

## Feeding and spatial ecology of mountain lions in the Mendocino National Forest, California

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Between 2010 and 2012, we studied the feeding and spatial ecology of mountain lions (*Puma concolor*) in the Mendocino National Forest, California, a single-ungulate system in which their main prey were black-tailed deer (*Odocoileus hemionus columbianus*). Mountain lions displayed relatively high ungulate kill rates ( $\bar{x} = 1.07$  ungulates/week, and  $\bar{x} = 5.78$  kg/day), and also displayed individual variation in diet composition. The majority (77.6%) of deer  $\geq 1$  year old killed by mountain lions were in fair or better condition despite possible observed selection towards deer in older age classes ( $\geq 9$  years old). Analyses of hunting behavior indicated that prey types were killed in varying proportions among different time periods, with fawns more frequently killed during diurnal hours. We also found differences in habitat characteristics between kill sites and subsequent feeding sites, with feeding sites lower in elevation, flatter in slope, and with greater canopy density. Individual 95% fixed kernel home ranges varied between 102 and 614 km<sup>2</sup>. Estimated population densities of mountain lions including known kittens were comparatively low (0.68 mountain lions/100 km<sup>2</sup>).

Keywords: black-tailed deer, diet composition, home range, kill rate, mountain lion, *Odocoileus hemionus columbianus*, population density, *Puma concolor*

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Mountain lions are the most widely distributed carnivore in the western hemisphere (Sunquist and Sunquist 2002), and across their distribution they exhibit localized approaches in foraging behavior and spatial use (Murphy and Ruth 2010, Hornocker and Negri 2010, Elbroch and Wittmer 2012). For example, high prey biomass and the lack of large mammalian competitors in steppe habitats in Chilean Patagonia result in frequent use of open habitats that are largely avoided in North America (Beier 2012, Elbroch and Wittmer 2012, Wilmers et al. 2013). More broadly, diet composition varies among ecosystems depending upon prey assemblages and prey densities and abundances (Murphy and Ruth 2010). In order to understand mountain lion ecology it is therefore important to understand distinct strategies for and adaptations to unique ecosystems and thus the ecology of local populations.

The feeding ecology of mountain lions has been studied intensively due, in part, to broad interest in their effects on local prey populations including game species. Nevertheless, there remain aspects of its feeding ecology that are under-studied or unknown. For example, ungulates are the main prey of mountain lions in terms of biomass (Hornocker 1970, Knopff 2010, Ruth and Murphy 2010). However, kill rate estimates have shown large variation among studies, and there is debate as to whether these differences are attributable to environmental conditions, including prey species, or methodological differences, either in the field or in statistical analyses (Knopff et al. 2010, Ruth and Murphy 2010, Elbroch et al. 2014). Also, studies using scat analyses indicate that smaller vertebrates are a frequent component of their diet, although their importance in terms of biomass remains debated (Murphy and Ruth 2010, Bacon et al. 2011). Previous research has also shown that individual mountain lions specialize in their selection of prey (Ross et al. 1997, Elbroch and Wittmer 2013a), which in turn may have significant implications for modeling predator-prey dynamics, particularly when evaluating the effects of predation on rare prey (Wittmer et al. 2014).

Understanding space use of mountain lions is also important to determine the effect of mountain lions on prey species. In particular, home range size and overlap among resident mountain lions determine population density, and therefore affect mountain lion predation on local prey populations. Home range size and use, however, vary among ecosystems based on prey availability and distributions (Grigione et al. 2002, Elbroch and Wittmer 2012), as well as the energetic demands of individual mountain lions (e.g., sex class, pregnancy, and age; Logan and Sweanor 2001, Grigione et al. 2002). In general, mountain lion home ranges are smaller and mountain lion population densities are higher in areas of high quality habitats (i.e., with high prey density; Logan and Sweanor 2001, Grigione et al. 2002, Shaw 2010).

In 2010, we initiated a study in the Mendocino National Forest, California, in order to further our understanding of the feeding and spatial ecology of mountain lions in the area. The Mendocino National Forest is an important public hunting area for black-tailed deer in California, and our goal was to evaluate the impact of mountain lion predation on black-tailed deer (*Odocoileus hemionus columbianus*). Particular objectives were to: (1) determine mountain lion diet composition and kill rates; (2) evaluate age-distribution and

condition of ungulate prey; (3) further understand the cryptic hunting behaviors of mountain lions; and (4) quantify home range sizes and the density of the mountain lion population.

## MATERIALS AND METHODS

*Study area.*—We conducted our study in and adjacent to the Mendocino National Forest, California, from June 2010 to November 2012. The Mendocino National Forest is considered one of the premier public hunting areas for black-tailed deer in California. An established network of dirt roads provides ready access and the area is close to major urban areas including the cities of Sacramento, San Francisco, and San Jose. Our mountain lion study was part of a much larger study aimed at quantifying the population dynamics of black-tailed deer in the area (Marescot et al. in press).

The study area encompassed approximately 1,000 km<sup>2</sup> and included portions of Mendocino, Tehama, Glenn, and Lake Counties (39° 42' N, 122° 55' W; Figure 1). Elevations in the study area ranged from 396 to 2,466 m, with moderately rolling terrain at lower elevations and moderately steep, mountainous terrain at higher elevations. Climate varied seasonally, with mean daily temperatures ranging from -1°C to 24°C and extreme temperatures ranging from -2°C to 45.5°C (NOAA-Mendocino Pass, CA Weather Station; <http://www.ncdc.noaa.gov/cdo-web/>). Mean annual precipitation averaged 132 cm; the majority of precipitation occurred from December through March with only trace precipitation from May through September (NOAA-Ukiah Municipal Airport, CA Weather Station; <http://www.ncdc.noaa.gov/cdo-web/>). Below 1,000 m precipitation was predominantly in the form of rain, while at higher elevations, snow was common.

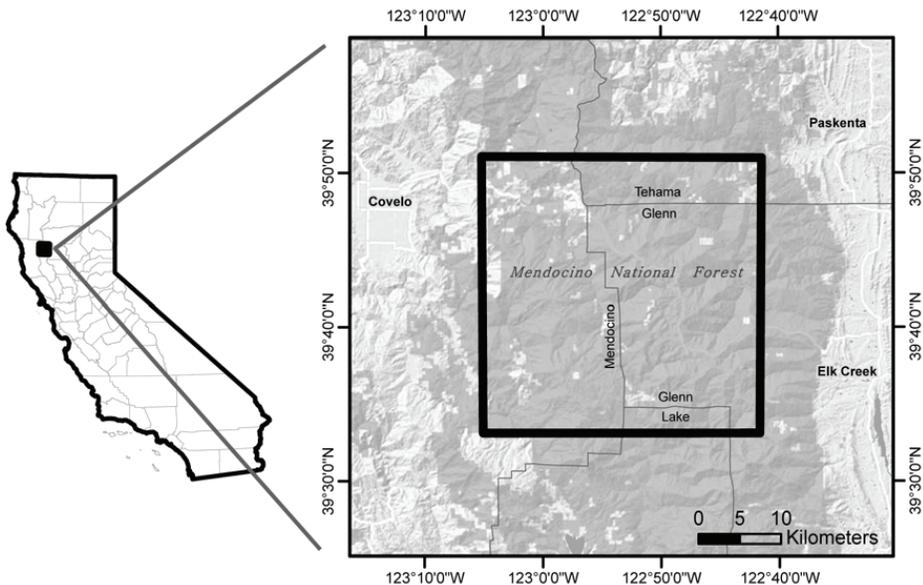


FIGURE 1.—Location of the study area, which included Mendocino National Forest and adjacent private lands, from 2010–2012. The study area is outlined by the thick black line, within the greater context of the North Coast Range and California.

Major habitat types based on the California Wildlife Habitat Relationships categories (Mayer and Laundenslayer 1988) changed with elevation, and included (in order of increasing elevation): blue oak (*Quercus douglasii*) woodland, annual grassland, montane hardwood conifer, Douglas fir (*Pseudotsuga menziesii*), mixed chaparral, montane hardwood, ponderosa pine (*Pinus ponderosa*), Klamath mixed conifer, montane riparian, and montane chaparral. Black-tailed deer were the most common large ungulate in the area. Other ungulates present include non-native wild pigs (*Sus scrofa*), tule elk (*Cervus elaphus nannodes*), and domestic cattle (*Bos taurus*), all of which occurred at very low densities. Competitors and scavengers noted at mountain lion kills included black bears (*Ursus americanus*), coyotes (*Canis latrans*), gray foxes (*Urocyon cinereoargenteus*), turkey vultures (*Cathartes aura*), and common ravens (*Corvus corvax*) (Allen et al. 2014a).

*Animal captures.*—Between June 2010 and November 2012, we captured mountain lions using trained hounds and box traps. Upon capture, mountain lions were anesthetized with Telazol® (tiletamine HCl and zolazepam HCl; Fort Dodge Animal Health, Fort Dodge, IA). Ketamine HCL (Ketaset®, Fort Dodge Animal Health, Fort Dodge, IA) was administered as needed to maintain anesthesia during processing. Once anesthetized, we determined the sex and then weighed, measured, and fitted each with an ear tag and a combined ARGOS satellite GPS/radio telemetry collar (Lotek 7000SAW, New Market, Ontario, Canada). We used measurements of gum-line recession to determine the age of captured mountain lions (Laundre et al. 2000), and classified them as subadults (<3 years) or adults (≥3 years). All capture methods were approved by an independent Institutional Animal Care and Use Committee at the University of California, Davis (Protocols 15341 and 16886), and by the Wildlife Investigations Laboratory of the California Department of Fish and Wildlife.

*Collar programming and field methods.*—We programmed collars to acquire GPS locations at 2-hr intervals, and downloaded location data via satellite every 3 days. We then displayed location data in ArcGIS 3.2 (ESRI, Redlands, CA) to visually identify clusters of GPS points and thus potential kill sites. In this study we defined GPS clusters as ≥5 locations (or a minimum of 8 hours between first and last locations) within 150 m of each other that contained at least one crepuscular or nocturnal location (Elbroch and Wittmer 2013a), and we attempted to visit every GPS cluster for each individual puma. We performed field investigations after downloads of Argos-relayed GPS locations and used handheld GPS units (Garmin 60csx) to locate possible prey remains.

We used the state of decay and locations of bite marks on prey carcasses to assess whether the prey had been killed or whether the mountain lion had been scavenging. We classified prey species through skeletal features and external characteristics (hair and pelage, or feathers). At each feeding site (and a subset of kill sites—see below) we recorded the elevation, overhead tree species, and determined the primary microhabitat type within a circle with diameter 20 m<sup>2</sup> and the carcass at its center, based on descriptions of Mayer and Laundenslayer (1988). We then used a concave spherical densiometer to measure the canopy cover and a clinometer to measure the slope of the feeding site.

We estimated the age of black-tailed deer killed by mountain lions to the closest month for individuals <1 year old based upon field observations and the assumption that fawns were born on June 16th of each year. We estimated the age of black-tailed deer for individuals 1–2.5 years old using tooth irruption patterns (Heffelfinger 2010), and for individuals >2.5 years old by cementum annuli analysis (Low and Cowan 1963; Matson's

Laboratory, Milltown, MT). We determined condition for adult black-tailed deer from the color and consistency of the bone marrow (Hornocker 1970), differentiating 4 categories: poor (red or red and pink marrow), fair (pink marrow), good (pink and white marrow), and excellent (white marrow). We estimated prey weights based on published literature: for deer, we used monthly sex-specific weights for fawns, and annual sex-specific weights for adults based on data from Sitka black-tailed deer (*O. h. sitkensis*; Parker et al. 1993); for other mammal species we used the mean weights described in Jameson and Peeters (2004), and for bird species we used the mean weights described in Sibley (2005).

*Statistical analyses.*—We used program *R* version 3.0.0 (R Core Team 2013) for our statistical analyses, except where noted. Following *R* guidelines (R Core Team 2013), we cite associated packages used in the analyses. In each statistical test, we considered  $P \leq 0.05$  to be statistically significant.

We determined the frequency of occurrence for each species in the diet of mountain lions through prey remains found at GPS clusters. We determined kill rates for each individual mountain lion for the entire time each had a functional GPS collar, with the duration of monitoring periods shown in Table 1. We calculated kill rates in terms of both number of individuals killed (animals/week) and biomass (kg/day) for each collared mountain lion. We calculated both types of kill rate for all prey items, and then separately for ungulates, with the number of ungulates killed per week allowing for comparison to previous studies of mountain lion kill rates (summarized in Table 1 of Knopff et al. 2010).

TABLE 1.—The kill rates and percent of diet made up of non-ungulates for mountain lions monitored during the study in the Mendocino National Forest, California, 2010–2012. The duration of the monitoring period for each mountain lion is shown in days. The percent of diet made up of non-ungulates was calculated by occurrence of individual animals over the course of the entire monitoring period. Kill rates were calculated for all prey species and just ungulates for GPS clusters of  $\geq 8$  hours, with kill rates of mass calculated as kg/day and kill rates of number of individuals calculated as animals/week.

ID	Monitoring Period (days)	Percent of Non-ungulates in Diet	Kill Rates			
			All Prey		Ungulates	
			Mass (kg/day)	Individuals (animals/week)	Mass (kg/day)	Individuals (animals/week)
F1	477	21.1%	4.78	1.12	4.68	0.88
F17	328	8.9%	5.82	1.20	5.81	1.09
F19	202	20.0%	4.37	0.87	4.34	0.69
F23	186	44.7%	5.27	1.81	4.77	0.98
F43	209	8.1%	10.27	2.08	10.26	1.91
M33	386	5.7%	6.84	1.29	6.71	1.20
M36	83	43.8%	4.37	1.35	3.92	0.76

We hypothesized that individual mountain lions would vary in the proportion of non-ungulate prey in their diet. For each individual mountain lion we categorized each animal killed as ungulate or non-ungulate, and then used a chi-square test with a 7x2 contingency table (Sokal and Rohlf 1987) to test for differences in the proportion of the two prey types among individual mountain lions. For our analyses of age and condition of deer killed by

mountain lions we only used kills where we found teeth (irruption  $n = 34$ , cementum annuli  $n = 38$ ) and long-bones ( $n = 89$ ) needed to determine these variables. We hypothesized that male and female black-tailed deer would be killed at different ages because in hunted populations with male-only harvest restrictions, there may be fewer male deer available in the old age class than sub-adult or prime age classes. Because of a low sample size in some classes, we used a Fisher's exact test (Sokal and Rohlf 1987) to test our hypothesis, with categories of sub-adults (1–2.5 years old), prime age (3–8 years old), and old ( $\geq 9$  years old) for deer of each sex.

We defined the time of kill for each prey carcass using the hour of the first waypoint at each mountain lion GPS cluster, 12 values available (0000, 0200, 0400, 0600, 0800, 1000, 1200, 1400, 1600, 1800, 2000, 2200). We then grouped times into 3 categories: nocturnal, diurnal, and crepuscular (times within 1 hour of sunrise and sunset), based on daily local sunrise and sunset times. We hypothesized that because mountain lions display specialization in their prey killed (Ross et al. 1997, Elbroch and Wittmer 2013a) and the timing of their feeding bouts (Pierce et al. 1998), that individual mountain lions might also vary in the times they hunt and kill prey. For each individual mountain lion we categorized each kill by time period, and used a Fisher's exact test to test for variation among individual mountain lions. We next split prey into 3 types: adult deer ( $\geq 1$  year), fawns ( $< 1$  year old), and non-ungulate prey. Because mountain lions are primarily nocturnal hunters (Currier 1983, Pierce et al. 1998, Sweanor et al. 2008), we expected that each prey type would be killed in higher proportions during the night, and hypothesized that prey types would not vary in their proportions among time periods. We categorized each kill by prey type and the categories of times of kill and used a chi-square test with a 2x3 contingency table (Sokal and Rohlf 1987) to test our hypothesis. We used a post-hoc Bonferroni test to determine where significant differences occurred.

On 13 occasions we determined the location where mountain lions killed black-tailed deer and compared their characteristics to matched, subsequent feeding sites. To find the kill site we followed the trails of mountain lions, backwards from the feeding site, to the point where the deer's tracks ended and the deer first hit the ground. At kill sites we recorded elevation, primary habitat type, overhead tree, canopy cover, and slope, following the same procedures as at feeding sites. We hypothesized feeding sites would be different from kill sites because mountain lions would choose concealment to feed (Murphy and Ruth 2010). We hypothesized that mountain lions would drag deer downhill (lower elevation) due to the mass of the deer and to flatter areas (less slope) for ease of feeding, while also choosing areas of high canopy cover to limit detection by avian scavengers (Elbroch and Wittmer 2013b). We first tested each variable (elevation, slope, and canopy cover) for normality with a Shapiro-Wilk normality test, and then tested for variance equality with a Levene's test (Sokal and Rohlf 1987). We then used a two-tailed Student's  $t$ -test with equal variances (Sokal and Rohlf 1987) to test for differences between kill and feeding sites for each variable.

We estimated home ranges of mountain lions for the total time they wore GPS collars in our study area using the fixed bivariate kernel method (Worton 1989). We first translated location data into R spatial data using the *sp* package (Pebesma and Bivand 2005, Bivand et al. 2008) and then used the *adehabitatHR* package (Calenge 2006) to estimate 95% kernel home ranges for each lion. We determined the kernel smoothing factor ( $h$ ) using least squares cross validation (Seaman and Powell 1996).

We calculated a minimum population density following methods outlined in Elbroch and Wittmer (2012) and Rinehart et al. (2014). We employed a density estimate for August–October 2011 using overlapping home ranges for that 3-month period. We based our minimum population estimate on our 402 km<sup>2</sup> ‘trapping area’ (Rinehart et al. 2014), an area in which we believe we had captured every resident mountain lion (based on the methods used in Smallwood and Fitzhugh [1993] we did not find any mountain lion tracks in the area that could not be accounted for by mountain lions wearing GPS collars). Using ArcGIS 9.3 we created 95% kernel home ranges for the 3-month period for each mountain lion by sex and age; we then summed the proportion of their overlapping home ranges within the trapping area (using Hawth’s tools and ArcGIS 9.3) to determine the density of adult resident mountain lions for each sex, and then overall for mountain lions (including juveniles and kittens) in the study area. To avoid bias associated with scaling a density to a different spatial extent than that of the study area, we then reported densities per 402 km<sup>2</sup> (Rinehart et al. 2014). With the understanding that we would negatively bias results by scaling down the population density, we also present densities per 100 km<sup>2</sup> for comparison with other studies.

## RESULTS

*Kill rate and diet composition.*—We captured 7 mountain lions (5 females, 2 males) and monitored each mountain lion for  $\bar{x} = 9.07 \pm 4.79$  *SD* months (Table 1). We conducted field investigations of 598 out of 609 identified GPS clusters, and we investigated the ARGOS-relayed GPS clusters within  $\bar{x} = 6.78 \pm 8.18$  *SD* (range 0–60) days after the mountain lion left the kill.

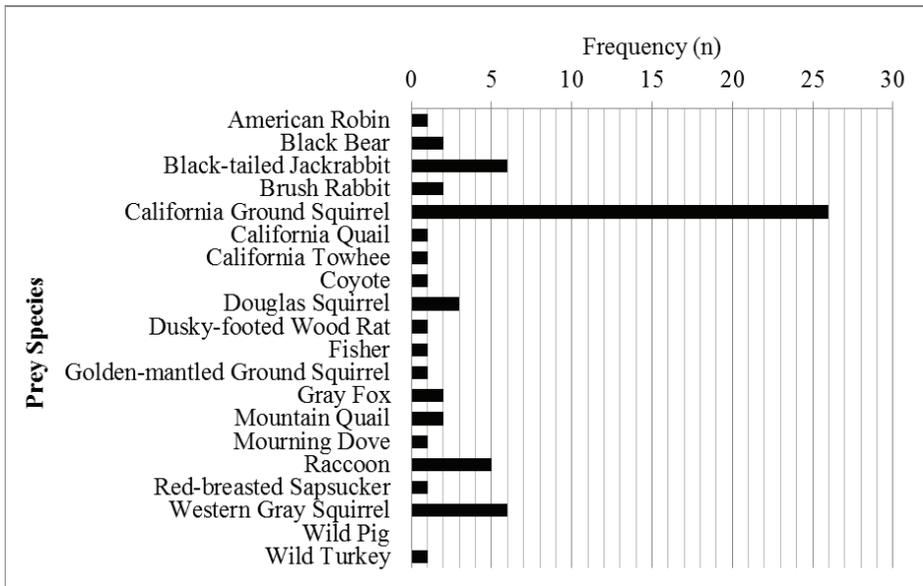


FIGURE 2.—The frequency of occurrence for each non-ungulate prey species we documented mountain lions eating during the study in the Mendocino National Forest, California, 2010–2012.

We identified 352 mountain lion kills, including 288 black-tailed deer, 2 black bears, and 62 small-to-medium sized vertebrates (Figure 2), as well as 4 acts of mountain lion scavenging. Kill rates for all prey species were  $\bar{x} = 1.39$  (95% CI = 1.07-1.70) animals/week, and  $\bar{x} = 5.96$  (95% CI = 4.40-7.51) kg/day (Table 1). Kill rates for ungulates were  $\bar{x} = 1.07$  (95% CI = 0.77-1.38) ungulates/week, and  $\bar{x} = 5.78$  (95% CI = 4.16-7.40) kg/day (Table 1). Black-tailed deer contributed 98.6% of prey biomass and 74.4% of deer killed by mountain lions were  $\geq 1$  year old.

*Hunting and feeding behavior.*—Our chi-square analysis revealed a significant difference among individual mountain lions in the proportion of non-ungulate prey in their diet ( $X^2_6 = 45.03$ ,  $P < 0.0001$ ) (Table 1). Our analysis revealed a sex-specific difference in the proportion of deer killed in different age classes ( $P_2 = 0.0378$ ) (Figure 3), with more females in the old age class than prime age class. The condition of black-tailed deer  $\geq 1$  year old killed varied, with 12.4% of individuals in excellent condition, 32.6% in good condition, 32.6% in fair condition, and 22.4% in poor condition.

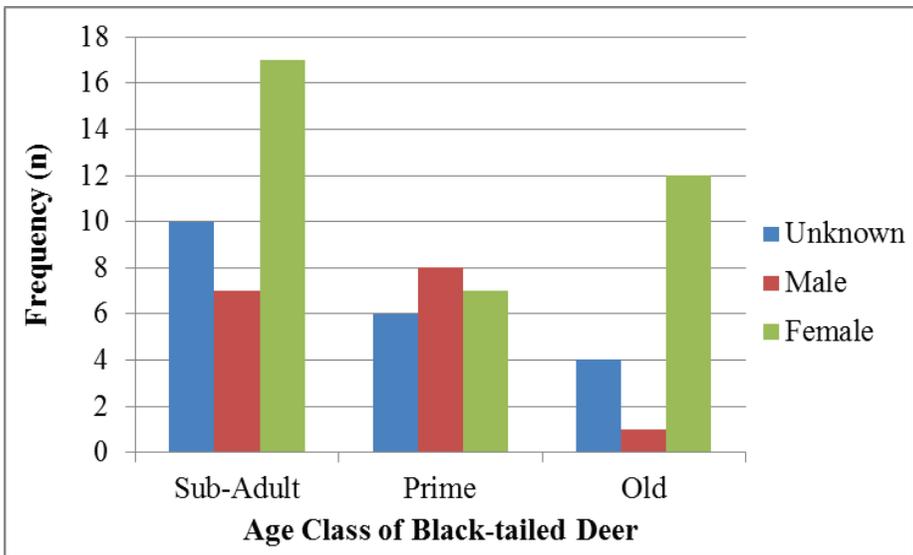
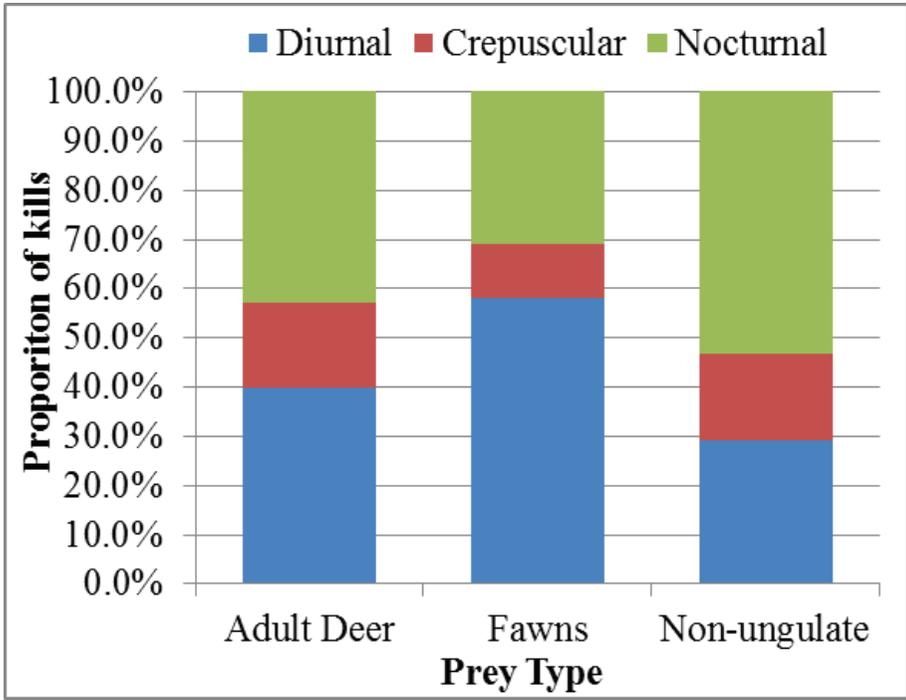


FIGURE 3.—The frequency of black-tailed deer killed by mountain lions among age and sex classes. Male, female, and unknown deer are shown by class, with sub-adult representing deer 1–2.5 years old, prime representing deer 3–8 years old, and old representing deer 9–22 years old. Sub-adult deer were aged using teeth irruption, while prime and old deer were aged using cementum annuli analysis. Mendocino National Forest, California, 2010–2012.

Our chi-square analyses did not reveal a significant difference among individual mountain lions in the time periods kills were made ( $X^2_{12} = 11.43$ ,  $P = 0.4927$ ), but did reveal significant differences in the time of kills for different prey types ( $X^2_4 = 12.82$ ,  $P = 0.0122$ , Figure 4). Our post-hoc analyses revealed fawns were more likely to be killed in diurnal periods ( $X^2_2 = 10.18$ ,  $P = 0.0061$ ), while non-ungulate prey were more frequently killed during nocturnal periods but were marginally insignificant ( $P = 0.0705$ ).



**Figure 4.**—The proportion of kills made by mountain lions for each prey type by time period. The time periods were grouped into 3 categories: nocturnal, diurnal, and crepuscular (within 1 hour of sunrise or sunset). Mendocino National Forest, California, 2010–2012.

Based on our 13 detailed site investigations, black-tailed deer were dragged  $\bar{x} = 21.7\text{m} \pm 4.28 \text{ SE}$  from the kill site to the feeding site. Approximately 40% of the feeding sites had different primary habitats and overhead tree species than the kill sites. The elevation at feeding sites was significantly lower than at kill sites ( $P_{12} = 0.0325$ ), with feeding sites  $\bar{x} = 5.77\text{m} \pm 2.39 \text{ SE}$  lower in elevation than kill sites. The slope at feeding sites was significantly flatter than at kill sites ( $P_{12} = 0.0174$ ), with feeding sites  $\bar{x} = 13.54^\circ \pm 5.02 \text{ SE}$  flatter in slope than kill sites. The canopy cover at feeding sites was significantly more dense than at kill sites ( $P_{12} = 0.0101$ ), with the canopy cover of feeding sites  $\bar{x} = 29.4\% \pm 10.2 \text{ SE}$  more dense than kill sites.

*Home range sizes and population density.*—Ninety-five percent kernel home ranges were  $\bar{x} = 266 \pm 116 \text{ km}^2$  for 4 adult females,  $102 \text{ km}^2$  for 1 subadult female,  $348 \text{ km}^2$  for 1 adult male, and  $142 \text{ km}^2$  for 1 subadult male (Table 2). We calculated a snapshot, minimum population density of  $1.74/402 \text{ km}^2$  ( $0.43/100 \text{ km}^2$ ) for adult female mountain lions and  $0.49/402 \text{ km}^2$  ( $0.12/100 \text{ km}^2$ ) for adult males. Total mountain lion density in the study area including known kittens was  $2.75/402 \text{ km}^2$  ( $0.68/100 \text{ km}^2$ ).

TABLE 2.—The characteristics and home range sizes of mountain lions in the Mendocino National Forest, California, 2010–2012. The age, age class and weight at original capture are shown, along with the number of GPS points used in the home range analyses. Home ranges (km<sup>2</sup>) were calculated using 95% kernels for the entire time the mountain lion was collared.

ID	Age (years)	Class <sup>a</sup>	Weight (kg)	Number of GPS Points	95% Kernel home range km <sup>2</sup>
F1	6.5	AF	34.6	5342	614.1
F17	1.4	SF	31.5	3695	102.4
F19	4.1	AF	33.6	1565	148.1
F23	4.2	AF	49.5	2125	158.6
F43	3.1	FG	38.1	2035	143.5
M33	7.0	AM	59.1	4255	347.8
M36	2.5	SM	48.1	971	141.8

<sup>a</sup>AF = Adult Female; AM = Adult Male; SF = SubadultFemale;  
SM= Subadult Male; FG = Family Group

## DISCUSSION

We found relatively high ungulate kill rates, with mean kill rates of 1.07 (95% CI = 0.77–1.38) ungulates/week among the highest kill rates reported for mountain lions to date (see summary in Table 1 of Knopff et al. 2010). These results, however, may be a consequence of intensive field methods rather than an indication of true differences in the feeding ecology of mountain lions in our study area, or an effect of the smaller ungulate size in our study area (Laundre 2008, Elbroch et al. 2014). Alternatively, the high kill rates may be due to interactions with competitors, particularly black bears. Black bears are a dominant scavenger (Allen et al. 2014a), and researchers have recently hypothesized that black bear kleptoparasitism may result in increased kill rates of mountain lions (Murphy et al. 1998, Allen et al. 2014b, Elbroch et al. 2014). Allen et al. (2014b) reported that kill rates in summer and fall when black bears were active in our study area were substantially higher than kill rates in winter and spring when black bears were predominately hibernating. Elbroch et al. (2014) reported that kill rates in three study areas with different scavenger communities were all higher than predicted by energetic needs of mountain lions.

We found high non-ungulate prey diversity when compared to previous studies that used GPS cluster methods to find mountain lion kills. Individual mountain lions also varied in the amount that non-ungulate prey species contributed to their diet, lending further support to previous research showing that individual mountain lions exhibit variation in prey selection (e.g., Ross et al. 1997, Elbroch and Wittmer 2013a). GPS cluster investigations may estimate different diet composition as compared to diets determined with scat analyses (Murphy and Ruth 2010, Bacon et al. 2011), due to the difficulty of finding small prey items. However, although our study likely underestimated small prey items, it further emphasized

that studies utilizing intensive GPS investigation are capable of describing small prey in diet composition (Pitman et al. 2014). We did not record any predation on tule elk or wild pigs, and this may be due to their low density in the study area or the fact that they are recent (elk) or novel (pigs) additions to the local prey community (*sensu* Novaro et al. 2000). Wild pigs are a pest species in California, and our results suggest that managers may not be able to depend on mountain lions to slow further range extensions.

Despite the diversity of non-ungulate prey species we observed, black-tailed deer were the most important prey of mountain lions (98.6% of biomass), the majority of which (77.6%) were judged to have been in fair or better condition. The lack of deer in poor body condition killed by mountain lions in our study is similar to previous results (i.e., 80% of deer killed by mountain lions in good body condition; Pierce et al. 2000), and might be indicative of good health of the local deer population. The age structure of adult female deer killed by mountain lions, however, was skewed towards older individuals. As can be expected in a black-tailed deer population in which only males are heavily-hunted, only two male deer were killed past prime age and more females killed were in the old age class than in the prime age class. This included an individual aged 22 years old (based on cement-annuli results; Matson's Laboratory LLC, Missoula, MT), and our results may suggest increased success of killing individuals past their prime age, or a much older deer population than is common in California.

Our analyses of hunting behaviors suggest that we may need to rethink some assumptions used in previous studies. Mountain lions are predominantly active during nocturnal and crepuscular hours (Currier 1983, Pierce et al. 1998, Sweanor et al. 2008), and it has thus been generally assumed that most of their kills occur during these periods. However, our results showed variation in time of kill by prey type, but also lower proportions of prey killed during nocturnal periods than expected. For example, adult black-tailed deer were killed in similar proportions during nocturnal and diurnal time periods, while deer <1 year old were killed significantly more frequently during diurnal time periods. This suggests that mountain lions are hunting during diurnal hours as opportunities arise, especially during summer when young ungulates are available. This result is in contrast to previously published studies (Currier 1983, Pierce et al. 1998, Sweanor et al. 2008) and may have led researchers to underestimate kill rates. Additionally, many studies attempting to link predation and predation risk to habitat have used the location of prey remains (e.g. Atwood et al. 2007, Elbroch and Wittmer 2012, Apps et al. 2013). However, our results showed that the location of prey remains were different than the location of the actual kill in many respects, including primary habitat type. Kill sequences often occur over large areas, and if we inferred predation risk from habitat where prey remains were found, we would be evaluating preferences for feeding sites of mountain lions rather than habitats where deer are at risk of being killed. Future studies should take this assumption into account and attempt to define the scale of risk and locate kill sites when describing habitat-specific risks for prey.

The population density in our study area was lower than in many other studies, while observed home ranges were in the published range for mountain lions (Logan and Sweanor 2010). The reasons for the observed low population densities, however, are unclear. Hunting of mountain lions in California has been prohibited since 1972 (Torres et al. 1996) and mountain lion populations from coastal California have historically had high population densities (Roberson and Lindzey 1984). For example, Hopkins et al. (1986) reported densities of 3.6/100 km<sup>2</sup> in a coastal area in central California, almost 6 times higher than the densities we observed. Instead our population density was more comparable to the

lowest recorded mountain lion population densities of 0.37/100 km<sup>2</sup> reported by Lindzey et al. (1994) in Utah. Given the high abundance of black-tailed deer in the study area (20 deer/km<sup>2</sup>; D. Casady, unpublished data) it is doubtful that the low mountain lion density was caused by low prey density. We speculate that low mountain lion densities were more likely a consequence of other factors such as illegal hunting or interference competition with dominant scavengers such as black bears. For example, previous studies have shown that poaching can greatly reduce mountain lion population densities (0.3-0.74/100 km<sup>2</sup> in areas with poaching compared to 1.55-2.89/100 km<sup>2</sup> in areas without poaching) (Paviolo et al. 2009). Alternatively, the usurpation of kills by bears has been reported to force solitary felids to kill deer more frequently (Krofel and Kos 2010, Krofel et al. 2012), and this may also be true of mountain lions, with lower available energy potentially resulting in low recruitment rates. Unknown factors or interplay between poaching and usurpation of kills by black bears could also account for low mountain lion densities in the study area. High ungulate kill rates together with seemingly low densities of mountain lions in our study area could have important implications for the future dynamics of black-tailed deer in the Mendocino National Forest.

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