The difference between killing and eating: ecological shortcomings of puma energetic models

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Abstract. Bioenergetic modeling is employed to estimate the energetic demands of many cryptic carnivores and their kill rates needed to meet their energetic requirements. We tested two prevalent assumptions driving energetic modeling of predator kill rates: (1) morphological and physiological information (weight, energetic demands of activity patterns) of individual predators are sufficient to accurately predict their kill rates, and (2) kill and consumption rates are equivalent (meaning that carnivores consume all of what they kill). We did this by testing whether two independent energetic models accurately predicted puma (*Puma concolor*) kill and consumption rates in three study systems in North and South America with variable ecology, including climate and prey assemblages. Our results demonstrated that current puma energetic models drastically underestimate actual puma kill rates quantified through intensive field monitoring. We concluded that puma energetic models more realistically estimate puma consumption rates needed to meet metabolic requirements. Puma kill rates determined from field efforts were not explained by puma weight (in kg) or activity patterns (in distance traveled), which were the variables used in energetic models. Our kill rates in kg/day determined from field investigations of GPS clusters were the highest reported to date and statistically equivalent across three distinct ecosystems, a range of puma characteristics, variable lengths of monitoring, variable daily distances traveled, and across systems with 1–3 ungulate prey. In contrast, puma kill rates in ungulates/week differed across study areas, suggesting that kill rates described in kilograms per day are better suited for comparing puma kill rates across systems while kill rates in terms of ungulates per unit time are better suited for modeling predator-prey dynamics for a particular ecosystem. Based on these results we concluded that energetic models using morphological and physiological variables alone were insufficient to predict kill rates, and proposed that rather than focusing future research on refining current energetic models, future research should be directed at understanding the behavioral ecology driving carnivore kill rates.

Key words: bioenergetic modeling; California; Colorado; kill rates; kleptoparasitism; Patagonia; predation; Puma concolor.

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INTRODUCTION

Understanding the effects of predators on prey has long been a focus of ecological research (e.g., Elton 1924). Kill rates, defined as the numbers of prey killed per individual predator per unit time (Holling 1959), are possibly the most fundamental component of ecology required for modeling predator-prey dynamics (e.g., Lotka-Volterra equations; Lotka 1925, Volterra 1926). Estimates of kill rates have increased our understanding of dynamic species interactions in complex multi-species communities, including apparent competition affecting rare prey (Holt and Lawton 1994, Wittmer et al. 2013), predation-mediated Allee effects (McLellan et al. 2010), and the effects of kleptoparasitism on the fitness of subordinate competitors (Gorman et al. 1998, Elbroch and Wittmer 2013a). Accurate estimates of kill rates are also essential for managers charged with setting sustainable harvest quotas for game species coexisting with native predators (e.g., White and Lubow 2002), and developing conservation strategies for species negatively affected by predation, including those in reintroduction programs (e.g., Rominger et al. 2004, Wittmer et al. 2013).

For cryptic species, kill rates are difficult, if not impossible to quantify through direct observation in natural environments. Bioenergetic modeling, based upon basal metabolic rates (BMR) (Kleiber 1961) and the energetic costs associated with activity (Ackerman et al. 1986, Gorman et al. 1998), has thus been employed to estimate the energetic demands of many carnivores and subsequently the kill rates needed to meet these energetic requirements (e.g., wolves, *Canis lupus*, in Glowacinski and Profus 1997). BMRs have traditionally been scaled from $M^{0.75}$ in vertebrates, where M is mass in kilograms (Kleiber 1961, Hudson et al. 2013), and activity patterns and their associated energetic budgets have been derived from bioenergetic studies of both captive and free-ranging animals (Weiner 1989).

Pumas (*Puma concolor*) are a solitary, large carnivore widespread throughout the western hemisphere, and a species in which bioenergetic modeling has made important contributions to our understanding of both its foraging ecology and its impacts on prey (Robinette et al. 1959, Hornocker 1970, Ackerman et al. 1986, Laundre

2005). In contrast, published kill rates quantified through field efforts have been highly variable and rarely align with model predictions (Laundré 2008, Knopff et al. 2010, Ruth and Murphy 2010b). Until recently, puma field research has been almost entirely reliant upon triangulation of animals tagged with VHF transmitters over multiple days, a method that likely underestimates actual kill rates because of the difficulty in finding kills at which pumas remained for less than 24 hours (Merrill et al. 2010, Elbroch and Wittmer 2013b). Recent GPS technology, however, has revolutionized research methods on the foraging ecology of cryptic carnivores (Knopff et al. 2010, Merrill et al. 2010, Elbroch and Wittmer 2013b). New puma research based on field investigations of GPS clusters has suggested that actual puma kill rates are significantly higher than those predicted by puma energetic models (Knopff et al. 2010, Elbroch and Wittmer 2013b), despite improved data on puma activity patterns and associated refinements of puma energetic models (Laundré 2005).

Prevalent energetic models for carnivores, including pumas, remain strictly physiological, meaning that predicted kill rates are quantified based upon morphology (mass in kilograms) and energy budgets (either in terms of activity coefficients determined from captive and field trials [pumas in Ackerman et al. 1986], activity time [wild dogs, *Lycaon pictus*, in Gorman et al. 1998] or distance traveled [pumas in Laundre 2005]). Puma energetic models have incorporated variable female reproductive status to account for the increased energetic demands of families over individuals (Ackerman et al. 1986, Laundre 2005), however, other important aspects of puma ecology remain unaccounted for in current energetic models. For example, pumas abandon large amounts of prey carcasses due to harassment by scavengers, which influences how much meat pumas consume, and potentially their kill rates as well (Murphy 1998, Ruth and Murphy 2010a, Elbroch and Wittmer 2013b).

The objectives of our research were to test two prevalent assumptions driving the energetic modeling of predator kill rates: (1) that morphological and physiological information of individual predators alone are sufficient to accurately predict kill rates (e.g., Ackerman et al. 1986, Laundré 2005), and (2) that kill and consumption

rates are equivalent (meaning that carnivores consume all of what they kill [Vucetich et al. 2012]). We do not dispute that energy consumption is driven by species morphology (size) and physiology (energetic budgets based on activity), but rather aimed to quantify potential differences between consumption and kill rates as a means to explore the importance of incorporating additional ecological context into bioenergetic modeling of predator kill rates, and predator impact on prey populations. We hypothesized that puma bioenergetic models would correctly estimate puma consumption rates, which account for their energetic requirements for survival, but would underestimate the amount of prey killed by pumas needed to acquire their energetic needs because they do not consume all of what they kill (Elbroch and Wittmer 2012*b*).

We achieved our objectives by comparing puma kill rates determined through intensive field investigations at three independent field sites in North and South America, with kill rates calculated using two independent puma energetic models (Ackerman et al. 1986, Laundré 2005). We measured kill rates in kilograms of prey killed per day (kg/day) to compare these three methods. The three study areas were representative of some of the significant variation in the environmental conditions pumas encounter across their range, both in terms of climate and ungulate prey assemblages. Further, we compared kill rates for these three study areas in terms of ungulates killed per week (ungulates/week) to compare our findings with previous research (summarized in Table 1 in Knopff et al. 2010), and tested whether any variation in kill rates across study areas was driven by differences in research methods, as proposed by Knopff et al. (2010) and Ruth and Murphy (2010*b*), or the number of types of ungulate prey in the system, as proposed by Laundré (2008).

METHODS

Study areas

Our first study site (Patagonia) was located in the southern portion of Chile's Aysén District, north of Lago Cochrane in central Chilean Patagonia (W 47.800, S 72.000). The area covered approximately 1200 km^2, and included the 69 km^2 Lago Cochrane National Reserve, the 690 km^2 private Estancia Valle Chacabuco, and approximately 440 of the 1611 km^2 Jeinimeni National Reserve (Elbroch and Wittmer 2012*a*). The land cover was characteristic of rugged Patagonia mountains containing a mixture of three dominant cover classes: open Patagonian steppe; high-elevation, deciduous forests dominated by lenga (*Nothofagus pumilio*); and lower elevation shrub communities dominated by ñirre (*N. antarctica*) interspersed with chaura (*Pernettya mucronata*) and calafate (*Berberis microphylla*) shrubs. Elevations ranged from 200 to 1,500 m above sea level (asl), temperatures averaged 6.5°C over the course of a year, and the area received approximately 800 mm of precipitation annually, with the majority falling as snow during the Austral winter (May–August) (Elbroch and Wittmer 2012*a*). Pumas in our Patagonian site were part of a diverse predator-prey system that included two native ungulate species, guanacos (*Lama guanicoe*) and huemul (*Hippocamelus bisulcus*) as well as domestic sheep (*Ovis aries*). Guanacos were the most abundant ungulate prey (88.6% of prey biomass), followed by domestic sheep (2.3% biomass), and finally rare and endangered huemul deer (0.5% of biomass) (Elbroch and Wittmer 2013*a*). Individual pumas were also known to prey on introduced European hares (*Lepus europaeus*) (8.5% of available prey biomass) (Elbroch and Wittmer 2012*a*). Eleven vertebrate species scavenged from puma kills, most notably Andean condors (*Vultur gryphus*) and culpeo foxes (*Lycalopex culpaeus*) (Elbroch and Wittmer 2012*b*).

Our second study site (Colorado) was located in western Colorado near the town of De Beque (W 39.385, S −108.324), and covered an area of approximately 1100 km^2. The area consisted of a matrix of public lands managed by the US Bureau of Land Management (BLM), interspersed with private inholdings of various sizes, most notably the approximately 800 km^2 High Lonesome Ranch, where the research was focused. The topography was rugged and consisted of flat valley bottoms between approximately 1500 and 1700 m asl, steep canyon walls, and plateaus ranging in elevation between 1800 and 3000 m asl. Valley bottoms and slopes were characterized by pinyon-juniper (*Pinus edulis* and *Juniperus* spp.) woodlands, interspersed with islands of Gambel oak (*Quercus gambeli*), and

Table 1. Individual puma characteristics and the associated characteristics of each intensive monitoring period.

Puma ID	Monitoring period	Sex	Study site	Kitten status	Weight (kg)	Days of monitoring	Total distance traveled (km)	Mean daily distance moved (km)
PA_M2	M02_1	M	PAT	...	70	45	285.76	6.35
PA_M2	M02_2	M	PAT	...	70	30	573.6	19.12
PA_M3	M03_1	M	PAT	...	66	120	1604.64	13.37
PA_M3	M03_2	M	PAT	...	67	164	1943.36	11.85
PA_M4	M04_1	M	PAT	...	82	57	639.04	11.21
PA_F1	F01_1	F	PAT	4	35	202	4212.8	20.86
PA_F2	F02_1	F	PAT	1	32	62	1130.88	18.24
PA_F3	F03_1	F	PAT	1	38	169	1876	11.10
PA_F4	F04_1	F	PAT	2	36	89	799.36	8.98
PA_F4	F04_2	F	PAT	3	36	60	455.84	7.60
PA_F4	F04_3	F	PAT	4	36	272	1857.6	6.83
PA_F5	F05_1	F	PAT	1	38	53	344.32	6.50
PA_F5	F05_2	F	PAT	2	38	90	546.08	6.07
PA_F5	F05_3	F	PAT	3	38	60	986.72	16.45
CO_P01	P01_1	M	CO	...	46	354	1808.32	5.11
CO_P03	P03_1	M	CO	...	46	287	2568.512	8.95
CO_P05	P05_1	M	CO	...	66	55	548.992	9.98
CO_P06	P06_1	M	CO	...	65	155	2087.04	13.46
CO_P13	P13_1	M	CO	...	50	120	747.68	6.23
CO_P02	P02_1	F	CO	4	43	26	114.48	4.40
CO_P07	P07_1	F	CO	4	50	58	331.296	5.71
CO_P07	P07_2	F	CO	4	50	292	2226.797795	7.63
CO_P08	P08_1	F	CO	1	42	250	1663.2	6.65
CO_P09	P09_1	F	CO	4	44	221	1470.016	6.65
CO_P10	P10_1	F	CO	4	41	249	2244.4	9.01
CO_P12	P12_1	F	CO	1	48	180	1268.08	7.04
CA_M33	M33_1	M	CA	...	56	57	419.13	7.35
CA_M33	M33_2	M	CA	...	56	66	657.24	9.96
CA_M33	M33_3	M	CA	...	57	37	292.04	7.89
CA_M36	M36_1	M	CA	...	48	69	288.29	4.18
CA_F1	F01_1	F	CA	1	35	31	243.34	7.85
CA_F1	F01_2	F	CA	1	35	46	208.29	4.53
CA_F1	F01_3	F	CA	1	48	36	216.96	6.03
CA_F17	F17_1	F	CA	1	50	57	445.96	7.82
CA_F17	F17_2	F	CA	1	58	61	321.57	5.27
CA_F17	F17_3	F	CA	1	38	39	170.66	4.38
CA_F17	F17_4	F	CA	1	33	30	156.11	5.20
CA_F17	F17_5	F	CA	1	33	67	350.51	5.23
CA_F19	F19_1	F	CA	1	30	33	204.56	6.20
CA_F23	F23_1	F	CA	1	50	34	286.66	8.43
CA_F23	F23_2	F	CA	1	34	38	303.33	7.98
CA_F43	F43_1	F	CA	4	33	69	272.87	3.95
CA_F43	F43_2	F	CA	4	38	28	132.12	4.72
CA_F43	F43_3	F	CA	4	38	42	137.95	3.28
CA_F43	F43_4	F	CA	4	38	33	189.16	5.73

rangeland shrub communities (*Artemisia* spp. and *Atriplex* spp.). High-elevation plateaus included mixed conifer (*Pseudotsuga mensiesii* and *Pinus contorta*) and aspen (*Populus tremuloides*) forests, as well as rangeland shrubs. The area averaged 295 mm of precipitation annually, most of which fell as snow between December and March. Temperatures in the area were strongly seasonal, ranging from −10°C during winter to 33.8°C during summer; mean annual temperature was 8.1°C (NCDC COOP Station number 057031). The study area supported two native ungulate species, elk (*Cervus canadensis*) and mule deer (*Odocoileus hemionus*), and large numbers of cattle (*Bos primigenius*), although we never documented a puma killing cattle during the course of our study. Common additional prey species included American beavers (*Castor canadensis*) and North American porcupines (*Erethizon dorsatum*), and competitive scavengers regularly detected at puma kills included American black bears (*Ursus americanus*), coyotes (*Canis latrans*), Golden eagles (*Aquila chrysaetos*), and common gray foxes (*Urocyon cinereoargenteus*).

Our third study site (California) was located in

Northern California and included approximately 1024 km^2 of the Mendocino National Forest and surrounding private properties (W 39.738, S −123.160). Elevations ranged from 400 to 2450 m asl. Habitats varied across elevational gradients from grasslands and mixed chaparral at low elevations to Douglas fir (*Pseudotsuga menziesii*) stands at high elevations. The climate was strongly seasonal. Temperatures varied from −12°C to 45.5°C, and the mean annual temperature averaged 13.1°C (NCDC COOP Station #042081). Annual rainfalls in the area average approximately 1320 mm, predominantly falling between October and April either as rain at lower elevations or snow at higher elevations. Black-tailed deer (*O. h. columbianus*) were the only abundant ungulate prey in the area. There were increasing numbers of feral pigs (*Sus scrofa*) at lower elevations and we occasionally observed Tule elk (*C. e. nannodes*) dispersing through the study area, but we never documented predation on these species. Other documented prey species included black-tailed jackrabbits (*Lepus californicus*), northern raccoons (*Procyon lotor*), and California ground squirrels (*Otospermophilus beecheyi*). Regular competitive scavengers detected at puma kills were American black bears, common gray foxes, coyotes, turkey vultures (*Cathartes aura*), and common ravens (*Corvus corvax*).

Puma captures

We predominantly relied on hounds to capture pumas in all three study areas. Hounds forced pumas to retreat to a tree or rocky outcrop where we could safely approach them. Captures with hounds in Patagonia occurred during the Austral fall and winter (March–August 2008 and May–September 2009), during Colorado winters between February 2010 and March 2012, and throughout the year in California between December 2009 and November 2012. We also used box traps in Colorado and California during the same time periods when running hounds, and foot snares (described in Logan et al. 1999, Elbroch et al. 2013) in Colorado to capture pumas during warmer months. All traps were equipped with telemetry devices and monitored at minimum twice per day (1 hour after sunrise and again prior to midnight). In Patagonia and Colorado, pumas were anesthetized with keta-

mine (2.5–3.0 mg/kg) and medetomidine (0.075 mg/kg), and in California, pumas were anesthetized with approximately 2.2 mg /kg of Telazol (tiletamine HCl and zolazepam HCl; Fort Dodge Animal Health, Fort Dodge, IA). Pumas were processed, sampled, and fitted with either Argos or Iridium GPS collars (Lotek 7000SAW or Lotek Iridium 2D). The effects of medetomidine were reversed with atipamezole (0.375 mg/kg), and pumas were released at capture sites. All capture and handling procedures adhered to guidelines developed by the American Society of Mammalogists (Gannon and Sikes 2007) and were approved by the independent Institutional Animal Care and Use Committee at the University of California, Davis (Protocols 13252, 15341, 16645, 16886).

Calculating kill and consumption rates from field efforts

GPS collars placed on adult pumas were programmed to acquire location data at 2-hour intervals and transmit data through an Argos uplink at 3-day intervals, or twice daily via an Iridium uplink. Upon retrieval, location data received via satellite and downloaded directly from collars were displayed in ArcGIS 9.1. (ESRI, Redlands, CA), in which we calculated distances between consecutive puma locations. In Patagonia and Colorado, we defined GPS clusters (Anderson and Lindzey 2003) as any ≥2 locations, and in California as any ≥3 locations, within 150 m of each other, and where a minimum of 1 GPS location was recorded during crepuscular or nocturnal periods, the exact timing of which varied with season. For 2 months at the start of our fieldwork, we investigated every cluster, even those made completely within daylight hours. However, because daytime clusters never revealed predation events and required significant time to check (each puma would make 1–3 short daytime clusters per day), we chose not to investigate clusters with durations completely within daylight hours for the remainder of the projects and to assume that they were day beds rather than kills. Ninety-three percent of all field investigations of clusters were conducted by CyberTracker-certified observers (Evans et al. 2009, Elbroch et al. 2011), ensuring a consistent field effort and expertise across study sites. Researchers transferred puma location data

to handheld GPS units, which they then used to guide them in the field to locate GPS clusters.

In all three study areas GPS locations were systemically searched to locate and identify prey remains, including hair, skin, rumen, and bone fragments. The state of prey remains, presence and location of bite marks, and body parts consumed were used to determine whether the puma had killed the animal or was scavenging. For all three study areas, we estimated age-specific weights of adult ungulate prey from literature sources and, to account for lower weights of juvenile animals, adjusted weights based on known growth rates using simple regressions of weight and age (see Appendix).

We quantified total kill rates (kg/day) for all prey killed for sampling periods where pumas were monitored continuously for a minimum of 4 weeks (Knopff et al. 2010, Elbroch and Wittmer 2013*a*) with the exception of one 26-day monitoring period. We did not include any periods in which Argos transmissions missed GPS locations for ≥1 night. For pumas in which there was a gap in monitoring, and thus two or more sampling periods of continuous monitoring greater than four weeks in length, we calculated kill rates for each period separately. We also calculated kill rates in terms of ungulates killed per week, to compare with previous research summarized in Knopff et al. (2010, Table 1). All ungulates, regardless of species, size or sex were treated equally when we quantified kill rates in ungulates/week.

We defined consumption rates as we did kill rates, in kg/day for the length of each monitoring period. We estimated consumption rates from the number of 24-hour periods that a puma was associated with the kill site, and employed results from feeding trials with captive pumas to estimate the amount of meat consumed during this time. Ackerman (1982) reported feeding trails for several pumas, mostly subadults, and Danvir and Lindzey (1981) reported feeding trials for an adult male. We decided to use the largest estimates for adult pumas to better reflect wild puma consumption rates, and to provide conservative estimates of how much meat pumas abandoned at carcasses. We assumed an initial consumption rate of 6.8 kg for the first 24-hour period, and then 4.1 kg for each successive 24-hour period. We chose this estimate for con-

sumption rather than subtracting the weight of prey remains from estimated live prey weights (e.g., Vucetich et al. 2012) because of the commonality of other scavengers feeding at puma kills while pumas were still utilizing the carcass (Elbroch and Wittmer 2012*b*), thus making it impossible to determine how much meat was eaten by pumas versus other animals. The numbers of kittens accompanying females were determined and monitored using a variety of methods, including incidental observations during captures of their mothers, direct observations, tracks in snow, and remote cameras at active kill sites. For females with kittens three months of age and older, we estimated the amount eaten by individual kittens by first estimating their weight as a fractional proportion of adult females and then multiplying said weight by the adult consumption rates reported above. Monthly weights of kittens were calculated from equations developed by Maehr and Moore (1992), and the equation constants suggested in Laundré and Hernández (2002). Kitten consumption rates were combined with that of their mother to estimate total feeding of family groups.

Calculating kill and consumption rates from energetic models

Ackerman et al. (1986) method.—We employed Ackerman et al.'s (1986) models to predict energy expenditures, consumption rates, and kill rates for each puma monitoring period as follows: $E_{Total} = E_{BMR} + E_{Act} + E_{Gro} + E_{Rep}$. The calculation, $E_{BMR} = 70 \times M^{0.75}$, represented the daily energy demands of basal metabolism in kcal/day, where M was a puma's weight at capture in kg. The calculation, $E_{Act} = E_{BMR} \times AC$, represented the additional daily energetic demands of physical activity in kcal/day, where AC represented activity constants dependent on the sex and reproductive status of the puma (AC = 2.43 for adult males, 1.56 for adult females without kittens, 1.67 for females with kittens, and 1.62 for kittens; Ackerman et al. 1986). The calculation,

$$E_{Gro} = \Delta Weight \times \left(\frac{1430}{e} \right),$$

accounted for the additional daily energetic demands of growth in kcal/day, where the average daily change in weight over the period

of monitoring was multiplied by the energetic value of puma flesh (1430 kcal/kg) divided by e, a 60% growth efficiency constant. The equation,

$$E_{\text{Rep}} = n_{\text{litter}} \times \left(\frac{E_{\text{cub}}}{e_2} \right),$$

accounted for the additional daily energetic demands of accompanying kittens for adult females in kcal/day, where n was the number of kittens in the litter, e_2 was the efficiency of energy transfer between mother and kitten (60% during lactation, 100% during gestation and post weaning), and the equation, $E_{\text{cub}} = E_{\text{BMR}} + E_{\text{Act}} + E_{\text{Gro}}$, accounted for the daily energetic demands of each kitten, as defined above. We estimated age-specific kitten weights with equations developed by Maehr and Moore (1992), and the equation constants suggested in Laundré and Hernández (2002).

We then defined the predicted daily consumption rate in kg/day as:

$$\text{Consump}_{\text{Ack}} = \frac{E_{\text{Tot}}}{0.87 \times 1890 \times 0.86},$$

where 0.87 was the fraction of energy derived from meat, 1890 kcal was the energetic value of deer meat, and 0.86 was the energetic value of the food post digestion and assimilation. Predicted daily kill rate in kg/day as was estimated as follows:

$$\text{KillRate}_{\text{Ack}} = \frac{\text{Consump}_{\text{Ack}}}{0.68},$$

where 0.68 accounted for the edible portion of adult ungulates (Wilmers et al. 2003).

Laundré (2005) method.—We employed Laundré's (2005) models to predict energy expenditures, consumption rates, and kill rates for each individual adult puma in each study area for variable monitoring periods as follows: $E_{\text{Total}} = 5.8 \times M^{0.75} \times t + 2.6 \times M^{0.60} \times d + (E_{\text{Kittens}})$. E_{Total} was energy expenditure measured in kilocalories, M was a puma's weight at capture in kg, t was time in hours for the monitoring period for which we calculated consumption and kill rates, and d was the distance traveled in kilometers for the duration of the monitoring period, determined by taking the sum of straight-line distances between consecutive GPS locations and multiplying by a correction factor of 1.6 (Elbroch and Wittmer 2012*a*).

The additional energetic costs of kittens (E_{Kittens}) for pregnant females were 14.8 kcal/day (0.008 kg deer) per kitten, and for lactating females, 381.1 kcal/day (0.202 kg deer) per kitten (Laundré 2005). We quantified the energetic demands of each dependent kitten >2 months old as an additional 1696 kcal/day (Laundré 2005).

We then defined the predicted daily consumption rate in kg/day as follows:

$$\text{Consump}_{\text{Lau}} = \frac{E_{\text{Tot}}}{1890 \times 0.86},$$

where 1890 was the energetic value of deer meat, and 0.86 was the energetic value of the food post digestion and assimilation. Predicted daily kill rates in kg/day were then estimated as follows:

$$\text{KillRate}_{\text{Lau}} = \frac{\text{Consump}_{\text{Lau}}}{0.68},$$

where 0.68 accounted for the edible portion of adult ungulates (Wilmers et al. 2003).

Comparing kill and consumption rates from energetic models with field-based kill rates

We employed mixed model analyses of variance (ANOVA) to test whether kill rates and consumption rates varied with the method used to quantify them (e.g., the two energetic models and field calculations), study site, or between males and females. Individual pumas were included as a random effect to account for variability among individuals. Where there were multiple monitoring periods for an individual puma, their kill and consumption rates were averaged across monitoring periods before analyses. We used a logarithmic transformation on kill and consumption rates to meet the assumptions of ANOVA and a post-hoc Tukey HSD test for comparisons of significant differences (Steel et al. 1997).

Testing for the significance of biological and ecological variables employed in bioenergetic modeling

We employed multiple linear regression to test whether puma weights and mean daily distances traveled held any predictive value for kill rates quantified from field efforts investigating GPS clusters. We used a root transformation on puma weights and a logarithmic transformation on mean daily distances traveled (km) for pumas

during their monitoring periods, and included individual pumas as a random effect, to account for variability amongst pumas.

We employed mixed model ANOVAs to test whether mean handling time, defined as the number of hours a puma was associated at a carcass, and mean meat abandoned by pumas in each monitoring period differed across study areas. These analyses were informed by field observations suggesting that handling time and meat abandoned might be potential explanatory variables in differences in kill rates we might detect across study sites. We employed a logarithmic transformation on mean handling time to meet the assumptions of ANOVA and included individual puma as a random effect. We standardized meat abandoned by unit time (meat abandoned/day), and estimated meat abandoned by subtracting our consumption estimates for individual pumas and families described above, from our estimates of available meat at a carcasses (Elbroch and Wittmer 2012b). We estimated that 68% of ungulate carcasses (Wilmers et al. 2003) and 95% of smaller prey were edible (Ackerman et al. 1986). We employed a root transformation on mean meat abandoned to meet the assumptions of ANOVA.

Field-based kill rate comparisons among pumas

Using mixed-model ANOVAs that incorporated individual pumas as a random effect, we tested whether transformed kill rates in terms of kg/day and ungulates/week created from investigating GPS clusters varied among study sites, between males and females, and the interaction between them when one or more of the variables proved significant. We then used the same tests to determine whether there were differences among females of different breeding status, however, we included samples of the same puma at different breeding stages as independent samples. We tested four classes: (1) not accompanied by kittens/not pregnant, (2) pregnant (3 month gestation), (3) nursing kittens (<3 months), and (4) accompanied by kittens ≥3 months, the age at which kittens are completely weaned and consume meat (Ackerman et al. 1986). When there was a significant result, we tested for which of the four breeding stages were statistically equivalent or different from each other using a post-hoc Tukey HSD test. We then

repeated the same analyses for transformed consumption rates created from field efforts.

RESULTS

Pumas, prey composition, and movements

Using satellite GPS technology, we monitored 26 individual pumas (10 males, 16 females) in three study sites over 45 intensive monitoring intervals ranging from 26 to 368 days (Table 1).

In Patagonia, we monitored 8 pumas (3 males, 5 females) for a total of 14 intensive monitoring periods ranging from 45 to 272 days (males = 83.2 ± 56.7 days, females = 117.4 ± 78.3 days [mean ± SD]). Males weighed 72.8 ± 8.1 kg and females 35.8 ± 2.5 kg. We conducted field investigations of Argos-relayed GPS clusters within 11 ± 12 days of the time the puma left the area. We investigated 694 GPS clusters and identified 433 kill sites and 6 acts of puma scavenging. Prey included 350 ungulates (7 huemul deer, 41 domestic sheep, and 302 guanacos), and 83 small to medium-sized vertebrates (Elbroch and Wittmer 2013b). Pumas moved an average 11.8 ± 5.1 km/day during intensive monitoring intervals. Additional information on puma status can be found in Table 1.

In Colorado, we monitored 11 pumas (5 males, 6 females) during 11 monitoring periods ranging from 26 to 368 days (males = 194.2 ± 123.1 days, females = 182.3 ± 97.0 days). Male weights averaged 54.6 ± 10.1 kg and females averaged 44.7 ± 3.6 kg (Table 1). We investigated 1001 GPS clusters and documented 437 predation and 8 scavenging events. On average, we investigated clusters identified from functioning satellite collars ($n = 9$) within 5.9 ± 7.9 days of the puma leaving the area, and for collars ($n = 2$) which stored GPS data only, we investigated clusters within 168.0 ± 91.1 days of occurrence. Prey included 337 ungulates (71 elk and 266 mule deer) and 106 small to medium-sized vertebrates. Pumas on average moved 7.6 ± 2.5 km/day.

In California, we monitored 7 pumas (2 males, 5 females) over a total of 19 intensive monitoring periods ranging from 28 to 69 days (males = 57.3 ± 14.4 days, females = 42.9 ± 13.9 days). Male pumas weighed 48 and 56 kg, females averaged 38.1 ± 5.1 kg (Table 1). We conducted field investigations of GPS clusters within 6.6 ± 7.4 days of the time the puma left the area. We

investigated 396 GPS clusters, and identified 215 kill sites and 4 acts of puma scavenging. Prey included 176 black-tailed deer, 1 American black bear, and 38 small to medium-sized vertebrates. All observed incidents of scavenging were upon black-tailed deer carcasses. Pumas on average moved 6.1 ± 1.8 km/day.

Kill and consumption rates determined from energetic models, and comparisons among model predictions and field observations

Kill rates differed depending upon the method employed to estimate them (Ackerman et al. 1986, Laundré 2005, our field based method) ($F_{2,64.3} = 77.87$, $P < 0.0001$). The results of our Tukey HSD showed that each method of determining kill rate yielded statistically different results. Mean kill rates were 4.04 ± 2.75 kg/day of prey for the energetic models of Ackerman et al. (1986), 2.44 ± 1.10 kg/day of prey for the energetic models of Laundré (2005), and 10.10 ± 4.10 kg/day of prey for the field efforts investigating GPS clusters (Table 2). Puma kill rates did not differ across study sites ($F_{2,23.7} = 1.66$, $P = 0.21$) (Table 2) or between males and females ($F_{1,24.9} = 0.00$, $P = 0.73$). Kill and consumption rates in kg/day for individual pumas determined with all three methods in all study sites are found in Table 2.

The method of determining consumption rate (Ackerman et al. 1986, Laundré 2005, our field based method) yielded significantly different results ($F_{2,61.7} = 23.21$, $P < 0.0001$) (Table 2). The Tukey HSD indicated that each method of determining consumption rate yielded statistically different results. Mean consumption rates over complete monitoring periods were 2.75 ± 1.87 kg/day of prey for the energetic models of Ackerman et al. (1986), 1.66 ± 0.75 kg/day of prey for the energetic models of Laundré (2005), and 3.35 ± 1.77 kg/day of prey estimated from the time pumas remained at GPS clusters. Our estimated consumption rates determined from time pumas were associated with carcasses did not vary among study sites ($F_{2,21.5} = 0.91$, $P = 0.42$) or between males and females ($F_{1,22.0} = 1.91$, $P = 0.18$).

Assessing biological and ecological variables employed in bioenergetic modeling

Neither puma weight ($F_{1,41.23} = 0.06$, $P = 0.82$) or mean daily distance traveled by pumas ($F_{1,41.5} = 1.22$, $P = 0.29$) (Table 1) explained variation in kill rates among study sites (Tables 2 and 3). We did not detect a difference in mean handling time among pumas in different study areas ($F_{2,23} = 1.67$, $P = 0.21$) (Table 3). We did not detect differences in the mean amount of meat abandoned across study sites ($F_{2,22} = 2.38$, $P = 0.10$), nor between meat abandoned by males versus females ($F_{1,22} = 2.16$, $P = 0.16$) (Table 3).

Comparing kill and consumption rates among pumas from field efforts

When assessing kill rates in kg/day determined using field investigations of GPS clusters (Table 2), neither study site ($F_{2,33.7} = 0.91$, $P = 0.41$) or sex ($F_{1,41.8} = 0.01$, $P = 0.93$) provided significant variation among kill rates. When assessing kill rates among females of different breeding status, there was a difference between their kill rates ($F_{3,26.1} = 3.64$, $P = 0.03$) (Table 2). Females with kittens >3 months old killed significantly more prey than females without kittens (category 1), however, females of categories 2–4 were statistically equivalent. When assessing kill rates in ungulates/week, study site proved a significant source of variation ($F_{2,22} = 3.62$, $P = 0.04$), but there were no differences between male and female kill rates ($F_{1,22} = 0.98$, $P = 0.33$) (Table 3). The results of the Tukey HSD test showed that kill rates in ungulates/week in California were higher than those in Colorado ($P = 0.03$), but that kill rates in ungulates/wk in Patagonia and Colorado ($P = 0.34$), and California and Patagonia ($P = 0.42$) were statistically equivalent.

When assessing the consumption rates determined from handling times quantified from GPS location data, we did not detect differences among study sites ($F_{2,21.1} = 0.89$, $P = 0.43$), or between the sexes ($F_{1,22.1} = 1.85$, $P = 0.19$) (Table 2). Given that we added additional consumption estimates for kittens to their mother's consumption rates, not unexpectedly females of different breeding status showed variable consumption rates ($F_{3,37.2} = 6.04$, $P = 0.002$). Females with dependent kittens ≥3 months were estimated to consume more than females in any of the remaining three categories.

Table 2. Comparative kill and consumption rates for all pumas (kg/day) as determined by the bioenergetics modeling of Ackerman et al. (1986), bioenergetics modeling of Laundré (2005), and from field methods for all intensive puma monitoring periods.

Puma ID	Field calculated consumption rate (kg/day)	Field calculated kill rate (kg/day)	Ackerman predicted consumption rate (kg/day)	Ackerman predicted kill rate (kg/day)	Laundré predicted consumption rate (kg/day)	Laundré predicted kill rate (kg/day)
PA_M2	2.42	17.4	2.64	3.89	1.63	2.40
PA_M2	2.46	20	2.64	3.89	1.71	2.51
PA_M3	2.27	12.9	2.53	3.72	1.66	2.44
PA_M3	2.13	14.6	2.56	3.76	1.66	2.44
PA_M4	1.91	7.9	2.98	4.38	1.91	2.81
PA_F1	4.31	14.8	3.89	5.72	2.90	4.27
PA_F2	1.71	10	1.10	1.61	1.02	1.51
PA_F3	4.96	21.4	4.52	6.65	2.24	3.30
PA_F4	1.81	5.75	2.55	3.75	1.04	1.52
PA_F4	5.06	15.05	1.91	2.81	1.91	2.81
PA_F4	5.3	12.91	4.89	7.19	2.78	4.09
PA_F5	1.15	1.21	1.25	1.84	1.04	1.53
PA_F5	1.93	5.38	3.28	4.82	1.05	1.55
PA_F5	2.75	4.81	2.32	3.41	2.49	3.67
CO_P01	3.14	14.62	1.96	2.88	1.21	1.77
CO_P03	2.23	12.21	1.93	2.84	1.26	1.85
CO_P05	1.2	7.07	2.53	3.72	1.61	2.37
CO_P06	2.07	13.08	2.50	3.68	1.64	2.42
CO_P13	2.27	6.78	2.12	3.11	1.33	1.96
CO_P02	3.31	5.48	11.13	16.37	1.11	1.64
CO_P07	4.76	9.79	3.53	5.19	3.04	4.47
CO_P07	5.63	8.67	4.02	5.91	1.64	2.41
CO_P08	3.3	12.74	1.35	1.98	1.12	1.65
CO_P09	4.23	10.2	3.99	5.87	3.67	5.39
CO_P10	7.18	13.3	5.26	7.74	2.91	4.27
CO_P12	1.8	6.06	1.49	2.19	1.24	1.82
CA_M33	1.67	6.51	2.25	3.30	1.40	2.06
CA_M33	2.39	7.6	2.25	3.30	1.44	2.11
CA_M33	3.36	9.08	2.25	3.31	1.41	2.07
CA_M36	3.03	5.99	1.99	2.93	1.21	1.77
CA_F1	2.17	8.31	1.23	1.81	1.04	1.52
CA_F1	2.63	7.41	1.16	1.71	0.95	1.39
CA_F1	2.23	5.64	1.49	2.19	1.23	1.81
CA_F17	2.43	7.01	1.52	2.24	1.28	1.88
CA_F17	3.18	7.56	1.71	2.51	1.40	2.06
CA_F17	2.89	8.3	1.25	1.84	1.02	1.50
CA_F17	3.85	10.28	1.13	1.66	0.93	1.36
CA_F17	3.38	7.04	1.13	1.66	0.93	1.36
CA_F19	2.31	9.98	1.05	1.54	0.87	1.28
CA_F23	2.87	10.45	1.52	2.24	1.29	1.89
CA_F23	3.45	8.7	1.14	1.67	0.96	1.42
CA_F43	7.12	10.42	4.42	6.50	2.70	3.96
CA_F43	4.61	8.35	5.32	7.83	2.80	4.12
CA_F43	4.69	13.23	5.56	8.18	2.84	4.17
CA_F43	9.11	16.34	5.58	8.20	2.81	4.14

DISCUSSION

Our results demonstrate that current puma energetic models drastically underestimate their actual kill rates, as quantified with GPS technology and intensive field monitoring ($\bar{X} = 4.04$ kg/day for Ackerman et al. [1986], 2.44 kg/day for Laundré [2005], 10.10 kg/day for our field-based calculations). Further, our results suggest that energetic models using morphological and phys-

iological variables alone are insufficient to predict kill rates. Despite the significant variation encompassed by our data in terms of characteristics of individual pumas and their movements from three different study areas, neither weight in kg nor activity in terms of mean daily distances traveled, was a significant predictor of observed kill rates. Basic metabolic rates and animal physiology are essential in creating minimum energetic budgets for species, but our

Table 3. Number of kills, kill rates in ungulates/week, mean handling times, and mean meat abandoned for all pumas and intensive monitoring periods.

Puma ID	Number of kills	Number of ungulate kills	Kill rate (ungulates/week)	Mean handling time (24-hr periods)	Mean meat abandoned/day (kg)
PA_M2	7	7	1.09	4.14	9.35
PA_M2	5	5	1.17	3.29	10.42
PA_M3	40	40	2.33	1.48	7.72
PA_M3	34	34	1.45	1.29	6.63
PA_M4	10	10	1.23	2.00	5.51
PA_F1	38	38	1.32	2.00	5.62
PA_F2	10	9	1.02	2.00	5.12
PA_F3	50	42	1.74	1.90	9.75
PA_F4	29	7	0.55	1.90	2.81
PA_F4	13	6	0.70	2.48	4.01
PA_F4	68	60	1.54	1.86	3.96
PA_F5	17	0	0.00	1.00	0.05
PA_F5	19	8	0.62	2.00	1.89
PA_F5	17	13	1.52	1.88	0.84
CO_P01	95	50	0.99	2.24	7.34
CO_P03	54	29	0.71	2.31	6.47
CO_P05	9	7	0.89	1.14	2.40
CO_P06	30	25	1.13	2.80	7.25
CO_P13	14	8	0.47	4.08	2.06
CO_P02	6	6	1.62	1.67	0.42
CO_P07	6	6	0.72	5.80	5.03
CO_P07	54	54	1.29	2.63	2.96
CO_P08	44	38	1.06	4.20	5.46
CO_P09	32	30	0.95	2.77	2.55
CO_P10	61	52	1.46	2.53	2.14
CO_P12	20	18	0.70	3.50	2.39
CA_M33	10	9	1.11	1.90	2.76
CA_M33	15	15	1.59	1.69	2.88
CA_M33	10	8	1.51	2.80	2.82
CA_M36	16	10	1.01	3.31	1.17
CA_F1	9	7	1.58	1.56	3.67
CA_F1	8	7	1.07	3.13	2.37
CA_F1	9	7	1.36	2.00	1.16
CA_F17	12	12	1.47	2.33	2.33
CA_F17	14	13	1.49	2.86	1.96
CA_F17	8	8	1.44	3.00	2.76
CA_F17	9	7	1.63	3.56	6.41
CA_F17	13	11	1.15	3.85	1.41
CA_F19	9	7	1.48	1.67	4.51
CA_F23	11	9	1.85	1.82	4.24
CA_F23	14	7	1.29	2.20	2.67
CA_F43	18	17	1.72	2.22	1.41
CA_F43	10	8	2.00	1.60	1.07
CA_F43	16	13	3.14	1.44	8.54
CA_F43	13	12	2.55	1.62	2.01

data suggest that energetic models solely based on these variables will almost certainly underestimate kill rates for pumas, and may do so for other carnivores as well.

Both energetic models better approximated our estimates of consumption rates based upon the time pumas remained at GPS clusters and estimates of handling time ($\bar{X}$ = 2.75 kg/day for Ackerman et al. [1986], 1.66 kg/day for Laundre [2005], 3.35 kg/day for field-based calculations); the 95% CIs for consumption predictions by the Ackerman et al. [1986] model overlapped with

our field estimates. Nevertheless, we realize our estimates for consumption rates based on handling time were coarse, determined from captive animal trials and the number of 24-hour blocks a puma was associated with a carcass. Thus, we would interpret our consumption estimates with caution. In fact, actual puma consumption rates may be higher given that wild pumas almost certainly exhibit higher activity levels than their captive counterparts. Yet even with these limitations, our findings suggest that both puma energetic models failed to predict puma kill rates

in natural settings, but that they might be more realistically estimating puma consumption rates and the amount of meat a wild puma needs to sustain itself.

Our kill rates in kg/day determined from field investigations of GPS clusters were statistically equivalent across three distinct ecosystems ranging from warm summers and cool winters in relatively dry Western Colorado to cool, open steppe grasslands in Chilean Patagonia, to mountain Mediterranean climates in northern California. Our kill rates in kg/day were also equivalent across a range of puma weights (largest male at 82 kg; smallest female at 32 kg), sex, three of four breeding categories of females, length of monitoring periods, and mean daily distances traveled. Finally, our kill rates in kg/day were consistent across systems where pumas relied on 1 to 3 ungulate prey species of varying sizes. In our study, heavier pumas did not kill more prey (in kg) than lighter pumas, females did not kill more than males, and only females with kittens >3 months of age killed more than solitary, non-pregnant females. The remarkable consistency in puma kill rates we documented across such incredible ecological variability was unexpected; perhaps these findings were artifacts of small sample sizes, or perhaps they suggest that kill rates are driven by "partial prey consumption" (e.g., Vucetich et al. 2012) and other ecology, rather than physiology.

We did, however, find differences in kill rates across study sites, when measured in terms of ungulates killed per week. This was likely due to the great variation in ungulate sizes we encountered in our three study sites (from adult deer and sheep in California and Patagonia weighing 40 kg to bull elk in Colorado weighing up to 385 kg), and the potential for further differences in kill rates due to species-specific vulnerability of smaller juveniles to puma predation (Knopff et al. 2010). Our results thus emphasized the importance of comparing puma kill rates in different systems with different prey assemblages in kg/day. In contrast, kill rates in terms of prey numbers killed per unit time are essential to predator-prey modeling and a critical metric when considering puma kill rates in a specific ecosystem on a specific prey (e.g., Holling 1959).

Our kill rates of 10.10 kg/day (95% CI = 8.90–11.30 kg/day) determined by investigating GPS clusters in the field are the highest reported for pumas to date, and only overlap with previous estimates reported by Knopff et al. (2010) (8.28 kg/day, 95% CI = 7.13–9.41 kg/day). Our kill rates in ungulates/week were also higher than essentially all previous estimates from field data (see Table 1 in Knopff et al. 2010). On average, pumas in our study areas killed 3 times more meat in kg than they consumed, and about 50% more ungulates (in terms of numbers) than previously reported (Table 1 in Knopff et al. 2010). This has important implications for predator-prey modeling and subsequent management of both pumas (and sensu other large carnivores) and their ungulate prey. Given that puma predation is a significant cause of mortality for many North American game species (e.g., bighorn sheep, *Ovis canadensis* [Johnson et al. 2013]; mule deer [Forrester and Wittmer 2013]) underestimating their kill rates and those of other predators may be a contributing factor to their observed or suspected declines. For game species, underestimating the number of prey being killed by predators may also lead to human harvest quotas that are set too high; the emergent effects of potentially excess human harvest in combination with higher actual predator kill rates could certainly contribute to ungulate declines (e.g., Eberhardt et al. 2007). Further, pumas are significant predators of domestic animals (Kissling et al. 2009, Zarco-González et al. 2012), and any attempt at modeling bioeconomic impacts of livestock losses to predators would be sensitive to biased estimates of kill rates. Last, kill rates in ungulates per predator per unit time are also integral in models used to predict predator densities based on prey abundances (e.g., Karanth et al. 2004). Underestimating actual kill rates would thus result in overestimates of predator densities that could be sustained by a given prey population.

The mechanism for the large discrepancy between the number of ungulates killed and actual consumption rates remains unclear. Whether pumas are such efficient predators that they choose to abandon large quantities of meat, or whether they relinquish kills to dominant competitors is still a question in need of answering. Perhaps pumas follow rules of optimal foraging theory (MacArthur and Pianka 1966), and abandon carcasses like "patches" in

marginal value theorem (Charnov 1976), when the benefits of remaining with the carcass diminish to a yet undetermined tipping point (Carbone et al. 2005, Vucetich et al. 2012). Research from Patagonia revealed that scavenging condors increased puma kill rates by reducing puma handling time at carcasses (Elbroch and Wittmer 2013*a*), and Murphy (1998) proposed similar effects due to scavenging bears in North America. The influence of kleptoparasitism on other carnivore foraging ecology has also been well documented in wolves and African wild dogs (Gorman et al. 1998, Carbone et al. 2005, Kaczensky et al. 2005).

Our results elucidate the clear difference between killing and eating, and question the suitability of energetic models solely based on morphological and physiological parameters when attempting to predict kill rates and thus quantify the effects of predators on their prey. Further, our results suggest that refining the energetic budgets for species are unlikely to improve predictive accuracy of current models used to estimate carnivore kill rates. In this example, our data are clear: pumas consistently kill (in kg/day) significantly more than they consume across diverse ecosystems with different prey assemblages. Based on these results we propose that rather than focusing on refining current energetic models, future research should be directed at understanding the behavioral ecology driving carnivore kill rates and the meat they abandon. Models that incorporate these important aspects of carnivore ecology will be better suited to quantify and predict the significant roles top carnivores play as keystone species subsidizing diverse scavengers and decomposers (DeVault et al. 2003, Elbroch and Wittmer 2012*b*) and shaping ecological communities. Further, these models may aid in quantifying the effects of kleptoparasitism on carnivore kill rates and fitness (Gorman et al. 1998, Elbroch and Wittmer 2013*a*), and the indirect effects scavengers may have on prey populations (Elbroch and Wittmer 2013*a*, Moleón et al. 2014).

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Supplemental Material

Appendix

Estimating Prey Weights

In Patagonia, the age of guanacos up to 24 months old were determined using tooth eruption sequences in the lower mandible (Raedeke 1979). We estimated the monthly weights of 1-year (chulengos) and 2-year guanacos using linear growth estimates, a birth weight of 12.7 kg, and 1-yr and 2-yr weights of 42 kg and 100 kg, respectively (Sarno and Franklin 1999). Guanacos >2 years of age were estimated to weigh 120 kg (Raedeke 1979).

The only data available for growth rates in huemul was an estimated birth weight of 5 kg (Flueck and Smith-Flueck 2005). Therefore, we applied growth allometry for the structurally similar mule deer (*Odocoileus hemionus*; 0.21 kg/day; Anderson and Wallmo 1984) to estimate weights of huemul <1 year old. We estimated weights of huemul ages 1–3 based on growth rates reported for mule and white-tailed deer (*O. virginianus*) (Putman 1988). We used adult huemul (>3 years) weights of 65 kg (Iriarte 2008). The ages of huemul up to 3.5 years old were estimated using tooth eruption sequences. For small prey, we assumed 4 kg for European hares (Elbroch and Wittmer 2013*b*), 2 kg for Patagonian haired armadillos (*Chaetophractus villosus*) (Iriarte 2008), 9 kg for culpeo foxes (Iriarte 2008), and 6.4 kg for upland geese (*Chloephaga picta*) (Todd 1996).

In Colorado we estimated age and sex-specific weights for ungulates using published literature. Mule deer and elk birth weights were estimated at 4 kg (Pojar and Bowden 2004) and 16.7 kg (Smith et al. 2006), respectively. We used documented weights at 6, 12, 24, and 36 months (Dean et al. 1976, Bergman 2011) to estimate monthly weights with simple linear regression. Male and female mule deer were given the same weight up to 24 months old, after which females were assumed to stop growing (Armstrong et al. 2011), while males grew to 36 months. Monthly weight estimates for elk were sex specific from neonate to 36 months (Dean et al. 1976, Smith et al. 2006). Where sex could not be determined from prey remains at the kill site, we used an average of male and female weights for the respective age in months. Non-ungulate prey items were given a single weight estimate from published records (Armstrong et al. 2011).

In California, we calculated the age of black-tailed deer to the closest month for individuals <1 year based on average fawning dates in the study area, and for individuals >1 year based on tooth eruption and wear to the closest year (Heffelfinger 2010). We determined sex-specific weights for each year based on Parker et al. (1993). For other mammals we used the average weights listed by Jameson and Peeters (2004), while for birds we used the average weights listed in Sibley (2005).