

Can't bear the competition: Energetic losses from kleptoparasitism by a dominant scavenger may alter foraging behaviors of an apex predator



Maximilian L. Allen^{a,*}, L. Mark Elbroch^b, Heiko U. Wittmer^c

^aIllinois Natural History Survey, University of Illinois, 1816 S. Oak Street, Champaign, IL 61820, USA

^bPanthera, 8 West 40th Street, 18th Floor, New York, NY 10018, USA

^cSchool of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington 6140, New Zealand

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Abstract

The interspecific interactions of apex predators are integral to the function of ecological communities, but most studies have focused on understanding their top down effects. Kleptoparasitism (the stealing of procured food) by dominant scavengers can have negative effects on populations and behaviors of apex predators. We captured 7 pumas (*Puma concolor*) and fitted them with GPS collars to investigate potential kill sites ($n = 352$), some of which we monitored with camera traps ($n = 58$). We analyzed whether observed kleptoparasitism by American black bears (*Ursus americanus*) affected puma energetics and foraging behavior. We found that black bears were the most frequent scavenger of puma kills (72.4%), and we documented bears scavenging puma kills during every month. The top model for bear detection of puma kills included prey size, temperature, and canopy cover, with bears more likely to scavenge from adult black-tailed deer (*Odocoileus hemionus columbianus*) carcasses in warmer temperatures and under dense canopy cover. When black bear scavenging occurred, pumas spent 22% less time at their kill and incurred energetic losses. In response, pumas shortened their inter-kill intervals by 1.3 days thus increasing their kill rates. Our results demonstrate how a dominant scavenger directly mediates the foraging behavior of an apex predator. These results suggest that community interactions do not necessarily start at the top in top-down systems, and the effects of predators on prey populations can only be understood within their respective ecological communities.

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Interspecific interactions (i.e., predation, competition, parasitism/disease) are integral to the structure and function of ecological communities and ecosystems. Apex predators, in particular, are known for their important top-down effects on ecosystems (Estes & Palmisano 1974; McLaren & Peterson 1994; Ripple et al., 2014). Apex predators can both directly and indirectly affect their prey populations (Estes &

Palmisano 1974; Ripple et al., 2001) and, due to resulting changes in both the abundance and distribution of their often-larger bodied prey, initiate trophic cascades more frequently than smaller predators (DeLong et al., 2015). Apex predators, however, also have to mitigate negative effects of direct and indirect interactions with other species in their ecological communities. For example, juveniles of apex predators are sometimes killed by other predators (Ruth et al., 2011), and predators affected by parasitism/

*Corresponding author.

E-mail address: maxallen@illinois.edu (M.L. Allen).

disease have been shown to change their hunting behavior (Cross et al., 2016). When multiple large-bodied predators overlap, competition for prey can also result in subordinate species having to shift their diet (i.e., resource partitioning; Hayward et al., 2006).

Scavenging and kleptoparasitism (the stealing of already procured food; Krofel et al., 2012) are increasingly recognized as important interspecific interactions, but their direct and indirect effects on other species within ecological communities can be difficult to quantify. Effects of dominant scavengers that steal and displace subordinate predators from their ungulate kills include: reductions in energetic intake (Carbone et al., 1997; Krofel et al., 2012), reduced subordinate predator abundances (Gorman 1998, Krofel & Jerina 2016), and changes in hunting and other behaviors exhibited by the subordinate species (Carbone et al., 1997; Krofel et al., 2012). Ultimately, the effects of scavengers on predators are likely species-specific. For example, social predators can often consume large portions of their prey before scavengers are able to exploit it, although there is intraspecific competition within the group (Gorman 1998). In contrast, solitary predators often consume large prey over multiple days and are thus more prone to losing food to scavengers (Allen, Elbroch, Wilmers & Wittmer, 2015; Krofel et al., 2012). Fear of the apex predator appears to limit losses to some species (Allen, Elbroch et al., 2015), but does not appear to be an effective strategy against dominant scavengers which can overpower solitary carnivores (Allen, Elbroch et al., 2015; Krofel & Jerina 2016; Krofel et al., 2012).

Bears are dominant scavengers known to outcompete many other species for carrion (Allen, Elbroch et al., 2015; Krofel et al., 2012). Bears are able to detect animal carcasses quickly, with experimental work showing that American black bears (*Ursus americanus*; hereafter black bears) detected carcasses on average 2 days (48.5 hours) after being placed on the landscape (Allen, Elbroch et al., 2015). Importantly, their large body size allows bears to usurp carcasses from apex predators (Allen, Elbroch et al., 2015; Krofel & Jerina 2016; Krofel et al., 2012). For example, brown bears (*Ursus arctos*) in Europe have been found to usurp 32% of Eurasian lynx (*Lynx lynx*) kills and lynx feeding time at these kills was reduced by 47%, leading to increases in lynx kill rates and overall energetic losses of 41% (Krofel et al., 2012). The relationship between pumas (*Puma concolor*) and black bears in North America is likely similar. Puma kill rates increase during seasons when black bears are active (Clark et al., 2014; Elbroch et al., 2015) and this is assumed to be because of direct competition with black bears. For example, pumas immediately abandoned 72% of their ungulate kills once they were detected by black bears (Allen, Elbroch et al., 2015), indicating the subordinate status of pumas. Nevertheless, determining the impacts of bear scavenging on puma kill rates is complicated by the fact that pumas generally select smaller prey (e.g., neonate ungulates) and increase their kill rates in the warmer months when bears are most active, regardless of the presence of bears.

Therefore, the impacts of bears on puma foraging behaviors may be marginal in comparison to the influence of prey size (Clark et al., 2014).

Our goal was to increase our understanding of how kleptoparasitism by black bears affects puma energetics and foraging behavior. To meet this goal, we examined the following objectives and hypotheses: 1) We compared the correlative strength of monthly bear scavenging and monthly mean prey weight with monthly inter-kill intervals, as a first step in determining which variable more influences puma kill rates. 2) We tested factors which might determine whether black bears detected and scavenged from a puma kill. Among *a-priori* models that we tested, our primary hypothesis was that black bears would more likely detect and feed from larger kills (i.e., adult black-tailed deer; *Odocoileus hemionus columbianus*) during warmer temperatures (when bears are active), but that additional landscape variables would not explain kleptoparasitism from bears (e.g., Elbroch et al., 2015). 3) We determined the direct effects of black bear kleptoparasitism on puma feeding time (number of hours in two-hour increments that a puma was associated with its kill), kg of meat consumed, and percent of the edible meat consumed (amount consumed/available to consume at a kill). We expected bears feeding on puma kills to reduce all three variables because they are a dominant scavenger (e.g., Allen, Elbroch et al., 2015, Krofel et al., 2012). 4) We determined how kleptoparasitism by black bears affected the subsequent inter-kill interval (days from making one kill to making next kill). We hypothesized that inter-kill intervals of pumas would decrease after losing a carcass to a bear, so that they could recoup energetic losses to bears. 5) We determined if pumas killed more small prey (fawns and other prey) during the months that they suffered the highest rates of black bear kleptoparasitism of adult deer (e.g., Krofel et al., 2012). We hypothesized that pumas would vary the amount of adult deer that they ate each month due to kleptoparasitism by bears (see above), and hypothesized that pumas would shift to consuming more small prey in months with higher kleptoparasitism (positive correlation), and as they consumed less adult deer (negative correlation).

Materials and methods

Study area

Our study extended across approximately 1,000 km² centered on the Mendocino National Forest in northern California (Fig. 1). Terrain varied from valley bottoms as low as 396 m to steep and rugged slopes at elevations of up to 2,466 m. Mean daily temperatures ranged from -1°C to 24°C and mean annual precipitation was 132 cm. Habitats were primarily forested, but varied with elevation and vegetation communities. For a full description of the study area see Allen et al., and Wittmer (2015b). Black-tailed deer were the only resident ungulate and primary prey of pumas in the

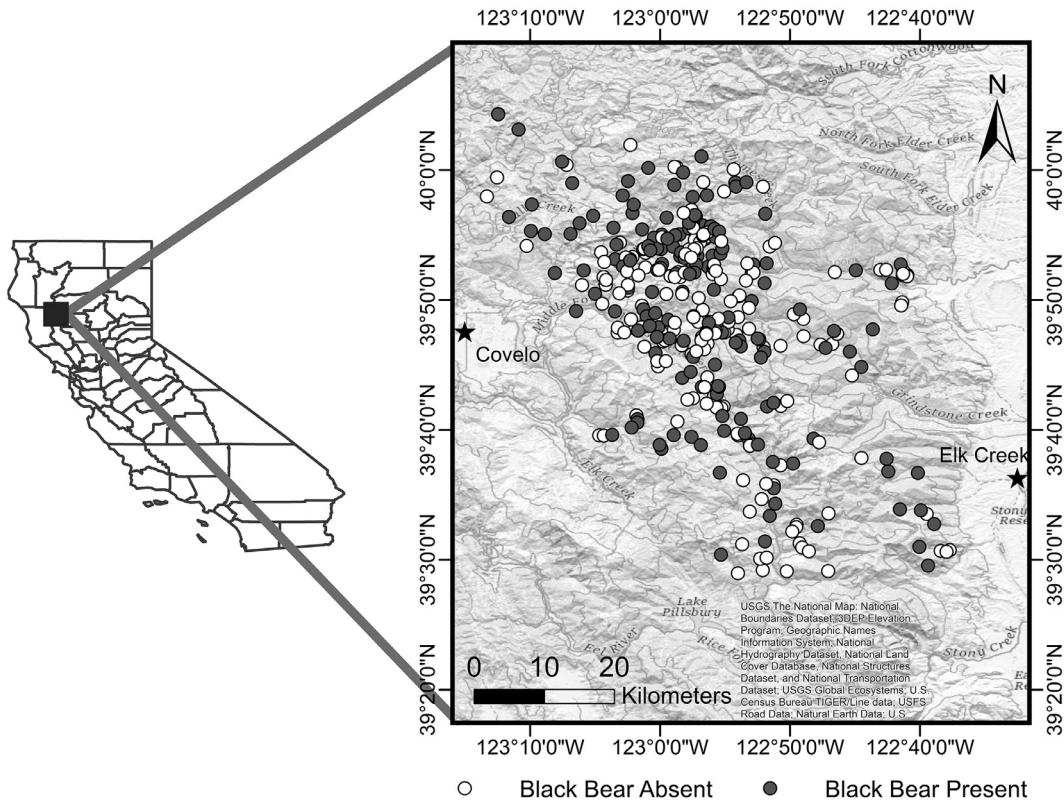


Fig. 1. The study area in Mendocino National Forest in northern California, with the location of puma kill sites documented during the study.

study area (Allen, Elbroch et al., 2015). Pumas occurred at low densities ($0.68/100 \text{ km}^2$; Allen, Elbroch et al., 2015), while high black bear abundance explained much of the observed spatial variability in mortality risk of fawns during summer (Forrester & Wittmer 2019).

Field methods

We captured pumas using hounds and box traps from June 2010 to November 2012 as detailed in Allen et al. (2015b) and fit each puma with a satellite GPS collar (Lotek 7000SAW, New Market, Ontario). All capture and field 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, and conformed to all laws in the USA. We programmed collars to collect a GPS location every 2-hrs and downloaded GPS locations via satellite every 3 days. We identified potential kills as clusters of activity with ≥ 5 GPS locations (minimum of 8 hours between first and last locations) within 150 m of each other that contained at least one crepuscular or nocturnal location (Allen, Elbroch et al., 2015).

We visited clusters within $\bar{x} = 6.78 \pm 8.18 \text{ SD}$ (range 0–60) days after the puma departed the kill. At potential kills we investigated the site for predation events and determined

the prey species killed by pumas by identifying remains (bones, hair/feathers) found at each GPS cluster. This resulted in documentation of 352 kills, of which 64 were non-ungulate prey (Table 1). We also documented visual signs of

Table 1. Counts of non-ungulate prey killed by pumas in the study.

| Prey type | n |
|--|----|
| American robin, <i>Turdus migratorius</i> | 1 |
| American black bear, <i>Ursus americanus</i> | 2 |
| Black-tailed rabbit, <i>Lepus californicus</i> | 6 |
| Brush rabbit, <i>Sylvilagus bachmani</i> | 2 |
| California ground squirrel, <i>Otospermophilus beecheyi</i> | 26 |
| California quail, <i>Callipepla californica</i> | 1 |
| California towhee, <i>Melozone crissalis</i> | 1 |
| Coyote, <i>Canis latrans</i> | 1 |
| Douglas squirrel, <i>Tamiasciurus douglasii</i> | 3 |
| Dusky-footed woodrat, <i>Neotoma fuscipes</i> | 1 |
| Fisher, <i>Pekania pennanti</i> | 1 |
| Golden-mantled ground squirrel, <i>Callospermophilus lateralis</i> | 1 |
| Gray fox, <i>Urocyon cinereoargenteus</i> | 2 |
| Mountain quail, <i>Oreortyx pictus</i> | 2 |
| Mourning dove, <i>Zenaida macroura</i> | 1 |
| Northern raccoon, <i>Procyon lotor</i> | 5 |
| Red-breasted sapsucker, <i>Sphyrapicus ruber</i> | 1 |
| Western gray squirrel, <i>Sciurus griseus</i> | 6 |
| Wild turkey, <i>Meleagris gallopavo</i> | 1 |

scavengers at each kill site, including black bears (indicated by multiple scats in the immediate area of the kill). In addition, we deployed infrared video camera traps at 58 active puma kills on average 39.8 (52.9 SE) hours after the puma made the kill, to document feeding activity of pumas and potentially black bears. We set the camera traps to record continuous activity at each kill, with 60 s of video recorded at each trigger and a 1 s refractory period. We used this data to determine detection time and amount of scavenging at this subset of kills. We documented the elevation, slope, aspect, and canopy cover at each kill site. Finally, we determined the temperature and precipitation for each kill site using data from a local weather station for the day the kill was made.

Estimation of mass and consumption

To determine the mass of prey, we used the monthly sex-specific weights of fawns, and the annual sex-specific weights of adults based on Parker, Gillingham, Hanley, and Robbins (1993). We estimated the age of fawns (<1-year-old) to month assuming a birth date of June 16th (Allen, Elbroch et al., 2015), and of adults using tooth eruption patterns (Heffelfinger, 2010) and cementum annuli analysis (Low & Cowan 1963) via Matson's Laboratory (Milltown, MT). For other mammals we used the mean mass based on Jameson and Peeters (2004). For birds we used the mean mass based on Sibley (2005).

We considered the time of kill to be the time associated with the first GPS point of a cluster and time of abandonment to be the time of the last GPS point of a cluster. We defined feeding time as the duration a puma was at a kill site from kill to abandonment (Krofel et al., 2012), and defined inter-kill interval as the duration from the time a kill was made to the time the subsequent kill was made (Knopff et al., 2010). We determined feeding time and inter-kill interval in 2-hr increments based on the GPS data, but excluded the inter-kill interval for the kills where we did not visit the next sequential potential kill ($n = 5$).

Field experiments by Wilmers et al., and Getz (2003) found that 68% of ungulates was edible, and we calculated the edible portion of puma kills as
estimated mass \times 0.68.

We based our active consumption rates on those of Elbroch et al., and Wittmer (2014) (6.8 kg for the initial 24 hours of the kill, and 4.1 kg for subsequent 24-hour periods of the kill; based on experimental work by Ackerman, 1982, Danvir & Lindzey 1981), and estimated the total kg consumed at each kill in two-hour intervals based on the feeding time of the puma. For one female (F43) with known yearling kittens ($n = 2$), we summed the kitten consumption rates with those of their mother (e.g., Elbroch et al., 2014). We also calculated the percent of each kill consumed as
kg consumed/kg available.

Statistical analyses

We used program R version 3.3.1 (R Core Team 2016) for all of our statistical analyses, and in each analysis, we considered $p \leq 0.05$ to be statistically significant. We determined the distribution for our data before deciding on the specific model to run in each analysis, and used the lme4 package (Bates et al., 2015) for generalized linear mixed effect models (GLMMs) and the nlme package (Pinheiro et al., 2013) for linear mixed effect models (LMMs).

First, we used LMMs to determine if the overall amount of meat consumed by pumas, the amount of adult deer consumed by pumas, or the amount of small prey (fawns and other prey) varied by month. We used each of the variables of interest (kg of meat consumed, kg of adult deer consumed, kg of small prey consumed) as our dependent variable, the identity of pumas as a random effect, and the given month as a fixed independent effect with the lowest or highest mean as the comparison. Second, we used non-parametric Spearman rank correlation coefficients to determine if the monthly mean of small prey consumed significantly correlated with the amount of adult deer consumed and the percent of adult deer scavenged by bears.

Following Clark et al. (2014), we began by conducting pair-wise Pearson's correlation analyses between monthly inter-kill intervals and 1) monthly mean prey size (kg), 2) the monthly proportion of all kills at which we documented bears, and 3) the monthly proportion of adult deer kills at which we documented bears. In terms of puma diet, deer comprised 98.6% of local prey biomass (Allen, Elbroch et al., 2015), and evidence of bears at kills was almost certainly more easily detected than that of other scavengers. These analyses were meant to help us determine whether mean prey size or bear scavenging more strongly impacted inter-kill rates across months. We reported R^2 values and P values based on an alpha of 0.05.

To determine which factors allow black bears to detect and scavenge from a puma kill we used a series of *a-priori* binomial GLMMs with a logit link based on a set of common variables (Table 2). We used a binary dependent variable (whether bears scavenged from the kill, yes-no), the identity of the puma as a random effect, and all other variables as independent effects. In the models we considered three types of puma kills: adult deer, fawns, and other prey (birds, carnivores, lagomorphs, and squirrels). We compared models in an AIC framework using the AIC weight (w), and considered models with the highest cumulative w to be our top models (Burnham & Anderson 2002).

To determine the direct effects of black bear kleptoparasitism on puma feeding time, meat consumed, and percent of edible carcass consumed we used LMMs to compare these variables at kills that were detected/not detected by bears. We used each of the variables of interest (puma feeding time, meat consumed, and percent of edible carcass

Table 2. *A-priori* variables and underlying reasons for black bears detecting kills made by pumas.

| Variables | Reason |
|---------------|---|
| Type of kill | Bears will be able to detect large carcasses more easily and also be motivated to find larger carcasses due to the larger potential energetic rewards for their efforts |
| Temperature | Bears will be able to detect carcasses more easily with warmer temperatures and in seasons when they are active |
| Precipitation | Weather will be the key aspects affecting whether bears can detect carcasses, being able to detect carcasses better with higher temperatures and less precipitation |
| Slope | Bears will detect carcasses on flatter slopes |
| Canopy cover | Bears will be able to detect and exploit carcasses in areas with less dense canopy cover |

consumed) as our dependent variables, the identity of pumas as a random effect, and an interaction between the presence of bears and kill type (with adult deer as our contrast) as our fixed independent effects.

To determine how kleptoparasitism by black bears affected the subsequent inter-kill interval we used LMMs to compare these variables for kills that were detected/not detected by bears. We used inter-kill interval as our dependent variable, the identity of pumas as a random effect, and an interaction between the presence of bears and kill type (with adult deer as our contrast) as our fixed independent effects.

Results

Patterns in energetics by month

Pumas varied significantly in the overall amount of meat they consumed each month. Pumas consumed the least

amount of meat in April (48.9 kg ±19.3 SE), significantly less than in six other months ($p \leq 0.03$) with the most meat consumed in January (88.1 kg ±15.0 SE). In October through January ≥80 kg were consumed by pumas, but <70 kg were consumed in April, July, August and September.

Pumas also varied significantly in the amount of meat consumed from adult deer and small prey (fawns and other prey) each month. Pumas consumed the least meat from adult deer in August (40.3 kg ±18.6 SE), significantly less than in six other months ($p \leq 0.03$) with the most in January (84.7 kg ±16.9 SE) (Fig. 2). Pumas consumed the largest amount of small prey in October (19.8 kg ±4.5 SE), significantly more than in 6 other months ($p \leq 0.03$), and the least amount in April (0 kg) (Fig. 2).

The amount of small prey consumed in a given month had a significant negative correlation with the amount of deer consumed ($r = -0.59$, $p = 0.04$), meaning that pumas consumed more small prey in months when they consumed fewer adult deer. The amount of small prey consumed in a given month had a significant positive correlation with the percent of deer scavenged by bears ($r = 0.63$, $p = 0.03$), meaning that in months when bears were scavenging from more of the adult deer killed by pumas, pumas ate more small prey.

Monthly inter-kill rates correlated highly with the monthly proportion of adult deer kills at which we documented bears ($r = 0.80$, $p = 0.002$), and monthly mean prey size ($r = 0.79$, $p = 0.002$), and, to a lesser degree, the monthly proportion of all kills at which we documented bears ($r = 0.67$, $p = 0.02$). This suggests that variable inter-kill rates were better explained by the inclusion of bear scavenging, rather than seasonal variation in mean prey size alone.

Black bear detection of and feeding at puma kills

We documented black bear activity at puma kills during every month of the year. Our top model for bear detection of

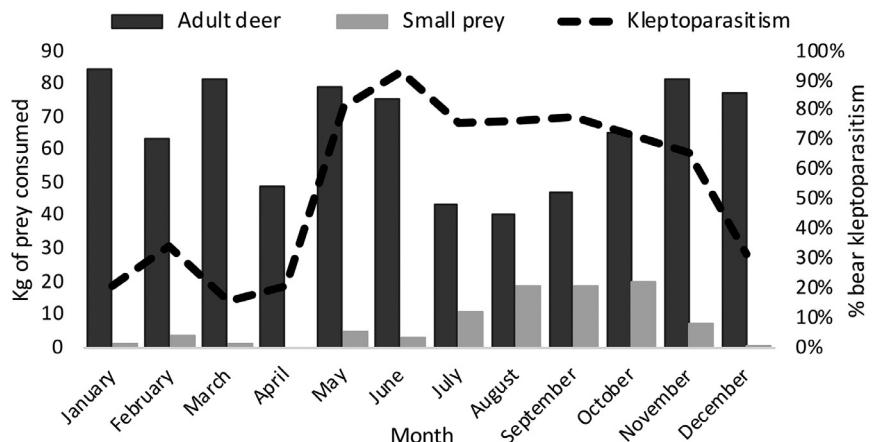


Fig. 2. The monthly values of the kg consumed by pumas of adult deer and small prey, as well as the percent of adult deer kleptoparasitized by black bears.

Table 3. Results of our Generalized Linear Mixed Model analyses for black bear detection and scavenging of kills made by pumas. We rank the competing models by their AIC weight (w).

| Variables | AIC | ΔAIC | wAIC |
|--|-------|-------|------|
| Kill Type + Temperature + Canopy Cover | 365.5 | 0.0 | 0.89 |
| Kill Type + Temperature | 369.7 | 4.2 | 0.11 |
| Kill Type | 385.9 | 20.4 | 0.00 |
| Canopy Cover | 471.0 | 105.5 | 0.00 |
| Temperature + Canopy Cover + Slope | 471.3 | 105.8 | 0.00 |
| Canopy Cover + Slope | 472.2 | 106.7 | 0.00 |
| Temperature | 472.8 | 107.3 | 0.00 |
| null | 473.5 | 108.0 | 0.00 |
| Slope | 474.3 | 108.8 | 0.00 |
| Temperature x Precipitation | 476.3 | 110.8 | 0.00 |

puma kills was *type of kill + temperature + canopy cover* ($w = 0.89$; Table 3), while the second best model was *type of kill + temperature* ($w = 0.11$). Based on odds ratios in the top model, adult deer (0.22), kills associated with warmer temperatures (-10.85), and kills with denser canopy cover (-1.31) were more likely to be found than fawns (0.16) or other prey species (0.01). The odds ratios in the second best model were essentially the same except for a substantial increase in the odds ratio of adult deer to 2.45. Specifically, black bears scavenged from 66.5% of adult deer kills (including a maximum of 94% in June, and >75% from May through September; Fig. 2), but only 32.9% of fawns and 3.4% of other prey.

Black bears were the most frequent scavenger detected at the 58 puma kills we monitored with camera traps, and displaced pumas from the carcass at 29 of these kills (50%). Bears were detected at nearly twice as many kills ($n = 42$, 72.4%) as the next most frequent scavenger (gray fox, *Urocyon cinereoargenteus*; $n = 22$, 37.9%). Bears detected carcasses more quickly than other scavengers, being the first or second scavenger at 73.8% ($n_{\text{first}} = 21$, $n_{\text{second}} = 10$) of kills monitored with cameras. At these kills, black bears had a mean total feeding time of 145.9 (95% CI 98.5–193.2) minutes.

Black bear effects on consumption

In the absence of black bears, pumas on average spent 3.17 (± 0.28 SE) days feeding at adult deer kills. The presence of bears significantly affected puma feeding time ($p = 0.0001$), resulting in an average decrease of 0.71 days (± 0.18 SE) during which the puma fed on the carcass. As compared to how long pumas fed on adult deer, pumas fed on fawns 1.91 days (± 0.23 SE) shorter ($p < 0.0001$). In the presence of bears, however, pumas increased their average feeding time on fawns by 0.77 days (± 0.36 SE) ($p = 0.03$). Pumas also fed on average 2.07 fewer days (± 0.23 SE) at other prey kills ($p < 0.0001$) than they did at adult deer kills.

Bears had no effect on puma feeding time at non-ungulate kill sites.

Pumas consumed 17.2 kg (± 1.4 SE) of meat at adult deer kills in the absence of black bears. The presence of bears significantly affected the amount of meat consumed by pumas at their kills ($p = 0.02$), and on average, pumas suffered losses of 2.03 kg (± 0.88 SE). In comparison to the amount of meat pumas ate at adult deer kills, pumas consumed 11.23 kg (± 1.11 SE) less meat at fawn kills ($p < 0.0001$) and 15.57 kg (± 1.10 SE) less meat at other prey kills ($p < 0.0001$). The presence of bears did not have an effect on how much meat pumas consumed at fawn kills or other prey kills.

In the absence of black bears, pumas consumed 56% ($\pm 0.5\%$ SE) of adult deer kills, whereas in the presence of bears, pumas consumed 6.6% (± 3.1 SE) less of the carcass ($p = 0.04$). As compared with the percentage of the carcass pumas consumed at adult deer kills, pumas consumed 25.5% (± 4.0 SE) more of each fawn kill ($p < 0.0001$) and 45.1% (± 3.9 SE) more of other prey kills ($p < 0.0001$). Bears did not impact the percentage of the carcass pumas consumed at fawn kills or other prey kills.

Effect of black bears on subsequent puma predation behavior

In the absence of black bears, the inter-kill interval for pumas was 6.84 (± 0.61 SE) days. The presence of bears significantly affected the subsequent inter-kill interval for pumas ($p = 0.02$), and on average decreased the interval by 1.34 days (± 0.55 SE). In the absence of bears, pumas inter-kill interval also decreased 3.17 days (± 0.69 SE) following smaller fawn kills ($p < 0.0001$) and 2.78 days (± 0.68 SE) following other prey kills ($p < 0.0001$). We did not detect a significant effect of bear presence on intervals following fawn kills and other prey kills.

Discussion

Pumas in our study area have the highest ungulate kill rates reported for the species across their range (reviewed in Cristescu et al., 2020). We attempted to provide a mechanistic understanding of how kleptoparasitism by a dominant scavenger (black bear) in our system may have mediated their foraging behavior. Our results show that 1) monthly inter-kill rates correlated most strongly with the monthly proportion of deer kills detected by bears, closely followed by monthly mean prey size; 2) black bears were more likely to scavenge from adult black-tailed deer than either fawns or other prey species; 3) when black bears scavenged from adult deer kills, pumas spent less time feeding at the kill and thus incurred energetic losses; 4) the behavioral response of pumas was to kill prey more frequently (shorten their inter-kill interval); and 5)

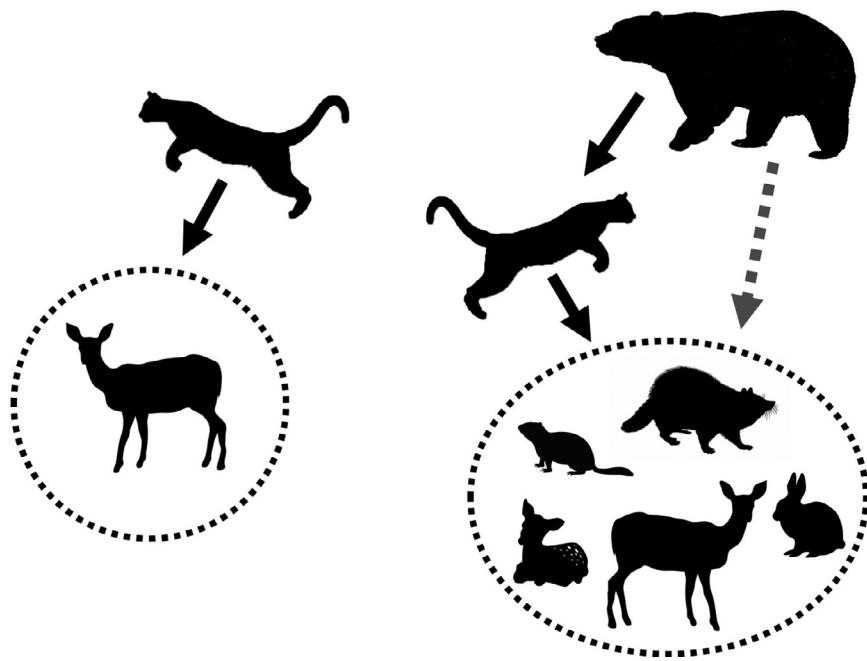


Fig. 3. A conceptual figure, showing that in months with little black bear kleptoparasitism pumas primarily prey on deer, but in months with high black bear kleptoparasitism pumas diversify the prey they kill and consume.

pumas increased the proportion of their diet that was small prey during months when kleptoparasitism by black bears was most frequent. The direct energetic losses caused by black bears were substantial (>10 kg in many months with high bear activity); we documented bears actively feeding for ~2.5 hours at each kill, during which bears can consume large amounts of meat (see Appendix A). The kleptoparasitism by bears thus appears to have mediated changes in puma foraging behavior (Fig. 3). The effect of these changes on prey (i.e., deer) populations remains unclear. While the partitioning of different life stages of the same prey (i.e., bears preying primarily on neonates (Forrester & Wittmer 2019) and pumas on adult deer (Allen, Elbroch et al., 2015) should theoretically facilitate coexistence among competing predators (De Roos et al., 2008), the combined effects of low fawn survival mostly due to bear predation, and low summer adult survival, mostly due to puma predation, caused a decline in the local deer population. Therefore, increased kill rates of pumas due to kleptoparasitism by bears may have contributed to observed declines in the local deer population (Marescot et al., 2015).

The potential fitness consequences for apex predators experiencing bear kleptoparasitism are not understood, and we currently do not know the thresholds for energetic losses due to kleptoparasitism that would lower fitness for pumas (Elbroch et al., 2017). The spring peak in bear scavenging corresponds with the kitten-rearing season for Eurasian lynx, and therefore kleptoparasitism by bears could lead to direct decreases in kitten survival (Krofel et al., 2012). In contrast, pumas exhibit summer birth pulses in ecosystems with cold, snowy winters, but do not exhibit a defined birth season in more moderate climates. Further, pumas care

for kittens for longer time periods than Eurasian lynx. These distinctions may buffer pumas from any impact of kleptoparasitism on kitten survival when they are youngest, but increase the impacts of bear kleptoparasitism on the long term survival of their kittens as they age. Pumas do not appear to have behaviors that can limit detection by black bears, as caching of kills has been found to be ineffective to deter bear scavenging (Elbroch et al., 2015).

Pumas also killed more small prey in the months in which they experienced the highest kleptoparasitism by bears. This relationship does not necessarily infer causation, but it may indicate a behavioral strategy in which pumas can consume small prey fast enough to avoid detection and kleptoparasitism by bears. Alternatively, puma prey switching to smaller prey in warmer months may also reflect changes in prey availability and vulnerability, as has been documented in pumas (e.g., Wilckens et al., 2015) and other carnivores (e.g., gray wolf, *Canis lupus*; Metz et al., 2012). There are comparatively few studies of the seasonal prey selection of pumas in the absence of bears. One, however, conducted in Chilean Patagonia did reflect puma prey switching to newborn ungulates in the summer months (Elbroch & Wittmer 2013), suggesting that in our study area, puma switching to fawns was at least in part explained by their availability and vulnerability (Knopff et al., 2010). The presence of black bears had no effect on the consumption of fawns and other prey species, likely because pumas are able to consume them entirely over shorter periods of time (Knopff et al., 2010). Somewhat counterintuitively, there was an increase in the time pumas spent at fawn kills that were found by bears, but this is likely because bears found larger fawns during the latter parts of the year.

Pumas in our study system did exhibit habitat selection when hunting deer but not when hunting other prey (Cristescu et al., 2019), suggesting other prey may be opportunistically killed rather than selected for. Scavenging of ungulate kills by dominant brown bears may have led Eurasian lynx to evolve for killing smaller prey in addition to ungulates (Krofel et al., 2012), but pumas are generally thought to be ungulate specialists, at least in North America (see review in Ruth & Murphy 2010). However, small prey are more difficult to detect than ungulate prey (Allen, Elbroch et al., 2015; Bacon et al., 2011) and most algorithms to determine kill sites from GPS data only focus on prey >8 kg in mass (Knopff et al., 2010). Studies from South America also indicate a greater proportion of non-ungulate prey in puma diets (Ruth & Murphy 2010), but are often based on scat analyses that underestimate ungulate prey and overestimate smaller prey when compared to studies based on GPS cluster investigation (Bacon et al., 2011). The difficulty in detecting small prey from GPS cluster investigations likely led to us underestimating their importance to puma diet. Our analyses suggest that small prey are not consumed as much as adult deer (the only ungulate in the system), but may be an important energy source to compensate for losses to black bears.

Black bears were more likely to find kills of adult deer during warmer temperatures. Most black bears hibernate at some point during the winter, which may create a competition refuge for pumas (Elbroch et al., 2015). Despite hibernation, we documented bears scavenging from puma kills during every month of the year, but scavenging was most frequent at adult deer kills during June (94%). This peak in early summer is the same as found for brown bears at Eurasian lynx kills (Krofel et al., 2012). This may suggest that scavenging is most important during the period when bears emerge from hibernation but before the peak of fawn availability and mast crops mature. This also suggests that pumas, lynx and other apex predators may facilitate bear populations. Such seasonal facilitation via kleptoparasitism has been suggested for smaller carnivores feeding at apex predator kills (e.g., red fox, *Vulpes vulpes*; Helldin & Danielsson 2007), but not for dominant, apex predators.

Because pumas are apex predators that have important effects on their ecosystems, it is important to consider how their populations may be affected by increasing bear populations and the indirect effects on ecosystems. We have shown how black bears directly affect pumas and their predation behavior, but more importantly, these effects likely ripple through the ecosystem and may become more pronounced with increasing bear densities. Kleptoparasitism by bears directly causes increases in puma inter-kill intervals and may thus indirectly cause higher mortality for the deer population, in addition to directly being a large source of fawn mortality (Forrester & Wittmer 2019). Alternatively, bear scavenging at puma kills may satiate bears and reduce bear predation on ungulate neonates, and therefore bear kleptoparasitism may ultimately be of compensatory impact on

ungulate dynamics. In areas where puma predation is the main cause of adult deer mortality (e.g., Marescot et al., 2015), increasing puma kill rates in response to kleptoparasitism may have negative consequences for ungulate populations and community structure (e.g., Ripple et al., 2001). These direct and indirect effects that black bears have on ecosystems are particularly important because black bears are one of the few large carnivores that are currently expanding their range (Ripple et al., 2014). The effects of black bears on pumas are likely linked to bear density (e.g., Krofel & Jerina 2016), and the increasing restrictions on bear hunting regulations (e.g., outlawing the use of trained hounds) in many jurisdictions may lead to decreases in harvest and greater population increases for black bears. Thus, resource managers need to consider possible effects of changes in management of one species as they can directly affect the populations and conservation of others (Krofel & Jerina 2016).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:[10.1016/j.baae.2021.01.011](https://doi.org/10.1016/j.baae.2021.01.011).

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