Original Article

Nowhere to hide: pumas, black bears, and competition refuges

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One hypothesis for how carnivores with overlapping ecology coexist in natural systems is through heterogeneous competition landscapes, in which subordinates utilize "competition refuges" to mitigate risks associated with dominant competitors. We tested for the effects of American black bear (*Ursus americanus*) kleptoparasitism on puma (*Puma concolor*) foraging in 2 systems in North America. We also tested whether partial prey consumption exhibited by pumas in the presence of bears was better explained by rules of optimal foraging or by kleptoparasitism by black bears, and whether pumas utilized spatial competition refuges to mitigate competition with bears over carcass remains. Puma kill rates in ungulates/wk were equivalent across study systems, but 48% greater in the bear season than the no-bear season. Our analyses of handling time did not support the notion that partial prey consumption exhibited by pumas followed patterns of optimal foraging. Rather, puma handling time and prey consumption were better explained by the presence of bears. Surprisingly, pumas did not utilize spatial competition refuges to mitigate competition with black bears, and instead our results suggested they increase their kill rates to compensate for losses. Our results linking high seasonal kill rates of a top predator with kleptoparasitism by a dominant competitor provide strong evidence that the effects of predation can only be understood within a community framework. In particular, we propose that future predation studies should differentiate between relative contributions of predators and competitors on prey dynamics. Further, our results suggest kleptoparasites may indirectly impact prey populations through their effects on top predators.

Key words: **competition refuges, interference competition, kill rates, kleptoparasitism, predation, *Puma concolor*, *Ursus americanus*.**

INTRODUCTION

That dominant competitors exclude or limit subordinate competitors is a foundation principle of ecology, resulting in the traditional view that competitors may only coexist in natural communities through the divergence of ecological niches (MacArthur and Levins 1967). Competitors, however, frequently coexist, and numerous hypotheses have been proposed to explain patterns and conditions for sympatry. Evidence suggests that subordinate competitors may persist in the presence of a dominant competitor: 1) by shifting their resource use to mitigate competition overlap (e.g., Glen and Dickman 2008), 2) through the influences of external ecological processes (e.g., apparent competition scenarios reducing the dominant competitor through a shared predator, Roemer et al. 2002; or where intraspecific competition is greater than interspecific competition, MacArthur and Levins 1967), 3) through behavioral

strategies exhibited by the subordinate competitor that may buffer them from competition (e.g., temporal partitioning of shared resources; Hayward and Slotow 2009), or 4) where dominant foragers only partially consume their prey and the "scraps" subsidize the subordinate forager (Mittler 1997). Another hypothesis often attributed to large carnivores, is that competition landscapes are heterogeneous and that subordinate competitors utilize temporal or physical "competition refuges," in which they can either avoid or mitigate risks associated with interactions with dominant competitors (Durant 1998, 2000; Broekhuis et al. 2013, Elbroch and Wittmer 2013).

Negative interactions among sympatric carnivores include interference competition, exploitation competition, and predation risks associated with direct harassment and/or intraguild killing (Durant 1998, 2000; Odden et al. 2010; Krofel et al. 2012; Vanak et al. 2013). Kleptoparasitism, one of the most common forms of competitive species interactions, has been shown to influence carnivore foraging and fitness. For example, kleptoparasitism by brown bears

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(*Ursus arctos*) decreases European lynx (*Lynx lynx*) handling times and increases lynx kill rates in summer (Krofel et al. 2012), kleptoparasitism by Andean condors (*Vulture gryphus*) decreases puma handling times and increases puma kill rates (*Puma concolor*) in Patagonia (Elbroch and Wittmer 2013), and kleptoparasitism by spotted hyenas (*Crocuta crocuta*) and African lions (*Panthera leo*) decreases wild dog (*Lycaon pictus*) and cheetah (*Acinonyx jubatus*) handling times in southern and central Africa throughout the year (Creel and Creel 1996; Carbone et al. 2005; Hayward et al. 2006; Broekhuis et al. 2013). Kleptoparasitism can also lead to fitness consequences for predators. Both wild dog and cheetah densities are reduced in the presence of high densities of spotted hyenas and lions, and leopard (*Panthera pardus*) numbers are reduced in the presence of higher tiger (*Panthera tigris*) densities, at least in part due to kleptoparasitism and harassment at kills (Creel and Creel 1996; Durant 1998; Durant 2000; Odden et al. 2010; Harihar et al. 2011).

Interference competition at predator kills may also increase carrion availability, and indirectly influence ecosystem structure and stability (Barton et al. 2013; Moleón et al. 2014). Kleptoparasitism, for example, may be a potential mechanism explaining the sometimes large discrepancy between the number of animals and associated calories that carnivores kill versus consume (Elbroch et al. 2014). Other research, however, has suggested that the discrepancy between predator kill and consumption rates may reflect satiation (Holling 1966) or optimal foraging instead. Following principles of optimal foraging, the amount of "partial prey consumption" exhibited by predators should correlate with kill rates and be reflective of prey availability, rather than influenced by external or internal constraints, such as competitive scavengers (Lucas and Grafen 1985; Vucetich et al. 2012).

Pumas are a solitary, large carnivore and a subordinate competitor to American black bears (*Ursus americanus*) where they co-occur in western North America and southern Florida (Murphy et al. 1998; Ruth and Murphy 2010; Allen et al. 2014a). Pumas are specialist hunters of medium and large ungulates, whereas black bears are generalist foragers of diverse foods. Black bears are also dominant scavengers of large carcasses, and their presence at carcass resources has been shown to reduce the diversity of other vertebrate scavengers present, as well as the feeding times of those scavengers (Allen et al. 2014a). Therefore, pumas and black bears exhibit minimal niche overlap, except in early summer when they are direct competitors for newborn ungulate prey (e.g., elk [*Cervus elaphus canadensis*] calves; Griffin et al. 2011). Black bears, however, also exhibit kleptoparasitism of puma kills when they are active, and black bear kleptoparasitism is suspected to be a significant influence on puma foraging, if not fitness (Murphy et al. 1998; Allen et al. 2014b).

Our overall objective was to determine whether kleptoparasitism by a dominant competitor influenced foraging of a top predator. We tested whether partial prey consumption exhibited by pumas in the "bear season" was better explained by rules of optimal foraging or by kleptoparasitism by black bears. We focused on black bears over other scavenger species because of their dominant role at carcasses and their tendency to displace pumas from their kills (Murphy et al. 1998; Allen et al. 2014a). Following optimal foraging theory, we hypothesized that puma carcass utilization would be negatively correlated with their kill rates, and that partial prey consumption of carcasses would not be correlated with search times preceding kills (*sensu* Vucetich et al. 2012). Support for optimal foraging theory would suggest that pumas abandon scraps that black bears capitalize upon, facilitating the coexistence of these 2

competitors in space (Mittler 1997). Nevertheless, we also hypothesized that the presence of a bear at a specific puma kill would result in shorter handling times at that kill, and shorter search times between that kill and a puma's subsequent kill; in other words, we expected black bears to increase puma kill rates and to increase the amount of carrion on the landscape produced by pumas.

Given the energetic costs of losing carcasses, we also hypothesized that pumas would actively mitigate the potential effects of kleptoparasitism by disproportionally killing prey in competition refuges that reduced the risk of carcass detection by black bears during summer. To test this hypothesis, we developed resource selection functions (RSF; Manly et al. 2002) of verified puma kills in summers to determine the spatial attributes that explained the time until a bear detected a puma kill. We expected our RFSs to identify spatially explicit areas in which puma kills were either slowly or never detected by bears.

METHODS

Study areas

Our first study site was located in western Colorado near the town of De Beque (WGS84 N 39.385, W −108.324; Figure 1a). The core of our study area was approximately 1100 km², approximately half of which was managed by the High Lonesome Ranch. Interspersed parcels of public lands were managed by the US Bureau of Land Management. The topography was rugged and consisted of flat valley bottoms approximately 1500–1700 m asl, steep canyon walls, and elevated plateaus ranging between 1800–3000 m asl. Lower elevations were characterized by pinyon-juniper (*Pinus edulis* and *Juniperus* spp.) woodlands, interspersed with stands of Gambel oak (*Quercus gambelii*), and rangeland shrub communities (*Artemisia* spp. and *Atriplex* spp.). Higher elevations were characterized by mixed conifer (*Pseudotsuga mensiesii* and *Pinus contorta*) and aspen (*Populus tremuloides*) forests, as well as rangeland shrubs. Mean annual precipitation was 295 mm, most of which fell as snow between December and March. Temperatures were strongly seasonal, ranging from −10°C during winter to 33.8°C during summer with a mean annual temperature of 8.1°C (NCDC COOP Station number 057031).

Pumas in our Colorado study area primarily preyed on elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*). Additional small prey species included American beavers (*Castor canadensis*) and North American porcupines (*Erethizon dorsatum*). In addition to black bears, coyotes (*Canis latrans*), Golden eagles (*Aquila chrysaetos*), and common grey foxes (*Urocyon cinereoargenteus*) were also regularly detected at puma kills (Elbroch et al. 2014).

Our second study site was approximately 1000 km² and located almost completely within the Mendocino National Forest in Northern California (WGS84 N 39.738, W −123.160; Figure 1a). Elevations ranged from 400 to 2450 m asl with steep elevational gradients. Vegetation included mixed oak woodlands (*Quercus* spp.), dense chaparral, and grasslands at low elevations, whereas mid elevations were mainly comprised of mixed coniferous forests (*Pinus* spp. and *Pseudotsuga menziesii*). High elevations were a mix of fir forests (*Abies* spp.), shrub communities (*Ceanothus* spp. and *Prunus* spp.), and scattered dry and wet meadows dominated by exotic annual grasses. Climate was strongly seasonal. Mean annual precipitation was 1320 mm, and predominantly fell between October and April as rain at lower elevations and snow at higher elevations. Temperatures typically ranged from −12°C to 45.5°C, with
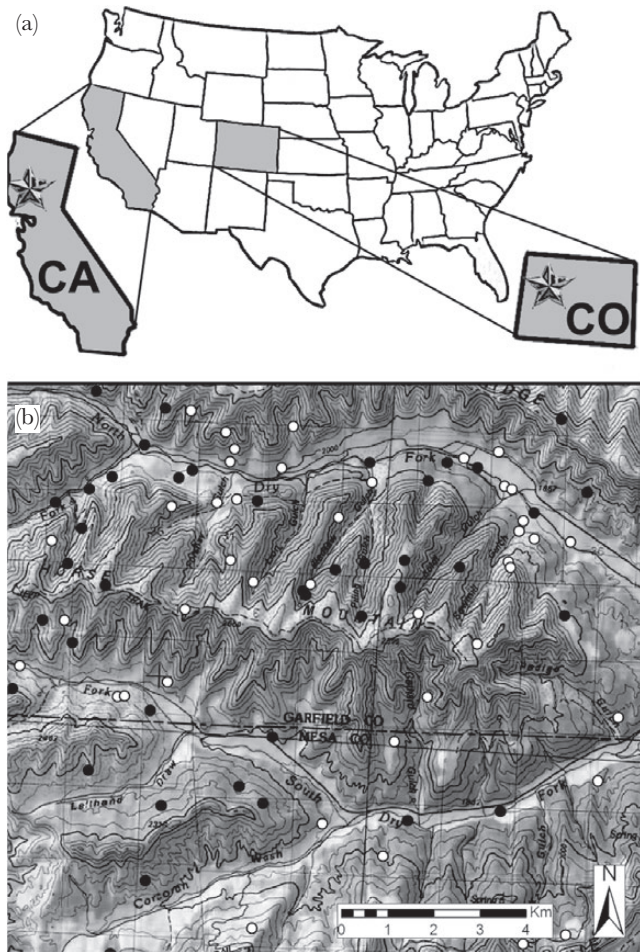
Figure 1
(a) The location of the 2 study areas in the United States; northern California (CA) and northwestern Colorado (CO). (b) An example of kill locations used in the RSF analyses that illustrates that kills detected quickly and slowly by black bears were often adjacent and in similar areas. Black points represent kills which were discovered by a black bear within 48 h, and white points are kills discovered by bears ≥96 h after they were made or not at all.

a mean annual temperature of 13.1°C (NCDC COOP Station # 042081).

Black-tailed deer (*O. h. columbianus*) were the only ungulate prey killed by pumas in the California study area. Additional prey species included black-tailed jackrabbits (*Lepus californicus*), northern raccoons (*Procyon lotor*), and California ground squirrels (*Otospermophilus beecheyi*; Allen et al. 2014b). In addition to black bears, we regularly detected common grey foxes, coyotes, turkey vultures (*Cathartes aura*), and common ravens (*Corvus corvax*) at puma kills (Allen et al. 2014a).

Puma captures

Between February 2010 and March 2012, we captured 11 pumas (5 males, 6 females) in Colorado, and between December 2009 and November 2012, we captured 7 pumas (2 males, 5 females) in California. Specific puma attributes and capture methods are detailed in Elbroch et al. (2014). All capture and handling procedures adhered to guidelines developed by the American Society of Mammalogists (Sikes et al. 2011) and were approved by the

independent Institutional Animal Care and Use Committee at the University of California, Davis (Protocols 15341, 16645, and 16886).

Collar programming and field efforts

Pumas were fitted with either Argos or Iridium GPS collars (Lotek 7000SAW or Lotek Iridium 2D). Collars placed on pumas were programmed to acquire locations at 2-h intervals and transmit data through an Argos uplink at 3-day intervals, or twice daily via an Iridium uplink. On retrieval, all location data were displayed to identify GPS clusters associated with potential kill sites (Anderson and Lindzey 2003). In Colorado, we defined clusters as any ≥2 locations ≥2 h apart, and in California as any ≥2 locations ≥8 h apart, within 150 m of each other, and where at minimum 1 location was recorded during crepuscular or nocturnal periods (Elbroch et al. 2014). Puma location data were transferred to handheld GPS units to locate clusters in the field.

In both study areas, GPS locations were systemically searched to locate and identify prey remains, including hair, skin, rumen, and bone fragments. The state of prey remains, presence and location of bite marks (e.g., throat, nose, or back of head to indicate predation), and body parts consumed were used to determine whether the puma had killed the animal or was scavenging. In circumstances where pumas were still feeding on carcasses, we placed remote video cameras (Bushnell Trophy Cam, Bushnell Outdoor Products, Overland Park, KS). Ninety-three percentage of all field investigations of clusters were conducted by CyberTracker certified observers (Elbroch et al. 2011), ensuring a consistent field effort and expertise across study sites. We estimated age-specific weights of adult ungulate prey from literature sources and, to account for lower weights of juvenile animals, adjusted weights based on known growth rates using simple regressions of weight and age (Elbroch et al. 2014). The presence of black bears at puma kills was determined from video footage, footprints, scats, and other associated signs.

Defining handling time, search time, and kill rates

We calculated handling times, search times, and kill rates for 2 seasons for each study site, but rather than using arbitrary calendar seasons, we assigned "bear" and "no-bear" seasons for each study site. We defined the "bear" season in Colorado as April 20th through November 2nd each year, because these were the earliest and latest dates bears were detected at puma kills during the study. Defining a bear season in California was more problematic, because bears were detected at puma kills at least once in every month of the year. However, because bear detection at puma kills declined drastically between December 1st and March 31st, we chose to define the bear season as April 1st through November 30th each year.

We defined the handling time as the total hours from the first to the last GPS location recorded within 150 m of verified kill sites (Elbroch et al. 2014), even when the puma moved away from the area and then returned during the period it was utilizing the carcass (e.g., traveled to a resting site in a different location or traveled to retrieve kittens). We only quantified handling time for the subset of kills in which Argos and GPS performance allowed us to accurately identify the start and end of each kill, which required continuous GPS locations leading up to and away from a kill.

We defined search time as the total hours between the last GPS location within 150 m of a verified kill site and the first GPS location within 150 m of the subsequent verified kill site (Elbroch and Wittmer 2013). Thus we divided puma activity into 2 phases: searching and handling, choosing not to differentiate from among the other behaviors that occurred within each phase (e.g., resting).

We quantified puma kill rates in 3 different ways for sampling periods in which pumas were monitored continuously for a minimum of 4 weeks in a single season (bear vs. no-bear), with the exception of one 26-day monitoring period (Elbroch et al. 2014). We did not include any periods in which Argos transmissions missed GPS locations for ≥1 night. For pumas in which there was a gap in monitoring, and thus 2 or more sampling periods of continuous monitoring greater than 4 weeks in length, we calculated kill rates for each period separately. We quantified kill rates in kg per day for all prey killed in each sampling period. We also calculated kill rates in terms of 1) animals/wk and 2) ungulates/wk. All ungulates, regardless of species, size or sex were treated equally when we quantified kill rates in ungulates/week.

Effect of season on puma handling times, search times, and kill rates

We first tested for differences in puma foraging explained by season or study site. We employed a series of generalized linear models (GLIM; SAS 9.3, SAS Institute, Cary, NC) with a binomial distribution, logit link function, and in which individual puma was included as a random effect, to test whether there were differences in 1) mean prey size killed by pumas, 2) mean puma handling time, 3) mean puma search time, or 4) mean puma kill rates for our predictor variables, season, and study site. We also incorporated an interaction term between season and study site in all analyses.

Testing whether partial prey consumption exhibited by pumas in the bear season was better explained by optimal foraging or black bear kleptoparasitism

We employed a multivariate approach to test whether prey weight (in kg), the presence of a black bear(s), the search time leading up to the kill, or study site held explanatory power for handling time at each kill ≥40 kg. Only kills investigated within 21 days from when the puma abandoned the kill were included in analyses to ensure the accuracy of detecting bear presence. We also employed a ≥40 kg cutoff for prey weight to minimize the potential bias small prey have on handling time and the potential that bears were not detected at small prey kill sites. A 40 kg cutoff also ensured that pumas might abandon meat for reasons other than smaller prey size or the presence of bears, such as satiation or optimal foraging (*sensu* Vucetich et al. 2012). Prior to the statistical analysis, we tested for collinearity between independent variables with pairwise coefficient correlations and used ($|r| < 0.5$) for retaining variables.

We then employed a GLIM, with a Poisson distribution, logarithmic link function, and individual puma as a random effect (SAS 9.3, SAS Institute). We ran all possible combinations of all variables and used Akaike's Information Criterion adjusted for small sample size (AIC_c, ΔAIC_c, and Akaike weight w_i; Burnham and Anderson 2002) for each model output to determine variables that influenced handling time in the bear season. Models separated by ≤2 AIC_c units of the best supported model were considered equally supported (Burnham and Anderson 2002).

Testing whether puma search time in the bear season was influenced by black bear kleptoparasitism

As a further test of the influence of black bear kleptoparasitism on puma foraging behaviors, we employed a GLIM, with a Poisson distribution, logarithmic link function, and in which individual puma was included as a random effect, to test whether the handling time at each kill ≥40 kg (in h), the presence of a black bear(s) at that kill, or study site held explanatory power for the next search time in sequence. Only kills investigated within 21 days from when the puma abandoned the kill were included in this analysis (see "Testing whether partial prey consumption exhibited by pumas in the bear season was better explained by optimal foraging or black bear kleptoparasitism"). When we ran the full model, the analysis did not converge. Based on our above analysis on handling time, which showed study site was not a significant variable, we removed study site as a covariate and ran the model with only handling time and bear presence as potential explanatory variables.

Testing for competition refuges in which pumas avoided black bear kleptoparasitism

To test for possible competition refuges of pumas from kleptoparasitism of black bears, we compared environmental variables at cougar kill sites where a bear was detected within 48 hours of when the kill was made to sites where bears were detected ≥96 h after the kill was made or not at all (Figure 1b), with conditional logistic regression (PROC LOGISTIC; SAS 9.3, SAS Institute, Inc. Manly et al. 2002; Boyce 2006):

$$w(x) = \exp\left(\beta_0 + \beta 1 x_1 + \beta 2 x_2 \cdots + \beta k x_k\right),$$

where $w(x)$ is the probability of selection as a function of covariate x, with coefficient $\beta k x_k$ and intercept β_0. Each puma was considered as a stratified variable to control for variation among individuals (i.e., individuals were sampling units), and the logistic model was conditioned on that variable. Prior to any statistical analyses, we used a correlation matrix to evaluate collinearity ($|r| > 0.5$) among the following predictor variables: elevation, slope, aspect, vector ruggedness measure (VRM; Sappington et al. 2007), distance to nearest river, and habitat type. In California, we classified 4 distinct habitat types: deciduous forests, conifer forests, shrublands, and meadows. Due to the greater habitat variability in Colorado, we classified 6 distinct habitat types: deciduous forests, conifer forests, mixed forests, pinyon-juniper forests, shrublands, and meadows. Zero predictor variables were correlated (all $|r| < 0.5$) and therefore all variables remained in our analysis. We conducted separate RSFs for each study site. We intended to use model-averaged parameter estimates and unconditional standard errors (SE) to assess the influence of each predictor variable on resource selection (Burnham and Anderson 2002) and to create probability surfaces to identify spatial refuges (Manly et al. 2002), however, zero variables were significant in any of the models (all $P > 0.25$) and therefore we did not proceed with this step.

RESULTS

Puma monitoring and prey indices

We monitored 18 pumas for 21 blocks of ≥28 days during bear seasons (monitoring interval = 143±58 days, mean ± SD), and 8 pumas for 13 monitoring blocks during no-bear seasons (monitoring interval = 62±32 days, mean ± SD; Supplementary Table S1). In Colorado, we investigated 1001 GPS clusters of pumas and documented 437 predation and 8 scavenging events, of which 3 were

intraspecific kleptoparasitism. On average, we investigated clusters from functioning collars ($n = 9$) within 5.9 ± 7.9 days (mean ± SD, range 0–31) of the puma leaving the area, and for collars which stored GPS data only ($n = 2$), we investigated clusters within 168.0 ± 91.1 days (mean ± SD, range 63–189). Prey included 337 ungulates (71 elk, of which 30 were calves ≤6 months, and 266 mule deer, of which 84 were fawns ≤6 months) and 106 smaller vertebrates (Elbroch et al. 2014). In California, we investigated 598 out of 609 GPS clusters of pumas within 6.8 ± 8.2 days (mean ± SD, range 0–60) of the time the puma left the kill. We identified 352 prey (288 black-tailed deer, of which 75 were fawns ≤6 months, and 62 small prey, Allen et al. 2014b) and 4 scavenging events, of which 2 were intraspecific kleptoparasitism.

Black bears were detected at 47.8% and 77.2% of kills ≥40 kg, as determined from cameras and associated signs during the bear season in Colorado and California, respectively (Supplementary Table S1). Cameras were placed at 47 active puma kills in Colorado and 58 active kills in California during the bear season. In Colorado, bears displaced pumas at 29 kills with cameras, and pumas returned only once to 3 of these kills (10%) after the appearance of the bear. In California, bears displaced pumas at 29 kills with cameras, and pumas returned only once to 8 of these kills (28%) after the appearance of the bear (Supplementary Video S1). During 1 incident of kleptoparasitism in California, an adult female puma returned and killed a 3-year-old female bear that had initially displaced her from her kill.

Effect of season on puma handling times, search times, and kill rates

Prey size differed between study sites ($F_{1,750} = 81.87$, $P < 0.0001$), seasons ($F_{1,750} = 42.68$, $P < 0.0001$), and the interaction between study site and season was also significant ($F_{1,750} = 16.70$, $P < 0.0001$). Prey size in Colorado was 55.9 ± 2.62 kg (mean ± SD) during the bear season and 105.2 ± 10.30 kg (mean ± SD) during the no-bear season. Prey size in CA was 28.71 ± 1.16 kg (mean ± SD) during the bear season and 38.4 ± 2.66 kg (mean ± SD) during the no-bear season. Handling time varied between seasons ($F_{1,750} = 42.68$, $P < 0.0001$), but not between study sites ($F_{1,750} = 0.53$, $P = 0.47$) or with the interaction between study site and season ($F_{1,750} = 0.04$, $P = 0.84$). Handling times averaged 43.2 ± 35.2 h (mean ± SD) during the bear season and 89.1 ± 67.0 h (mean ± SD) during the no-bear season. Search time varied between season ($F_{1,750} = 14.83$, $P < 0.0001$), but not between study sites ($F_{1,750} = 1.17$, $P = 0.28$) or with the interaction between study site and season ($F_{1,750} = 0.07$, $P = 0.80$). Search times averaged 69.4 ± 70.6 h (mean ± SD) during the bear season and 98.7 ± 74.6 h (mean ± SD) during the no-bear season.

Kill rates in animals/wk differed significantly between seasons ($F_{1,18} = 21.67$, $P = 0.0002$), but not study sites ($F_{1,18} = 0.18$, $P = 0.68$) or with the interaction between study site and season ($F_{1,18} = 0.34$, $P = 0.57$). Kill rates were 1.48 ± 0.46 animals/wk (mean ± SD) during the bear season and 0.84 ± 0.28 animals/wk (mean ± SD) during the no-bear season (Figure 2). Kill rates in ungulates/wk also differed significantly between seasons ($F_{1,18} = 12.48$, $P = 0.0024$), but not study sites ($F_{1,18} = 0.05$, $P = 0.83$) or with the interaction between study site and season ($F_{1,18} = 0.69$, $P = 0.42$). Kill rates were 1.14 ± 0.35 ungulates/wk (mean ± SD) during the bear season and 0.77 ± 0.23 ungulates/wk (mean ± SD) during the no-bear season (Figure 2). In contrast, kill rates in kg/day were equivalent across seasons ($F_{1,18} = 0.18$, $P = 0.68$), but differed between study sites ($F_{1,18} = 11.08$, $P = 0.0037$). The interaction between study site and season was not significant ($F_{1,18} = 0.94$, $P = 0.34$). Measured in kg/day, kill rates were higher in Colorado (9.0 ± 3.7 kg/day, mean ± SD) than in California (6.0 ± 2.0 kg/day, mean ± SD).

Testing whether partial prey consumption exhibited by pumas in the bear season was better explained by optimal foraging or black bear kleptoparasitism

Our AIC_c comparisons identified 1 top model, that outperformed all others (>2 AIC difference) and accounted for 84% of AIC weights (Table 2). Our top model showed that puma handling time during the bear season was explained by the preceding search time leading up to the kill ($F_{1,293} = 22.51$, $P < 0.0001$), prey size ($F_{1,293} = 64.57$, $P < 0.0001$), and the presence of a bear ($F_{1,293} = 47.92$, $P < 0.0001$). Handling time increased following longer search times and as prey weight increased, but decreased with the presence of a bear (Figure 3).

Testing whether puma search time in the bear season was influenced by black bear kleptoparasitism

Puma search time after each kill during the bear season was explained by both the handling time at the kill ($F_{1,283} = 27.38$, $P < 0.0001$), and the presence of a bear ($F_{1,283} = 35.90$, $P < 0.0001$).
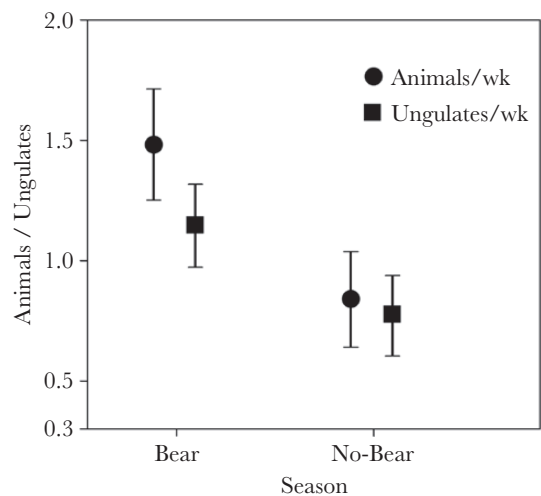

Figure 2
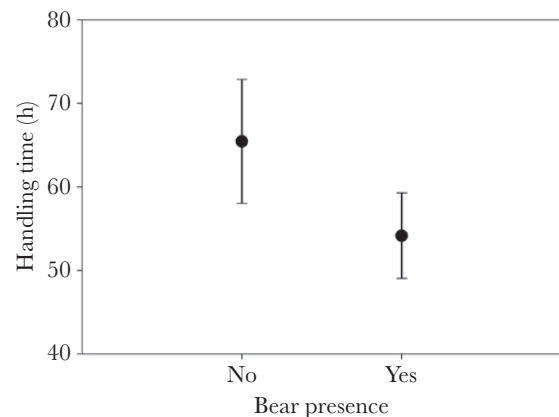Comparative mean ± 1 SD kill rates in animals and ungulates/week across bear and no-bear seasons.

Figure 3
Comparative mean ± 1 SD handling times (hours) at kills ≥40 kg with and without bears present, in the bear season.

Search times after kills with longer handling times were longer, and search times after kills at which a bear was present were shorter.

Testing for competition refuges in which pumas avoid black bear kleptoparasitism

In Colorado, we utilized 67 kills at which a bear was detected within 48 h of when the kill was made, and 242 kills at which a bear was detected ≥96 h from the time of kill or not at all, to test for possible competition refuges for pumas. Corresponding sample sizes in California were 83 and 75, respectively. We did not detect any significant spatial patterns explaining the time until a bear detected puma kills in either Colorado or California, meaning that the probability of a bear finding a puma kill was equivalent across the landscape. There was no difference in elevation, slope, aspect, VRM, distance to nearest river, or habitat type (all $P > 0.25$) between kills detected quickly by bears and kills detected more slowly or not at all.

DISCUSSION

Our results demonstrated the strong potential negative effects of kleptoparasitism by dominant competitors on foraging of top predators, and suggested that when predators lack for spatial competition refuges, top predators may mitigate the effects of kleptoparasitism by increasing their kill rates. Our analyses of handling time during the bear season did not support the notion that partial prey consumption exhibited by pumas followed patterns of optimal foraging. Instead, puma handling time and prey consumption at individual kills in the bear season were better explained by the presence of bears. Unlike wolves (*Canis lupus*) feeding on moose (*Alces alces*; Vucetich et al. 2012), there was a significant explanatory relationship between the search time preceding a kill and the handling time at that kill. When pumas searched longer for prey in the bear season, they remained with carcasses longer. These results suggested that when pumas partially consumed prey in the bear season, it was unlikely because they had met their energetic requirements (i.e., satiation in Holling 1966), or abandoned meat because of a behavioral decision that indicated prey were abundant and easy to catch (i.e., optimal foraging in Vucetich et al. 2012).

Prey size, naturally, explained handling time, but handling times at large carcasses were also shorter at kills where bears were present than at kills where they were not (Figure 3). Search times after kills at which bears were present were also shorter than after kills where bears were absent. Together, these results suggest that puma kill rates were influenced by black bear kleptoparasitism in 2 ways: first, puma kill rates were likely increased in the presence of bears because pumas consumed less of their kills when being quickly displaced by bears, and second, pumas killed their next prey more quickly when displaced by a bear at their last kill. Increased kill rates were likely reflective of energetic losses as well, both in terms of losing calories to competitors and in expending additional calories to hunt more frequently. Further, when the effects of bears are considered in addition to the potential effects of other scavengers (e.g., Allen et al. 2014a), our results were likely conservative estimates of the effects of kleptoparasitism on puma foraging.

Puma kill rates in animals/wk were equivalent across study systems, but 77% greater in the bear season than the no-bear season. Puma kill rates in ungulates/wk were also equivalent across study systems, and 48% greater in the bear season than the no-bear season. Higher puma kill rates in summer, however, are explained by more than just bear kleptoparasitism; pumas increase their kill rates because of changes in prey vulnerability (e.g., the ungulate birth

pulse, Knopff et al. 2010) and likely because higher temperatures increase invertebrate activity (Ray et al. 2014) and rates of spoilage (Bischoff-Mattson and Mattson 2009). Pumas also exhibited shorter handling and search times as well as killed smaller prey in the bear season. The difference in mean prey size may have been influenced by seasonal availability, as for example, some small prey like ground squirrels (*Spermophilus* spp.) and newborn ungulates are only summer fare (e.g., Knopff et al. 2010). Alternatively, differences in prey size across seasons may have been reflective of larger behavioral decisions exhibited by pumas. Like cheetahs (Hayward et al. 2006), pumas may select smaller prey that are easier to catch during the bear season to mitigate potential competition with black bears over carcass remains.

Most surprisingly, results from our RSF analysis did not support our hypothesis that pumas would identify and utilize competition refuges to mitigate losses to black bears. None of the explanatory landscape variables we included in our analysis proved to hold predictive power over whether a black bear would detect and usurp a puma's kill quickly or not. Unlike cheetahs, wild dogs, and leopards, which exhibit varied behavioral strategies and utilize spatial and temporal refuges to mitigate competition with dominant African lions and hyenas (Vanak et al. 2013), pumas could not hide from black bears. We did not detect any spatial characteristics that explained the timing it took black bears to discover puma kills, and pumas did not hunt in spatial refuges that mitigated competition with black bears. Given the number of recent studies utilizing RSFs to link habitat use to reduced survival probabilities of prey (e.g., DeCesare et al. 2014), the lack of spatial competition refuges for pumas may indicate that fitness consequences for pumas in these systems are not serious enough to force changes in their foraging behavior or an inability to avoid a dominant scavenger that is also a habitat generalist. This suggests the only relief from bear kleptoparasitism provided pumas in both study systems was a temporal refuge when bears entered hibernation.

The impacts of kleptoparasitism by a dominant competitor on top predator kill rates raises questions about the ecological influences of competitors on ecological communities. As the only top predator in our 2 study systems, pumas almost certainly selected for areas with high prey densities (Carbone and Gittleman 2002), if not for areas that mitigated competition with black bears in summers. Because the timing of kleptoparasitism by black bears appeared homogenous across the landscape, pumas could only defend their kills to mitigate the effects of black bears, or increase their kill rates to compensate for their losses. Consequently, a dominant competitor may indirectly impact prey populations through increasing top-down control exhibited by a top predator (Figure 4); this may be especially relevant to understanding predation on rare prey in multi-prey systems (e.g., Elbroch and Wittmer 2013). Alternatively, it is also possible that a predator could exhibit prey switching to mitigate the effects of the competitor, and avoid increasing total predation rates on specific prey. Carcasses stolen from top predators by dominant competitors may also subsidize competitor populations, which may be predators themselves. The question remains as to whether puma subsidies to black bears increase bear numbers and bear predation of newborn ungulates (Figure 4; Griffin et al. 2011), or whether puma subsidies buffer ungulates from direct predation by bears.

The top-down effects of predators on their ungulate prey has long been hotly debated (e.g., Wilby and Orwin 2013), even while there is increasing evidence that scavengers and carrion subsidies may indirectly influence prey through increasing top-down forces (Elbroch
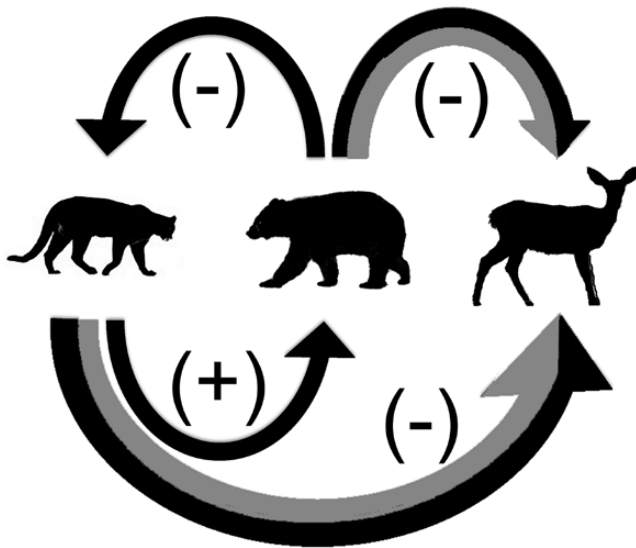
Figure 4
Conceptual model of how interference competition by a dominant competitor might influence prey dynamics through a top predator. The "+" sign indicates positive contributions, and the "−" sign indicates a negative influence. Pumas provide subsidies to black bears, but negatively impact deer numbers. Black bears negatively influence pumas through kleptoparasitism and negatively impact deer through fawn predation. The grey portions of the arrows connecting bear to deer, and pumas to bears are the potential additional impacts due to interference competition. Black bears increase puma kill rates, thus the grey represents this additional impact. Pumas potentially subsidize bear populations, which in turn predate on deer fawns.

and Wittmer 2013, Moleón et al. 2014, Pereira et al. 2014). New and improved GPS technologies have shown that carnivore kill rates, including those of pumas, are higher than previously assumed and cannot be explained by energetic requirements alone (Elbroch et al. 2014). Our results linking high seasonal kill rates of a top predator with kleptoparasitism by a dominant competitor provides strong evidence that predation can only be understood within a community framework (Moleón et al. 2014). This framework must simultaneously evaluate the direct influence of predators on prey and the availability of carrion, in combination with the effects of carrion, scavengers, and competitors on predator foraging and prey populations. Such community approaches to predation studies are needed to understand whether predator foraging behaviors in general already account for the ubiquitous effects of kleptoparasitism, or whether there are indeed thresholds of kleptoparasitism that increase predation rates. Only then will be able to differentiate the relative contributions of predators and competitive scavengers on prey dynamics.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

FUNDING

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