Games of risk and reward in carnivore communities

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Abstract

Mesopredator release theory suggests that dominant predators suppress subordinate carnivores and ultimately shape community dynamics, but the assumption that subordinate species are only negatively affected ignores the possibility of facilitation through scavenging. We examined the interplay within a carnivore community consisting of cougars, coyotes, black bears, and bobcats using contemporaneous Global Positioning System telemetry data from 51 individuals, diet analysis from 972 DNA-metabarcoded scats, and data from 128 physical investigations of cougar kill sites, 28 of which were monitored with remote cameras. Resource provisioning from competitively-dominant cougars to coyotes through scavenging was so prolific as to be an overwhelming determinant of coyote behavior, space use, and resource acquisition. This was evident via strong attraction of coyotes to cougar kill sites, frequent scavenging of cougar-killed prey, and coyote diets that nearly matched cougars in the magnitude of ungulate consumption. Yet coyotes were often killed by cougars and used space to minimize encounters, complicating the fitness benefits gained from scavenging. We estimated that 23% (95% CI: 8–55%) of the coyote population in our study area was killed by cougars annually suggesting that coyote interactions with cougars are a complex behavioral game of risk and reward. In contrast, we found no indication that bobcat space use or diet was influenced by cougars. Black bears avoided cougars, but there was no evidence of attraction to cougar kill sites, and much lower levels of ungulate consumption and carcass visitation than for coyotes. Interspecific interactions among carnivores are multifaceted encompassing both suppression and facilitation.

Significance Statement

An incomplete understanding of the total influence top predators exert on subordinate species hinders our ability to anticipate the effects that changing carnivore populations will have in ecological communities. Here we show that cougars are the architects of a complex behavioral game of risk and reward, as subordinate or co-occurring carnivores are both provisioned and preyed on by the top predators. Each co-occurring carnivore species considered here employed a different strategy to approach the risk-reward tradeoff suggesting there are multiple viable solutions to the game. By not considering the multitude of effects top predators have on other carnivores, we are missing important linkages in terrestrial food webs.

Main Text

Introduction

The mesopredator release hypothesis posits a trophic cascade wherein larger-bodied and competitively-dominant predators suppress subordinate predators with consequences for prey populations (1-4). Such suppression is often the result of interspecific killing which may be so pervasive as to account for one- to two-thirds of the total mortality of terrestrial carnivores (5-7). Subordinate species may respond to this risk by altering their space use or activity patterns to minimize the probability of encounters with dominant predators (8, 9), but nonetheless, the antagonism between predator species can result in reductions in density or complete exclusion of subordinate carnivores from certain habitats or regions (4, 10, 11).

The assumption that only negative interactions influence carnivore community structure is likely overly simplistic because scavenging of dominant predator kills can also provision subordinate species (7, 12, 13). While the prey killed by dominant predators may represent a 'fatal attraction' that leads mesopredators to their death, the energetic rewards from scavenging in some cases may outweigh the risks (14). For example, if the risk of scavenging is the same as hunting alternative prey but yields a higher probability of finding food, the fitness-maximizing decision for the subordinate or co-occurring species should be to scavenge (Fig. 1; *SI Appendix*,

Text S1). But as risks associated with scavenging increase, the optimal choice becomes a more nuanced function of the relative risk versus reward and depends on the energetic state of the potential scavenger (Fig. 1a; *SI Appendix*, Text S1). And, of course, the scavenger must make this assessment under imperfect knowledge of the risk involved. Thus, the decision for a subordinate species to scavenge from a dominant species represents a complex behavioral game of risk and reward (Fig. 1b). How the costs and benefits of interactions with dominant predators influence the overall fitness of subordinate or co-occurring species has rarely been examined.

Understanding the intraguild dynamics of carnivores is critical to anticipating the ecosystem-level consequences of changing predator populations, but establishing the relative prevalence of suppression and facilitation among carnivores has remained intractable. Strong inference about the magnitude and direction of behavioral and population-level interactions among carnivores requires (1) quantifying the intraguild predation rate on subordinate or co-occurring carnivores, (2) understanding the extent to which subordinate or co-occurring carnivores utilize carrion from dominant predator kills, and (3) evaluating whether dominant predators or their kills influence the movements or space use of subordinate or co-occurring carnivores. Spatial avoidance of dominant predators and high rates of intraguild predation would suggest other carnivores are suppressed. By contrast, high utilization of dominant predator kills by subordinates would support the facilitation hypothesis. We note that while the literature often refers to the benefit conferred by scavenging as facilitation (7, 12, 14), this term implies no harm to the dominant species. If carrion is lost due to scavenging (15, 16), the phenomenon may be more appropriately termed parasitism, or more specifically, kleptoparasitism.

Here we quantify the influence of cougars (*Puma concolor*) on coyotes (*Canis latrans*), black bears (*Ursus americanus*), and bobcats (*Lynx rufus*). Cougars are widely considered dominant to coyotes and bobcats, and although previous researchers have suggested cougars are subordinate to black bears, the available literature suggests that cougars kill bears more often than the reverse (17). We therefore consider bears and cougars to be co-occurring and not necessarily fitting within a clear dominance hierarchy. We leveraged four empirical datasets including contemporaneous Global Positioning System (GPS) telemetry data of 51 individuals across the four species of carnivores, diet analysis from 972 DNA-metabarcoded carnivore scats, and data from 128 physical investigations of cougar kill sites, 28 of which were monitored for scavenging via remote cameras to evaluate how sympatric carnivores are influenced by cougars. We hypothesized that black bears, bobcats and coyotes could be unaffected by cougars (null hypothesis), negatively influenced by cougars (suppression hypothesis), positively influenced by cougars (facilitation hypothesis), or both positively and negatively affected by cougars (provision-predation hypothesis) (Fig. 1c). We used contemporaneous GPS data to infer whether each carnivore species altered movements due to the proximity of a cougar or cougar kill site. We hypothesized that carnivore species attracted to cougar kill sites would have a high frequency of carrion in their diet—suggesting facilitation from cougars—but would also be killed by cougars at higher rates than species that avoided cougar kill sites, indicating suppression. Together, these approaches provided a robust evaluation of the fine-scale behavioral interactions and facilitation versus suppression tradeoff among species within carnivore communities, which will be increasingly important as predator populations recover across portions of their former range and are extirpated in others.

Materials and Methods

Data collection. We collected data on four sympatric carnivore species (cougars, coyotes, black bears, and bobcats) in and adjacent to the Starkey Experimental Forest and Range in the Blue Mountains of northeastern Oregon, USA (Fig. 2 and *SI Appendix*, Text S2) between 2016 and 2020. We tagged 17 cougars (8M, 9F), 17 coyotes (10M, 7F), 11 black bears (7M, 4F), and 6 bobcats (3M, 3F) with GPS collars (Vectronic Aerospace or Lotek Wireless, Inc.) programmed to record positions every 2 or 3 hours (*SI Appendix*, Text S3). We used conservation detection dogs (18) to locate scats (*SI Appendix*, Text S4) and genetically confirmed 774 coyote scats, 85 black bear scats, 96 bobcat scats, and 17 cougar scats (19) that were DNA-metabarcoded for diet

analysis (*SI Appendix*, Text S5). We considered the frequency of occurrence of ungulates (i.e., deer spp. [*Odocoileus hemionus* and *O. virginianus*] and elk [*Cervus canadensis*]) in scats of subordinate carnivores as a qualitative but imperfect proxy for scavenging (14). Although each of these carnivore species can kill deer of all ages, elk consumption by coyotes and bobcats in particular is likely exclusively from scavenging because these species rarely kill elk calves in the region (20). In addition to inference from scat analysis, we further quantified cougar diets by conducting ground searches of clusters of cougar GPS locations indicating potential kill sites of tagged individuals (*SI Appendix*, Text S6) (21). At 28 of the 128 confirmed cougar kill sites, we deployed remote cameras (Bushnell Trophy Cam Aggressor, Browning Dark Ops HD Pro, and Reconyx HyperFire 2) to estimate scavenging rates by the other carnivores. We separately tallied the number of daily visits made by coyotes, bears and bobcats to cougar kill sites that were detected on camera, where a visit was defined as a detection separated by at least 30 minutes from another detection of a given species. We used negative binomial regression to model the number of daily visits to the carcass by a given species as:

$$\textit{number of daily visits} = \textit{cougar present} + \textit{ln(time since kill)} + \textit{prey size} + \textit{kill ID}$$

where cougar present (1/0) indicates whether the cougar was present at the kill that day, time since kill is the number of days since the kill was made, prey size (1/0) indicates whether the prey was large (adult ungulate) or not (young of the year ungulate), and kill ID is a random intercept identifying a given kill site.

Calculating Intraguild Predation Rate. At times, the prey items found at cougar kill sites were other carnivores which allowed us to calculate the proportion of cougar kills representing intraguild predation. Combining these data with information on contemporaneously-estimated carnivore densities (22) and cougar kill rates (21) from a recent study in the area allowed us to calculate intraguild predation rates, i.e., the proportion of the co-occurring carnivore population dying annually due to cougar predation. We calculated the intraguild predation rate on species *i* (P_i) as the number of individuals from species *i* killed per unit time (K_i) divided by the population density of species *i* (D_i) where K_i is the product of cougar population density (D_c) cougar kill rate (kills/year), R, and proportion of kills corresponding to species *i* (F_i):

$$P_i = \frac{K_i}{D_i} = \frac{D_c \times R \times F_i}{D_i}$$

We quantified uncertainty in P_i by propagating error inherent in each parameter using Markov Chain Monte Carlo simulations (*SI Appendix*, Text S7).

Step selection functions. We fit integrated step-selection functions (hereafter *SSFs*) (23, 24) to GPS collar data to estimate how coyote, bobcat, and bear movements were influenced by landscape variables, cougar proximity, or cougar kill site proximity. We included movement attributes as parameters in each model to reduce bias arising from sampling control locations (25) using a gamma distribution to characterize the natural log of step lengths and a von Mises distribution to characterize the cosine of turning angles (24, 26). We generated 20 random steps for each observed step (27). To ensure that territoriality did not bias inference, we did not allow the endpoints of random steps to fall outside a 1,000 m buffer of the 99% minimum convex polygon of each animal's territory. We did this to prevent detecting spurious avoidance behavior due to a random step occurring in an area for which the animal did not have uninhibited access due to territoriality.

We sought to identify whether landscape features and the proximity of a cougar (hereafter, 'distance to cougar' or D2C) or cougar kill site (hereafter, 'distance to kill' or D2K) influenced the movements of coyotes, bobcats, and bears. We calculated distance to cougar as the natural log-transformed Euclidean distance between each focal individual (coyote, bobcat, or bear) and the nearest GPS-collared cougar at that time to determine whether the subsequent

movements of the animal were toward or away from the cougar. To restrict encounters to only those in which the cougar could plausibly be detected by the subordinate species, we only allowed cougars within 1,000 m of the focal bear, bobcat, or coyote to influence the movements of the other carnivores by using a binary indicator for whether a cougar was present (hereafter, 'cougar present' or CP) (1/0) at each GPS fix. We cast 'distance to cougar' as an interaction term with 'cougar present' such that the term was nullified when the nearest known cougar was > 1,000 m away. We used a buffer of 1,000 m because that is the distance elk alter behavior in response to wolves (28) and has also been used to determine interaction distances between cheetahs (29). Further, it is implausible that species could detect cougars at distances greatly exceeding this value. However, to ensure this cutoff did not change our inference about the direction or magnitude of the effect of cougars, we replicated the analyses using additional cutoff values of 500 and 1,500 m. If GPS fixes between cougars and the other carnivores were not contemporaneous (i.e. falling on the same hour plus a tolerance of 300 seconds) due to misalignment or missed fixes, we imputed the location of the cougar using a correlated random walk (30). We allowed cougar locations to be imputed if a single GPS fix was missed but we censored location data for any gaps exceeding 6 hours.

We used this same approach to assess how carnivores responded to cougar kill sites by including a term for 'distance to kill,' calculated as the natural log of the Euclidean distance between each GPS position of a focal individual and the nearest cougar kill site. Potential kill sites were identified from clusters of sequential cougar GPS locations indicating reduced movement and were either confirmed via physical investigations or identified as probable kills using a predictive model (21) (*SI Appendix*, Text S6). We paired 'distance to kill' with a binary indicator variable describing whether there was a known or predicted cougar kill present (hereafter, 'kill present' or KP) (1/0) within a 3,000 m buffer of the focal individual. When there was not a kill within the buffer, the indicator variable took the value of zero and the whole term became null. If there was more than one kill within this buffer for a given individual at a given time, we considered only the distance to the most recent kill. Our assumption that carnivores could detect a carcass up to distances of 3,000 m was conservative; for example, one GPS-collared coyote in our study exhibited two bouts of directed travel of 2.2 km and 3.6 km outside its territory to feed on an elk carcass suggesting an ability to detect carrion from these distances (*SI Appendix*, Fig. S1). Further, previous studies report that coyotes can travel between 12.2 and 20.5 km to reach carcasses of domestic animals (31, 32), while arctic foxes routinely detect marine mammal carcasses at distances of at least 10 km (33). While less is known about olfaction distances in bears, it is reported that polar bears (*Ursus maritimus*) can detect seal breathing holes at distances of 3 km (34). While the available literature suggests 3,000 m is an appropriate value for a cutoff, we replicated each analysis using cutoffs of 2,000 m and 4,000 m to ensure inference was not an artifact of the buffer chosen.

To avoid data contamination due to old carcasses that no longer provided scavenging opportunities, we classified all kills occurring within 30 days of the focal fix as present by censoring kills exceeding this threshold. To quantify how movements of carnivores toward or away from the kill may change as the carcass aged, we created another variable cast as an interaction between the kill present indicator variable (KP), the natural log of the distance to kill (D2K), and the natural log of the time elapsed since the kill (hereafter, 'time since kill' or TSK). This interaction allowed the magnitude of avoidance or attraction to change as a function of the age of the carcass.

It is certain that at times additional cougars were present in the study area not monitored with GPS collars, so the inferences made about effects of cougars and their kill sites on the other carnivore species should be considered conservative. Thus, with complete information on all cougar and kill site locations, the D2C and D2K variables may have had larger effect sizes and/or smaller standard errors than reported here.

Before including cougar variables, we first fit models containing only landscape, and movement variable (hereafter, *habitat model*) according to

$$w(x) = exp(\boldsymbol{\beta} \times landscape\ variables + \beta_{turn\ angle} \times cosine(turn\ angle) + \beta_{step\ length} \times ln(step\ length))$$

where ‘landscape variables’ refer to the continuous variables *ln*(distance to open road), *ln*(distance to perennial water source), canopy cover, topographic ruggedness, and the factor variable potential vegetation type. *A priori*, we expected each of these landscape variables to influence resource selection of each of the species considered, so for simplicity we did not conduct model selection on subsets of these variables and instead retained them all.

We then added the cougar and kill site terms and used Akaike’s Information Criterion (AIC) (35) to assess whether this full model (hereafter, *habitat + cougar model*) outperformed the habitat-only model:

$$w(x) = \exp(\boldsymbol{\beta} \times landscape\ variables + \beta_{D2C} \times CP \times D2C + \beta_{D2K} \times KP \times D2K + \beta_{D2K \times TSK} \times KP \times D2K \times TSK + \beta_{turn\ angle} \times cosi$$

By setting $\beta_{D2K} \times \mathrm{KP} \times \mathrm{D2K} + \beta_{D2K \times TSK} \times \mathrm{KP} \times \mathrm{D2K} \times \mathrm{TSK}$ equal to zero and solving for TSK, we estimated the time until the effect of the kill becomes null. Assuming a kill site is initially a source of attraction that diminishes in time, this is estimated by

$$\exp\left(-\frac{\beta_{D2K}}{\beta_{D2K \times TSK}}\right)$$

We used the ‘amt’ package (26) in Program R 3.6.1 (R Development Core Team 2019) to format data, generate random steps, and fit models.

Evaluating Weight of Evidence for Facilitation, Suppression, and Null Hypotheses. We leveraged multiple independent datasets on the four carnivore species using a weight of evidence approach to determine whether cougars suppress and/or facilitate black bears, bobcats, and coyotes. *A priori*, we established the following criteria: 1) spatial avoidance of cougars would be evidence of suppression, attraction to cougars would be evidence of facilitation, and indifference toward cougars would support the null hypothesis, 2) spatial avoidance of cougar kill sites would be evidence of suppression, attraction to kill sites would be evidence of facilitation, and indifference toward kill sites would support the null hypothesis, 3) a higher frequency of ungulates found in scats of subordinate or co-occurring predators (a proxy for scavenging in our system) in similar proportions to those observed in cougar scats would suggest a higher degree of facilitation than would a lower frequency of ungulates found in scats, and no ungulates found in scats would support the null hypothesis, 4) higher scavenging rates would suggest a greater degree of facilitation than would lower scavenging rates, and the absence of scavenging would support the null hypothesis, and 5) any amount of intraguild predation by cougars on other carnivores would be evidence of suppression, whereas complete absence of intraguild predation would support the null hypothesis.

Results

Step selection functions. Coyotes, black bears, and bobcats each responded to a subset of landscape variables; most notably, bears and bobcats strongly selected for high canopy cover while coyotes avoided high canopy cover (Table 1 and SI Appendix; Fig. S2). Including the three cougar parameters (CP × D2C, KP × D2K, and KP × D2K × TSK) substantially improved model fit for bears (ΔAIC = 10.36) and particularly for coyotes (ΔAIC = 23.96), but the habitat-only model outperformed the habitat + cougar model for bobcats (ΔAIC = 2.69) (SI Appendix, Table S1). Notably, coyotes exhibited a strong attraction to cougar kill sites ($\beta = -0.26$, $p < 0.001$) which attenuated as the carcass aged ($\beta = 0.071$, $p < 0.001$; Fig. 3 and Table 1) and resulted in approximately 39 days of selection for cougar kill sites. Post-hoc analyses revealed that attraction of coyotes to cougar kill sites was driven primarily by resident male coyotes (SI Appendix, Text S9–S10, Table S2–S3). Coyotes avoided cougars ($\beta = 0.20$, $p = 0.014$; Table 1), but there was no evidence to suggest attraction to kill sites was diminished if a cougar was present at the kill, indicating coyotes may disregard the risk of cougars when a food reward is present (SI Appendix,

Text S11, Table S4). Bears were indifferent to kill sites ($\beta = 0.01$, $p = 0.93$) but actively avoided cougars ($\beta = 0.55$, $p \leq 0.001$; Table 1). Bobcats were indifferent to both cougars ($\beta = 0.26$, $p = 0.33$) and their kill sites ($\beta = 0.11$, $p = 0.54$; Table 1). For all species, the choice of buffer for determining whether a cougar (CP) or kill (KP) was present did not appreciably change inference about the direction or magnitude of these effects except that coyote avoidance of cougars was only evident when buffers 1,000 m or less were used (SI Appendix, Text S12, Table S5–S10).

Diet analysis. DNA metabarcoding of carnivore scats revealed a variable frequency of occurrence of deer and elk across species. In coyotes, elk and deer were present in 58% and 12% of scats, respectively (Fig. 4b). In bears, elk was found in 29% of scats and deer in 8% of scats (Fig. 4b). Zero bobcat scats contained elk and 8% contained deer (Fig. 4b). For cougars, 61% of scats contained elk and 22% contained deer. Investigations of 128 cougar kill sites with confirmed prey revealed that elk represented 64% and deer 16% of the prey items killed by cougars (Figs. 4a, 4b).

Scavenging Rates. We monitored 28 cougar kill sites containing ungulate prey using remote cameras to estimate scavenging rates. Cameras were placed an average of 4.4 (range: 0–16) days after the kill was made and were operational an average of 17.4 (range: 1–52) days. We documented coyotes present at 89% of carcasses, bears at 50% of the carcasses outside the hibernation period ($N = 22$), and zero bobcats were detected at cougar kills (Fig. 4c, 4d) during the period cameras were active. For coyotes, the negative binomial regression model predicted that one day after a large ungulate was killed, the carcass would receive 1.8 visits by coyotes but that the number of visits would be reduced by 27% with every additional ln(day) ($\beta = -0.31$, $p = 0.067$; Fig. 5a). The coyote visitation rate was expected to be 160% higher for a large ungulate than a juvenile ungulate ($\beta = 0.97$, $p = 0.059$) and was not influenced by cougar presence ($\beta = 0.43$, $p = 0.26$). The bear model predicted 0.36 visits by bears the day after a large ungulate was killed and that every additional ln(day) would reduce the number of visits by 52% ($\beta = -0.73$, $p = 0.051$; Fig. 5b). The number of daily bear visits was not influenced by the size of prey ($\beta = 0.39$, $p = 0.50$) nor whether a cougar was present ($\beta = -0.12$, $p = 0.89$). The intercepts were –0.81 ($p = 0.22$) and –1.32 ($p = 0.29$) for the coyote and bear models, respectively.

Intraguild Predation. Physical investigations of cougar kill sites indicated that coyotes represented 7.0% (9 of 128; 95% CI: 3.3–11.1%) of cougar kills (Fig. 4e, f). In eight cases coyotes were the only prey item found and were consumed by cougars, and in one case a dead coyote was found in conjunction with another prey item. In the latter scenario, the coyote was not consumed but exhibited trauma consistent with cougar predation and was presumably killed as it attempted to scavenge from the kill. One transient GPS-collared coyote in our sample was killed and consumed by an uncollared cougar outside the study area (Fig. 4e) and in another instance, a GPS-collared cougar killed and consumed a GPS-collared coyote in the study area. With all sources of uncertainty propagated, we estimated that annually, cougars kill approximately 23.0% (95% CI: 8.4–54.7%) of the coyote population according to:

$$\textit{Intraguild Predation rate} = \frac{(2.2\ \text{cougars}\cdot 100\ \text{km}^{-2})\times(54.5\ \text{kills}\cdot\text{cougar}^{-1}\cdot\text{year}^{-1})\times(0.07\ \text{dead coyotes}\cdot\text{kill}^{-1})}{33.9\ \text{coyotes}\cdot 100\ \text{km}^{-2}}$$

Weight of Evidence for Facilitation, Suppression, and Null Hypotheses. We found evidence of both facilitation and suppression of other carnivore species by cougars (Fig. 6). Most notably, coyotes exhibited facilitation in three of the five measures evaluated (statistically significant attraction to kill sites, frequent carrion in diet, and high scavenging rates) and indication of suppression in two measures (the presence of intraguild predation and avoidance of cougars). Bears showed evidence of facilitation in two measures (moderate scavenging rates and moderate levels of carrion in diet), suppression in one measure (statistically significant avoidance of cougars), and no evidence in two measures (absence of statistically significant attraction or avoidance of kill sites, absence of intraguild predation). We found no evidence that cougars

influenced bobcats in any of the five measures we evaluated, fully supporting the null hypothesis that cougars neither suppress nor facilitate bobcats.

Discussion

We combined contemporaneous GPS-tracking of four carnivore species, prey identification at cougar kill sites, diet analysis with DNA metabarcoding, and remote-camera monitoring of cougar kills to assess the relative strength of suppressive and facilitative forces between a competitively dominant predator and three subordinate or co-occurring predators. Our strongest evidence of facilitation suggested that resource provisioning from cougars to coyotes through scavenging was so ubiquitous as to be an overwhelming determinant of coyote behavior, space use, and resource acquisition. This finding was demonstrated through strong attraction of coyotes to cougar kill sites, coyotes scavenging nearly all carcasses at cougar kill sites that we monitored, and coyote diets that nearly matched cougars in the magnitude and composition of ungulate consumption. However, we also show that cougars readily killed coyotes as prey and to a much lesser degree from competitive interactions at kill sites. These previously unquantified interactions highlight a complex game of risk and reward as coyotes seek to maximize their fitness by scavenging while simultaneously evading cougars (7, 36).

Selective forces operating on coyote behavior influence their acceptance of risk while acquiring resources at cougar kills. By observing dead coyotes at 7% of cougar kill sites, we found the risk cougars pose to coyotes to be substantial. We estimated that each cougar killed approximately 3.8 coyotes annually, though we note previous studies in the region have reported less coyote predation (21, 37) so this value may partially be the result of a small sample size. Nonetheless, given a cougar density of 2.2 per 100 km^2 in our study area (22), this suggests that approximately 8.4 coyotes are killed per 100 km^2 per year. With a coyote density of 33.9 per 100 km^2, this level of mortality reflects 23.0% (95% CI: 8.4–54.5% when all sources of uncertainty are propagated) of coyotes killed by cougars annually. Thus, cougar predation is a very significant mortality source to coyotes, but coyotes nevertheless readily accept this risk to forage extensively on cougar kills. This risk may not be evenly shared by all coyotes, however, because many (6 of 9) of the coyotes killed by cougars were young (< 2 years old), indicating that breeding coyotes may gain the most benefit from scavenging while younger and dispersing coyotes may bear most of the intraguild predation cost. Therefore, cougar predation on coyotes is probably compensatory to some degree although we cannot confirm this with the available data.

Only 1 of 9 coyotes killed by cougars occurred at a kill site. While this is mildly suggestive of increased risk while scavenging because coyotes spend substantially less than 1/9 of their daily activity budget (2.67 hours daily) scavenging, this small sample size precludes statistical determination of how much, or if, predation risk per unit time is higher while actively scavenging. If risk from cougars is not higher at kill sites than elsewhere on the landscape, then scavenging becomes an even more appealing prospect (Fig. 1a). While heightened risk at cougar kill sites is intuitive, this may not be the case for several reasons. First, coyotes may exhibit heightened vigilance levels when scavenging if dominant predators are perceived to be near (38). Second, assuming cougars are satiated after feeding on a kill, they may have little motivation to kill coyotes if their primary reason for doing so is for consumptive purposes. Determining whether cougars kill coyotes for an immediate energetic gain or the long-term benefit of removing a competitor should be the focus of further study. Two lines of evidence suggest coyotes do not reduce their use of kill sites if cougars are present at the kill; terms accounting for this were not significant in either the regression model of kill site visits from camera data nor a post-hoc step-selection function with an added term indicating whether a cougar was on a kill in question (*SI Appendix*, Text S11).

Not all species showed such a strong influence from cougars. Black bears were indifferent to cougar kill sites as determined from step-selection functions using GPS data which was surprising given substantial bear scavenging of cougar prey has been previously documented in other studies (15, 16, 20, 39). Not only did step selection functions indicate no attraction toward cougar kills, scat analysis revealed deer and elk constituted only a moderate percentage of the diets of black bears. Because bears readily kill and consume deer and elk

neonates (40), a substantial proportion of ungulates in their diet may have come from direct predation. A lower rate of bear scavenging at cougar kills is further supported by camera data indicating that bears were less frequent visitors to cougar kills than were coyotes. The lack of attraction to kill sites as measured by GPS data suggests that the bears that did visit cougar-killed prey may have encountered them opportunistically, in contrast to coyotes which at times made long and directed movements toward kill sites. Further, bears may not have frequently overlapped with cougar kills for several reasons. First, bears exhibit seasonal movements following ephemeral resource pulses and in this region, these seasonal resources are often located in habitats not frequently used by cougars. Second, the time when bears are active (i.e. not denning) generally coincides with time periods in which cougars kill smaller prey (21) further limiting the potential for scavenging, particularly if coyotes arrive first. The selection coefficient for distance to kill still was not statistically significant when male and female bears were modeled separately; however, the direction of the coefficient suggested male bears tended to be slightly attracted to kill sites while female bears tended to avoid them (*SI Appendix*, Text S13, Table S11). This accords with previous studies of brown bears wherein females with cubs had a lower propensity to scavenge than males (41).

While bears neither selected for nor avoided cougar kills, step selection functions indicated that black bears did actively avoid cougars. This was unexpected because black bears often usurp cougar prey at kill sites in other areas (15, 16). However, two recent studies on cougar prey selection in an adjacent study area reported finding bears as prey items (21, 37) and other literature reports more instances of cougars killing black bears than the converse (17). Our results suggest that black bears in our system view cougars as sufficiently threatening that they utilize the landscape to reduce the risk of confrontation. When modeled separately, both male and female bears exhibited avoidance of cougars (*SI Appendix*, Text S13, Table S11). Because body size is a major determinant of intraguild conflict (6), it is possible that larger bears (either larger individuals or larger bear species) would be less risk averse toward cougars, but we did not have the data to assess this.

Previous research indicates that intraguild predation is most likely to operate between carnivore species that have intermediate body size differences, broad dietary overlap, and that are taxonomically related (5, 6). Despite their taxonomic relatedness to cougars, we found no evidence suggesting that bobcats were attracted to cougar kill sites or otherwise influenced by cougars (42). Previous studies have found variable levels of bobcat scavenging (15, 39), but our three data sources indicated very clearly that bobcats in this system are not scavenging from cougars. We found zero instances of elk in any of 96 bobcat scats and zero observations of bobcats at cougar kill sites. While 8% of bobcat scats contained deer, this could be explained by direct predation because bobcats kill deer in this system (43). By foregoing energetically profitable cougar kills, bobcats in this system are solving the game of risk and reward quite differently than are coyotes. This is expected when the availability of non-scavenged foods is higher, or body condition is high, thus obviating the need to incur risk, or if predation risk at kills is higher, which might be the case for solitary bobcats relative to group-living coyotes (Fig. 1a).

While we have assessed behavioral interactions among a dominance hierarchy of extant carnivores, gray wolves (*Canis lupus*) are now recolonizing much of western North America including our study area. At the time of data collection, wolves were only a minor presence on the landscape and very rarely killed or scavenged prey in our study area (ODFW, unpublished data). But as wolves become more prominent on the landscape, the interplay between carnivores in this system is likely to change. For example, wolves are likely to deposit carrion in more open grassland environments than do cougars. The larger viewsheds in such vegetation types may be attractive to coyotes seeking scavenging opportunities (44), but the increased post-encounter predation risk by a wolf pack versus a solitary cougar may shift coyote behavior toward increased avoidance of wolf kills. Future work might assess whether coyotes perceive the risk-reward landscape with wolves differently than that with cougars by monitoring selection for, and scavenging at, both cougar and wolf kills.

The extent to which scavenging by co-occurring carnivores affects cougars is not clear. Despite cougars being an average of 4–5 times larger than coyotes in this area, we observed at least one instance via remote camera monitoring of kill sites where coyotes displaced a cougar

from its kill. The cougar involved had dependent young that were likely nearby, which may have made it especially vulnerable or responsive to the mesopredators. A question with broader ecological significance, however, is whether cougars increase their kill rate due to lost feeding opportunities caused by scavengers. While others have shown that black bears often usurp cougar kills which may lead to an increase in kill rate (15, 16), there are many confounding factors such as spatiotemporal variation in prey size, composition, or density, seasonality of kills, carrion decomposition rates, etc. to consider this a generality for all scavengers. However, our camera monitoring of carcasses showed that coyotes often arrived and began scavenging before cougars abandoned their kills, so any loss of carrion should technically be considered kleptoparasitism and not facilitation *per se*.

To conclude, it is probably a gross oversimplification to propose that species interactions within terrestrial carnivore communities have either strictly positive, negative, or even neutral consequences (7). We demonstrated that coyotes, and a lesser extent bears, were confronted by the opposing effects of both facilitation (i.e. food provisioning) and suppression (i.e. death), yet bobcats were seemingly unaffected by a dominant predator. Scavenging carrion from dominant predators incurs both risk and reward, and thus the willingness to engage in this activity must be mediated by behavior. But why would coyotes, bears, and bobcats approach the risk-reward tradeoff so differently? One possible explanation is that the selective pressures favoring one risk aversion strategy over another operated differently by species. As the efficiency of acquiring alternative prey increases, scavenging becomes less advantageous (Fig. 1a) and this should cause species with higher proficiency finding alternative prey to scavenge less. The ability to perceive risk likely differs by species as well, and regardless of whether these are innate or learned behaviors, our results suggest that the propensity to meet energetic demands by scavenging is variable across species, with neither strategy appearing to have an obvious fitness benefit over the other. This suggests that there are likely to be multiple viable strategies to solve this complex behavioral game.

Acknowledgments

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Figures and Tables

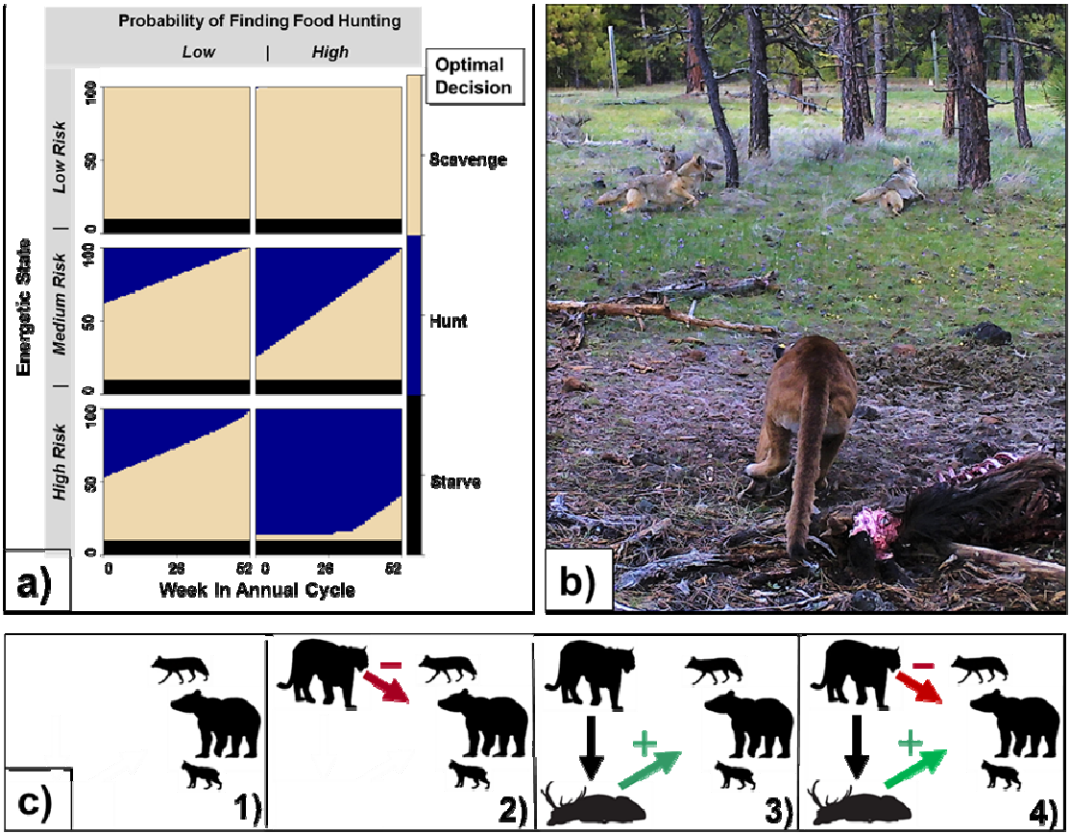

Figure 1. a) Predictions from a two patch dynamic state variable model used as an illustrative example. The conceptual model predicts the fitness-maximizing decision where the choices are to scavenge (patch 1, tan shading) or forego the scavenging opportunity and hunt alternative prey (patch 2, blue shading). The optimal decision in this theoretical model depends on the risk, quantified as daily probability of death, and reward, quantified as probability of finding food. The fitness-maximizing decision depends not only on risk and reward of each patch, but also the energetic state of the scavenger (y-axis) and the week within an annual cycle (x-axis). b) Interaction between coyotes and a cougar at a kill site monitored by remote camera. c) Possible influences of dominant predators in a carnivore community: 1) dominant predators do not influence other carnivores (null hypothesis), 2) dominant predators negatively influence other carnivores through interference competition or interspecific killing (suppression hypothesis), 3) dominant predators positively influence other carnivores due to resource provisioning via scavenging (facilitation hypothesis), and 4) dominant predators both positively and negatively influence other carnivores (provision-predation hypothesis).

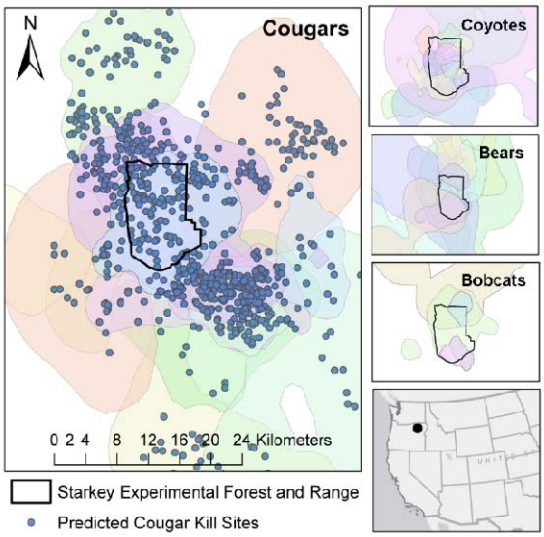

Figure 2. Study area. Left panel: Known and predicted cougar kill sites (blue points) and 95% kernel density home range estimates (colored polygons) for collared cougars. Right panels, top to bottom: coyote, black bear and bobcat 95% kernel density home range estimates (colored polygons). All panels: Starkey Experimental Forest and Range (black polygon).

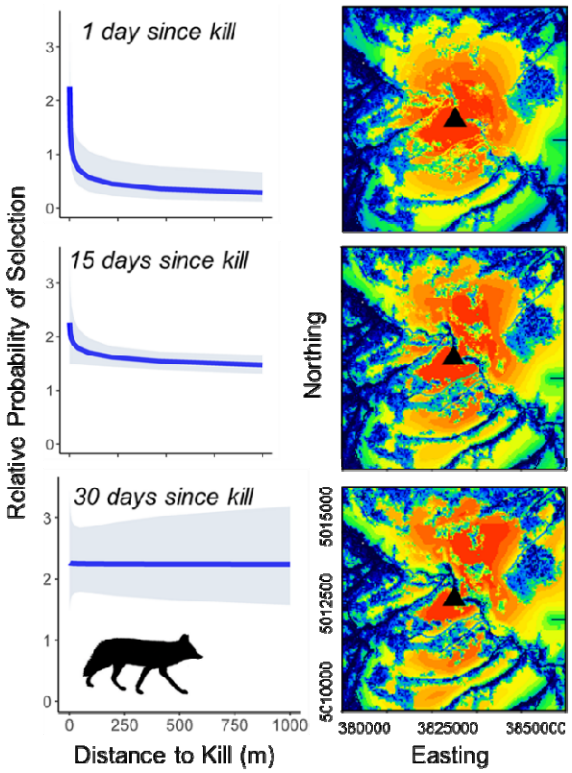

Figure 3. Attraction of coyotes to cougar kill sites. The first column presents marginal response plots for step selection functions showing the relative probability of selection as a function of the distance to the kill site. The second column presents predictive maps showing the relative probability of selecting for areas on the landscape as a function of the distance to the nearest kill site (black triangle). Warm colors indicate selection and cool colors indicate avoidance. In both columns, each row shows the predicted response at 1, 15, and 30 days after the kill was made.

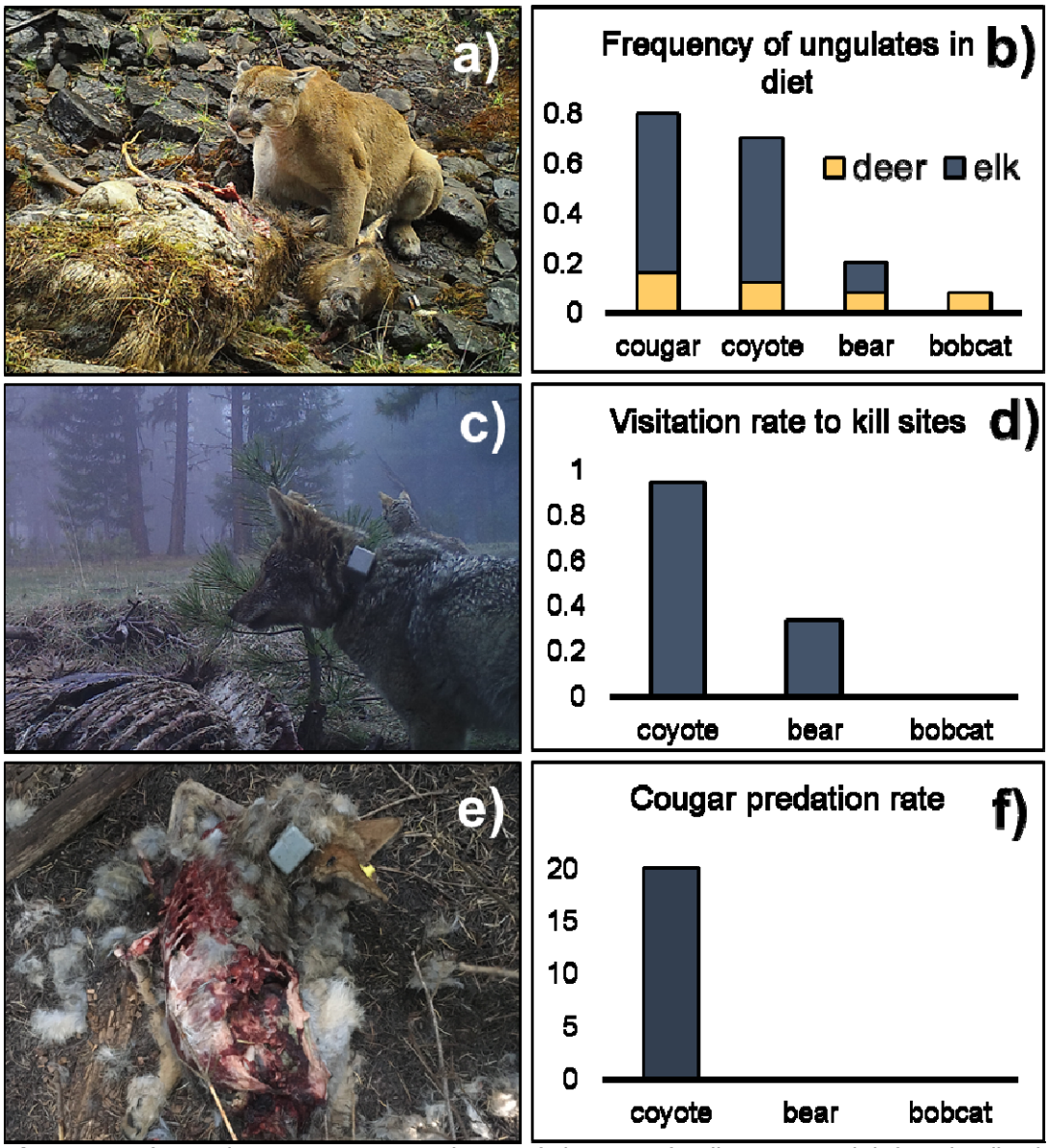

Figure 4. Left panel: Remote camera photos of a) cougar feeding on an adult female elk, c) coyotes scavenging a cougar kill, e): coyote killed by cougar. Right panel: plots showing b) percentages of deer and elk in carnivore diets determined from DNA-metabarcoding of scats (except for cougars in which diet estimates came from kill site investigations), d) scavenging rates of carnivores at cougar kill sites documented by remote cameras, and f) the estimated proportion of the population killed annually by cougars.

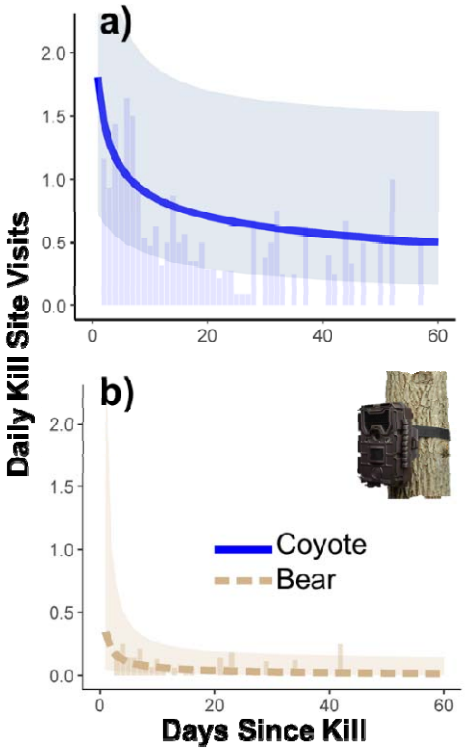

Figure 5. Remote-camera based estimates of daily visits to cougar kill sites by coyotes (panel a) and black bears (panel b). The thick line displays the predicted number of visits for coyotes (solid blue line) and bears (dotted tan line). Shaded regions indicate 95% confidence interval for the predictions. The vertical bars display the mean number of visits for every day since the kill was made, across all kill sites monitored (N = 28). The predictions assume that the kill was a large ungulate (i.e., the binary factor variable for prey size = 1) and that a cougar was present (i.e., the binary factor variable for cougar present = 1).

	GPS collars		Scats	Cameras	Clusters
	Cougar presence	*Kill site presence*	*Diet*	*Carcass Visitations*	*Intraguild predation*
	Suppression	**Facilitation**	**Facilitation**	**Facilitation**	**Suppression**
	Suppression	**Null**	**Facilitation**	**Facilitation**	**Null**
	Null	**Null**	**Null**	**Null**	**Null**

Figure 6. Weight of evidence for support of suppression, facilitation, and null hypotheses regarding the influence of a dominant predator, cougars, on subordinate or co-occurring carnivores: coyotes, bears, and bobcats.

Table 1. Parameter estimates for landscape and cougar variables influencing the relative probability of selection in step-selection functions in coyotes, black bears, and bobcats. PVT = potential vegetation type, CP = cougar present, D2C = distance to nearest cougar, KP = kill present, D2K = distance to nearest kill, and TSK = time since kill.

	Coyote			Bear			Bobcat		
	β	*SE*	*P*	*β*	*SE*	*P*	*β*	*SE*	*P*
CP × D2C[1]	0.20	0.08	0.01	0.55	0.15	<0.01	0.26	0.26	0.33
KP × D2K[1]	-0.26	0.05	<0.01	0.01	0.10	0.93	0.11	0.17	0.54
KP × D2K[1] × TSK[1]	0.07	0.02	<0.01	-0.02	0.04	0.59	-0.08	0.07	0.26
Canopy Cover	-0.13	0.01	<0.01	0.36	0.01	<0.01	0.32	0.01	<0.01
Distance to Road[1]	0.09	0.01	<0.01	0.13	0.01	<0.01	0.10	0.02	<0.01
Distance to Water[1]	0.02	0.01	0.01	-0.01	0.01	0.44	0.01	0.02	0.45
Ruggedness	-0.06	0.01	<0.01	0.16	0.01	<0.01	0.02	0.02	0.23
PVT, Wet Forest[2]	-0.09	0.02	<0.01	0.42	0.03	<0.01	0.98	0.07	<0.01
PVT, Dry Forest[2]	-0.08	0.02	<0.01	0.26	0.03	<0.01	0.71	0.07	<0.01
PVT, Other[2]	-0.25	0.15	0.09	1.39	0.11	<0.01	1.26	0.31	<0.01
Step Length[1]	0.03	<0.01	<0.01	0.04	0.01	<0.01	0.05	0.01	<0.01
Turning Angle[3]	-0.09	0.01	<0.01	0.04	0.00	<0.01	0.22	0.02	<0.01

[1]Indicates the variable was natural log transformed; [2]the reference category was Grassland; [3]indicates the cosine of the variable was used.