Research Article

Cougar Kill Rates and Prey Selection in a Multiple-Prey System in Northeast Oregon

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ABSTRACT Cougars (*Puma concolor*) are a primary predator of mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) throughout western North America. Effective management of predator-prey systems requires a solid understanding of kill rates, prey use, and selection. We implemented a 3-year study in northeast Oregon to investigate cougar diet, kill rates, and prey selection in a multiple-prey system to assess the degree to which patterns in cougar predation may be generalizable across systems and to identify selective predation patterns of cougars that may affect ungulate populations. We marked 25 adult cougars with global positioning system (GPS) collars and monitored predation sequences for 7,642 days to identify kill sites. In field investigation of kill sites, we identified remains of 1,213 prey items killed by cougars, of which 1,158 (95.4%) were native ungulates. On average, cougars killed 1.03 ungulates/week (95% CI = 0.92–1.14), but kill rates varied by season, sex, and reproductive status of cougars. Cougars killed ungulate prey 1.55 (95% CI = 1.47–1.66) times more frequently during summer (May–Oct) than winter (Nov–Apr). Kill rates were higher in summer because juvenile ungulates were the most frequently killed prey item and were smaller than prey killed in winter. Female cougars with kittens >6 months old killed prey more frequently than males, solitary females, and females with kittens <6 months old likely in response to the increased energetic burden of raising kittens. Male cougars killed larger prey than females, which likely explains why males killed at similar rates as solitary females, despite the larger body size of males. We documented patterns in prey selection influenced by season and demographic classification of cougars. Diets of male cougars included roughly equal amounts of elk (52.2%) and deer (47.8%), whereas diets of females were dominated by deer (74.6%). Male and female cougars displayed strong patterns of selection for elk calves during summer. During winter, female cougars selected deer fawns and males selected elk calves. Female cougars with kittens >6 months old demonstrated little selection for any age class or species of prey, highlighting an opportunistic foraging strategy to maximize energy gains while feeding young. Across all cougars, we observed a pattern of selection for adult male deer during winter but not summer and did not observe patterns of selection for adult elk according to sex. Our results strongly supported the hypothesis proposed by [Knopff et al. (2010) Journal of Wildlife Management, 74: 1435–1447] that cougar predation is influenced by season and demographic classifications of cougars and our results provide strong evidence that this hypothesis should be generalizable to other areas. The patterns of selection for juvenile elk and deer suggested wildlife managers should consider the potential negative effects of cougars on ungulate populations in areas where juvenile recruitment has been chronically low. © 2014 The Wildlife Society.

KEY WORDS *Cervus elaphus*, cougar, elk, kill rate, mountain lion, mule deer, *Odocoileus hemionus*, Oregon, predation, prey selection, *Puma concolor*, ungulate mortality.

Effective management of predator-prey systems requires an understanding of predator kill rates and abundance

(Anderson and Lindzey 2003, Vucetich et al. 2011) and prey selection patterns in multiple-prey systems (Robinson et al. 2002). Throughout western North America, cougars (*Puma concolor*) are one of the primary predators of mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus nelsoni*). Survival rates of cougars in Oregon are some of the highest reported (Clark et al. 2014), which has allowed populations in Oregon to steadily increase statewide since the mid-1990s (Keister and van Dyke 2002, Oregon Department of Fish and Wildlife [ODFW] 2006) and obtain high densities in northeast Oregon (Davidson et al. 2014). Concurrent with

increases in cougar populations many mule deer and elk populations have declined (ODFW 2003, 2011, 2012), leading to speculation that cougars may be responsible for ongoing ungulate population declines; however, little empirical evidence exists to support this speculation. A substantial body of literature relates to cougar kill rates and prey use (see Murphy and Ruth 2010 for a summary). However, many of these studies investigated predation patterns during only part of the year, were based on small samples sizes, and/or used different methods to estimate kill rates and prey use of cougars, which often resulted in contradictory findings. Furthermore, cougar predation may be influenced by prey availability (Spalding and Lesowski 1971, Leopold and Krausman 1986, Murphy 1998), climate (Dalrymple and Bass 1996), and habitat use of prey (Williams et al. 1995, Nowak 1999), which can all be variable among ecosystems. Therefore, practitioners current-ly do not know to what extent kill rates, prey use, and selection may be generalized among study areas, and extrapolation of these predation patterns from other areas may lead to unwarranted conclusions regarding the effect of cougars on ungulate populations.

Season may be an important source of variation influencing kill rates and prey use of cougars, but reported effects of season have often been contradictory. Whether these differences among study areas are attributable to ecological or methodological differences is not well known because sampling intervals (i.e., seasonal vs. annual), sample sizes, and methods (e.g., snow-tracking, energetics models, and location clusters) have varied greatly among studies. For example, cougars may kill more frequently during summer when juvenile ungulates are most available (Nowak 1999, Laundré 2008, Knopff et al. 2010) or they may kill more frequently during winter when ungulates are nutritionally stressed and cougars have increased thermoregulatory burdens (Hornocker 1970, Murphy 1998). However, in the most comprehensive study of cougar predation patterns to date, cougars killed 1.5 times more frequently during summer when cougar diets were dominated by juvenile ungulates (Knopff et al. 2010). Seasonal patterns in prey use by cougars may also be due to variability in vulnerability of prey over the course of the year (Lima and Dill 1990). Knopff et al. (2010) found that cougar diets changed throughout the year where cougars killed juvenile ungulates most frequently during summer, male ungulates most frequently during fall, and female ungulates most frequently during spring, which was attributable to changes in prey vulnerability over the course of the year.

Kill rates and prey use of cougars can vary by sex and reproductive status (Knopff et al. 2010, White et al. 2011), but a large degree of variation exists in reported magnitudes and differences in kill rates among sexes of cougars (see summary in Knopff et al. 2010). Cougars are sexually dimorphic with males being approximately 1.5 times larger than females (Logan and Sweanor 2001). As a result, diets of male cougars are expected to include higher proportions of larger prey (Knopff et al. 2010, White et al. 2011). Furthermore, because of their larger body size (Logan and Sweanor 2001), males are hypothesized to kill more frequently than females to meet their energetic requirements. However, males may actually kill less frequently than females in multiple-prey systems because their diets include a greater proportion of large prey (Knopff et al. 2010). Female cougars provide food for their dependent kittens (Logan and Sweanor 2001), so females with kittens are expected to kill more frequently than those without kittens (Knopff et al. 2010). As a result of increased energetic burdens associated with raising kittens, females with kittens may include a greater proportion of larger prey in their diets where they use an opportunistic foraging strategy by killing prey as it is encountered (Emmons 1987, Novaro et al. 2000).

Documenting prey selection patterns is critical to understanding effects of predators on prey because selection for individuals with high reproductive values (e.g., prime-age females) can magnify the effect of predators on prey populations (MacArthur 1960). In multiple-prey systems, understanding selective predation patterns is important because prey selection can increase effects of predators on prey populations compared to uniform prey use (Rosenzweig 1978, Mills 2007). This can be especially true in cases where predator numbers are determined by primary prey densities, but the predator selectively preys upon a secondary prey species, causing a disproportionate effect on secondary prey (Messier 1994, Sinclair et al. 1998). Disproportionate predation on secondary prey by cougars has been docu-mented in systems where mountain caribou (*Rangifer tarandus caribou*; Wittmer et al. 2005), Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*; Johnson et al. 2012), mule deer (Robinson et al. 2002, Cooley et al. 2008), and porcupine (*Erethizon dorsatum*; Sweitzer et al. 1997) served as secondary prey species for cougars.

We conducted a 3-year study to document kill rates, prey use, and prey selection of a sample of adult cougars in a multiple-prey system. Our primary objective was to determine if cougar predation patterns can be generalized among study areas, and to do this we retested the objectives of Knopff et al. (2010) including: 1) how frequently do cougars kill ungulates, 2) does season influence cougar kill rates, prey use, and selection, 3) does sex and reproductive status of females influence predation patterns, and 4) do cougars select juvenile ungulates or kill prey at random? We hypothesized male cougars should kill more frequently than females because of their larger body size and females with kittens would kill more frequently than females without kittens because of increased energetic burdens associated with raising kittens. We also hypothesized that cougar predation would follow the reproductive vulnera-bility hypothesis (Lima and Dill 1990), where vulnerability to predation of female ungulates was highest prior to parturition, males were most vulnerable during the rut, and juveniles were most vulnerable for the first few months after birth. Given that cougars in northeast Oregon killed a large percentage of radiocollared elk calves during the first 6 months after parturition (Rearden 2005, B. Johnson, ODFW, unpublished data), we hypothesized cougars would select juvenile elk during summer but switch to

alternative prey (i.e., deer) during winter when fewer calves were killed by cougars. Finally, we hypothesized that male cougars would have a higher proportion of larger prey (e.g., adult elk) in their diets than female cougars because their larger body size would allow them to more effectively capture and handle larger prey.

STUDY AREA

We studied cougar predation in Mt. Emily Wildlife Management Unit (WMU) located in the Blue Mountains of northeast Oregon, USA from 2009 to 2012 (Fig. 1). Mt. Emily WMU covers 1,992 km^2 and ranges in elevation from 360 to 1,850 m. Land ownership was a mixture of private, public, and tribal lands (Confederated Tribes of the Umatilla Indian Reservation; CTUIR). Public lands were managed by United States Forest Service (Wallowa–Whitman and Umatilla National Forests) and State of Oregon. Land management practices on private lands varied by elevation, with low elevations dominated by commercial agriculture and forested habitats managed as industrial forests or grazing rangelands. Vegetation patterns within the study area were strongly influenced by topography, aspect, and elevation. Low elevation sites on the west side of the study area were dominated by exposed upland slopes and a mixture of hawthorn (Crataegus columbiana), willow (Salix spp.), and blackberry (Rubus armeniacus) in riparian areas. Scattered ponderosa pine (Pinus ponderosa) and black cottonwood (Populus trichocarpa) were found in riparian areas. High elevation sites on the central and eastern side of the study area were dominated by mixed-conifer stands with exposed southern aspects. Common tree species included ponderosa pine, Douglas-fir (Pseudotsuga menziesii), grand fir (Abies grandis), larch (Larix occidentalis), and lodgepole pine (P. contorta).

Since receiving formal protection in the 1960s, cougar populations in Oregon have increased from isolated populations in northeast and southwest Oregon to widespread distributions throughout the state (Keister and van Dyke 2002, ODFW 2006). Minimum indices of cougar population size generated from population reconstruction indicated that cougar populations in Mt. Emily WMU have remained relatively stable since the late 1980s (B. Johnson, ODFW, unpublished data). Based on population reconstruction of harvested cougars (Lancia et al. 2005), the minimum number of cougars in the Mt. Emily WMU over the past 10–15 years was 40–55 individuals (B. Johnson, ODFW, unpublished data). End of winter population estimates (ODFW, unpublished data) estimated from POP-II population models (Bartholow 1992) indicated mule deer ($n = 4,800$ adults) were the most abundant ungulate available to cougars in our study area followed by elk ($n = 2,850$ adults), and white-tailed deer ($n = 2,500$ adults; O. virginanus). Population estimates over the past 20 years, indicated elk populations declined 50% (5,500 to 2,850 adults), mule deer populations increased 74% (2,700 to 4,800 adults), and minimum counts of white-tailed deer indicated they increased from extremely low densities to spatially restricted high densities (M. Kirsch, ODFW, personal communication).

Approximately 1,700 km^2 (85%) of summer range for deer and elk occurred within Mt. Emily WMU. Defined winter
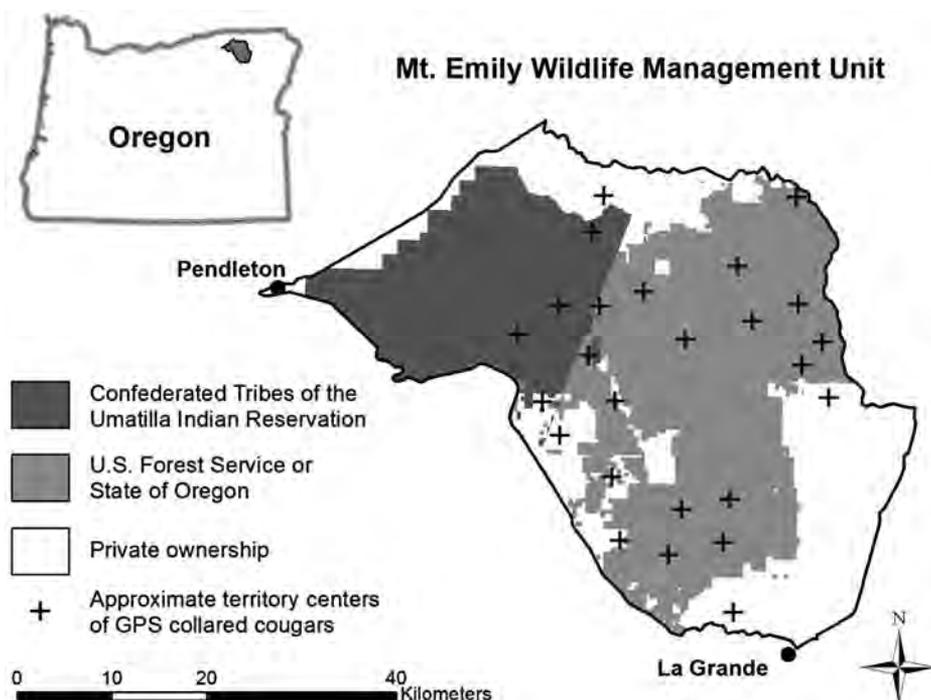

Figure 1. Location of the Mt. Emily Wildlife Management Unit in northeast Oregon, USA, and approximate center points of territories of cougars monitored with global positioning system (GPS) collars to determine kill rates and prey selection in a multiple-prey system from 2009 to 2012.

ranges for mule deer and elk covered 595 (30%) and 868 (45%) km² , respectively, of the Mt. Emily WMU (ODFW, unpublished data) and were located at lower elevations on the eastern and western portions of the study area. Some mule deer, elk, and cougars used high elevation, exposed, southern aspects during winter outside defined winter range boundaries. White-tailed deer occurred at relatively high densities on the northwest side of the study area but were relatively rare throughout the remainder of the study area. Based on minimum counts, moose (*Alces alces*) occurred at very low numbers (<10; M. Kirsch, personal communication). Trend counts indicated approximately 500 feral horses (*Equus caballus*) were located on the CTUIR, but none were observed outside the CTUIR (C. Scheeler, CTUIR, personal communication). Seasonal grazing allotments authorized approximately 4,900 domestic sheep (1 Jun–9 Oct) and 525 cattle on Forest Service managed lands (6 Jun–31 Oct; B. Lathrop and A. Johnson, U.S. Forest Service, Wallowa–Whitman and Umatilla National Forests, personal communication), and 700 cattle (1 May–14 Jun and 30 Sep–15 Nov) on CTUIR lands (G. Schumacher, CTUIR, personal communication). In addition, an unknown number of domestic livestock were present seasonally or annually on private property. Black bear (*Ursus americanus*), coyote (*Canis latrans*), and bobcat (*Lynx rufus*) were common, and no wolf (*C. lupus*) packs were documented within Mt. Emily WMU during our research.

METHODS

Cougar Capture and Monitoring

We captured cougars with use of trained hounds according to procedures outlined and approved by the Starkey Experimental Forest and Range, Animal Care and Use Committee (Starkey Experimental Forest and Range IACUC No. 92-F-0004) and followed the guidelines of the American Society of Mammalogists for use of wild mammals in research (Sikes and Gannon 2011). We treed cougars and immobilized them with a mixture of Ketamine (200 mg/mL; Fort Dodge Animal Health, Fort Dodge, IA) and xylazine (20 mg/mL; Rompun®; Bayer, Inc., Shawnee Mission, KS) at a dosage of 0.4 mL per 10 kg of body mass and administered via remote injection from a dart gun. Upon immobilization, we weighed, sexed, and aged cougars. Whenever possible, we extracted the first premolar of adult cougars for cementum annuli analysis to determine age (Trainer and Matson 1988). We also obtained field estimates of cougar age using evidence from tooth wear (Ashman et al. 1983, Shaw 1986), gum-line recession (Laundré et al. 2000), and pelage spotting progression (Shaw 1986). We classified cougars as dependent kittens (<1 year), subadults (independent females <2 years and males <3 years), and adults (females ≥2 years and males ≥3 years). We used a different classification for sub-adult males and females because males typically did not establish a territory until 3 years of age, and we did not want to place global positioning system (GPS) collars on males that may disperse from our study area. We marked adult cougars with a GPS collar (Lotek 4400S or Lotek 7000SA; Lotek

Engineering, Newmarket, ON, Canada) until our supply of GPS collars was depleted and then marked additional adults with very high frequency (VHF) radiocollars (Telonics MOD-600; Telonics, Inc., Mesa, AZ) to monitor survival and aid recapture if a GPS collar became available. We attached 2 permanent, numbered ear tags to uniquely identify each cougar. Prior to release, we administered yohimbine (0.125 mg/kg; Yobine®; Lloyd Laboratories, Shenandoah, IA) as an antagonist for xylazine.

We programmed GPS collars to acquire 6 locations per day (0300, 0600, 1200, 1800, 2100, 2400 hours). For unknown reasons, acquisition success of GPS collars placed on males was substantially lower than those on females; consequently, we increased the location acquisition schedule for collars placed on males to 9 locations per day (0130, 0300, 0430, 0600, 1200, 1800, 1930, 2100, 2230, 2400 hours) to improve our ability to locate kills (Knopff et al. 2009). We continuously monitored individual cougars until their collar failed, the cougar died, or the study ended. We used both ultra-high frequency (UHF) and ARGOS platform GPS collars in our study. We switched to ARGOS platform GPS collars during the later portion of the study to reduce the number of fixed-wing aircraft flights required to download GPS locations from collars. For cougars fitted with UHF GPS collars (Lotek 4400S), we downloaded locations fortnightly via a remote communication link from a fixed-wing aircraft or from the ground. For cougars fitted with ARGOS platform GPS collars (Lotek 7000SA or Lotek 7000SAW), we retrieved location data via a satellite communication link every 5–10 days.

Locating Kill Sites and Identifying Prey Remains

We used an algorithm developed by Knopff et al. (2009) to identify potential kill sites of cougars from clusters of GPS locations based on the following criteria: ≥2 locations within 200 m occurring within 6 days, with additional locations added if they were obtained within 6 days of the last location included in the cluster. This algorithm was designed to locate prey items >8 kg (Knopff et al. 2009) so the potential existed for us to miss small prey items killed by cougars. We located potential kill sites using geographic coordinates of the geometric center of location clusters, and systematically searched 8 transect lines positioned on cardinal compass bearings (e.g., N, NE, E) out to 50 m, walked 20 m to the right, then zigzagged back to the cluster center. If additional GPS locations fell outside the 50-m radius, we searched a 25-m radius around each GPS location using the approach outlined above. After locating prey remains at a location cluster, we looked for evidence of cougar predation (e.g., bite or claw marks on the hide, puncture marks on the skull or neck) or sign (i.e., bed sites, scat, tracks or a cached or covered carcass; Shaw 1977) to assign the carcass as a cougar kill. If the available evidence indicated the animal was not killed by a cougar (e.g., natural causes, hunter- or vehicle-killed), we assigned the remains as a scavenging event. We determined the species of prey by using skeletal, anatomical, and pelage characteristics (Moore et al. 1974, Verts and Carraway, 1998, Jacobson 2004). We assigned ungulate prey to 1 of 3 age

classes: juvenile (<1 year), yearling (1 year), and adult (≥2 yr). We determined age of prey using body size or tooth eruption and wear patterns (Schroeder and Robb 2005). We determined sex of yearling and adult ungulates using the presence of antler pedicels. We recorded undetermined species, age class, or sex of prey as unknown. We assigned a date to predation events using the date of the first GPS location included in the cluster and assigned each predation event to summer or winter. We assigned summer to kill dates between 1 May and 31 October to include the ungulate birth pulse, snow-free period, and emergence of black bears from their dens. We assigned an approximate live weight estimate of identified ungulate prey based on age and sex of animals captured during field studies or published values (Appendix 1). We used bear sign (e.g., scat or tracks) combined with disturbance of a kill site (e.g., scattered prey remains) to document visitation of a cougar kill by a black bear.

We developed models to predict the presence of kills at GPS location clusters using data from all GPS-collared female cougars monitored during the first year of our study for both summer ($n = 612$ clusters; May–Oct) and winter ($n = 381$ clusters; Nov–Apr) monitoring periods to eliminate searches at GPS location clusters that had a low probability of having a kill present. After the first year of the study, data on location clusters of males was insufficient to develop a predictive model, so we surveyed all location clusters of males for the duration of the study. We used logistic regression (Hosmer and Lemeshow 2000) to model the presence or absence of a cougar kill at a GPS location cluster. We coded GPS location clusters where we located a cougar-killed ungulate as kills (1) and those where we did not locate a prey item or located a non-ungulate prey was as a non-kill (0). We censored from the analysis GPS location clusters associated with capture locations and nursery sites where females had kittens. We developed a candidate set of models based on attributes of GPS location clusters that included 1) corrected points, the number of locations obtained at the cluster divided by the fix rate success; 2) fidelity, the number of locations in the cluster minus the number of fixes away from the cluster; 3) average distance, the mean distance from locations in the cluster to the cluster center; 4) binary day period, equal to 1 if >24 hours were spent at the cluster and equal to 0 if <24 hours were spent at the cluster; and 5) day period, the number of 24-hour periods with at least 1 location at the cluster. When developing the candidate model set, we used the following guidelines: 1) corrected points must be included in the model, 2) models would either include binary day period or day period, not both, and 3) the only interaction term considered was between corrected points and average distance. We used Akaike's Information Criteria corrected for small sample sizes (AIC$_c$) to rank candidate models (Burnham and Anderson 2002). We used the best-ranked model to distinguish between kill and non-kill sites.

After initial development of models used to determine the presence of a kill at GPS location clusters, we also used trained dogs to locate prey remains, where a human observer directed the dog to search the area around the cluster using the search pattern outlined above. Detection dogs located kills faster (4 min vs. 16 min, respectively), searched non-kill sites faster (18 min vs. 40 min, respectively), and appeared to locate kill remains more frequently than human observers (43% vs. 35% of clusters surveyed, respectively). However, detection dogs and human observers found kills at similar rates after accounting for the probability of the cluster containing a kill (e.g., clusters with a 0.20–0.39 probability of containing a kill, dogs located a kill at 43.8% of clusters vs. 40.5% for human observers; Clark 2014). Consequently, we had no reason to believe that the use or non-use of dogs influenced our results.

Kill Rates
We estimated seasonal kill rates of ungulates by cougars for adult males and females, adult females with kittens <6 months old, and adult females with kittens >6 months old. We used a ratio estimator (ungulate kills/week) of kill rates because they are more conservative and less biased than other methods (i.e., days between consecutive kills; Hebblewhite et al. 2003) but require longer monitoring intervals to obtain reasonable estimates (Knopff et al. 2009, 2010). We included individual cougars in our analysis if they were monitored ≥42 days during a particular season. We used a 42-day cutoff because this retained the majority of cougars while censoring short monitoring periods. We determined the reproductive status of female cougars by visiting nursery sites, collaring at least 1 dependent kitten, observing tracks of kittens at kill sites, or visually observing kittens. We did not monitor the reproductive status of females daily, and we may have incorrectly classified the reproductive status of females over short time periods (e.g., <2 weeks). We used 2-way analysis of variance (ANOVA) and Tukey's honest significance test to test for effects of season, sex, and reproductive status of cougars on kill rates (Day and Quinn 1989).

To further investigate temporal variation in cougar kill rates, we assessed correlations between mean proportion of juvenile ungulates in cougar diets, mean prey size (kg), mean proportion of cougar kills visited by bears, and mean inter-kill intervals (i.e., number of days between consecutive kills) at monthly intervals. We used inter-kill intervals because they are less biased over short monitoring periods than ratio estimators (Hebblewhite et al. 2003). For individual cougars, we calculated inter-kill intervals, proportion of juvenile ungulates in cougar diets, prey size (kg), and proportion of cougar kills visited by bears at monthly intervals, and obtained mean values across all cougars for subsequent analysis. We conducted simultaneous, pair-wise Pearson's correlations between mean inter-kill intervals, weight of prey killed by cougars, and the proportion of cougar kills visited by black bears at monthly intervals in program R using function corr.test in the psych package (R Development Core Team 2011). We used a Bonferroni adjustment to correct for multiple comparisons and an alpha of 0.05 to determine significant correlations.

Prey Availability and Selection

We determined proportions of species, sex, and age classes of prey available to cougars within Mt. Emily WMU using a combination of POP-II derived population estimates (Bartholow 1992) and herd composition data obtained during helicopter flights that were provided by ODFW and CTUIR (Appendix S1). We pooled data for all deer species because most deer of unknown species killed by cougars were fawns ($n = 79$; 62.7%), and censoring these prey would have underestimated use of fawns by cougars. For deer and elk, we used separate but similar approaches to calculate the proportion of individuals within each sex and age class (Clark 2014; Appendix S1). We generated seasonal estimates of prey availability that we based on estimates at the start of each season. We calculated mean herd composition values and population estimates for each ungulate species from population estimates provided by ODFW and CTUIR from 2009 to 2012 to obtain a single point estimate of prey availability over the duration of our study (Appendix S1).

We calculated separate seasonal, genus (i.e., *Odocoileus* or *Cervus*), and age class (i.e, juvenile, yearling, or adult) selection ratios for each sex and reproductive status of cougars. Within each sex and demographic classification of cougars, we pooled kills from individuals to define use under Design I (Thomas and Taylor 1990) and compared this to available prey within the study area using:

$$\hat{w}_i = o_i / \pi_i$$

where $\hat{w}_i$ is the selection ratio for prey item i, o_i is the proportion of prey item i in the diet, and π_i is the proportion of species i available in the study area (Manly et al. 2002). We tested the null hypothesis that cougars had similar proportions of prey in their diets regardless of sex or reproductive status (χ^2_{L1}; Manly et al. 2002:eq. 4.26) and if any classification of cougar non-randomly used prey (χ^2_{L2}; Manly et al. 2002:eq. 4.27). Selection ratios and associated confidence intervals <1 indicate use lower than available, and those >1 indicate selection. Where selection ratios and associated confidence intervals overlapped 1, we concluded use in proportion to availability. We compared selection ratios among demographic classifications (e.g., selection vs. use in proportion to availability vs. use lower than available) to determine where patterns of selection differed among demographic classifications of cougars.

We conducted 1 additional analysis (χ^2_L; Manly et al. 2002:eq. 4.11) to determine if cougars seasonally selected for a particular sex of adult deer or elk. For this analysis, our sample of adult deer and elk with known sex killed by cougars was limited (deer: summer = 108, winter = 63; elk: summer = 14, winter = 39), so we pooled seasonal data for all cougars regardless of cougar sex or reproductive status to increase sample sizes and decrease Type II errors (Zar 1999). We made the assumption that kills where we were able to determine the sex of prey were representative of all adult deer and elk killed by cougars (i.e., our ability to determine sex of cougar-killed prey was not biased towards a particular sex).

RESULTS

We captured 9 adult male and 16 adult female cougars and fitted them with GPS collars. Of the 16 females, 11 transitioned between reproductive classifications at least once. We monitored predation sequences for 7,642 cougar-days ($n = 25$, $\bar{x} = 318 \pm 49$ days/cougar, range = 38–850 days) from April 2009 to April 2012, which represented 20.9 cougar-years. We monitored cougars more days during the summer (4,286 days, $n = 22$, $\bar{x} = 195 \pm 27$ days/cougar, range = 2–184 days) than the winter (3,356 days, $n = 22$, $\bar{x} = 153 \pm 25$ days/cougar, range = 7–181 days). We monitored female cougars more days (5,518 days, $n = 16$, $\bar{x} = 368 \pm 67$ days/cougar, range = 59–850 days) than males (2,124 days, $n = 9$, $\bar{x} = 236 \pm 64$ days/cougar, range = 38–634 days). We visited 3,365 GPS location clusters and located the remains of 1,213 prey items at 1,172 clusters. The median number of days between the date a cluster was formed and when the cluster was surveyed was 21 days ($\bar{x} = 28$ days, SD = 25). Even though most edible biomass was consumed before kill sites were located, we successfully identified species, age, and sex of prey from skeletal remains for animals killed throughout the year.

Model for Predicting the Presence of a Kill

Our best model for determining the presence or absence of a kill at a GPS location cluster during summer was (Table S1):

$$-3.453 + 0.691 \times CP + 0.073 \times FID + 0.003 \times AD - 0.003 \times (CP \times AD)$$

where CP is the corrected number of points in the cluster, FID is cluster fidelity, and AD is the average distance of all points in the cluster from the cluster center. Our best model for determining the presence or absence of a kill at a GPS location cluster during winter was (Table S2):

$$-4.868 + 0.577 \times CP + 0.046 \times FID + 0.027 \times AD - 0.004 \times (CP \times AD)$$

and included the same variables as the summer model. We used a probability cutoff of 0.12 and 0.06 during summer and winter, respectively to define a kill location because they allowed >20% of clusters not to be surveyed, while missing <1% of kills (Clark 2014).

Prey Use and Scavenging

Of the 1,213 cougar kills, 95.5% were deer or elk and 4.5% included carnivores (badger [*Taxidea taxus*], black bear, cougar, and coyote), small mammals (beaver [*Castor canadensis*], opossum [*Didelphis virginana*], raccoon [*Procyon lotor*], snowshoe hare [*Lepus americanus*], and woodrat [*Neotoma* spp.]), and birds (dusky grouse [*Dendragapus obscurus*], ruffed grouse [*Bonasa umbellus*], ring-necked pheasant [*Phasianus colchicus*], and turkey [*Meleagris gallopavo*]; Table 1). Domestic sheep were the only domestic livestock killed by cougars during our study, but this was rare (<0.5% of all kills).

Deer (mule deer and white-tailed deer combined) were the most common ungulate (68.6%) in cougar diets followed by elk (31.4%). Estimates of live weight biomass of cougar-

Table 1. Seasonal comparison of cougar diets for adult males, solitary females, adult females with kittens <6 months old, and adult females with kittens >6 months old. Results were from 1,213 predation events for 25 cougars in northeast Oregon, USA from 2009 to 2012.

	Adult male				Adult female no kittens				Adult female with kittens <6 months old				Adult female with kittens >6 months old			
	Summer		Winter		Summer		Winter		Summer		Winter		Summer		Winter	
Prey type	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n
Individual species																
White-tailed deer	11.7	21	11.6	13	6.7	17	20.2	20	18.6	34	6.0	3	18.7	37	25.5	35
Mule deer	17.9	32	32.1	36	42.4	108	62.6	62	43.2	79	74.0	37	38.9	77	40.9	56
Unknown deer species[a]	9.5	17	5.4	6	11.0	28	2.0	2	9.3	17	10.0	5	19.7	39	8.8	12
Elk	46.9	84	47.3	53	38.0	97	14.1	14	23.5	43	8.0	4	18.2	36	24.1	33
Other[b]	14.0	25	3.6	4	2.0	5	1.0	1	5.5	10	2.0	1	4.5	9	0.7	1
Condensed ungulate categories																
Deer	45.5	70	50.9	55	61.2	153	85.7	84	75.1	130	91.8	45	81.0	153	75.7	103
Elk	54.5	84	49.1	53	38.8	97	14.3	14	24.9	43	8.2	4	19.0	36	24.3	33
Ungulates by age class																
Fawn	25.3	39	17.6	19	38.8	97	36.7	36	36.4	63	34.7	17	31.2	59	31.0	39
Yearling deer	2.6	4	6.5	7	5.6	14	8.2	8	9.8	17	4.1	2	11.6	22	10.3	13
Adult deer	15.6	24	17.6	19	14.4	36	33.7	33	28.3	49	46.9	23	32.3	61	33.3	42
Unknown age deer[c]	1.9	3	9.3	10	2.4	6	7.1	7	0.6	1	6.1	3	5.8	11	7.1	9
Calf	39.6	61	16.7	18	36.8	92	9.2	9	23.7	41	2.0	1	14.8	28	11.1	14
Yearling elk	8.4	13	5.6	6	1.2	3	1.0	1	1.2	2	2.0	1	2.1	4	1.6	2
Adult elk	5.8	9	26.9	29	0.8	2	4.1	4	0.0	0	4.1	2	2.1	4	5.6	7
Unknown age elk[c]	0.6	1	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0

[a] Insufficient prey remains were present to accurately determine species; most (62.7%) of unidentified remains were fawns.
[b] Other prey items included badger, beaver, black bear, cougar, coyote, domestic sheep, opossum, raccoon, and turkey.
[c] Insufficient evidence was present to accurately assign the prey item to the correct age class.

killed deer (50.1%) and elk (49.9%) were similar. In instances where we distinguished between deer species ($n = 667$), mule deer were the most common species in cougar diets (73.0%). Cougars killed 764 deer during our study, and fawns (46.5%) were the most frequently killed age class, followed by adults (36.1%), yearlings (11.0%), and unknown age deer (6.4%). Adults comprised the greatest amount of deer biomass killed by cougars (60.4%) followed by fawns (18.9%), yearlings (13.0%), and unknown aged deer (7.7%). Cougars killed 364 elk during our study. Calves (75.3%) were the most frequently killed age class of elk, followed by adults (15.7%), yearlings (8.8%), and unknown age elk (0.2%). Adults comprised the greatest amount of elk biomass killed by cougars (42.8%) followed by calves (39.1%) and yearlings (18.1%). Cougar diets differed by sex (Table 1) with elk more common in diets of males (52.2%) than females (25.4%; $\chi_1^2 = 66.91$, $P < 0.001$). The proportion of deer in diets of solitary females ($\chi_1^2 = 18.36$, $P < 0.001$) and females with kittens >6 months old ($\chi_1^2 = 5.41$, $P = 0.02$) increased from summer to winter. In contrast, proportion of deer in the diets of male cougars ($\chi_1^2 = 0.56$, $P = 0.46$) and female cougars with kittens >6 months old ($\chi_1^2 = 0.99$, $P = 0.32$) was similar between seasons.

We documented 50 instances of scavenging by cougars, which represented 4% of all prey remains. Of the 25 cougars monitored, 15 (60.0%) scavenged at least once, and males (5 out of 9; 55.6%) and females (10 out of 16; 62.5%) scavenged at similar rates ($\chi_1^2 = 0.12$, $P = 0.73$). Most carcasses scavenged by cougars were ungulates (44 of 50; 88%) that were killed by hunters or vehicles. Cougars also scavenged discarded livestock remains ($n = 4$), illegal bear bait ($n = 1$), and a black bear ($n = 1$). One female was responsible for 15 of the 50 instances of scavenging. This female resided where remains of human-killed ungulates and domestic livestock were discarded at illegal dump sites along a remote gravel road and vehicle-killed animals from an adjacent highway were present.

Kill Rates
We used a subset of 1,099 ungulate kills to calculate kill rates, which represented 62 season and demographic-specific monitoring intervals ≥ 42 days. Annually, cougars killed 1.03 (95% CI = 0.92–1.14) ungulates per week; however, kill rates (ungulates/week) of cougars were influenced by sex, reproductive status, and season ($F_{4,57} = 14.51$, $P < 0.001$; Fig. 2a). Cougars killed 1.55 (95% CI = 1.47–1.66) times more frequently during summer than winter, and female cougars raising kittens >6 months old killed more frequently than other cougars. We observed substantially higher kill rates of cougars during the ungulate birth pulse (May–Jul) and lower kill rates during winter (Dec–Mar) when average size of prey killed by cougars was greater (Fig. 2b). We observed significant correlations between mean monthly cougar inter-kill intervals (i.e., days between consecutive kills) and average weight of prey ($R^2 = 0.85$, $P < 0.001$; Fig. 3a), and proportion of cougar kills visited by black bears ($R^2 = 0.52$, $P = 0.02$; Fig. 3b). Weight of prey killed by cougars was negatively correlated with proportion of cougar kills visited by black bears ($R^2 = 0.49$, $P = 0.01$) because black bears emerge from their dens during months when juvenile ungulates dominate cougar diets. Therefore, temporal variation in kill rates of cougars is best explained by weight of prey killed by cougars and secondarily by proportion of cougar kills visited by black bears. Weight of
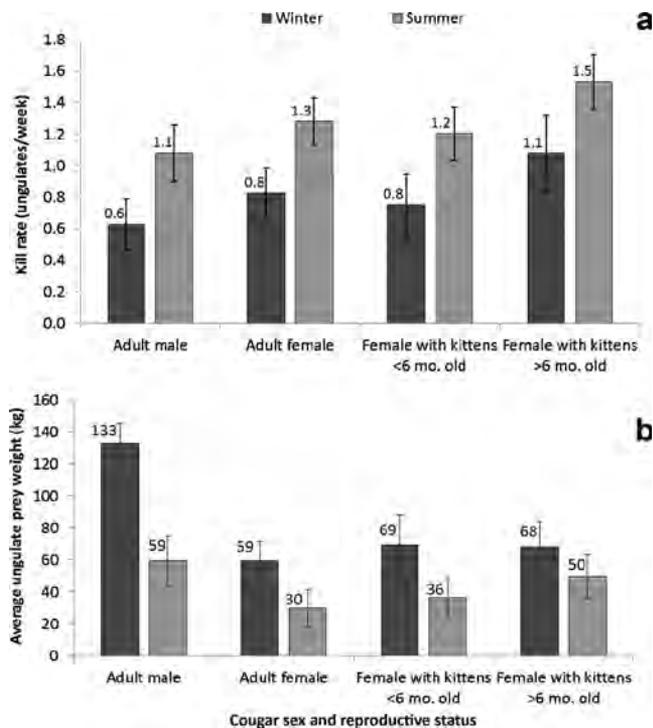
Figure 2. Seasonal estimates of cougar kill rates expressed as (a) frequency and (b) average prey size killed by cougars and associated 95% confidence intervals for each of 4 demographic classifications of cougars. Results were from 1,099 consecutive predation events from 21 cougars fitted with global positioning system collars in northeast Oregon, USA, from 2009 to 2012.

prey killed by cougars was negatively correlated with the proportion of juvenile ungulates in the diet of cougars ($R^2 = 0.64$, $P = 0.002$), indicating that cougars killed most frequently when juvenile ungulates dominated their diets (Table 1).

Prey Availability and Selection

Deer were the most abundant prey available throughout the year in our study area, juveniles of all species were the most common ungulate prey during summer, and adult deer and elk were the most abundant prey during winter (Table 2). Percentage of adult male deer and elk available to cougars was lower in winter because of legal harvest (Table 2).

Selection for genus and age class of prey.—We determined genus and age class of 744 of 766 ungulates killed by cougars during summer. Across all cougars, fawns ($n = 258$; 34.7%) were the most frequently killed prey, followed by elk calves ($n = 222$; 29.8%) and adult deer ($n = 170$; 22.8%). However, prey use differed according to cougar sex and reproductive status ($\chi^2_{L1} = 101.46$, $P < 0.001$; Table 1) and at least 1 demographic classification of cougars non-randomly used prey ($\chi^2_{L2} = 441.19$, $P < 0.001$). Male cougars killed all age classes of deer and adult elk in lower proportion than their availability but selected calf and yearling elk during summer (Fig. 4a). Regardless of reproductive status, female cougars killed adult elk in lower proportion than their availability, and used fawns and yearling deer and elk in proportion to their availability during summer. Females without kittens
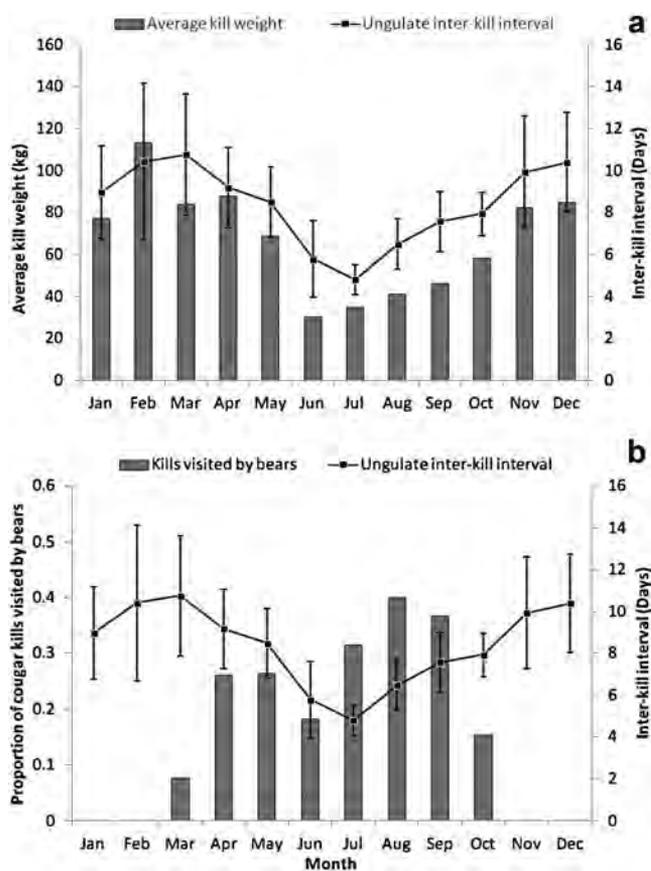

Figure 3. The average ungulate inter-kill interval and associated 95% confidence interval in each month versus the (a) average size of prey killed by cougars and (b) proportion of cougar kills visited by black bears in northeast Oregon, USA, from 2009 to 2012. We derived monthly average prey weights and the proportion of cougar kills visited by black bears using 1,158 ungulate kills where estimated weight and date of death was known. We estimated inter-kill intervals using data from 25 cougars where the date of the previous kill was known.

Table 2. The estimated number and percentage of deer and elk available to cougars according to age class and sex during the summer and winter in the Mt. Emily Wildlife Management Unit in northeast Oregon, USA from 2009 to 2012.

Prey species	Age class[a]	Summer[b]		Winter[b]	
		N	%	N	%
Deer[c]	Fawn	6,640	35	1,640	14
	Yearling	1,502	8	1,061	9
	Adult	5,798		4,853	
	Male	1,372	7	773	7
	Female	4,426	23	4,080	35
	Total deer	13,940		7,554	
Elk	Calf	2,000	10	1,000	9
	Yearling	304	2	220	2
	Adult	2,982		2,704	
	Male	688	3	541	4
	Female	2,290	12	2,163	19
	Total elk	5,286		3,924	
	Total prey	19,226		11,478	

[a] Fawn and calf = <1 year old, yearling = 1 year old, adult = ≥2 years old.
[b] Summer = May to October, Winter = November to April.
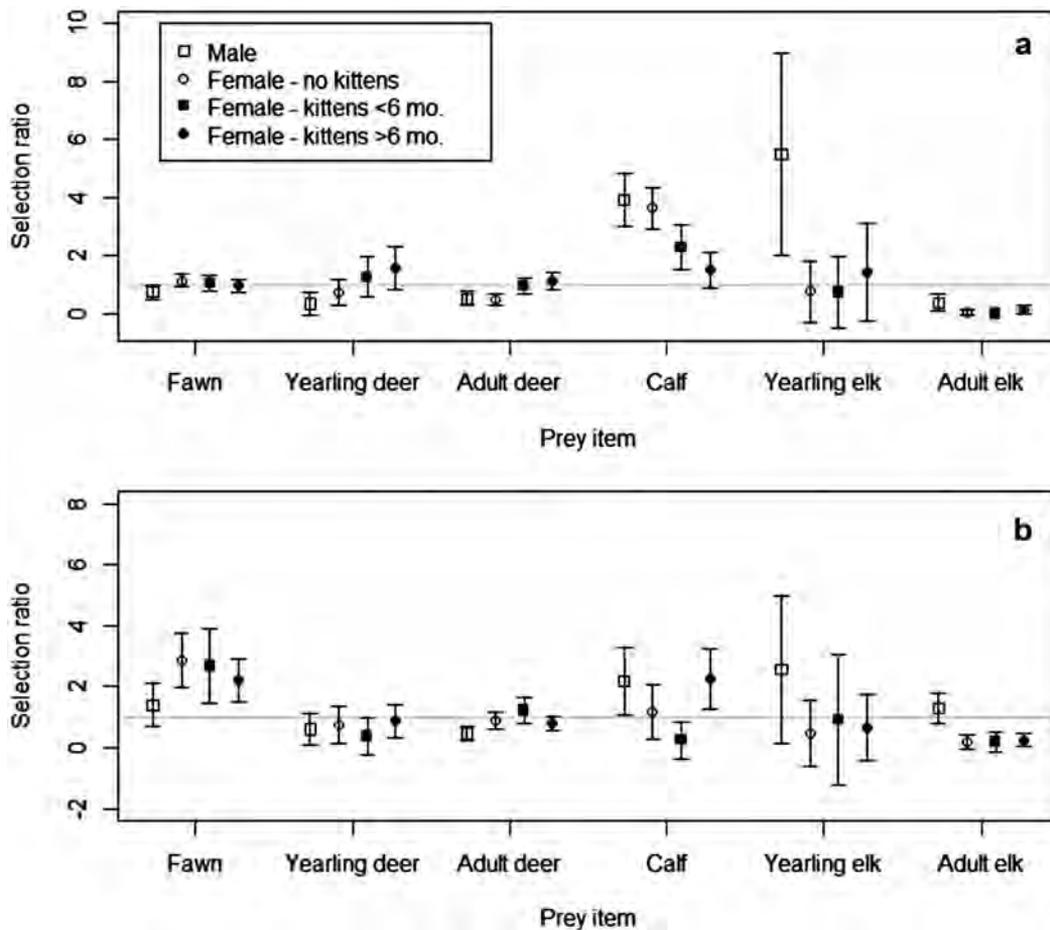[c] Combined populations of mule deer and white-tailed deer.

Figure 4. Prey selection ratios of cougars with 95% confidence intervals according to genus and age class of prey during (a) summer and (b) winter in northeast Oregon, USA, from 2009 to 2012. Population selection ratios were generated by comparing population level use to population level availability (Manly et al. 2002:eq. 4.10). The horizontal gray line represents a selection ratio of 1.0, which indicates use of prey in proportion to availability. Point estimates and associated 95% confidence intervals that are above the gray line indicate selection, whereas those that are below the gray line indicate prey was killed in lower proportion than available.

and those with kittens <6 months old selected elk calves during summer, but females with kittens >6 months old killed calves in proportion to their availability. Females without kittens killed adult deer in lower proportion to their availability during summer, whereas females with kittens killed adult deer in proportion to their availability (Fig. 4a).

We determined genus and age class of 352 out of 381 ungulates killed by cougars during winter. Across all cougars, adult deer were the most frequently killed prey ($n = 117$; 33.2%) followed by fawns ($n = 111$; 31.5%) during winter. However, prey use differed according to cougar sex and reproductive status ($\chi^2_{L1} = 68.03$, $P < 0.001$; Table 1) and at least 1 demographic classification of cougars non-randomly used prey ($\chi^2_{L2} = 170.92$, $P < 0.001$). During winter, male cougars selected elk calves, deer fawns, yearling deer and elk, and adult elk in proportion to their availability, and killed adult deer in lower proportion than their availability (Fig. 4b). Regardless of reproductive status during winter, female cougars selected fawns but used yearling deer, adult deer, and yearling elk in proportion to their availability, and killed adult elk in lower proportion then their availability. Selection patterns for elk calves by females during winter

varied by reproductive status. Females without kittens, with kittens <6 months old, and with kittens >6 months old killed elk calves in proportion to their availability, in lower proportion then their availability, and selected calves, respectively (Fig. 4b).

Selection for sex of adult deer and elk.—We determined sex of 108 and 63 adult deer killed by cougars during the summer and winter, respectively. Cougars did not select for either sex of adult deer during summer ($\chi^2_L = 0.57$, $P = 0.45$; Fig. 5a) but selected for adult, male deer during winter ($\chi^2_L = 13.30$, $P < 0.001$; $w_i = 1.89$, 95% CI $= 1.37$–2.41) and preyed on adult females proportionally less than their availability ($w_i = 0.73$, 95% CI $= 0.57$–0.89; Fig. 5a). Cougars killed a large percentage of adult male deer between August and November (48%), immediately prior to and during the rut, and most adult female deer were preyed on immediately prior to parturition between April and July (51%; Fig. 6a). We determined the sex of 14 and 39 adult elk killed by cougars during the summer and winter, respectively. We found no evidence cougars selected by sex of adult elk during the summer ($\chi^2_L = 0.02$, $P = 0.88$) or winter ($\chi^2_L = 0.11$, $P = 0.74$; Fig. 5b). Although we did not observe selection
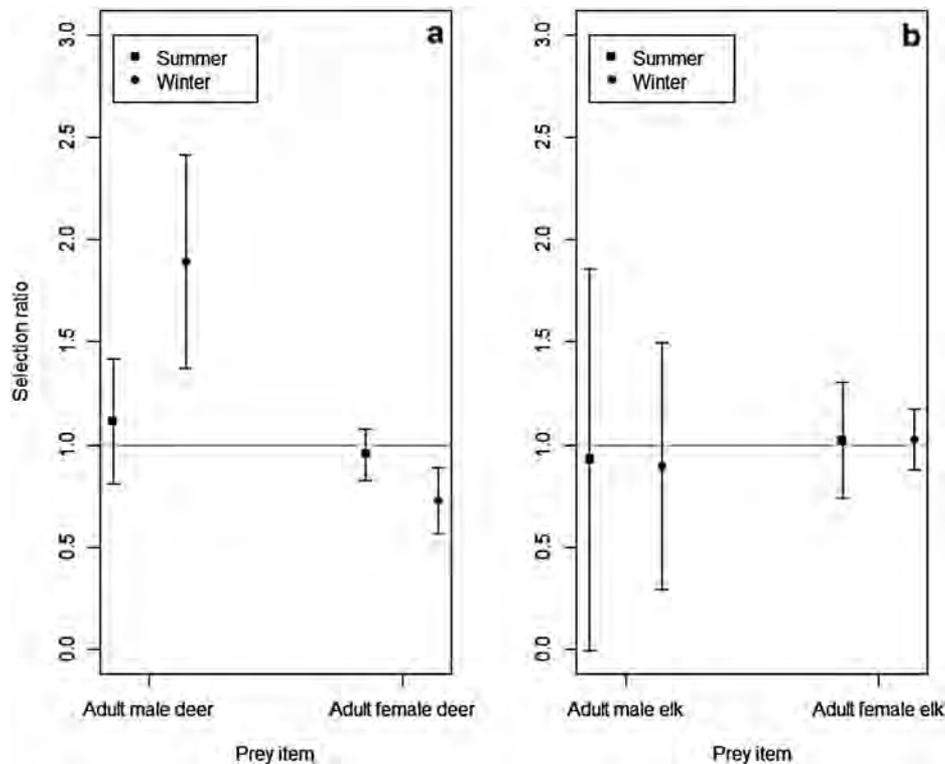
Figure 5. Prey selection ratios of cougars with 95% confidence intervals, by season, according to sex of prey for (a) adult deer and (b) adult elk in northeast Oregon, USA, from 2009 to 2012. Population selection ratios were generated by comparing population level use to population level availability (Manly et al. 2002:eq. 4.10). The horizontal gray line represents a selection ratio of 1.0, which indicates use of prey in proportion to availability. Point estimates and associated 95% confidence intervals that are above the gray line indicate selection, whereas those that are below the gray line indicate prey was killed in lower proportion than available.

for male elk, most were killed during or immediately after the rut (Fig. 6b), and most (80%) male elk were killed by male cougars. Sixty-three percent of female elk killed by cougars were killed prior to parturition between February and May (Fig. 6b).

DISCUSSION

Kill Rates

The kill rates documented in our study (0.90–1.33 ungulates/week) were at the upper range of published estimates (0.47–1.31 ungulates/week) for cougars in North America (Table 3); however, our results were consistent with those from west-central Alberta using identical methods (Knopff et al. 2010). Differences in kill rates calculated using GPS location clusters (this study, Knopff et al. 2010) compared to previous research are likely attributable to differences in methodology rather than biological differences. Kill rates estimated from snow-tracking provided seasonal estimates, which may not accurately reflect annual kill rates (this study, Knopff et al. 2010). Studies implemented using VHF telemetry often used small sample sizes with short monitoring intervals and estimation of kill rates over short monitoring intervals can often lead to biased kill rate estimates (Hebblewhite et al. 2003). Estimates of kill rates calculated using energetic models (Laundré 2005) were substantially lower than kill rates generated from field

sampling of GPS location clusters (Table 3), which was not surprising given that energetic models often underestimate kill rates of carnivores (Peterson and Ciucci 2003).

Although GPS location cluster data likely provides the least biased kill rate estimates, the method we used to locate cougar kills (Knopff et al. 2009) potentially caused us to miss small prey items such as young fawns and calves immediately following their birth. Newborn fawns (3–4 kg) represented about half of the biomass killed per day by cougars (Knopff et al. 2010, Clark 2014) but were smaller than the size of prey the cluster sampling technique was designed to locate (>8 kg; Knopff et al. 2009). Therefore, we acknowledge the possibility we did not document all fawns killed by cougars, which may have resulted in our underestimation of kill rates during and immediately following the ungulate birth pulse. This potential bias would be less evident for newborn elk calves because their birth weight (approx. 18 kg) is greater than the daily biomass killed by cougars (6–11 kg prey/day; Knopff et al. 2010, Clark 2014). Minimum prey size of cougars during winter was >30 kg; therefore, we likely documented all cougar kills for this time of year. Despite the possibility of underestimating kill rates during June and July when fawns are <8 kg, this would not invalidate our conclusion that cougar kill rates will be greater during summer when cougar diets are dominated by juvenile ungulates. Future investigations of cougar kill rates using GPS technology should consider increasing location
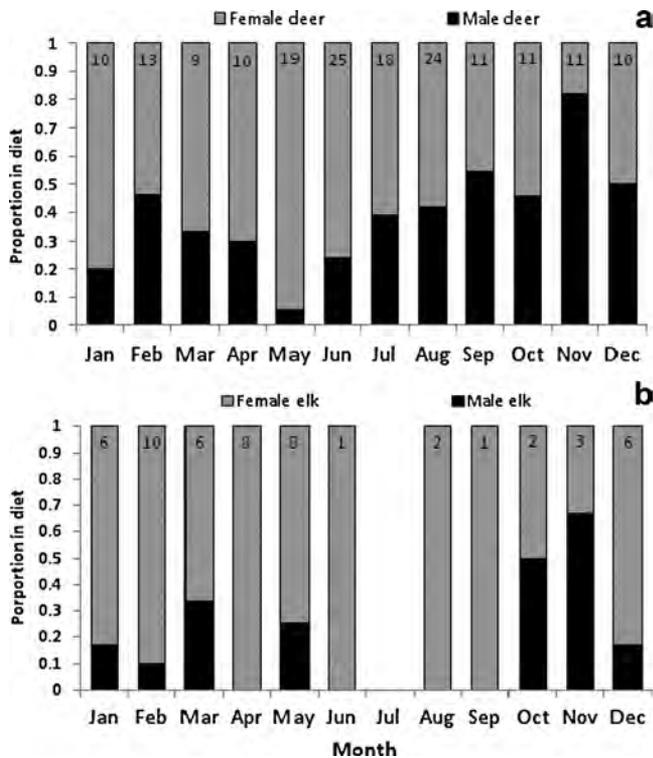
Figure 6. Monthly proportions of adult male and female (a) deer and (b) elk in the diets of 25 cougars in northeast Oregon, USA, from 2009 to 2012. We determined proportions from 234 adult deer and 53 adult elk where we were able to accurately determine the age and sex of prey. The values at the top of the bars indicated the number of individuals that were killed by cougars each month.

unlikely to occur because cougars are subordinate to other large carnivores at kill sites and cougars rarely scavenge kills of smaller predators (Murphy and Ruth 2010). The rate of scavenging in our study (approx. 4%) was similar to other studies (Logan and Sweanor 2001, Bauer et al. 2005, Knopff et al. 2010) suggesting our estimates of kill rates and prey use were not biased by scavenging. Kill-sharing by cougars could also positively bias kill rates, but given the low rate of interactions between independent cougars (Logan and Sweanor 2001), we believe this source of bias was minimal in our study.

The strong alignment between our results and those of Knopff et al. (2010) indicated cougar kill rates are influenced by season, sex, and reproductive status of females, and these patterns are generalizable among areas. We observed relatively minor differences in kill rates compared to those of Knopff et al. (2010). Cougars in west-central Alberta killed larger prey (e.g., moose and feral horses) and more biomass of prey (9.73 kg/prey/day; Knopff et al. 2010) than cougars in our study (e.g., elk and deer; 8.05 kg/prey/day; Clark 2014). Larger prey have a higher percentage of inedible biomass (e.g., bones and rumen content), which may explain why cougars in our study killed more frequently (kills/week) than those in Alberta (Table 3). Cougars kill more frequently during summer because cougar diets are dominated by juvenile ungulates (this study, Knopff et al. 2010). Kill rates of females with kittens were greater than solitary females (this study, Knopff et al. 2010, White et al. 2011) because family groups have higher collective energetic requirements (Ackerman et al. 1986, Anderson and Lindzey 2003, Knopff et al. 2010). In our study and Knopff et al. (2010), females did not increase kill rates until kittens were >6 months old (Fig. 2a), which suggested small kittens (<15 kg) do not place a high energetic burden on females. However, females were mostly restricted to nursery sites the first 30 days after

acquisition schedules during summer to identify the degree to which small ungulate prey are not documented immediately following the ungulate birth pulse. Incorrectly classifying scavenging events as cougar kills can positively bias kill rates (Anderson and Lindzey 2003), but this is

Table 3. Published estimates of the number of ungulates killed per week by cougars in western North America from 1970 to 2012.

| Source | Study area | Primary prey[a] | Kill rate[b] | | | | | | | Estimation technique[c] | Calculation technique[d] |
			UM	UF	ADM	SAM	ADF	SAF	FG		
Hornocker (1970)	ID	MD, E							1.17	Snow-tracking	Ratio
Shaw (1977)	AZ	MD					0.67		1.03	Model (LC-R)	NA
Ackerman et al. (1986)	UT	MD			0.83		0.44		0.67–2.26	Model (E)	NA
Ackerman et al. (1986)	UT	MD							1.57	Radiotelemetry	IKI
Harrison (1990)	BC	BS, MD							1.67	Radiotelemetry	IKI
Murphy (1998)	WY	E, MD			0.94	0.64	0.64	0.69	0.98	Radiotelemetry	IKI
Nowak (1999)	OR	MD, E					1.01		0.88	Radiotelemetry	IKI
Anderson and Lindzey (2003)	WY	MD, E			0.91	0.74	1.01	0.97	1.31	Model (LC-G)	Ratio
Laundré (2005)	ID	MD			0.37		0.29		0.85	Model (E)	NA
Mattson et al. (2007)	AZ	E, MD			0.95	0.88	0.76	1.17		Model (LC-G)	IKI
Cooley et al. (2008)	WA	WT, MD	0.74	0.91					1.20	Radiotelemetry	IKI
Laundré (2008)	ID	MD			0.47		0.49		0.59	Model (LC-R)	Ratio
Knopff et al. (2010) [e]	AB	WT, MD, E, MO			0.67	0.59	0.80	0.46	0.90–1.30[f]	GPS Telemetry	Ratio
This study[e]	OR	MD, E, WT			0.90		1.03		1.00–1.33[f]	GPS Telemetry	Ratio

[a] MD = mule deer, WT = white-tailed deer, MO = moose, BS = bighorn sheep, E = elk.
[b] Kill rate = ungulates/week: UM = unknown age male cougar, UF = unknown age female cougar, ADM = adult male, SAM = sub-adult male, ADF = adult female, SAF = sub-adult female, FG = family group. Blank cells indicate no estimates were calculated or provided.
[c] Estimates were generated from either direct visitation of kills in the field (snow-tracking, radiotelemetry, GPS telemetry), or indirectly with models (E = energetic, LC-R = radiotelemetry location model, LC-G = GPS location model).
[d] Kill rates were calculated using a ratio estimate or inter-kill interval (IKI). NA indicates not applicable.
[e] Females that transitioned between reproductive classifications had >1 kill rate calculated.
[f] Kill rates were calculated separately for females with kittens <6 months old (lower value) and >6 months old (upper value).

kittens were born and did not make many kills (D. Clark, Oregon State University, unpublished data). This caused lower kill rates during the first 30 days after kittens were born (summer = 0.99 kills/week, winter = 0.66 kills/week) compared to when kittens were 31–180 days old (summer = 1.36 kills/week, winter = 0.83 kills/week). Kill rates of females when kittens were 31–180 days old were intermediate to solitary females and females with older kittens, which suggested small kittens do place increased energetic demands on females. Male cougars killed larger prey than females (this study, Knopff et al. 2010), allowing males to potentially consume roughly 2 times more ungulate biomass per day than solitary females, and 1.5 times more than females with kittens (after accounting for body mass of kittens; Clark 2014). Male cougars may kill more frequently than females because of their larger body size (Logan and Sweanor 2001) or because home ranges of male cougars are approximately 2–3 times larger than those of females (Ross and Jalkotzy 1992, Spreadbury et al. 1996, Logan and Sweanor 2001), which require males to expend additional energy to traverse and defend their home ranges. Movement rates of GPS-collared cougars supported this assertion because male cougars (3.95 km/day) traveled 1.57 (95% CI = 0.59–2.55) km farther per day than females (2.38 km/day; $t_{22} = 3.31$, $P = 0.003$; D. Clark, Oregon State University, unpublished data).

Prey Use and Selection

Seasonal-, sex-, and reproductive status-specific patterns of prey use by cougars we observed were similar to those reported in west-central Alberta despite differences in vegetation and predator and prey guilds (Knopff et al. 2010). Combined, these results indicated cougar predation patterns follow the reproductive vulnerability hypothesis (Lima and Dill 1990) where cougars disproportionately prey upon juvenile ungulates during summer, male ungulates during fall, and female ungulates during winter and late spring, rather than killing prey at random, and this pattern likely holds throughout the geographic range of cougars.

Cougars are strongly dimorphic and it is hypothesized males are able to effectively capture larger prey because of more physical strength, which reduces their risk of injury during prey capture (Sunquist and Sunquist 1989, Iriarte et al. 1990). The consistently higher proportion of elk and other large ungulates in diets of male cougars compared to females in this and other systems support this hypothesis (Anderson and Lindzey 2003, Knopff et al. 2010, White et al. 2011). Diets of male cougars may also contain greater amounts of large prey to avoid intraspecific competition with females (Knopff et al. 2010) or to reduce time spent acquiring, processing, and feeding on prey, thus supporting optimal foraging theory, and allowing increased time for territorial defense and reproductive opportunities (Mattson et al. 2007). Differences in prey use and selection patterns by female cougars appear to balance increased energetic requirements needed to raise kittens with reducing risk of injury when capturing prey (this study, Knopff et al. 2010).

Female cougars with kittens >6 months old demonstrated minimal patterns in selection of prey, suggesting an opportunistic foraging strategy to take advantage of every opportunity to kill prey as encountered, except for adult elk (this study, Ross and Jalkotzy 1996, Mattson et al. 2007). In contrast, solitary females have lower energetic burdens than females with kittens, which may allow them to take fewer risks and prey upon smaller, weaker prey (this study, Murphy 1998, Knopff et al. 2010, White et al. 2011).

Our results and those of Knopff et al. (2010) indicated that most adult male elk and deer were killed by cougars during and after the rut, and most adult female elk and deer were killed by cougars immediately prior to parturition, which supported the reproductive vulnerability hypothesis (Lima and Dill 1990). Although our general results indicated an increase in adult male deer and elk being killed during and after the rut, cougars in our study did not select adult elk by sex, which was similar to the findings of Spreadbury (1989) and contradictory to other studies (Hornocker 1970, Kunkel et al. 1999, Anderson and Lindzey 2003). The lack of selection for male elk by cougars suggested that despite that male elk may be physically weakened following the rut, their large body size and weaponry (i.e., antlers) presented an extreme risk of injury to cougars (Hornocker 1970, Murphy 1998). Alternatively, habitat use patterns by male elk may reduce their susceptibility to cougar predation. Male elk tend to use more southerly aspects farther from ecotones than female elk (Skovlin et al. 2002) and these areas likely lack sufficient stalking cover for cougars to effectively capture elk. We expect the pattern of smaller male ungulates (i.e., deer) being selected by cougars during the fall and winter when they may be physically weakened because of rut activities should hold true in other areas, but the degree to which larger male ungulates (i.e., elk) are selected by cougars is still not well understood.

The strongest patterns of prey selection we documented were a seasonal shift in selection from elk calves to deer fawns between summer and winter. Cougars likely disproportionately preyed upon juvenile ungulates (this study, Hornocker 1970, Ross and Jalkotzy 1996, Knopff et al. 2010) because juveniles present very little risk of injury to cougars (Sunquist and Sunquist 1989) and are more naïve than adults (Geist 1982). We expect this pattern of disproportionate predation on juvenile ungulates can be generalized across systems with a defined ungulate birth pulse. Our estimates of prey selection may be biased slightly because of miscalculations of prey use or availability. For reasons previously outlined, we believe our estimates of prey use were largely unbiased. If our population estimates or herd composition data were biased, our estimates of prey availability would also be biased, which could affect our results (Manly et al. 2002). To address this concern, we conducted 2 post-hoc analyses where we doubled the size of either the elk or deer population. When we doubled the size of the deer population, patterns of selection were identical to what we reported, but strength of selection for elk calves during summer increased. When we doubled the size of the elk population, deer fawns were selected by female cougars

during summer and winter. Given these findings, our results were robust to inaccuracies in estimates of prey availability; however, we acknowledge this potential bias and patterns of selection of juvenile ungulates during summer may be greater than we documented.

The shift in selection from elk calves to deer fawns represented an optimal foraging strategy that balanced the risk of injury or ease of capture with energetic reward. Even though both fawns and calves were safe prey to capture, calves had a larger energetic reward (18 kg at birth) compared to fawns (3–4 kg at birth) during summer. By winter, fawns weighed approximately 30–45 kg, which represented an increased energetic benefit to cougars compared to summer but less risk of injury than larger elk calves (>80 kg). The seasonal selection patterns of elk calves by cougars in our study corresponded with patterns of mortality and survival of elk calves in northeast Oregon (Rearden 2005) and southeast Washington (Myers et al. 1999). Monthly survival rates of elk calves in northeast Oregon increased in a log-linear fashion from birth until they plateaued in November (i.e., the first 4–5 months of life). Thereafter, few calves were killed by cougars (Rearden 2005), suggesting calves were experienced or large enough to escape predation by cougars or presented a substantial risk of injury to cougars during capture. By the start of winter, approximately 50% of elk calves had died (Rearden 2005), and their decreased abundance likely reduced encounter rates between cougars and elk calves, which may have caused cougars to switch to more abundant alternative prey (i.e., fawns). Alternatively, the lack of selection for elk calves during winter could be attributable to changes in habitat use by elk. During winter and spring, elk occupy winter range habitat that typically occurs on south facing slopes (Skovlin et al. 2002), which in our study area consists of areas lacking vegetative structure (Franklin and Dyrness 1973). This shift to south facing aspects may make elk less vulnerable to predation during winter because these areas lack stalking cover for cougars. However, male cougars were still effective predators of elk throughout the year (Table 1, Fig. 4) and we contend seasonal patterns of selection for elk calves were attributable to an optimal foraging strategy used by cougars.

Selection of a secondary prey species by a generalist predator whose numbers are determined by a primary prey species can result in population declines for the secondary prey species or allow predators to maintain secondary prey at low densities (Messier 1994, Sinclair et al. 1998). This phenomenon has been termed apparent competition because the asymmetrical influence of a shared predator on secondary prey can appear as if the 2 prey populations are in direct competition (Holt 1977, Holt and Lawton 1993). Apparent competition, mediated by cougars, has been suggested in systems with mule deer and mountain caribou (Wittmer et al. 2005), mule deer and bighorn sheep (Johnson et al. 2012), white-tailed deer and mule deer (Robinson et al. 2002, Cooley et al. 2008), and mule deer and porcupine (Sweitzer et al. 1997) but not deer and elk. Cougar densities are likely determined primarily by the densities of their primary prey (i.e., most common prey item in diets; Logan

and Sweanor 2001, Laundré et al. 2007, Pierce et al. 2012) and secondarily by territory defense and behavioral mechanisms (Hornocker 1970, Logan and Sweanor 2001) raising the possibility that apparent competition could occur in areas with high deer densities. Since the mid-1990s, mule deer and white-tailed deer populations have increased in the Mt. Emily WMU (ODFW, unpublished data) resulting in relatively dense deer populations (approx. 290 adults/ 100 km^2). Concurrent with increased deer densities in Mt. Emily WMU since the mid-1990s, the elk population has declined, suggesting that apparent competition between deer and elk, mediated by cougars, could be occurring in the Mt. Emily WMU and presents a possible mechanism by which cougars limit elk but not deer populations. The potential limiting effect of cougars on elk populations is likely to occur because of selective predation on elk calves, which should result in variable or reduced calf survival. Variation in recruitment and population growth rate of elk is strongly correlated with variation in calf survival (Raithel et al. 2007, Harris et al. 2008, Clark 2014).

MANAGEMENT IMPLICATIONS

General patterns of cougar predation are emerging throughout their geographic range in western North America. These patterns suggest cougars kill more frequently during summer when diets are dominated by juvenile ungulates and less frequently during winter when diets include a higher proportion of ungulates with higher body mass. Although these broad patterns in cougar predation should be generalizable across the range of cougar distribution, we expect cougar diets and prey selection patterns to vary as a function of prey composition. For example, in systems with only deer, differential prey use by male and female cougars may not be as pronounced because opportunity for dietary segregation is limited. In multiple-prey systems, the strong selection for juvenile ungulates suggests cougars may have a disproportionate effect on these segments of ungulate populations. In elk populations, managers should consider cougars as a potential mechanism causing variable or low recruitment. Managers may be able to identify populations experiencing high levels of cougar predation by conducting herd composition surveys during late-summer or fall because most elk calves are killed by cougars during summer. However, other predators (e.g., black bears, wolves, and grizzly bears [*Ursus arctos*]; White et al. 2010, Griffin et al. 2011) or habitat conditions (Middleton et al. 2013) may be responsible for early mortality of elk calves and make it difficult to determine if cougars are negatively effecting recruitment in multiple-predator systems. Late-fall and early-winter herd composition surveys may be ineffective at assessing the effects of cougars on recruitment of deer because cougars continued to select fawns during winter. Furthermore, we advise managers to carefully consider all factors that may contribute to variability in juvenile recruitment because predation on juveniles may be largely compensatory mortality and other factors may be regulating recruitment in ungulate populations (Ballard et al. 2001, Bishop et al. 2009, Hurley et al. 2011).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix 1

Weights (kg) of ungulates used to calculate kill rate (kg/day) and prey composition (biomass) of cougars in northeast Oregon, USA, from 2009 to 2012.

Age and sex of prey	Species			
	Mule deer[a]	White-tailed deer[b]	Unknown deer[c]	Elk[a]
Adult male	75	68	72	315
Adult female	65	59	62	217
Yearling (12–23 months)	50	45	48	179
Juvenile[d] (11 months)	44	40	42	138
Juvenile (10 months)	41	37	39	129
Juvenile (9 months)	38	35	36	119
Juvenile (8 months)	35	31	33	109
Juvenile (7 months)	31	28	30	98
Juvenile (6 months)	27	24	26	87
Juvenile (5 months)	13	21	22	75
Juvenile (4 months)	19	17	18	62
Juvenile (3 months)	14	13	14	50
Juvenile (2 months)	10	9	10	39
Juvenile (1 month)	7	6	6	28
Juvenile (0 month)	4	3	4	18
Adult—unk sex[e]	70	64	67	266
Yearling or adult[f]	58	52	55	198

[a] Estimates of adult and yearling weights were calculated by taking the mean of fall and spring weights of mule deer captured in northeast Oregon (ODFW; unpublished data). Female elk weight estimates were calculated by taking the mean of fall and spring weights of elk captured in northeast Oregon (ODFW; unpublished data); male elk were assumed to be 1.45 times larger than females (Hudson et al. 2002).
[b] We calculated white-tailed deer weights by assuming they weighed approximately 90% of the weight of a similar aged mule deer.
[c] Average of mule deer and white-tailed deer estimates.
[d] Median weights of juvenile age classes per month were obtained from a von Bertanlanffy growth equation of the form $M(t) = A[1 - 1/3e^{-K(t-I)}]^3$, where $M(t)$ = mass (kg) at age t, A = max. weight (adult female), K = growth rate (we used 0.0049 for deer and 0.0042 for elk), and I = age at inflection point (140 days).
[e] Calculated using the average of adult male and female weights for each species.
[f] Calculated using the average of yearling female and adult female weights for each species. This value was used when we were unable to determine if prey item was a yearling or adult.