. F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology* 78:1–27.
- Klare, U., J. F. Kamler, and D. W. Macdonald. 2011. A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Review* 41:294–312.
- Knopff, K. H., A. A. Knopff, and M. S. Boyce. 2010. Scavenging makes cougars susceptible to snaring at wolf bait stations. *Journal of Wildlife Management* 74:644–653.
- 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.
- Kortello, D. A., E. T. Hurd, and D. L. Murray. 2007. Interactions between cougars (*Puma concolor*) and gray wolves (*Canis lupus*) in Banff National Park, Alberta. *Ecoscience* 14:214–222.
- Laundré, J. W., and L. Hernández. 2010. What we know about pumas in Latin America. Pages 76–90 in M. Hornocker and S. Negri, editors. *Cougar ecology and conservation*. University of Chicago Press, Illinois, USA.
- Litvaitis, J. A. 2000. Investigating food habits of terrestrial vertebrates. Pages 165–190 in L. Boitani and T. K. Fuller, editors. *Research techniques in animal ecology. Controversies and consequences*. Columbia University Press, New York, New York, USA.
- Marucco, F., D. H. Pletscher, and L. Boitani. 2008. Accuracy of scat sampling for carnivore diet analysis: wolves in the Alps as a case study. *Journal of Mammalogy* 89:665–673.
- Merrill, E., H. Sand, B. Zimmermann, H. McPhee, N. Webb, M. Hebblewhite, P. Wabakken, and J. L. Frair. 2010. Building a mechanistic understanding of predation with GPS-based movement data. *Philosophical Transactions of the Royal Society B* 365:2279–2288.
- Moore, T. D., L. E. Spence, C. E. Dugnolle, and W. G. Hepworth. 1974. Identification of the dorsal guard hairs of some mammals of Wyoming. Wyoming Game and Fish Department, Cheyenne, USA.
- Murphy, K., and T. K. Ruth. 2010. Diet and prey selection of a perfect predator. Pages 118–137 in M. Hornocker and S. Negri, editors. *Cougar ecology and conservation*. University of Chicago Press, Illinois, USA.
- Musiani, M., and P. C. Paquet. 2004. The practices of wolf persecution, protection and restoration in Canada and the United States. *Bioscience* 54:50–60.
- Newsome, R. D., and R. L. Dix. 1968. The forests of the Cypress Hills, Alberta and Saskatchewan, Canada. *American Midland Naturalist* 80:118–185.
- Pattie, D., and C. Fisher. 1999. *Mammals of Alberta*. Lone Pine, Edmonton, Alberta, Canada.
- Phillips, D. L., S. D. Newsome, and J. W. Gregg. 2005. Combining sources in stable isotopes mixing models: alternative methods. *Oecologia* 144:520–527.
- Quigley, H., and M. Hornocker. 2010. Cougar population dynamics. Pages 59–75 in M. Hornocker and S. Negri, editors. *Cougar ecology and conservation*. University of Chicago Press, Illinois, USA.
- Reed, J. E., W. B. Ballard, P. S. Gipson, B. T. Kelly, P. R. Krausman, M. C. Wallace, and D. B. Wester. 2006. Diets of free-ranging Mexican gray wolves in Arizona and New Mexico. *Wildlife Society Bulletin* 34:1127–1133.
- Reynolds, J. C., and N. J. Aebischer. 1991. Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the fox *Vulpes vulpes*. *Mammal Review* 21:97–122.
- Rominger, E. M., H. A. Whitlaw, D. L. Weybright, W. C. Dunn, and W. B. Ballard. 2004. The influence of mountain lion predation on bighorn sheep translocations. *Journal of Wildlife Management* 68:993–999.
- Ross, P. I., M. G. Jalkotzy, and M. Festa-Bianchet. 1997. Cougar predation on bighorn sheep in southwestern Alberta during winter. *Canadian Journal of Zoology* 74:771–775.
- Ruth, T. K., P. C. Buotte, and H. B. Quigley. 2010. Comparing ground telemetry and global positioning system methods to determine cougar kill rates. *Journal of Wildlife Management* 74:1122–1133.
- Sand, H., B. Zimmerman, P. Wabakken, H. Andren, and H. C. Pedersen. 2005. Using GPS technology and GIS cluster analyses to estimate kill rates in wolf–ungulate ecosystems. *Wildlife Society Bulletin* 33:914–925.
- Thompson, D. R., S. J. Bury, K. A. Hobson, L. I. Wassenaar, and J. P. Shannon. 2005. Stable isotope in ecological studies. *Oecologia* 144:517–519.
- Treves, A., and K. U. Karanth. 2003. Human–carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* 17:1491–1499.
- van Dijk, J., K. Hauge, A. Landa, R. Andersen, and R. May. 2007. Evaluating scat analysis methods to assess wolverine *Gulo gulo* diet. *Wildlife Biology* 13(Suppl 2):62–67.
- Weaver, J. L. 1993. Refining the equation for interpreting prey occurrence in gray wolf scats. *Journal of Wildlife Management* 57:534–538.
- 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.
- Woodroffe, R. 2000. Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation* 3:165–173.
- Zimmermann, 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: Rodgers.