

Seasonal variation in the feeding ecology of pumas (*Puma concolor*) in northern California

M.L. Allen, L.M. Elbroch, D.S. Casady, and H.U. Wittmer

Abstract: Direct effects of predators depend upon factors that can vary across seasons, including variations in the abundance and vulnerability of migrating prey. Past studies show conflicting results of whether puma (*Puma concolor* (L., 1771)) feeding ecology varies among seasons. We employed GPS collars to study puma feeding ecology in a single-prey system with migratory black-tailed deer (*Odocoileus hemionus columbianus* (Richardson, 1829)). We hypothesized that puma feeding ecology would vary based on changes in prey abundance and spatial distribution, as well as competition with scavengers and decomposers. Our results supported these hypotheses. Kill rates in number of ungulates/week were significantly higher in summer and autumn than in winter, likely owing to the increased availability and density of black-tailed deer fawns. The handling times of black-tailed deer ≥ 1 year old were significantly higher in winter than in spring, summer, or autumn. We speculated that reduced handling time in summer may have been influenced by black bear (*Ursus americanus* Pallas, 1780) kleptoparasitism and the decomposition of kills. Pumas killed black-tailed deer at higher elevations in summer than in winter, spring, or autumn, and the elevations correlated significantly with seasonal elevations used by black-tailed deer, suggesting that pumas exhibited seasonal foraging behaviours and tracked prey availability in a system with migrating prey.

Key words: black-tailed deer, kill rate, migration, *Odocoileus hemionus columbianus*, prey distribution, *Puma concolor*.

Résumé : Les effets directs de prédateurs dépendent de facteurs qui peuvent varier selon les saisons, y compris des variations de l'abondance et de la vulnérabilité de proies migratrices. Des études antérieures ont produit des résultats contradictoires quant à d'éventuelles variations de l'écologie alimentaire du cougar (*Puma concolor* (L., 1771)) selon la saison. Nous avons utilisé des colliers GPS pour étudier l'écologie alimentaire du cougar dans un système à proie unique, à savoir le cerf mulet migrateur (*Odocoileus hemionus columbianus* (Richardson, 1829)). Nous avons postulé que l'écologie alimentaire du cougar variait selon les variations de l'abondance et de la répartition spatiale des proies, ainsi que la concurrence de détritivores et de décomposeurs. Nos résultats appuient ces hypothèses. Les taux de capture en ongulés/semaine étaient significativement plus élevés à l'été et l'automne qu'à l'hiver, vraisemblablement en raison de la disponibilité et la densité accrues de paons de cerf mulet. Les temps de consommation de cerfs muets de ≥ 1 an étaient significativement plus élevés en hiver qu'au printemps, en été et en automne. Nous pensons que les temps de consommation plus courts durant l'été pourraient avoir été influencés par le kleptoparasitisme d'ours noirs (*Ursus americanus* Pallas, 1780) et la décomposition des captures. Les cougars tuaient des cerfs muets à de plus hautes altitudes en été qu'en hiver, au printemps et en automne, et les altitudes étaient significativement corrélées aux altitudes saisonnières fréquentées par les cerfs muets, ce qui donne à penser que les cougars faisaient preuve de comportements d'alimentation saisonniers et suivaient la disponibilité des proies dans un système à proies migratrices. [Traduit par la Rédaction]

Mots-clés : cerf mulet, taux de capture, migration, *Odocoileus hemionus columbianus*, répartition des proies, *Puma concolor*.

Introduction

Keystone effects of top-level predators on prey populations and ecosystems are well established (Estes 1996; Ripple and Beschta 2004). The direct effects of predators on their prey, however, are dependent on factors that may vary among seasons. In many terrestrial ecosystems, for example, ungulates migrate following changes in plant phenology to increase their access to forage, to avoid deep snows that limit their mobility and access to resources, and to reduce predation risk (Fryxell and Sinclair 1988; Hebblewhite and Merrill 2007). Ungulate migrations therefore result in significant redistributions of resources making it necessary for predators to respond to spatial and temporal variation in prey availability. Recent studies using GPS-collar technology have shown that top-level predators respond to seasonal variation in

prey availability and vulnerability in numerous ways, including temporal changes in diet and species-specific kill rates (Sand et al. 2008; Knopff et al. 2010; Metz et al. 2012; Elbroch et al. 2013; Gervasi et al. 2014).

Pumas (*Puma concolor* (L., 1771)) are solitary top-level predators that prey upon ungulates throughout their range in North America and South America (Sunquist and Sunquist 2002), and there are conflicting results and hypotheses concerning seasonal variation in puma feeding ecology (Knopff et al. 2010; Ruth and Murphy 2010a). Among kill rates, for example, previous studies have shown either no variation among seasons, an increase in winter, or an increase in summer (Knopff et al. 2010; Elbroch et al. 2013). Knopff et al. (2010) found higher kill rates in summer and hypothesized that was due to the increased availability of ungulates born

Received 1 December 2013. Accepted 25 March 2014.

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in early summer, which are easier to prey upon than adult ungulates. In contrast, [Hornocker \(1970\)](#) hypothesized ungulate kill rates would be lower in summer due to the increased availability of small nonungulate prey. Changes in seasonal kill rates may also be driven by ungulate migrations. [Cooley et al. \(2008\)](#) and [Pierce et al. \(1999\)](#) found that pumas followed migratory deer herds, but [Cooley et al. \(2008\)](#) did not find variation in kill rates among seasons. In contrast, [Elbroch et al. \(2013\)](#) reported that pumas in the southern Yellowstone ecosystem remained in place and prey switched from abundant migratory elk (*Cervus canadensis* Erxleben, 1777) in winter to abundant migratory deer in summer.

The seasonal behaviours of competitive scavengers and decomposers may also result in seasonal variation in puma kill rates. For example, brown bears (*Ursus arctos* L., 1758) increase kill rates of Eurasian lynx (*Lynx lynx* (L., 1758)) only during summer ([Krofel and Kos 2010](#); [Krofel et al. 2012](#)), while Andean Condors (*Vultur gryphus* L., 1758) have been shown to increase puma kill rates throughout the year ([Elbroch and Wittmer 2013b](#)). Invertebrate and microbial decomposers also consume and spoil carcasses in warm seasons ([Bischoff-Mattson and Mattson 2009](#)). Finally, statistical methods may have played a role in the conflicting results of seasonal variation, as most past studies of seasonal variation in puma feeding ecology are based on two season models that may be less effective than four-season models for detecting variation among seasons ([Metz et al. 2012](#)).

We employed Argos-GPS collars to study the feeding ecology of pumas in the Coast Range of northern California. Our objective was to understand the feeding ecology of pumas in a system where the availability and distribution of their sole ungulate prey, black-tailed deer (*Odocoileus hemionus columbianus* (Richardson, 1829), varied seasonally. Black-tailed deer in the study area exhibit elevational migrations, a behaviour hypothesized to be related to the seasonal availability of forage ([Loft et al. 1984](#); [Pierce et al. 1999](#)). Predators sometimes focus on killing young ungulates during summer ([Owen-Smith 2008](#)), and ungulate species synchronize their births to flood the ecosystem with young and limit the impact of predators ([Estes 1976](#); [Rutberg 1987](#)). Black-tailed deer in our study area exhibited a birth pulse at high elevations in June. In addition, our study area supported an abundant population of black bears (*Ursus americanus* Pallas, 1780), a dominant scavenger that is capable of usurping kills from pumas ([Ruth and Murphy 2010b](#)). Many black bears hibernate and were therefore more active in the study area from May to November. Possible causes of seasonal variation are sometimes confounding because they occur in conjunction with each other, making studies from different ecosystems necessary to determine broad ecological patterns. Our study area, with a single prey that migrates and exhibits a birth pulse and with also a seasonally abundant dominant scavenger, therefore offers an opportunity to examine the possible causes of variation in puma feeding ecology among seasons.

We hypothesized that the feeding ecology of pumas in our study area would vary among seasons, due to changes in the availability of migrating deer populations as well as activity patterns of competitors. Furthermore, we hoped to assess for potential biases introduced by sampling kill rates or prey selection in one season ([Metz et al. 2012](#)), by comparing foraging ecology across seasons. To determine whether puma feeding ecology varied among seasons, we studied (i) puma kill rates, (ii) mean daily movements of collared pumas, (iii) puma handling times of adult deer and their correlation with black bear presence, (iv) the elevation at which black-tailed deer were killed, and (v) whether the elevations used by black-tailed deer correlated with the elevations used by pumas. Based on [Knopff et al. \(2010\)](#) and the increased availability of black-tailed deer fawns during the birth pulse in summer, we hypothesized that puma kill rates (number of ungulates/week and kg/day) would be higher in summer and autumn than in winter and spring. Based on [Cooley et al. \(2008\)](#) and [Pierce et al. \(1999\)](#), we hypothesized that mean daily movements of pumas would be

shorter in winter when black-tailed deer populations were more concentrated than during other seasons. We also hypothesized that puma handling time of black-tailed deer ≥ 1 year old would be lowest in summer and autumn when bears were most active and higher temperatures tend to spoil meat faster and increase decomposition from invertebrates ([Bischoff-Mattson and Mattson 2009](#); [Ruth and Murphy 2010b](#); [Krofel et al. 2012](#)). Last, we hypothesized that pumas would track migrations of black-tailed deer and that there would be significant correlation between the elevation of puma kills and the elevations used by black-tailed deer; we expected pumas and deer to be lowest in winter and highest in summer ([Pierce et al. 1999](#); [Cooley et al. 2008](#)).

Materials and methods

Study area

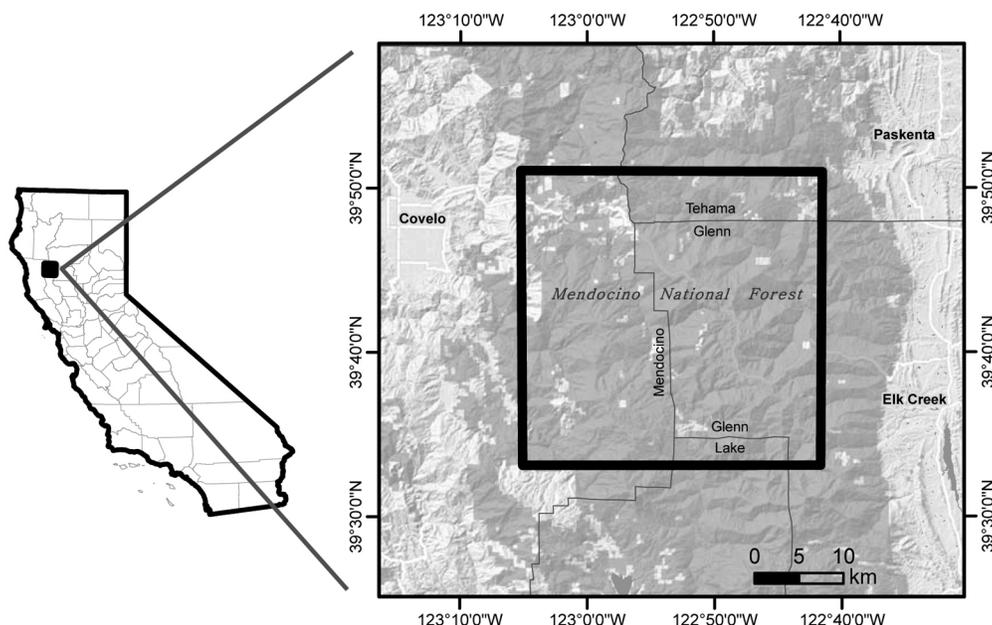
We conducted our study in the Mendocino National Forest, California, and surrounding private properties. Our study area encompassed approximately 1024 km² and included portions of Mendocino, Tehama, Glenn, and Lake counties ([Fig. 1](#)). Elevations in the study area ranged from 396 to 2466 m, with moderately rolling terrain at lower elevations and moderately steep, mountainous terrain at higher elevations. Climate varied seasonally, with mean daily temperatures ranging from -1 to 24 °C and extreme temperatures ranging from -12 to 45.5 °C. Mean annual precipitation averaged 132 cm; the majority of precipitation occurred from December through March with only trace precipitation from May through September. Below 1000 m, precipitation was predominantly in the form of rain, while at higher elevations, snow was common. Meteorological data were obtained from National Oceanic and Atmospheric Administration weather stations (Mendocino Pass, California, for temperature, and Ukiah Airport, California, for precipitation).

Major habitat types based on the California Wildlife Habitat Relationships categories ([Mayer and Laundenslayer 1988](#)) changed with elevation, including (in order of increasing elevation): annual grassland, montane hardwood conifer, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), mixed chaparral, montane hardwood, ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson), Klamath mixed conifer, and montane chaparral. Black-tailed deer were functionally the only large ungulate in the study area. Non-native wild pigs (*Sus scrofa* L., 1758) and tule elk (*Cervus canadensis nannodes* Merriam, 1905) from a past reintroduction project were present at very low densities or traversing through the study area, but were not preyed upon by pumas ([Allen 2014](#)). Smaller prey species included black-tailed jackrabbits (*Lepus californicus* Gray, 1837) and California ground squirrels (*Otospermophilus beecheyi* (Richardson, 1829)), while common competitors and scavengers at puma kills included black bears, coyotes (*Canis latrans* Say, 1823), gray foxes (*Urocyon cinereoargenteus* (Schreber, 1775)), Turkey Vultures (*Cathartes aura* (L., 1758)), and Common Ravens (*Corvus corax* L., 1758) ([Allen 2014](#)).

Animal captures

Between June 2010 and December 2012, we captured seven pumas with trained hounds and box traps. Upon capture, pumas were anesthetized with Telazol® (tiletamine HCl and zolazepam HCl; Fort Dodge Animal Health, Fort Dodge, Iowa, USA). Ketamine HCl (Ketaset®; Fort Dodge Animal Health) was administered as needed to maintain anesthesia during processing. Once anesthetized, the sex and mass of the pumas were determined, and the pumas were then fitted with an ear tag and a combined Argos satellite GPS/radiotelemetry collar (Lotek 7000SAW; Lotek Wireless Inc., Newmarket, Ontario, Canada). We used measurements of gum-line recession to determine the age of captured pumas ([Laundré et al. 2000](#)) and classified them as subadults (< 3 years) or adults (≥ 3 years). We concurrently captured 27 adult female black-tailed deer from July 2009 to August 2010 using methods

Fig. 1. A map of the study area, which included Mendocino National Forest and adjacent private lands. The study area is outlined by the thick black line, within the greater context of the North Coast Range and California.



described by Casady and Allen (2013) and fitted them with a combined store-on-board GPS/radiotelemetry collar (either Lotek Wireless Inc. or Telonics Inc., Mesa, Arizona, USA). All capture methods were approved by an independent Institutional Animal Care and Use Committee at the University of California, Davis, and the Wildlife Investigations Laboratory of the California Department of Fish and Wildlife.

Collar programming and field methods

We programmed deer collars to acquire GPS locations at 5 h intervals and retrieved GPS locations and elevations when collars automatically dropped off at the end of their life expectancy. We programmed puma collars to acquire GPS locations at 2 h intervals and downloaded location data via satellite every 3 days. Location data of pumas were displayed in ArcGIS version 3.2 and we visually identified GPS clusters. In this study, we defined potential kill sites as GPS clusters with ≥ 5 locations (or where pumas were present for at least 8 h) within 150 m of each other that contained at least one crepuscular or nocturnal location (Elbroch and Wittmer 2013a). We performed field investigations after downloads of Argos-relayed GPS locations and investigated GPS clusters in search of prey remains after loading them onto handheld GPS units (Garmin 60csx).

We used the age of the prey remains, evidence of evisceration and caching, parts of the body consumed, and the location of bite marks to determine whether the prey had been killed by a puma or whether the puma had been scavenging. We classified prey species through skeletal features and external characteristics (hair and pelage, or feathers). We documented black bear presence (i.e., tracks and scat) at the feeding sites of black-tailed deer ≥ 1 year old that we visited ≤ 28 days of it being created. We determined the age of black-tailed deer to the closest month for individuals < 1 year old based upon field observations and the assumption that the mean date of birth for fawns was 16 June of each year. We estimated the age for individuals > 1 year based on tooth eruption and wear to the closest year based on Heffelfinger (2010). We calculated prey masses based on published literature. We determined sex-specific masses for black-tailed deer fawns for each month, and for adults for each year based on estimates for Sitka black-tailed deer (*Odocoileus hemionus sitkensis* Merriam, 1898) presented in Parker et al. (1993). For all other animals, we used the

mean of masses described in Jameson and Peeters (2004) and Sibley (2005).

Statistical analyses

We used program R version 3.0.0 (R Core Team 2013) for our statistical analyses. Following R guidelines (R Core Team 2013), we cite associated packages used in the analyses. Before each statistical analysis, we tested each continuous variable data set for normality with Shapiro–Wilk’s normality test and then tested for variance equality with Levene’s test (Sokal and Rohlf 1987). In each statistical test, we considered $p \leq 0.05$ to be statistically significant. We calculated post hoc effect sizes as Cohen’s d scores (Cohen 1992) for statistically significant results, and we considered scores of 0.20 to be small effects, 0.50 to be medium-sized effects, and 0.80 to be large effects (Cohen 1992).

For our analyses, we used a definition of season based on weather and ecological patterns in the study area. Winter included December, January, and February, and was characterized by high precipitation and black-tailed deer living in concentrated winter groups at low elevations. Spring included March, April, and May, and was characterized by black-tailed deer moving higher in elevation following the melting snowpack. Summer included June, July, and August, and was characterized by hot temperatures and black-tailed deer giving birth on fawning grounds. Autumn included September, October, and November, and was characterized by black-tailed deer rut and migration to lower elevation winter range.

For each season, we calculated ungulate kill rates for the monitored pumas (in both number of ungulates/week and kg/day), mean daily movement rates, handling times of deer ≥ 1 year old, and elevation where pumas killed deer. We calculated ungulate kill rates (number of ungulates/week and kg/day) for each monitoring period. We calculated mean daily movement rates (km/day) for each individual puma for each season following the procedures of Elbroch and Wittmer (2012). We used days as samples when at least eight waypoints had been collected. We calculated the distance between consecutive GPS points using the haversine formula for great-circle distances (Sinnott 1984) and summed these figures for each day. We sampled the mean daily movement rates for each individual puma for each season that they were monitored. We defined handling time as the amount of time (h)

that pumas spent at each kill site (Elbroch and Wittmer 2013b). We quantified handling time as the total number of hours spent at the kill from the first to last GPS location within 150 m of the kill site; this included the time pumas moved away from the kill site, for example, to bed for the day and later returned to feed again. We only used black-tailed deer ≥ 1 year of age to eliminate variation in time spent at kills due to the smaller mass of fawns. We recorded the elevation of each black-tailed deer killed by each individual puma.

We used a series of five mixed-model analyses of variance (ANOVAs) using the nlme package (Pinheiro et al. 2013) to test for seasonal variation. We used mixed-model ANOVAs to control for variation in sample sizes and possible behavioural differences among individual pumas. The dependent variables included puma kill rates in number of ungulates/week, puma kill rates in kg/day, puma mean daily movement rates, puma handling times of black-tailed deer ≥ 1 year old, and elevations at which pumas killed black-tailed deer. For the two kill rates and mean daily movement rates, our sampling unit was each complete season. Based on Knopff et al. (2009), we included seasons where the individual puma was monitored for at least 28 consecutive days. For puma handling times of black-tailed deer ≥ 1 year old and elevations at which pumas killed black-tailed deer, each black-tailed deer was the sample unit and we then analysed across seasons.

We used the mixed-model ANOVAs to test if each of the dependent variables varied across seasons. In each mixed-model ANOVA, we used the independent variables of season (assigned as fixed effects) and individual pumas (assigned as a random effect). The dependent variables of handling times of deer ≥ 1 year old and elevation at which pumas killed black-tailed deer lacked normality and homoscedasticity, therefore we performed a logarithmic transformation on the data to meet the assumptions of the ANOVA (Sokal and Rohlf 1987). When we found significant differences using the mixed-model ANOVA in the “number of ungulates/week” kill rate among seasons, we performed post hoc pairwise comparisons using Tukey’s honestly significant difference (HSD) method for adjusting p values in the lsmeans package (Lenth 2013) to determine where the differences occurred.

We determined if a black bear had detected a puma kill by documenting black bear tracks and scat concentrated at the cache site. To examine if handling times of deer ≥ 1 year old were correlated with the percentage of puma kills detected by black bears in each season, we first used a $2 \times 4 \chi^2$ contingency table to determine if black bear detection of puma kills varied by season. We then used a linear regression analysis to determine if there was a significant correlation between handling times of adult deer and detection by black bears, using the seasonal mean handling times of adult deer as our dependent variable and the seasonal mean percentage of puma kills detected by black bears as our independent variable.

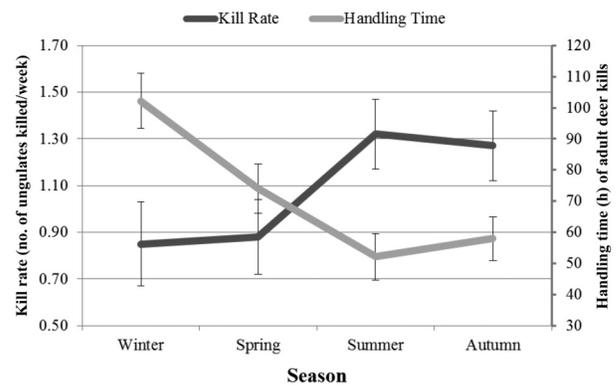
We performed an additional analysis to test if the monthly elevations used by black-tailed deer correlated with the monthly elevations at which pumas killed black-tailed deer. We calculated the mean monthly elevation used by each individual black-tailed deer that we monitored and then calculated the mean elevation used by the population from values of each individual black-tailed deer. We calculated the mean elevation at which pumas killed black-tailed deer for each month for each individual puma and then calculated the mean elevation for the population from the values of each individual puma. We used the monthly mean elevations at which pumas killed black-tailed deer as our dependent variable and used the monthly means of elevation used by black-tailed deer as our independent variable. Because of the lack of normality and homoscedasticity, we performed a logarithmic transformation on each set of the data to meet the assumptions of the linear regression (Sokal and Rohlf 1987).

Table 1. Physical characteristics and monitoring period for each puma (*Puma concolor*), including age and mass at initial capture, age and sex class, and days in their continuous monitoring periods.

| ID | Age (years) | Mass (kg) | Age and sex class | Continuous monitoring period (days) |
|-----|-------------|-----------|-------------------|-------------------------------------|
| F1 | 6.5 | 34.6 | AF | 477 |
| F17 | 1.4 | 31.5 | SF | 328 |
| F19 | 4.1 | 33.6 | AF | 202 |
| F23 | 4.2 | 49.5 | AF | 186 |
| F43 | 3.1 | 38.1 | FG | 209 |
| M33 | 7.0 | 59.1 | AM | 386 |
| M36 | 2.5 | 48.1 | SM | 83 |

Note: Age and sex class categories are adult female (AF), adult male (AM), subadult female (SF), subadult male (SM), and family group (FG).

Fig. 2. Mean monthly kill rates and handling times of black-tailed deer (*Odocoileus hemionus columbianus*) ≥ 1 year old for each season by pumas (*Puma concolor*). Kill rates and handling times were created for each individual puma for each month that they were monitored and were then pooled by season to test if the mean monthly puma kill rates and handling times varied across seasons. Values include standard errors.



Results

We captured seven pumas and monitored each puma for 9.07 ± 4.79 months (mean \pm SD) (Table 1). We conducted field investigations of a total of 598 out of 609 GPS clusters within 6.78 ± 8.18 days (mean \pm SD) (range 0–60 days) of the time the puma left the kill. We identified 352 kills, of which 288 were black-tailed deer. Black-tailed deer contributed 98.6% of the biomass of the prey killed by pumas. During summer, fawns accounted for 39.8% of ungulates killed by pumas and 10.2% of ungulate biomass killed by pumas. In autumn, fawns accounted for 27.5% of ungulates killed by pumas and 14.0% of ungulate biomass killed by pumas.

For kill rates in number of ungulates/week, our mixed-model ANOVA analysis revealed a significant difference among seasons ($F_{[3,14]} = 5.14$, $p = 0.0133$; Fig. 2). Our post hoc Tukey’s HSD analyses revealed that kill rates in summer were significantly higher than in winter or spring ($p_{\text{winter}} = 0.0272$, $d_{\text{winter}} = 1.08$; $p_{\text{spring}} = 0.0158$, $d_{\text{spring}} = 1.02$; Table 2) and that kill rates in autumn were also significantly higher than in winter or spring ($p_{\text{winter}} = 0.0437$, $d_{\text{winter}} = 0.95$; $p_{\text{spring}} = 0.0048$, $d_{\text{spring}} = 0.90$; Table 2). Ungulate kill rates in kg/day did not differ among seasons ($F_{[3,14]} = 0.56$, $p = 0.6487$; Table 2). Mean daily movement rates also did not differ among seasons ($F_{[3,14]} = 0.57$, $p = 0.6473$; Table 2).

For the handling times of black-tailed deer ≥ 1 year old, our mixed-model ANOVA analysis revealed a significant difference among seasons ($F_{[3,201]} = 10.69$, $p < 0.0001$; Fig. 2). Our post hoc Tukey’s HSD analyses found handling times in winter significantly higher than in spring, summer, or autumn ($p_{\text{spring}} = 0.0240$, $d_{\text{spring}} = 0.60$; $p_{\text{summer}} < 0.0001$, $d_{\text{summer}} = 1.06$; $p_{\text{autumn}} < 0.0001$, $d_{\text{autumn}} = 0.94$; Table 2). Handling times in spring were higher

Table 2. Mean monthly values for variables used in our analyses of variation across seasons of puma (*Puma concolor*) kill rates of black-tailed deer (*Odocoileus hemionus columbianus*).

| Season | Kill rate (no. of ungulates/week) | | Mass kill rate (kg/day) | | Daily movements (km/day) | | Elevation of deer kills (m) | | Handling time (h) of ≥ 1 year old deer | |
|--------|-----------------------------------|-----------|-------------------------|-----------|--------------------------|-----------|-----------------------------|-----------|---|------------|
| | Mean | 95% CI | Mean | 95% CI | Mean | 95% CI | Mean | 95% CI | Mean | 95% CI |
| Winter | 0.85 | 0.51–1.20 | 6.00 | 3.95–8.05 | 6.88 | 4.71–9.04 | 1006 | 840–1172 | 102.2 | 85.0–119.4 |
| Spring | 0.88 | 0.56–1.20 | 5.63 | 3.73–7.52 | 6.54 | 4.55–8.53 | 1012 | 857–1166 | 74.0 | 58.6–89.5 |
| Summer | 1.32 | 1.03–1.62 | 6.40 | 4.67–8.14 | 7.13 | 5.23–9.03 | 1307 | 1167–1446 | 52.1 | 37.6–66.5 |
| Autumn | 1.27 | 0.98–1.55 | 6.74 | 5.05–8.43 | 7.78 | 6.03–9.53 | 1168 | 1031–1305 | 58.0 | 44.3–71.7 |

Note: Values were averaged for each individual puma for each month that they were monitored and were then pooled by season to test if puma behaviours varied across seasons. Mean values are reported with 95% confidence intervals (CI).

than in summer or autumn, but were marginally insignificant ($p_{\text{summer}} = 0.0566$, $d_{\text{summer}} = 0.15$; $p_{\text{autumn}} = 0.1181$, $d_{\text{autumn}} = 0.11$; Table 2), possibly due to our low sample size of pumas. Our χ^2 test showed that detection of puma kills by black bears varied by season ($\chi^2_{[3]} = 24.16$, $p < 0.0001$), with 31.6% in winter, 70.3% in spring, 87.2% in summer, and 80.3% in autumn. Our linear regression analysis revealed a significant relationship between puma handling time of adult deer and detection rates of puma kills by black bears ($R^2 = 0.98$, $p = 0.0114$).

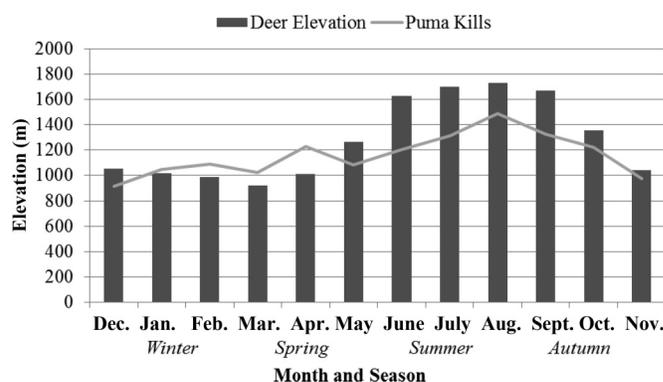
For elevation at which pumas killed black-tailed deer, our mixed-model ANOVA analysis revealed a significant difference among seasons ($F_{[3,279]} = 10.42$, $p < 0.0001$; Table 2). Our post hoc Tukey's HSD analyses indicated that kills in summer occurred at significantly higher elevations than in winter, spring, or autumn ($p_{\text{winter}} = 0.0001$, $d_{\text{winter}} = 0.49$; $p_{\text{spring}} = 0.0002$, $d_{\text{spring}} = 0.45$; $p_{\text{autumn}} = 0.0178$, $d_{\text{autumn}} = 0.22$), while kills in autumn were apparently at higher elevation than either winter or spring but were marginally insignificant ($p_{\text{winter}} = 0.0689$, $d_{\text{winter}} = 0.27$; $p_{\text{spring}} = 0.0739$, $d_{\text{spring}} = 0.23$). Additionally, our linear regression analysis showed a relationship between the monthly elevation at which pumas killed black-tailed deer and the monthly elevations used by black-tailed deer ($R^2 = 0.67$, $p = 0.0012$; Fig. 3).

Discussion

Our objective was to quantify the seasonal feeding ecology of pumas in a system with migrating prey. We studied four aspects of puma foraging ecology and the relationship between seasonal changes in black bear detection of puma kills and elevations used by black-tailed deer. Our results supported our hypothesis that pumas would exhibit seasonal variation in kill rates in number of ungulates/week. Our results did not support our hypothesis that pumas would exhibit variation among seasons in kill rates in kg/day, or in mean daily movement rates, although this may be partly due to our low sample size. We found that handling times of black-tailed deer ≥ 1 year old varied among seasons and were significantly correlated with detection of kills by black bears. Additionally, the elevation at which pumas killed black-tailed deer varied among seasons and the elevations where pumas killed deer were correlated with the elevations of marked black-tailed deer.

As noted by Metz et al. (2012), kill-rate metrics need to be interpreted with caution due to the biological differences in kill rates based on individuals per unit time and kill rates based upon mass per unit time. In our study, there was a significant difference in kill rates in number of ungulates/week among seasons, while there was no significant difference in kill rates in kg/day. Taken alone each kill-rate metric would tell a different story. Comparing kill rates in number of ungulates/week suggests that pumas exhibit strong seasonal variation, whereas comparing kill rates in kg/day suggests that regardless of number of animals killed per unit time, pumas kill an equivalent amount of meat. Kill rates in kg/day suggest that pumas might be following or meeting some energetic threshold irrespective of prey availability (Jeschke 2007). However, when observing the kill-rate metrics together, they point to the complexity of predator-prey relationships in a

Fig. 3. Elevations used by adult female black-tailed deer (*Odocoileus hemionus columbianus*) and elevation at which pumas (*Puma concolor*) kill black-tailed deer during each month of the year. Location data from GPS collars were averaged for each individual black-tailed deer for each month (dark gray bars). Elevations pumas killed black-tailed deer (gray line) were averaged for each individual puma for each month that they were monitored.



multipredator system. We found that pumas killed a greater number of black-tailed deer in summer and autumn, which coincided with the birth pulse of fawns in summer. Past studies have hypothesized that increases in puma and gray wolf (*Canis lupus* L., 1758) kill rates during summer were due to increased availability of vulnerable young ungulates (Sand et al. 2008; Knopff et al. 2010; Metz et al. 2012), and the number of fawns killed in summer and autumn in our study area supports this hypothesis. However, the notably lower handling times in summer and autumn may also have contributed to the increase in puma kill rates in summer and autumn and suggest that additional potential mechanisms may be influencing puma kill rates.

Handling times in winter were 196% greater than in summer and 176% greater than in autumn; this may be due to interactions with decomposers and dominant scavengers. Based upon research conducted by Bischoff-Mattson and Mattson (2009), we speculate that higher summer temperatures and increased invertebrate activity may lead to faster carcass decomposition and could therefore shorten handling times by pumas. In addition, interactions with black bears may also be causing a decrease in handling times during summer and autumn when black bears are most active. For example, brown bears have been shown to exact foraging costs on solitary felids, including forcing the abandonment of carcasses (Krofel and Kos 2010; Krofel et al. 2012). If black bear kleptoparasitism is the cause of the large reductions in handling times of deer > 1 year old, this could have important ecological influences, including causing pumas to hunt and kill more frequently during seasons when black bears are most active. Our results therefore support the conclusions of Elbroch and Wittmer (2013b), which suggest that future analyses of large carnivore kill

rates should take into account energetic losses to the scavenger guild to understand their influence on ecological communities.

The seasonal variation in the elevation where pumas killed black-tailed deer was correlated with the spatial distribution of black-tailed deer. The change in elevation of puma kills and their correlation with black-tailed deer elevation use supports the findings of Pierce et al. (1999) and Cooley et al. (2008) that pumas in our study area followed migrations of black-tailed deer. This is to be expected in a system where pumas rely on one ungulate species and different from populations where pumas do not need to follow migratory prey if other ungulate prey become seasonally available (Elbroch et al. 2013). Black-tailed deer exhibit a birth pulse and change their spatial distribution to concentrate their populations at high elevations during fawning. There are many reasons for this seasonal pattern, including changing availability of forage, accessibility of escape cover, and to lower the predation risk of newborn fawns. However, because pumas made kills where deer were most abundant in each season and puma kill rates were highest in summer, contrary to our expectations, migration of black-tailed deer did not appear to decrease puma predation. Thus, we now hypothesize that elevational migrations exhibited by black-tailed deer in our study area may not have been to reduce puma predation on neonatal fawns, but perhaps instead may have been to reduce age-specific predation risk from other predators that focus on fawns, such as coyotes, bobcats (*Lynx rufus* (Schreber, 1777)), and black bears (e.g., Griffin et al. 2011).

In summary, we found that puma kill rates and feeding ecology varied among seasons due to seasonal variation in behaviour and abundance of their prey and competitors. Ecologists have long noted that ungulates are limited by both the top-down and the bottom-up forces that structure ecosystems (Hopcraft et al. 2010; Forrester and Wittmer 2013). Here, we provide evidence that a top predator, in turn, is directly influenced by the seasonal behaviour of their main prey and apparently by scavengers. Our results highlight the importance of future research that aims to understand the mechanisms driving seasonal variation in the feeding ecology of pumas and other carnivores, including a mechanistic understanding of how scavengers influence puma foraging and how pumas alter their behaviour to compensate for changing densities and behaviours of their prey.

Acknowledgements

The California Department of Fish and Wildlife, the University of California at Davis, and the California Deer Association generously provided funding for the project. M. Allen was supported by a Victoria University of Wellington tuition scholarship. We thank B. Millsap, C. Wiley, and D. Tichenor for their expertise and help in capturing pumas, K. Cripe Fien for ArcGIS support, and J. Golla, B. Evans, R. Carrothers, J. Smith, G. Schmidt, B. Milano, C. Wallace, and P. Johnston for their help on the project.

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