



Management and Conservation Article

Cougar Kill Rate and Prey Composition in a Multiprey System

KYLE H. KNOPFF,¹ *Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada*

ALIAH ADAMS KNOPFF, *Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada*

ANDREA KORTELO,² *Department of Fish and Wildlife, University of Idaho, Moscow, ID 83844-1136, USA*

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

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ABSTRACT Assessing the impact of large carnivores on ungulate prey has been challenging in part because even basic components of predation are difficult to measure. For cougars (*Puma concolor*), limited field data are available concerning fundamental aspects of predation, such as kill rate, or the influence of season, cougar demography, or prey vulnerability on predation, leading to uncertainty over how best to predict or interpret cougar–ungulate dynamics. Global Positioning System (GPS) telemetry used to locate predation events in the field is an efficient way to monitor large numbers of cougars over long periods in all seasons. We applied GPS telemetry techniques combined with occasional snow-tracking to locate 1,509 predation events for 53 marked and an unknown number of unmarked cougars and amassed 9,543 days of continuous predation monitoring for a subset of 42 GPS-collared cougars in west-central Alberta, Canada. Cougars killed ungulates at rates near the upper end of the previously recorded range, and demography substantially influenced annual kill rate in terms of both number of ungulates (subad F (SAF) = 24, subad M (SAM) = 31, ad M = 35, ad F = 42, ad F with kittens <6 months = 47, ad F with kittens >6 months = 67) and kg of prey (SAF = 1,441, SAM = 2,051, ad M = 4,708, ad F = 2,423, ad F with kittens <6 months = 2,794, ad F with kittens >6 months = 4,280). Demography also influenced prey composition; adult females subsisted primarily on deer (*Odocoileus* spp.), whereas adult males killed more large ungulates (e.g., moose [*Alces alces*]), and subadults incorporated the highest proportion of nonungulate prey. Predation patterns varied by season and cougars killed ungulates 1.5 times more frequently in summer when juveniles dominated the diet. Higher kill rate in summer appeared to be driven primarily by greater vulnerability of juvenile prey and secondarily by reduced handling time for smaller prey. Moreover, in accordance with predictions of the reproductive vulnerability hypothesis, female ungulates made up a higher proportion of cougar diet in spring just prior to and during the birthing period, whereas the proportion of males increased dramatically in autumn during the rut, supporting the notion that prey vulnerability influences cougar predation. Our results have implications for the impact cougars have on ungulate populations and have application for using cougar harvest to manage ungulates.

KEY WORDS Alberta, cougar, demography, kill rate, multiprey, predator control, *Puma concolor*, ungulate, vulnerability.

Effective management of predator–prey systems depends on reliable estimates of the components of predation such as kill rate and prey composition, and knowledge of the ecological factors causing these to vary. Obtaining necessary data for wide-ranging and elusive large carnivores can be difficult, resulting in gaps in our understanding of predation. For example, most studies of large carnivore predation on ungulates have been conducted during winter, leaving ecologists guessing about predation during the rest of the year (Sand et al. 2008). In the case of cougars (*Puma concolor*), important predators of ungulates throughout the Americas, 5 decades of research has provided information about their predatory behavior (Hornocker and Negri 2009). Yet a number of important ecological questions require additional attention.

For example, a fundamental component of cougar–ungulate interactions is the number of ungulates cougars kill annually; several studies have attempted to estimate cougar kill rate, but estimates vary among studies by >350% within cougar age–sex classes (e.g., 15 vs. 53 ungulates/yr for ad F; Table 1). Past estimates often were derived from potentially unreliable energetic models or models based on telemetry–location clusters (see discussion in Laundré 2005), and even when direct field observations were obtained, sample sizes tended to be small, monitoring durations short,

or both (Table 1). Methods for calculating kill rate also vary among studies, potentially biasing parameter estimates, especially over short monitoring intervals (Hebblewhite et al. 2003). Thus, the challenge is to determine whether the variation among studies can be ascribed to ecological differences versus errors associated with methods.

Season is a potential source of variation in cougar predation, but seasonal influences on cougar predation remain poorly documented. Most studies provide data from only one season, which may extrapolate poorly to annual predation rates (Sand et al. 2008). Even where seasonal variation has been considered for cougars, reported patterns are inconsistent. One hypothesis is that cougars kill ungulates more frequently in winter, either because they switch to nonungulate prey in summer, because harsh environmental conditions (e.g., deep snow) cause ungulates to congregate and become more vulnerable in winter, or to account for the extra energetic costs of thermoregulation (Hornocker 1970, Murphy 1998, Laundré 2008). An alternative hypothesis predicts higher kill rates in summer just after the ungulate birth pulse in May–June when vulnerable juveniles are plentiful (Nowak 1999, Laundré 2008). Evidence regarding these hypotheses is contradictory. For instance, Cooley et al. (2008) reported no effect of season on kill rate, whereas both Murphy (1998) and Nowak (1999) reported seasonal effects, but in opposite directions.

Demographic structure of predator populations can influence predation (Taylor 1984), and because hunting

¹ E-mail: kknopff@ualberta.ca

² Present location: Taricha Consulting, Nelson, BC V1L 5E3, Canada

Table 1. A review of published estimates of ungulate kill rate by cougars in North America during 1949–2009.

Source	Location	Primary prey ^a	Kill rate ^b						Estimation technique ^c	Calculation technique ^d	Sample size ^e	Monitoring period ^f
			UC	UM	UF	AM	SM	AF				
Connolly (1949)	UT	MD	0.73						Ratio	≥26	<4	
Hornocker (1970)	ID	MD, ELK	0.27–0.38						N/A	N/A	N/A	
Hornocker (1970)	ID	MD, ELK						1.17	Ratio	2	15	
Shaw (1977)	AZ	MD						1.04	N/A	4	N/A	
Ackerman et al. (1986)	UT	MD				0.83		0.67–2.26	N/A	N/A	N/A	
Ackerman et al. (1986)	UT	MD						1.57	IKI	2	11	
Harrison (1990)	BC	BS, MD						1.67	IKI	2	34	
Beier et al. (1995)	CA	MD	0.93						Ratio	≤26	N/A	
Murphy (1998)	WY	ELK, MD				0.94	0.64	0.69	Ratio	4	27	
Nowak (1999)	OR	MD, ELK		0.92					IKI	7	44	
Janis and Clark (2002)	FL	WTD, FH		0.90	1.33				IKI	8.5	136	
Anderson and Lindzey (2003)	WY	MD, ELK				0.91	0.74	1.01	Ratio	2.2	84	
Laundré (2005)	ID	MD				0.37	0.29	0.85	N/A	N/A	N/A	
Mattson et al. (2007)	AZ	ELK, MD				0.95	0.88	0.76	IKI	2.5	N/A	
Cooley et al. (2008)	WA	WTD, MD		0.74	0.91			1.20	IKI	<5	<11	
Laundré (2008)	ID	MD				0.47	0.49	0.59	Ratio	12.6	3	
Laundré (2008)	ID	MD				0.47	0.47	0.59	Ratio	7	51	
This study	AB	WTD, MD, MO				0.67	0.59	0.80	Ratio	10 ^h	152	

^a Prey constituting >20% of cougar diet or primary prey available to cougars where diet was not reported: MD = mule deer, WTD = white-tailed deer, MO = moose, BS = bighorn sheep, FH = feral hog (*Sus scrofa*).

^b Kill rate is ungulates/week: UC = cougar of unknown age-sex, UM = male cougar of unknown age, UF = female cougar of unknown age or reproductive status, AM = ad male, SM = subad male, AF = ad female, SF = subad female, FG = family group.

^c Kill rate was either estimated directly by visiting kills in the field (snow-tracking, radiotelemetry, or GPS telemetry), or indirectly using models (E = energetics model, LC-R = location cluster model based on radiotelemetry, LC-G = location cluster model based on GPS telemetry). In the case of Mattson et al. (2007) and Anderson and Lindzey (2003) field data were used to parameterize logistic-regression location cluster models, but the models were used instead of field data to estimate kill rates.

^d Calculation technique can be either ratio or inter-kill (see Hebblewhite et al. 2003).

^e Sample size is average no. of cougars used/demographic category estimate.

^f Monitoring period is average no. of days monitored/cougar used in each estimate.

^g These represent separate estimates for FG with kittens <6 months (lower estimate) and >6 months (higher estimate). Thus, we estimated kill rate for 6 cougar demographic classes, not 5.

^h We calculated kill rates more than once for the same cougar if it transitioned among demographic categories.

can affect cougar population structure (Robinson et al. 2008), understanding how cougar age, sex, and reproduction shape predation patterns can be important. Yet, although most studies indicate that kill rate varies among demographic classes of cougars (Table 1), the reported magnitude and direction of this variation is inconsistent and only Murphy (1998) and Anderson and Lindzey (2003) offer predation data for all age–sex classes from the same study site. The relative importance of other influences on kill rate such as metabolic requirements or experience remains unclear (Ackerman et al. 1986, Murphy 1998, Laundré 2005).

Finally, whether cougars are selective predators preferring vulnerable prey (as suggested by Pierce et al. 2000), or random predators that kill prey as available within normal prey size limits (as suggested by Husseman et al. 2003) has ecological consequences (e.g., Wilmsers et al. 2007). Additional data on seasonal predation may help to clarify the role of prey vulnerability as a determinant of cougar predation. The reproductive vulnerability hypothesis states that temporal variation in the reproductive physiology and behavior of animals will produce associated shifts in vulnerability to predation (Lima and Dill 1990). According to the reproductive vulnerability hypothesis, if cougars select vulnerable prey they should target female ungulates during late gestation and early postparturition (when they are burdened by a heavy fetus or young neonate) and males during the rut (when they are physically weakened by fighting, more solitary, and less vigilant; Fitzgibbon 1990a, Molinari-Jobin et al. 2004, Owen-Smith 2008). Similarly, cougars selecting for vulnerable prey should exhibit disproportionate predation on juvenile ungulates in early summer when they are especially weak and vulnerable (Fitzgibbon 1990b, Testa et al. 2000).

We provide data on cougar predation in a seasonal multiprey environment in west-central Alberta, Canada, to help answer the 4 key questions about cougar predation outlined above: 1) how many ungulates do cougars kill, 2) how does season influence cougar predation, 3) what effect does cougar population structure have on predation rates, and 4) do cougars target vulnerable prey? Specifically, we aimed to census cougar predation on ungulates during year-round monitoring of a sufficiently large number of cougars to provide accurate and precise seasonal estimates of kill rate and prey composition for different demographic classes of cougars. We used these data to test hypotheses about seasonal effects on cougar predation, hypotheses regarding the influence of experience or metabolic demands on cougar predation, and the hypothesis that reproductive and juvenile vulnerability influence cougar predation.

STUDY AREA

We studied cougar predation in west-central Alberta, Canada, during 1998–2008. We pooled data from 2 adjacent study areas representing one cougar population: Bow Valley (BV), including portions of Banff National Park, and Clearwater County (CC) east of the Banff and Jasper National Park Boundaries (Fig. 1). The region

contained alpine, subalpine, montane, and boreal foothills ecoregions. Conifer forests dominated the landscape and were primarily composed of lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), Englemann spruce (*P. engelmannii*), and Douglas fir (*Pseudotsuga menziesii*), with occasional pockets of black spruce (*P. mariana*) and tamarack (*Larix laricina*) in low-lying areas and subalpine fir (*Abies lasiocarpa*) at higher elevations. Aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*) were patchily distributed, as were grasslands. Elevation varied between 849 m and 3,102 m, and topographical complexity increased from flatlands in the east to rugged mountains in the west (Fig. 1). Higher elevations consisted primarily of alpine meadow, rock, and ice. Industrial, residential, and agricultural developments were common but varied in intensity throughout the study area. The region's climate consisted of wet springs, dry summers, and cold, snowy winters. Westerly winds, known locally as Chinooks, provided periodic warming during winter, confining substantial snow accumulation to higher elevations and north aspects.

Potential ungulate prey for cougars included elk (*Cervus elaphus*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), feral horses (*Equus caballus*), bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus*). Woodland caribou (*Rangifer tarandus*) were present at low density. Nonungulate prey included beaver (*Castor canadensis*), porcupine (*Erethizon dorsatum*), snowshoe hare (*Lepus americanus*), and grouse (family: Tetraonidae). Large domestic stock (e.g., cattle and llama) and pets (e.g., cats and dogs) were available as prey also, primarily on private lands in the eastern portion of CC. Other carnivores including bobcat (*Lynx rufus*), lynx (*L. canadensis*), coyote (*Canis latrans*), wolf (*C. lupus*), wolverine (*Gulo gulo*), black bear (*Ursus americanus*), and grizzly bear (*U. arctos*) were present as potential prey or competitors for cougars.

METHODS

Capture and Monitoring

Cougars were treed by hounds in winter and we immobilized cougars with chemical agents using a dart gun (Hornocker 1970). Procedures were approved by the University of Idaho Animal Care and Use Committee (no. 2002–20) in BV and the University of Alberta Animal Care Committee (no. 479505) in CC. In BV we captured 9 cougars between November 2000 and April 2003 using Ketamine (Vetalar®; Bioniche Animal Health Canada, Inc., Belleville, Ontario, Canada) and medetomidine (Zalopine®; Orion Corporation, Espoo, Finland) at an intended dose of 2.5 mg/kg and 0.08 mg/kg respectively. In CC, we captured 44 cougars between December 2005 and May 2008 using 3 mg/kg zolazepam–tiletimine (Telazol®; Fort Dodge Animal Health, Fort Dodge, IA) and 2 mg/kg xylazine (Rompun®; Bayer, Inc., Toronto, Ontario, Canada). We weighed, measured, sexed, and aged immobilized cougars. We estimated age using a combination of tooth color and wear characteristics (Ashman et al. 1983, Shaw 1986), pelage spotting progression (Shaw 1986), and gum-line

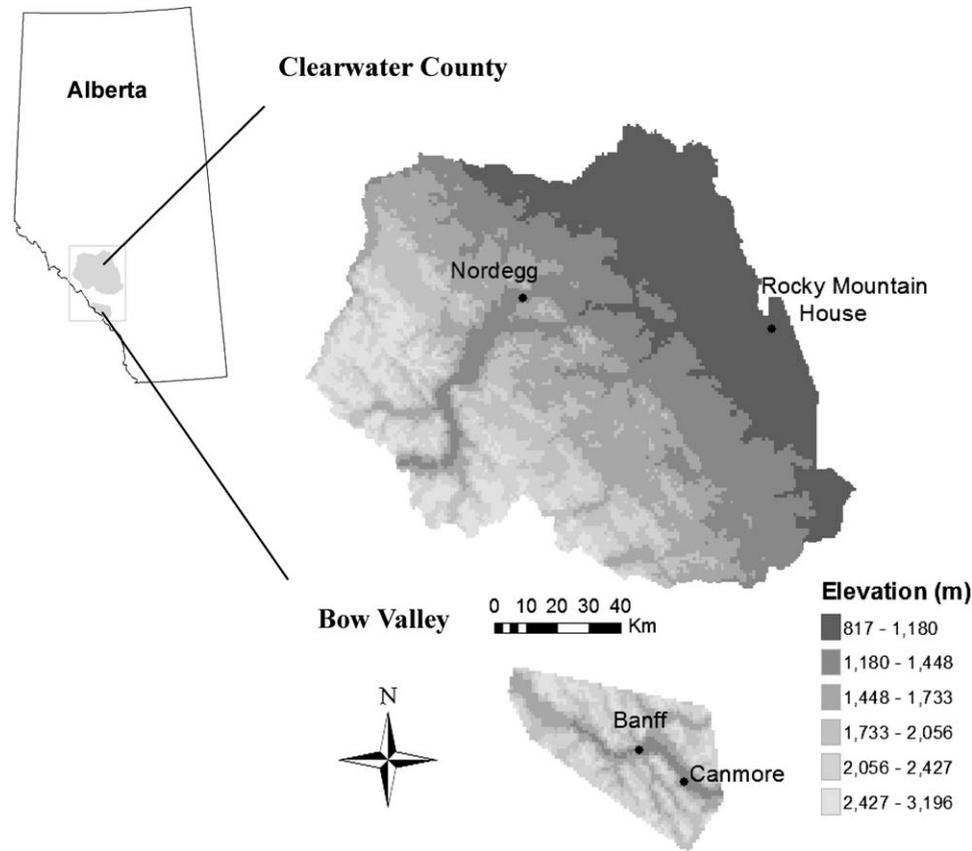


Figure 1. Map of Clearwater County (CC) and Bow Valley (BV) study area locations in west-central Alberta, Canada, where cougars were monitored from 1998 to 2008. Elevation and selected towns are displayed.

recession (Laundré et al. 2000). We classified cougars as kittens (still with mother), subadults (dispersal until 2.5–3 yr), or adults (>2.5–3 yr). We fitted cougars with one of 3 brands of Global Positioning System (GPS) radiocollar (Lotek 4400S [Lotek Engineering, Newmarket, Ontario, Canada]; H.A.B.I.T VHF/GPS [H.A.B.I.T Research, Victoria, British Columbia, Canada]; or Televilt GPS-Simplex [Televilt International, Ramsberg, Sweden]), or a Lotek LMRT-3 very high frequency (VHF) collar. Upon completion of handling, we gave cougars 0.125 mg/kg yohimbine (Yobine®; Lloyd Laboratories, Shenandoah, IA), to reverse xylazine, or 0.4 mg/kg atipamezole (Antisedan®; Pfizer Animal Health, Kirkland, Quebec, Canada), to reverse medetomidine, and released the animals.

We programmed GPS collars to obtain a location at either 2- or 3-hour intervals (i.e., 8–12 fix attempts/day). We attempted to download data from each collar fortnightly, and we visited clusters of GPS locations as soon as possible thereafter to identify predation events. We considered a cluster any combination of ≥ 2 locations occurring within 200 m and 6 days of each other (Knopff et al. 2009). In BV and prior to November 2007 in CC, we attempted to visit nearly all identified clusters. After 1 November 2007 in CC we employed a logistic regression model to screen clusters with a near-zero probability of predation from the set we visited in the field (Knopff et al. 2009). We also

opportunistically snow-tracked VHF-collared and uncollared cougars to locate predation events during 1998–2008.

Characteristics of Prey

We identified animal remains found at GPS location clusters as either predation or scavenging events provided there was evidence the cougar had killed or fed on the carcass. We assigned predation if we found remains with evidence of being killed by a cougar (e.g., bite marks and hemorrhaging on the neck or a clear predation sequence played out by tracks in the snow at fresh kills). Where such information was not available, we assigned predation if the age of the remains closely matched the dates over which the cluster was created and there was no evidence to contradict cougar predation. We assigned scavenging in cases where the animal had been killed by something other than a cougar (e.g., remains at a trapper bait station, or from a wolf-killed, hunter-killed, or road-killed animal) or if the carcass age greatly preceded the dates the cougar spent at the cluster (Knopff et al. 2010).

We identified prey species by anatomical, skeletal, and pelage characteristics (Stelfox 1993). We assigned prey to 1 of 3 age classes: young of the year (<1 yr), yearling (1–2 yr), or adult (>2 yr), as determined by size, degree of epiphyseal fusion, and tooth eruption and wear (Stelfox 1993). We used presence or absence of antlers or pedicles and other

Table 2. Ungulate weights we used to calculate kill rate (kg/day) and prey composition (biomass) for cougars in west central Alberta, Canada, during 2001–2008.

Age and sex class	Species				
	Deer	Elk	Moose	Bighorn sheep	Feral horse
Ad M	95 ^a	320 ^a	450 ^a	117 ^a	420 ^b
Ad F	70 ^a	230 ^a	418 ^a	65 ^a	420 ^b
Yearling (12–24 months)	55 ^c	181 ^c	330 ^c	51 ^c	331 ^c
YOY ^d (6–12 months)	38 ^c	124 ^c	226 ^c	35 ^c	227 ^c
YOY (3–6 months)	21 ^c	68 ^c	123 ^c	19 ^c	124 ^c
YOY (0–3 months)	10 ^c	33 ^c	60 ^c	9 ^c	61 ^c
Unknown	54 ^c	178 ^c	323 ^c	50 ^c	325 ^c

^a We obtained estimates from Renecker and Hudson (1993).

^b Estimated using known wt of similar-sized domestic horses.

^c We derived median wt for each nonad age class from a von Bertalanffy growth eq of the form $M(t) = A[1 - 1/3e^{-K(t - I)}]^3$, where $M(t)$ = mass (kg) at age t , A = max. wt (we used wt of ad F), K = growth rate (we used 0.0049), and I = age at inflection point (we used 140 days).

^d YOY = young of the yr.

cranial characteristics to determine sex (Stelfox 1993). If insufficient evidence existed to provide certain identification of species, age, or sex, we recorded ‘unknown.’ We assigned each predation event either to winter (15 Oct–14 Apr) or summer (15 Apr–14 Oct) using the date of the first GPS location at a predation cluster (GPS collared cats) or the estimated mortality date (for kills located via snow-tracking). We selected seasonal cutoffs to encompass broad shifts in temperature, daylight, and snow accumulation and to ensure the pulse in neonatal availability (i.e., May–Jun) was encapsulated within one season.

Because we usually visited kill sites after cougars had consumed their prey, we were unable to obtain biomass estimates in the field. Instead, we assigned approximate live weights to prey based on literature values (Table 2). For moose, elk, deer (white-tailed and mule deer combined), and bighorn sheep we assigned sex-specific weights to adults based on average values for Alberta ungulates (Renecker and Hudson 1993). Data on feral horse weights in west-central Alberta were unavailable, and we estimated average adult weight using known weight of similar-sized domestic horses. We obtained weights for yearling and young of the year ungulates using a von Bertalanffy growth equation of the form $M(t) = A[1 - 1/3e^{-K(t - I)}]^3$, where $M(t)$ = mass (kg) at age t , A = maximum weight ($t = \infty$), K = growth rate, and I = the age at inflection point (days; Monteith et al. 2009). We did not differentiate between sexes for juveniles and yearlings and we used adult female weights for each species (Table 2) to define A , and we assigned values to K (0.0049) and I (140) so that the resulting curve roughly approximated a number of published ungulate growth curves (e.g., Anderson et al. 1974, Hudson and Haigh 2002, Schwartz 2007, Monteith et al. 2009). We then assigned median weights from the curves to each of 4 age brackets (0–3 months, 3–6 months, 6–12 months, and 12–24 months; Table 2). If we could not determine ungulate age class, we assigned the yearling weight to the kill. If the prey was known to be an adult but we could not distinguish sex, we used the mean adult weight (i.e., [ad M + ad F]/2). Age–sex class was often difficult to determine for nonungulate prey (generally little remained of the carcass) and we assigned an average weight given by Soper (1964) for the species.

Prey Composition

We calculated species and age–sex composition of prey in cougar diets using all predation events where these prey characteristics were known. We calculated species composition both as percent frequency and percent biomass. We collapsed prey into 3 categories: small ungulates (e.g., deer, sheep, goats), large ungulates (e.g., elk, moose, feral horses), and nonungulate prey, and we used chi-square tests to compare prey composition among adult male, adult female, and subadult cougars and between seasons within demographic classes. We performed these and all other statistical analyses in STATA SE 9.0 (StataCorp, College Station, TX).

We also analyzed monthly variation in ungulate prey composition (we pooled data from all cougars) to test hypotheses about prey vulnerability. If cougars selected vulnerable prey, we expected greater representation by males in autumn, females in spring, and overrepresentation of juveniles immediately following the birth pulse. Assuming 80% of all ungulates in west-central Alberta were female with an annual fecundity rate of 1.5 gives a postbirth proportion of 54.5% juveniles in the ungulate population, which probably overestimates the true reproductive capacity of the ungulate guild occurring in west-central Alberta (Demarais and Krausman 2000). We therefore considered selection for juveniles to occur in months where they comprised >55% of predation events.

Kill Rate

Laundré (2005) points out that the best way to resolve disagreement over the number of ungulates cougars kill is to monitor predation sequences continuously in the field over long periods using GPS telemetry (e.g., Anderson and Lindzey 2003, Knopff et al. 2009). Although previous research has applied GPS telemetry to estimate cougar kill rate, estimates were obtained using models and not continuous monitoring (e.g., Anderson and Lindzey 2003, Mattson et al. 2007). In this study, we attempted to census cougar predation on ungulates over the duration each cougar was monitored. To ensure consistency and avoid potential bias in our kill rate estimates, we used only data from cougars wearing GPS telemetry collars where fix success was

>45% (Knopff et al. 2009). Although Knopff et al. (2009) suggest that monitoring periods must be long (preferably >100 days over a 180-day period) to reduce the influence of sampling error on kill rate estimation, restricting calculations to shorter monitoring periods that reflect changes in season and demography might be appropriate if these factors influence kill rate. We therefore calculated kill rates for all cougars continuously monitored for ≥ 4 weeks (28 days) in a given season and demographic class. We used a ratio estimator (Hebblewhite et al. 2003) because it is both more conservative and more accurate than the inter-kill method (e.g., Murphy 1998, Cooley et al. 2008), which truncates the denominator in the rate estimator to the period between the first and last kills in a predation sequence and eliminates monitoring periods where ≤ 1 kill was made. We used total monitoring time as the denominator for rate estimation and both number of kills and kg of prey as numerators, yielding frequency (events/week) and biomass (kg/day) metrics.

We calculated frequency metrics only for ungulates, because nonungulate prey <8 kg are likely to be underestimated in our sample (Knopff et al. 2009). We based biomass estimates on live weight of all prey and, therefore, overestimated cougar consumption. We did not attempt to correct for this overestimation because we did not measure loss to scavengers, decomposition, or carcass abandonment, and we were uncertain about the percent of prey biomass available for cougar consumption (e.g., $P > 90\%$ for neonates, an unknown quantity less for ad deer, and much less for ad moose or feral horses where cougars cannot access bones and marrow). Consequently, any correction factor we applied would be arbitrary.

To provide results comparable to other studies, we first calculated the average annual kill rate for cougars using individuals as the unit of analysis and pooling data across seasons and demographic classes. We then estimated season-specific kill rates for 6 cougar age-sex and reproductive classes: subadult female, subadult male, adult male, adult female, adult female with kittens <6 months, and adult female with kittens >6 months. We calculated kill rates more than once for an individual cougar in a given season if the animal transitioned between age or reproductive categories during the study. We visited den sites to obtain initial kitten counts and then used track counts in snow, dirt, or mud and occasional visual observations to monitor kitten retention. We aged kittens traveling with females at capture using spotting progression, body size, and track size, and counted them when treed or by snow-tracking.

We assessed the effect of season on kill rate while controlling for demographic variation using a 2-tailed paired t -test for individuals monitored ≥ 28 days in the same demographic class in both summer and winter. Next, we assessed the influence of demography on kill rate using a single factor analysis of variance in each season. Demographic and season-specific monitoring periods for each cougar were the units of analysis. Post hoc comparisons using Tukey's test determined which demographic classes differed (Day and Quinn 1989). We estimated annual kill

rates for each demographic class using the mean of season-specific values.

To test the hypothesis that kill rate increases as a consequence of the ungulate birth pulse in spring (e.g., Nowak 1999, Sand et al. 2008), we calculated the average interval between the first location fixes at consecutive predation events by month (intervals were assigned to the month in which they ended) for each cougar to determine whether the inter-kill interval (IKI) declined during and immediately after the birth pulse. We then evaluated the relationship between IKI and proportion of juvenile ungulates in monthly cougar diets using a Pearson's correlation. We used IKI for these analyses to avoid problems with calculating rates over extremely short monitoring periods (e.g., a few days) during months where monitoring was truncated due to capture or collar failure.

To provide a more mechanistic understanding of variation in cougar kill rates, we divided cougar IKI into search time (a function of the probability of encountering prey and the probability killing prey given an encounter) and handling time (time spent consuming prey). We defined handling time (hr) as the number of GPS locations obtained at a predation cluster divided by the collar fix success over the duration of the cluster and multiplied by the collar fix rate. We calculated search time by subtracting handling time of the prey killed at the beginning of an IKI from the total length of the interval. We could calculate negative search times if a second prey was killed (ending the initial IKI) while the first prey was still being handled (simultaneous handling of multiple prey). In such cases, we assigned search time as zero.

We tested the difference between average search and handling time during summer and winter using t -tests where each predation event was the unit of analysis. We also controlled for prey size (i.e., handling time/kg of prey) in a similar analysis to test the hypothesis that per-kg handling times will be reduced in summer, possibly as a consequence of increased contest competition with bears (e.g., Murphy et al. 1998) or more rapid decomposition of carcasses during warmer months. We then obtained monthly averages of search and handling time and correlated these with the proportion of juveniles in the diet to determine how each component of predation varied as a function of prey composition.

We regressed cougar body mass against kill rate (kg prey/day) in each season to test the hypothesis that kill rate is driven by metabolic requirements (Ackerman et al. 1986, Laundré 2005). We estimated weights for family groups by adding 15 kg/kitten <6 months old and 34 kg/kitten >6 months old to the capture weight of the mother. When comparing our regressions to those estimated in other studies (e.g., Laundré 2005) we first converted all kill rate estimates into kg of live weight/day. We also tested Murphy's (1998) hypothesis that cougar kill rate is related to experience and not necessarily metabolic needs alone. If this were true, adults should have higher kill rates (kg prey/kg cougar) than subadults. We excluded family groups because of different metabolic needs associated with kitten

Table 3. Seasonal comparison of the proportional frequency of prey in the diet of adult female, adult male, and subadult cougars. Results are presented for individual prey types and condensed prey categories using data from 1,428 predation incidents for 53 cougars in west-central Alberta, Canada, during 1998–2008.

Prey type	Ad F (%)		Ad M (%)		Subadult (%)	
	Summer (n = 557)	Winter (n = 406)	Summer (n = 107)	Winter (n = 114)	Summer (n = 153)	Winter (n = 91)
Individual prey types						
Beaver	4.67	1.72	9.35	5.26	15.03	4.40
Bighorn sheep	0.54	5.42	1.87	6.14	2.61	12.09
Coyote	2.50	3.20	0.00	0.88	1.96	4.40
Domestic	0.36	0.99	0.00	0.00	0.65	3.30
Elk	4.49	5.17	12.15	14.04	2.61	2.20
Deer	75.40	76.85	25.23	43.86	55.56	37.36
Feral horse	0.54	0.00	13.08	10.53	0.00	0.00
Moose	5.75	0.49	36.45	11.40	13.07	0.00
Porcupine	1.08	0.74	0.00	0.00	5.88	26.37
Other	4.67	5.42	1.87	7.89	2.61	9.89
Condensed categories						
Nonungulate	13.29	12.07	11.21	14.04	26.14	48.35
Small ungulate	75.94	82.27	27.10	50.00	58.17	49.45
Large ungulate	10.77	5.67	61.68	35.96	15.69	2.20

growth (Ackerman et al. 1986) and compared adult and subadult data for each season separately using 1-tailed *t*-tests.

RESULTS

Our sample of captured cougars included 30 adult females, 7 adult males, 6 subadult females, and 10 subadult males. Of these, 4 subadult females and 2 subadult males transitioned to adults and 9 adult females transitioned among reproductive classes while they were radiocollared. We monitored predation of 42 GPS collared cougars continuously over 9,543 cougar-days (\bar{x} = 227 days/cougar, SD = 127), split approximately evenly between summer (4,852 days) and winter (4,691 days) during 2002–2008. We visited approximately 3,700 GPS location clusters and snow-tracked cougars for >1,100 km, locating 1,509 predation events. We visited predation sites an average of 25 days (SD = 26) after kills were made and all edible biomass had generally been consumed by the time we arrived. Because smaller prey often was consumed completely, we infrequently determined age and sex for nonungulates and sex was almost never available from juvenile ungulates. However, we were able to identify species (with white-tailed and mule deer combined as deer) at 1,505 kills, age at 1,241 kills, and sex at 495 kills.

Prey Composition

Cougars killed a variety of wild prey including ungulates (white-tailed deer, mule deer, moose, elk, bighorn sheep, mountain goat, feral horses), carnivores (cougar, wolf, coyote, red fox [*Vulpes vulpes*], lynx, black bear, marten [*Martes americana*]), small mammals (beaver, porcupine, snowshoe hare, red squirrel [*Tamiasciurus hudsonicus*], hoary marmot [*Marmota caligata*]), and birds (grouse, ducks [*Anas* spp.], Canada geese [*Branta canadensis*], raven [*Corvus corax*]). The size of wild prey killed by cougars spanned 2 orders of magnitude ranging from red squirrels (0.35 kg) to adult moose and feral horses (>400 kg). Domestic animals

(e.g., llamas, cattle, dogs) comprised <1% of predation events.

Wild ungulates made up most prey we identified in both relative frequency (84%) and biomass (96%). Deer were the most prevalent ungulate (frequency = 64%, biomass = 51%), and of the cases where we could distinguish deer species (n = 541) white-tailed deer dominated (68%). Most ungulate prey were either young of the year (43%) or adults (45%) with yearlings making up the remainder. Cougars tended to kill younger animals, especially when preying on feral horses and moose (the largest prey available in W-central Alberta) for which nearly all predation events (86%) involved animals <2 years old. Female prey made up 58% of all predation events where we identified sex.

Cougars exhibited significant seasonal shifts in prey composition (ad M, χ^2_2 = 15.63, P < 0.001; ad F, χ^2_2 = 7.67, P = 0.022; SA, χ^2_2 = 17.29, P < 0.001). All

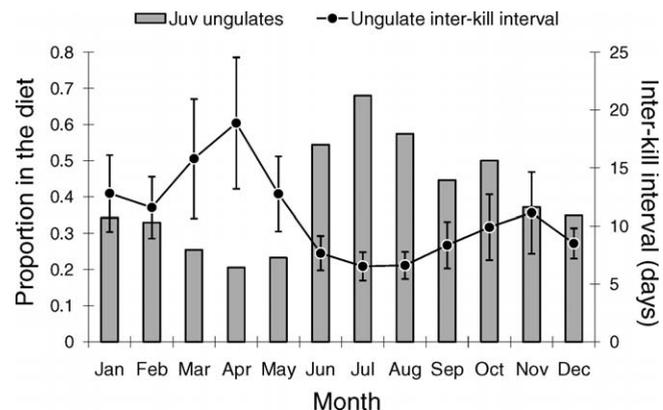


Figure 2. Monthly proportion of juvenile prey in cougar diet and the average ungulate inter-kill interval (bound by 95% CI) preceding kills made in each month in west-central Alberta, Canada during 2001–2008. We derived proportions from 1,229 kills where age of prey and date of death were known. We estimated inter-kill intervals for 42 cougars from 1,090 kills where the date of the preceding ungulate kill was known. Individual cougars were the unit of analysis in each month, and we pooled data from all cougar age–sex classes.

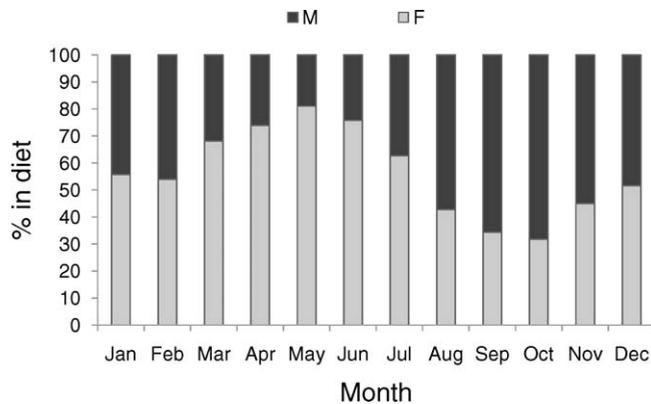


Figure 3. Monthly proportion of male and female ungulate prey in the diet of cougars in west-central Alberta, Canada during 1998–2008. We derived estimates from 489 predation events where we could unambiguously identify sex (i.e., skull or reproductive organs present) and month of death was known. Because we were rarely able to identify the sex of juvenile prey, we obtained >80% of the data presented here from adult and yearling prey.

demographic classes of cougar increased the proportion of large ungulates (e.g., moose, elk, feral horses) in their diet during summer, and in opposition to Hornocker's (1970) hypothesis that nonungulate prey would become increasingly important in summer, subadults shifted their diet to include almost twice as many nonungulate prey (especially porcupines) in winter (Table 3). The age structure of cougar prey varied by season and the proportion of juvenile ungulates found at predation events increased during summer ($\chi^2_2 = 43.70$, $P < 0.001$). Juvenile ungulates exceeded 55% of all prey killed by cougars (indicating selection) in July and August (Fig. 2). In these months, juvenile ungulates also accounted for up to 46% of the biomass killed by cougars. Although not different between seasons ($\chi^2_1 = 1.771$, $P = 0.183$), the proportion of male and female ungulate prey in cougar diet varied substantially by month over the course of the year (Fig. 3). Female ungulates were killed most often in April–June, whereas the proportion of males peaked during August–November.

Species composition of prey also varied among cougar age-sex classes ($\chi^2_4 = 295$, $P < 0.001$). Large ungulates made up 48.4% of ungulates killed annually by adult males, but only 8.6% and 10.7% of the prey killed by adult females and subadults, respectively. Nonungulate prey appeared more frequently in subadult diets (34.4%) than in those of either adult males (12.7%) or adult females (12.8%). Adult females focused predation on small ungulates (78.6%). When we considered biomass, the importance of large ungulates intensified for all age sex classes (ad M = 78.0%, ad F = 20.9%, SA = 25.2%), whereas the importance of nonungulates subsided (ad M = 2.0%, ad F = 3.4%, SA = 12.2%). Neither age ($\chi^2_4 = 1.41$, $P = 0.843$) nor sex ($\chi^2_2 = 0.74$, $P = 0.691$) of ungulate prey varied among sex and age classes of cougars.

Kill Rate

We estimated kill rate using a subset of 1,326 kills located at telemetry clusters during continuous monitoring of GPS collared cougars. We did not calculate kill rates for cougars

wearing H.A.B.I.T GPS collars because fix success averaged <35%. We calculated 85 season- and demographic-specific kill rates for which monitoring periods averaged 107 days (SD = 48.5). We did not calculate kill rate for 10 monitoring periods because their duration was <28 days. Cougar kill rate (not accounting for the influence of season or demography) averaged 0.8 ungulates/week (95% CI = 0.7–0.9) or 8.28 kg/day (95% CI = 7.13–9.41), but kill rates were variable among individuals (range = 0.24–1.38 ungulates/week and 2.88–18.60 kg/day). Moreover, ungulate IKIs varied over time for individuals. Cougars occasionally made kills in rapid succession, but we also documented 52 intervals between ungulate kills >3 weeks (21 days), the longest of which lasted 75 days. Cougars survived these periods by consuming other carnivores, small mammals, birds, or carrion.

We monitored 27 individual cougars that maintained demographic status across seasons. Using these paired data we found that, on average, cougars in west-central Alberta killed 1.49 times as many ungulates/week in summer ($\bar{x} = 0.951$ ungulates/week, 95% CI = 0.797–1.105) as in winter ($\bar{x} = 0.639$ ungulates/week, 95% CI = 0.497–0.782; $t_{26} = -5.358$, $P < 0.001$). Biomass killed also was higher in summer ($\bar{x} = 8.60$ kg/day, 95% CI = 6.68–10.52) than in winter ($\bar{x} = 7.79$ kg/day, 95% CI = 5.64–9.94), but not significantly so ($t_{26} = -0.931$, $P = 0.360$). Increased frequency of ungulate killing in summer occurred in tandem with increasing reliance on juvenile prey. Ungulate IKI varied substantially by month, reaching a high in April and dropping rapidly through the ungulate birth pulse (May–Jun) before increasing again after a low in July (Fig. 2). Monthly variation in IKI was strongly and negatively correlated ($R^2 = 0.74$, $P < 0.001$) with the proportion of juvenile ungulates in cougar diet (Fig. 2).

Average handling time of prey was 39% higher in winter ($\bar{x} = 78$ hr, SD = 63.8) than in summer ($\bar{x} = 56$ hr, SD = 46.8; $t_{1,239} = -6.703$, $P < 0.001$), and handling time was positively correlated with prey size ($R^2 = 0.21$, $P < 0.001$, $n = 1,240$). Thus, reduced inter-kill intervals in months where juveniles made up an increasing proportion of cougar diet were due in part to smaller prey. However, after controlling for prey size, we found that handling times were still 22% longer in winter ($\bar{x} = 2.20$ hr/kg, SD = 3.9) than summer ($\bar{x} = 1.81$ hr/kg, SD = 2.3; $t_{1,239} = -2.22$, $P = 0.013$), suggesting that other factors (e.g., scavenging by bears, more rapid carcass spoilage) might have contributed to the overall reduction in summer handling time.

Average duration of searching before making a kill also was lower in summer (summer = 117 hr, SD = 144; winter = 159 hr, SD = 207; $t_{1,036} = -3.78$, $P < 0.001$), contributing substantially to the overall reduction in inter-kill interval. Indeed, search time declined more than twice as fast as handling time for each incremental increase in the proportion of juvenile prey in cougar diet (Fig. 4). Thus, increased encounter rates via greater prey abundance, greater vulnerability of prey to attack once encountered, or seasonal changes in searching intensity contributed more to higher cougar kill rate in summer than did reduced handling time.

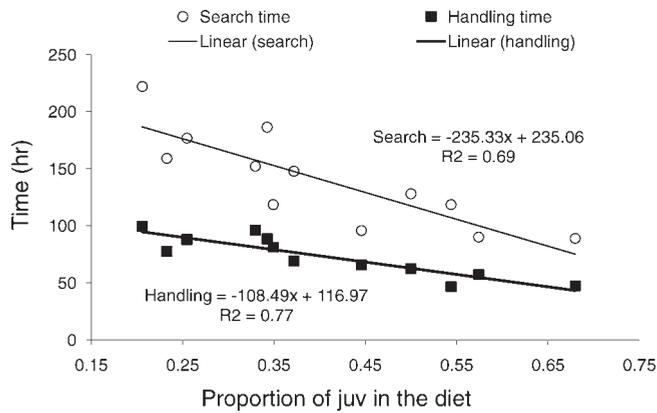


Figure 4. Relationship between the monthly proportion of ungulate juveniles in cougar diet and the average search and handling times during inter-kill intervals ($n = 1,211$) by month in west-central Alberta, Canada during 2001–2008. The best-fit linear regression equations and coefficient of variation (R^2) values are displayed.

Frequency of ungulate killing varied among cougar age-sex classes in both summer ($F_{5,30} = 6.85, P < 0.001$) and winter ($F_{5,43} = 13.3, P < 0.001$). Reproductive status had an especially profound impact: females with kittens >6 months old killed most frequently, followed by adult females with kittens <6 months old, adult females without kittens, adult males, subadult males, and finally subadult females (Fig. 5). Results of Tukey's pair-wise post hoc comparison revealed that statistical differences were driven primarily by adult females with kittens >6 months, which killed significantly more frequently than adult males and subadults of both sexes in winter and all demographic classes

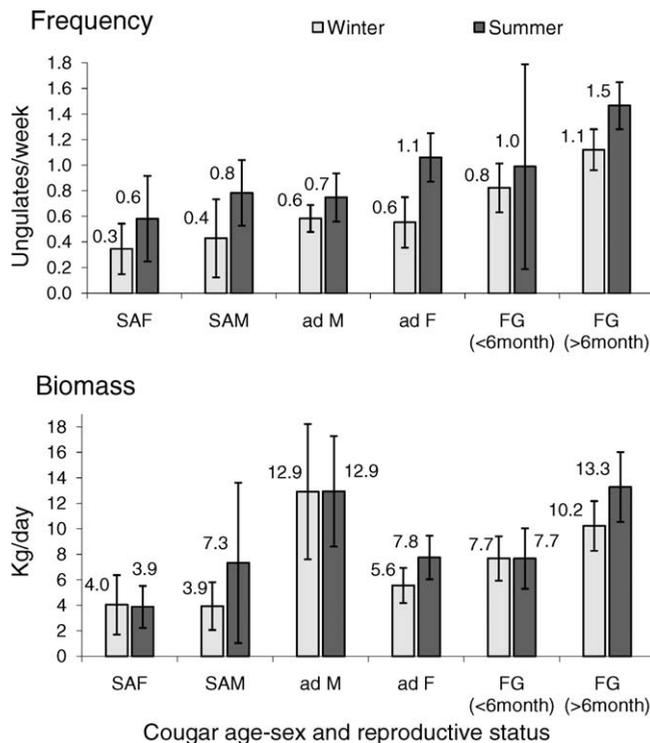


Figure 5. Cougar kill rates and associated 95% confidence intervals expressed as the frequency and biomass of prey for each demographic category and season in west-central Alberta, Canada during 2001–2008.

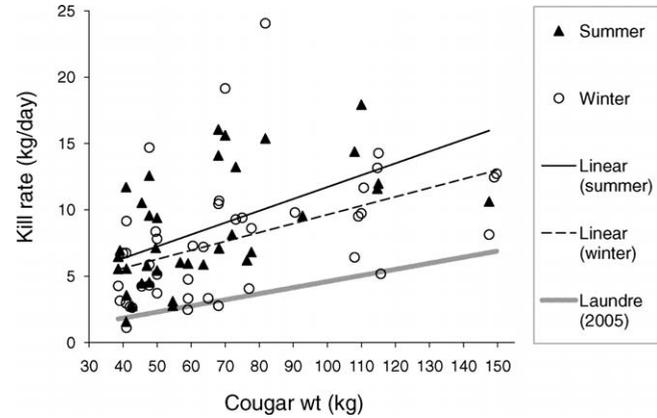


Figure 6. Relationship between cougar body mass (incorporating kitten wt for family groups) and kill rate (estimated live-wt biomass of prey) in summer and winter in west-central Alberta, Canada between 2001 and 2008. Also displayed is the relationship between cougar mass and kill rate predicted by Laundré's (2005) energetics model. We used Laundré's (2005) average daily requirement of 0.0363 kg of prey/kg of cougar/day divided by the constant 0.79 (= 0.0459) to convert edible biomass to live-weight biomass for comparison with our data.

except adult females with kittens <6 months in summer. The average number of ungulates killed per year was 24 for subadult females, 31 for subadult males, 35 for adult males, 42 for adult females, 47 for females with kittens <6 months, and 67 for females with kittens >6 months.

Biomass of prey killed by cougars also varied by demographic class in both seasons (summer: $F_{5,30} = 6.93, P < 0.001$; winter: $F_{5,43} = 9.27, P < 0.001$). Differences were primarily a result of the high biomass killed by adult males and females with kittens >6 months (Fig. 5). The wide confidence interval surrounding the summer biomass estimate for subadult males (Fig. 5) occurred because one approximately 2.5-year-old male (still without a home range) transitioned to killing moose like an adult male. The annual live-weight biomass of prey killed by cougars averaged 1,441 kg for subadult females, 2,051 kg for subadult males, 4,708 kg for adult males, 2,423 kg for adult females, 2,794 kg for females with kittens <6 months, and 4,280 kg for females with kittens >6 months.

Cougar body mass remained a significant predictor of the kg/day killed by cougars in both summer ($R^2 = 0.30$ and $P < 0.001$) and winter ($R^2 = 0.21$ and $P = 0.002$). However, coefficients of determination (R^2) indicate that most of the variation in kill rate remained unexplained by a model based on energetics alone. Experience, for instance, appeared to play a role and we found that after controlling for body mass, adults killed nearly twice as much as subadults in both summer (ad = 0.183 kg of prey/kg of cougar/day SA = 0.098 kg of prey/kg of cougar/day, $t_{25} = 4.078, P < 0.001$) and winter (ad = 0.148 kg of prey/kg of cougar/day, SA = 0.080 kg of prey/kg of cougar/day, $t_{27} = 2.628, P = 0.007$).

DISCUSSION

Kill Rate

Most of our annual kill rate estimates fell within the range of values reported for cougars elsewhere (Table 1), which is not surprising given the large variation among previous

estimates. Adult females and family groups in west-central Alberta tended to kill closer to the high end of earlier estimates, whereas adult males killed at the lower end (in terms of frequency, not biomass). The ratio method we used to calculate kill rate was substantially more conservative (i.e., >25%; Hebblewhite et al. 2003) than the IKI estimator used in most other field studies of cougar kill rate. Thus, the adult cougar kill rates we found were among the highest recorded using field data. Subadults were less effective predators, and our kill rate estimates were lower than those given previously (Table 1). Two of 3 previous estimates, however, used cluster models without visitation (e.g., Anderson and Lindzey 2003, Mattson et al. 2007), which tend to overestimate subadult kill rate (Anderson and Lindzey 2003; K. Knopff, University of Alberta, unpublished data).

3

Our kill rate estimates indicate that adult cougars are highly effective predators, killing at rates at the upper end of those recorded for wolves in both frequency and biomass (Peterson and Ciucci 2003, Sand et al. 2008, Webb 2009). Our estimates were inconsistent with lower proposed values based on energetics calculations and movement models for cougars during summer in Idaho, USA (Laundré 2005, 2008). The Idaho estimates differed from our summer estimates by as much as 365% in terms of frequency of killing and 538% in terms of prey biomass. Because kill rate fundamentally influences the effect predators have on their prey, the discrepancy between studies represents a substantial difference in the capacity for cougars to impact ungulates. For instance, Laundré et al. (2006) used a deterministic population model and kill rates derived from energetics calculations (Laundré 2005) to analyze cougar–mule deer dynamics in southern Idaho, concluding that cougars did not contribute to the decline or impede the recovery of mule deer between 1992 and 2004. Incorporating higher kill rate values we identified would alter this conclusion considerably.

Some of the discrepancies in kill rates in the literature (Table 1) are likely a result of inaccuracies associated with indirect methods or lack of precision due to small sample size in field-based studies. Energetics models often underestimate actual kill rates by large carnivores (Peterson and Ciucci 2003), and classification success of clustering models remains far from perfect, yielding reasonable estimates of kill rate only over long monitoring intervals and under circumstances where false positives and false negatives at individual location clusters cancel appropriately (Webb et al. 2008, Knopff et al. 2009). Some inconsistencies might be due to different ecological conditions among regions, but it is currently impossible to ascertain how much of the variation among studies can be ascribed to ecological vs. methodological differences. We believe that visiting GPS telemetry clusters in the field and using a ratio estimator to calculate kill rate represents the current gold standard in kill rate estimation for cougars (see reliability of results below) and future studies using similar techniques in other places will help better define the natural range of variation in cougar kill rate.

Influence of Season

Ungulate kill rate (frequency) increased by a factor of 1.5 during summer when cougars focused predation on smaller juvenile prey. This pattern is similar to that discovered by Sand et al. (2008) for wolves in Scandinavia and fails to support hypotheses predicting lower kill rate for large carnivores in summer (e.g., Hornocker 1970, Murphy 1998, Laundré 2008), which have led ecologists either to ignore seasonal differences in predation rates (Ballard et al. 1997, Laundré 2005, Varley and Boyce 2006, Laundré et al. 2006) or to assume that predation rates will be highest in winter (White and Garrott 2005, Stahler et al. 2006). Conversely, our results support the hypothesis that frequency of ungulate killing will increase in tandem with the pulse in neonate availability in early summer (Nowak 1999, Laundré 2008, Sand et al. 2008). This seasonal effect must be considered when estimating annual predation rates for ungulate populations subject to cougar predation.

There are 3 reasons why a similar seasonal pattern should be expected for all large carnivores occupying systems where ungulates exhibit a synchronized birth pulse. First, the ungulate birth pulse dramatically increases the density of prey available to a predator, which is expected to influence the functional response of unsatiated predators by increasing the probability of encounter (Holling 1959). Second, in contrast to a claim by Nilsen et al. (2009) that roe deer (*Capreolus capreolus*) fawns are invulnerable to predation by Eurasian lynx (*L. lynx*), most research indicates that ungulate neonates are highly susceptible to large carnivore predation (Fitzgibbon 1990b, Testa et al. 2000, Mech and Peterson 2003). Third, even if predators are satiated, handling times decrease when smaller prey are incorporated into the diet, resulting in a higher frequency of killing (Holling 1959). Some studies may have failed to identify higher kill rates for large carnivores in summer because methods in those studies did not permit researchers to locate many neonates or because sample size was too small (e.g., Jedrzejewski et al. 2002, Cooley et al. 2008, Nilsen et al. 2009).

Influence of Demography

Age–sex and reproductive class substantively influenced cougar predation patterns. Consequently, cougar population structure should be considered when investigating cougar–ungulate dynamics. Females with kittens displayed the highest frequency of predation, and although our results support the general consensus that family groups have higher kill rates than solitary cougars (Table 1), we did not find a pronounced increase in predation until kittens were older (i.e., >6 months), probably as a consequence of higher energetic requirements for larger kittens. Subadults, on the other hand, consistently killed less often, relied more heavily on nonungulate prey, and killed lower total biomass of prey than adults, supporting Murphy's (1998) hypothesis that experience is an important driver of cougar kill rate. Counterintuitively, we found that adult males killed ungulates less often than did smaller adult females, but this unexpected result is explained by the larger size of prey

killed by males. A focus on large ungulates might also explain why adult males in west-central Alberta killed less often than has been reported for males in other places where fewer species of large prey were available (Table 1). In some cases, therefore, kill rate comparisons might best be made using biomass, especially when comparing between sexes or among studies where the size of available prey differs.

Dietary segregation appears to be common in sexually dimorphic vertebrates (du Toit 2005, Breed et al. 2006), including cougars (Ross and Jalkotzy 1996, Murphy 1998, Anderson and Lindzey 2003). Presumably, a higher proportion of large ungulates in male cougar diet occurs because larger male body size reduces risks associated with attacking larger prey (Sunquist and Sunquist 1989, Iriarte et al. 1990). Yet, larger male body size does not explain why large prey should dominate male diets in systems where deer remain the most abundant prey, such as west-central Alberta (Webb 2009). An alternate explanation is that males focus on larger prey to reduce intra-specific competition with females and improve reproductive success.

Influence of Prey Vulnerability

Cougars in west-central Alberta killed primarily female ungulates just before, during, and just after the birthing period (Apr–Jun), males just before and during the rut (Sep–Nov; Fig. 3), and focused predation on juvenile ungulates in spring consistent with the reproductive and juvenile vulnerability hypotheses, reinforcing the notion that cougars select for vulnerable prey. Similarly, whereas cougars are capable of killing prey as large as adult moose and feral horses, prey of this size were rarely taken (<2% of prey weighed >400 kg). Most (74%) moose and feral horses killed by cougars were juveniles, and all cougar age–sex classes killed a higher proportion of large ungulate species (i.e., ad >200 kg) in summer when smaller juveniles were available (Table 3). This pattern is likely due to lower risks associated with attacking smaller prey (Sunquist and Sunquist 1989). Although our seasonal result is novel, that cougar predation on large ungulate species tends to focus on animals <1 year old has been well-documented (Hornocker 1970, Turner et al. 1992, Ross and Jalkotzy 1996, Murphy 1998, Husseman et al. 2003).

Although we were unable to distinguish relative contributions of elevated encounter rate (due to increased prey abundance), greater average susceptibility of prey to attack, or greater searching effort by cougars to higher kill rate in summer, these mechanisms were collectively more than twice as important as reduced handling time (Fig. 4). Because close grouping between mothers and young (e.g., moose) or hiding behavior of neonates (e.g., white-tailed deer) are strategies that limit searching efficiency during the pulse of juvenile availability in spring (Fitzgibbon 1990b, Fryxell et al. 2007), we suspect that high vulnerability of juveniles to attack when encountered is the dominant force driving elevated summer kill rates, which is further supported by selection for juveniles in summer (i.e., proportions in cougar diet higher than max. possible annual

production), even though encounter rates with juveniles might be low relative to older ungulates.

That vulnerability to attack might influence cougar predation runs contrary to the assumption that that felids kill prey as encountered (e.g., Wilmers et al. 2007). Rather, our results support studies that indicate selection for vulnerable individuals may be widespread in felid–ungulate systems (e.g., Pierce et al. 2000, Molinari-Jobin et al. 2004, Owen-Smith 2008). These patterns can be interpreted as part of a broader optimal foraging strategy where felids attempt to minimize risks associated with predation by targeting easier prey (e.g., Ross et al. 1995, Logan and Sweanor 2001, Owen-Smith 2008, Knopff et al. 2010).

Accuracy of Results

Three sources of bias in our GPS telemetry technique might have influenced our results. First, although probably rare, predation events might be missed because a cluster fails to form (we identified one case in BNP through snow-tracking where a kill was cached in a cave and no cluster was produced). Second, our cluster technique was designed to find prey >8 kg (Knopff et al. 2009) and prey less than or close to this value might be missed because handling time is too short to produce a cluster or because we did not locate remains at a cluster where prey was consumed (in some cases only a few tufts of hair and small bone fragments were all that remained of neonate kills). These sources of error would cause us to underestimate kill rate, especially during early summer when ungulate neonates dominated the diet. A third source of error might occur if we classified scavenging events as kills, inflating kill rate estimates and altering prey composition (Knopff et al. 2010). Scavenging at kills freshly made by other cougars can be especially difficult to identify, and this almost certainly occurred occasionally (we documented 4 cases of kill sharing by collared cougars with overlapping home ranges). On the other hand, we were able to identify scavenging events on numerous occasions and we have no reason to suspect that this source of error would be large enough to substantially alter our conclusions (Knopff et al. 2010).

Overall, the GPS telemetry approach we used had potential biases similar to radiotelemetry studies where researchers wait until carcasses are consumed before investigating predation sites, but our approach generated far more data. Moreover, potential biases associated with visiting telemetry clusters are fewer than those associated with estimating kill rate using models alone (Knopff et al. 2009). Snow-tracking can provide more detailed information, but logistical constraints restrict sample size and limit monitoring to winter. Consequently, our approach provides the best balance of accuracy and efficiency of currently available methods.

MANAGEMENT IMPLICATIONS

Our estimates of cougar kill rate and our findings concerning the influence of season, demography, and prey vulnerability on cougar predation patterns can be applied to better interpret and anticipate cougar–ungulate dynamics.

Our results also have application for cougar harvest management where cougar impacts on ungulate populations are cause for concern. Shifts toward a younger age structure or reductions in the proportion of females rearing kittens in hunted cougar populations (e.g., Stoner et al. 2006, Robinson et al. 2008) can reduce predation rates on ungulates, even if cougar density does not change, because subadults have lower kill rates than adults and females without kittens have lower kill rates than those with kittens. Likewise, changing the sex ratio of cougar populations via harvest (e.g., Anderson and Lindzey 2005) might be used to alter the impact cougars have on different species of ungulate in multiprey systems. Managers should be cautious when applying cougar harvest to enhance ungulate populations, however, because the benefit to ungulates will be situation-dependent, population-level predator control may not always produce the desired outcome for ungulates, and side-effects are possible, such as increased conflict with humans when average cougar age is reduced (Ballard et al. 2001, Lambert et al. 2006, Knopff and Boyce 2007).

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