

The Comparative Effects of Large Carnivores on the Acquisition of Carrion by Scavengers

Maximilian L. Allen,^{1,*} L. Mark Elbroch,² Christopher C. Wilmers,³ and Heiko U. Wittmer¹

1. School of Biological Sciences, Victoria University of Wellington, P.O. Box 600, Wellington 6140, New Zealand; 2. Panthera, New York, New York 10018; 3. Center for Integrated Spatial Research, Environmental Studies Department, University of California, Santa Cruz, California 95064

Submitted April 21, 2014; Accepted December 18, 2014; Electronically published March 19, 2015

Online enhancements: videos. Dryad data: <http://dx.doi.org/10.5061/dryad.dh2vr>.

ABSTRACT: Pumas (*Puma concolor*) and black bears (*Ursus americanus*) are large carnivores that may influence scavenger population dynamics. We used motion-triggered video cameras deployed at deer carcasses to determine how pumas and black bears affected three aspects of carrion acquisition by scavengers: presence, total feeding time, and mean feeding-bout duration. We found that pumas were unable to limit acquisition of carrion by large carnivores but did limit aspects of carrion acquisition by both birds and mesocarnivores. Through their suppression of mesocarnivores and birds, pumas apparently initiated a cascading pattern and increased carrion acquisition by small carnivores. In contrast, black bears monopolized carrion resources and generally had larger limiting effects on carrion acquisition by all scavengers. Black bears also limited puma feeding behaviors at puma kills, which may require pumas to compensate for energetic losses through increasing their kill rates of ungulates. Our results suggest that pumas provide carrion and selectively influence species acquiring carrion, while black bears limit carrion availability to all other scavengers. These results suggest that the effects of large carnivores on scavengers depend on attributes of both carnivores and scavengers (including size) and that competition for carcasses may result in intraguild predation as well as mesocarnivore release.

Keywords: carrion acquisition, competition, energy distribution, mesocarnivore, *Puma concolor*, scavenging, *Ursus americanus*.

Introduction

The effects of large carnivores in structuring ecological communities, including initiating trophic cascades, are well established (Estes and Palmisano 1974; Ripple et al. 2014). For example, by suppressing smaller carnivores, large carnivores have been shown to indirectly influence abundances

of other species, including birds and herbivores (Estes and Palmisano 1974; Rogers and Caro 1998; Courchamp et al. 1999; Prugh et al. 2009). Large carnivores also have cascading effects solely on other carnivores; increases in gray wolves (*Canis lupus*) in Minnesota resulted in suppression of coyotes (*Canis latrans*), which in turn allowed an increase in smaller red foxes (*Vulpes vulpes*; Levi and Wilmers 2012). Within their respective communities, large carnivores are thought to exert population-level influences on other species, either directly via predation or indirectly as a result of behavioral changes to avoid predation that result in lower fitness (Sargeant et al. 1987; Ripple et al. 2001, 2014; Ripple and Beschta 2004; Atwood et al. 2007). An underappreciated mechanism by which large carnivores might affect ecological communities is through their interactions with scavengers at carcasses, where they may increase access to carrion resources for some species and restrict access for others.

Scavenging is a widespread behavior whereby species compete for limited resources in order to gain nutritional benefits and increase individual fitness (Houston 1995; DeVault et al. 2003; Selva et al. 2003; Wilson and Wilkovich 2011). For example, numerous facultative scavengers use scavenging to increase their breeding success (e.g., Angerbjörn et al. 1991; Watson et al. 1992). In addition, recent studies have highlighted the importance of scavenging to ecosystem function and the transfer of energy between trophic levels (DeVault et al. 2003; Selva and Fortuna 2007; Wilson and Wolkovich 2011). Carcasses also appear to provide frequent opportunities for interactions among carnivores, and these interactions result in complex ecological relationships and resource partitioning (Root 1967; Houston 1995; Selva and Fortuna 2007).

Large carnivores not only provide carrion but also play an important role in how carrion is distributed among scavengers (e.g., Wilmers et al. 2003a; Elbroch and Wittmer 2012; Moleón et al. 2014). For example, large carni-

* Corresponding author. Present address: Center for Integrated Spatial Research, Environmental Studies Department, 1156 High Street, University of California, Santa Cruz, California 95064; e-mail: maxallen@ucsc.edu.

Am. Nat. 2015. Vol. 185, pp. 822–833. © 2015 by The University of Chicago. 0003-0147/2015/18506-5543\$15.00. All rights reserved.
DOI: 10.1086/681004

vores provide carrion throughout the year, rather than in the seasonal pulses characteristic of anthropogenic sources (Wilmers et al. 2003b). In addition to providing carrion, large carnivores are also capable of opening carcasses, allowing other species access to edible portions of the carcass (Selva et al. 2003). Large carnivores, however, also directly limit scavenger species at their kills and, through competition, limit the availability of carrion for other obligate and facultative scavengers when they themselves are scavenging (Hunter et al. 2006; Allen et al. 2014b).

Within western North American ecological communities, both pumas (*Puma concolor*) and black bears (*Ursus americanus*) are large carnivores that have the potential to affect other scavengers. Pumas are solitary predators that frequently kill ungulates while only occasionally scavenging themselves (Bauer et al. 2005; Knopff et al. 2010), and by regularly killing ungulates and other prey they act as an important source of carrion to scavenger communities (Elbroch and Wittmer 2012; Allen et al. 2014b). In contrast, black bears frequently kill newborn ungulates (Pelton 1982) but rarely kill adults (Svoboda et al. 2011). Therefore, black bears rarely provide carrion for scavengers and are instead a dominant scavenger of ungulates, including puma kills (Murphy et al. 1998; Ruth and Murphy 2010; Allen et al. 2014b). The influence of black bears on the acquisition of carrion by other scavengers, however, has been understudied.

The effects pumas and black bears have on the acquisition of carrion by scavengers is likely species specific. Previous research has shown that some scavengers access and exploit carrion better than others, as a result of differences in morphology and behaviors (Root 1967; Hertel 1994; Houston 1995; Cortés-Avizanda et al. 2012). Here, we evaluated the potential influences of competition on scavenging behaviors instead, and we attempted to determine how pumas and black bears affect the acquisition of carrion by scavenger classes and species. To address this question, we conducted a series of in situ experiments at black-tailed deer (*Odocoileus hemionus columbianus*) carcasses, comparing carrion acquisition at puma kills (video 1; videos 1–3 available online) to that at matching control carcasses and at a separate set of experimental carcasses where black bears were either present or absent. Specifically, we analyzed three aspects of carrion acquisition exhibited by each scavenger species: presence or absence at carcasses, total feeding time, and mean feeding-bout duration. We used presence as a proxy of the ability of scavengers to acquire energy from a given carcass, and we used total feeding time as a proxy for the amount of energy a scavenger was able to gain from a given carcass. Last, we used mean feeding-bout duration as a proxy for the effects of predation risk perceived by scavengers, because we hypothesized that a scavenger should exhibit shorter feeding bouts at carcasses with higher per-



Video 1: Still photograph from a video, available online, showing a male puma feeding on a black-tailed deer it killed.

ceived risk (Charnov 1976; video 2). We hypothesized that pumas and black bears would limit each aspect of carrion acquisition for all scavengers but that there would be variation in the magnitude of their limitation based on the body size of scavenger species.

Previous research demonstrated that pumas are subordinate to other large carnivores, including gray wolves, grizzly bears (*Ursus arctos*), jaguars (*Panthera onca*), and sometimes coyotes (*Canis latrans*; Ruth and Murphy 2010). We thus expected pumas to have a small effect on the acquisition of carrion by large carnivores. However, pumas are known to regularly kill smaller carnivores, and both mesocarnivores and small carnivores are present in the diet of pumas across much of their distribution (Murphy and Ruth 2010). Because of their dominance over mesocarnivores and small carnivores, we expected pumas to limit all three aspects of carrion acquisition by these classes. Pumas are also known to exhibit behaviors to minimize carcass detection by avian species, including caching of kills and moving kills to areas of dense overhead cover (Bischoff-Mattson and Mattson 2009; Ruth and Murphy 2010; Allen et al. 2015). Because of these behaviors, we expected pumas to limit the acquisition of carrion by avian scavengers, mainly by limiting their presence.

Black bears are capable of rapidly eating large amounts of food (video 3), including carrion, and their large body size allows them to exclude other species from carrion (Murphy et al. 1998; Allen et al. 2014b). On the basis of these observations, we hypothesized that black bears would be capable of monopolizing carrion resources, thereby limiting the presence and total feeding time of other scavengers. Despite their large size and occasional predation, black bears rarely kill other carnivores (Pelton 1982; Larivière 2001).



Video 2: Still photograph from a video, available online, showing an interaction between scavengers, where a gray fox flees from an approaching bobcat.

This suggests that other scavengers are not frequently in danger of injury or death from scavenging black bears, and we therefore hypothesize that black bears would have small limitations on mean feeding-bout duration of other scavengers.

Methods

Study Area

We conducted our study in the Mendocino National Forest, California. The study area encompassed approximately 1,000 km² (fig. 1). The area was primarily forested, with elevations ranging from 396 to 2,466 m and the majority of precipitation occurring from December through March. The habitat and meteorological aspects of the study area have been described in detail elsewhere (Allen et al. 2014a). Black bears occurred at high population densities despite hunting pressure (Forrester 2014). Pumas were legally protected from hunting, occurred at low population densities, and were the only predator in the system known to frequently kill adult ungulates (Allen et al. 2014a). Black-tailed deer were the most common large-ungulate prey of pumas, while wild pigs (*Sus scrofa*) and tule elk (*Cervus elaphus nannodes*) were present at very low densities but were not preyed on by pumas (Allen et al. 2014a). Intraguild predation by pumas was noted in the study area, with pumas killing black bears, coyotes, gray foxes, and raccoons (Allen et al. 2015).

Experimental Design and Field Methods

From January 2010 to November 2012, we used motion-triggered video cameras with infrared flash to record and

compare scavenger activity at different types of black-tailed deer carcasses. Because of the different spatial scales that can determine the scavenger assemblage present at a carcass, we designed our study to account for spatial characteristics and autocorrelation by determining the carcass location on the basis of habitat. For pumas, we compared the acquisition of carrion by scavengers at kills made by pumas ($n = 58$) to that at control carcasses ($n = 58$) with matching habitat characteristics that we placed simultaneously on the landscape. For black bears, we distributed black-tailed deer carcasses in varied habitats across the study area and compared scavenger carrion acquisition at carcasses where black bears were present ($n = 33$) to that at carcasses where they were absent ($n = 46$). For puma control carcasses and the black bear experiments, we used black-tailed deer killed through vehicle collisions that were fresh and in good condition, allowing us to replicate the freshness and decomposition state of actual puma kills.

Between June 2010 and December 2012, we captured seven pumas and fitted them with a combined ARGOS satellite GPS/radio telemetry collar (Lotek 7000SAW, New Market, ON; Allen et al. 2014a). In order to find fresh puma kills, we downloaded the location data via satellite connection every 3 days and investigated any GPS clusters where a monitored puma had spent at least 2 h within 150 m and appeared to still be present on the same day as the Argos-relayed GPS downloads (Allen et al. 2014b). We approached these potential feeding sites during midday, when pumas were least active, confirmed their continued presence with very-high-frequency telemetry, and limited the duration of our visits at the site in order to limit disturbance of the puma and avoid possible carcass abandonment. We secured the carcass with a wire cable to hold it within 1 m of



Video 3: Still photograph from a video, available online, showing a black bear scavenging on the carcass of a black-tailed deer.

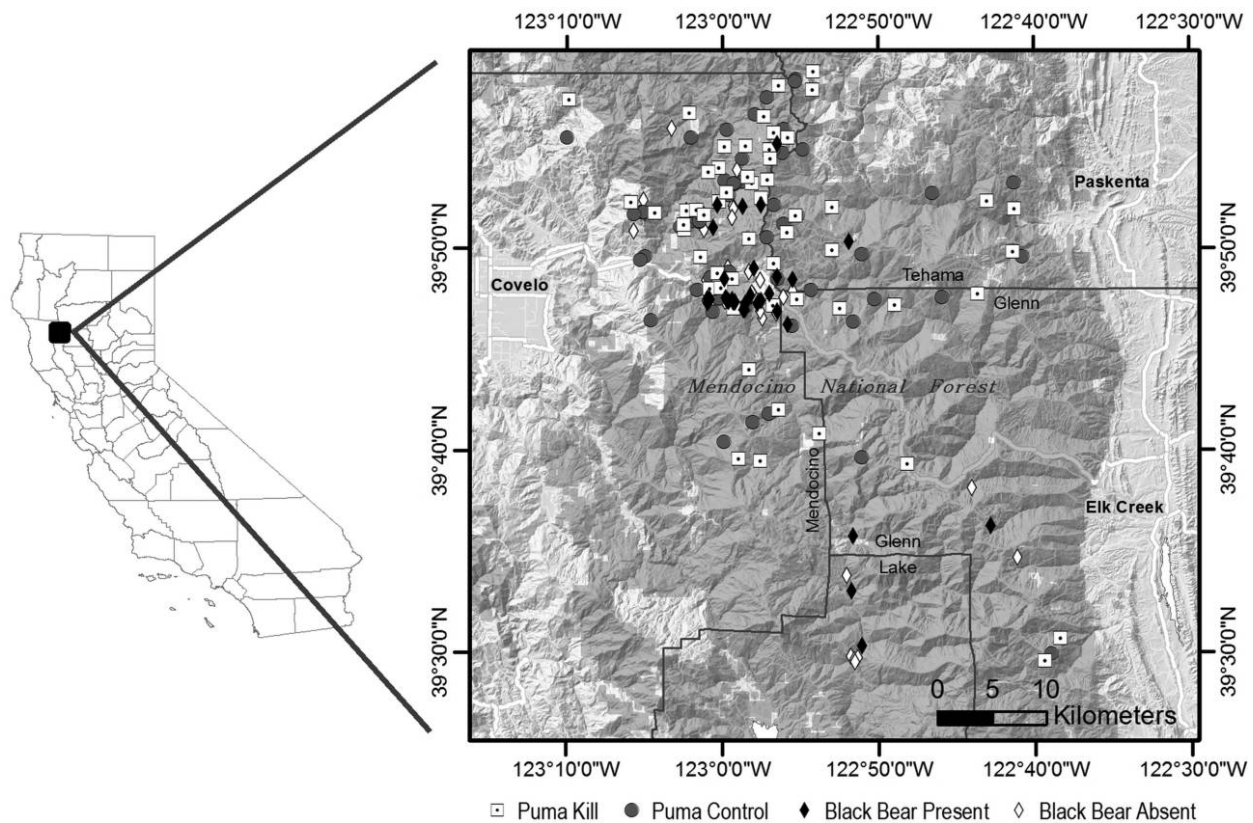


Figure 1: Map of the study area in Mendocino National Forest. Each carcass type is noted on the map to show the distribution, within the greater context of the Northern Coast Ranges.

its location for monitoring and then deployed a motion-triggered camera (Bushnell ScoutCam, Overland Park, KS) to document the feeding behaviors of scavengers at the kill. We set the motion-triggered cameras to record the maximum amount of activity, with 60 s of video recorded at each trigger and a pause of 1 s before becoming active at the next trigger. We recorded the habitat characteristics of the site and then found the site for the puma control carcass by matching the habitat characteristics as closely as possible to, in order of importance, (1) primary habitat type, (2) overhead tree species, (3) canopy cover, (4) secondary habitat type, (5) distance to secondary habitat, and (6) elevation. Before arriving at the site of the control carcass, we prepared a black-tailed deer carcass to provide an equivalent amount of meat in the same stage of decomposition as at the puma kill and then secured the carcass and deployed another camera.

For the black bear experiments, we placed 100 black-tailed deer carcasses in a variety of habitats, in order to increase detection probabilities for all vertebrate scavengers present in our study area. We secured each carcass in place with a wire cable and monitored the carcass for scavenger feeding behaviors with a motion-triggered video cam-

era with infrared flash (Cuddeback IR, De Pere, WI). We set the motion-triggered cameras to record the maximum amount of activity, with 30 s of video and a pause of 60 s before the next trigger. In order to understand the possible effects of black bears on other scavengers, we divided carcasses into those where black bears were “present” (defined as carcasses at which they were the first or second scavenger to arrive) and those where black bears were “absent” (defined as carcasses at which they were either completely absent or one of the last scavengers to arrive and at which they spent ≤ 10 min). We removed carcasses from our analyses (1) when black bears had an unknown influence (i.e., when they were the third or later scavenger to arrive and spent > 10 min at the carcass; $n = 10$) or (2) when carcasses had incomplete data because of camera malfunctions or camera displacements by black bears ($n = 11$).

Statistical Analyses

To determine the influences of pumas and black bears on scavengers, we considered three aspects of carrion acquisition: “presence,” “total feeding time,” and “mean feeding-out duration.” Presence was calculated as the percentage

of carcasses at which each scavenger species or class was recorded. We calculated the duration of a given feeding bout by subtracting the time at the start of a visit from the time at the end of a visit. For visits of less than 30 s, we considered the species or class present for 1 min rather than 0 min, and we rounded all other visits to the closest minute. Total feeding time was calculated as the sum of all feeding bouts at a given carcass, and mean feeding-bout duration was calculated as the mean duration of all feeding bouts at a given carcass.

We used generalized linear models (GLMs) to analyze each aspect of carrion acquisition, using the program R (ver. 3.1.0; R Development Core Team 2014). The data for these analyses are available in the Dryad Digital Repository (<http://dx.doi.org/10.5061/dryad.dh2vr>; Allen et al. 2015). In each analysis, we considered $P \leq .05$ to be significant and $P \leq .1$ to be marginally significant. We first tested for the effects of pumas and black bears on scavenger species and then analyzed scavengers by classes, with each scavenger species placed into one of four classes according to their body mass (table 1). We used each aspect of carrion acquisition as our dependent variables and chose the appropriate distribution on the basis of the error residuals. We used a binomial distribution with a logit link for presence, a Gamma distribution with a log link for total feeding time, and a Gaussian distribution with a log link for mean feeding-bout duration. We used carcass type as our first independent variable (first puma kill vs. control, then black bear present vs. absent). For our species analyses, we also included the corresponding value of carrion acquisition by the other nine most frequent scavengers as independent variables. For our class analyses, we included the corresponding value of carrion acquisition by the three other classes. Finally, we analyzed the effects of black bears on pumas, including puma carrion acquisition and feeding at their own kills. At puma kills, we compared puma total feeding time and mean feeding-bout duration before and after the arrival of black bears. We used puma total feeding time and mean feeding-bout duration as the dependent variables and whether the feeding occurred before or after bear arrival as the independent variable. As described

above, we used a Gamma distribution with a log link for total feeding time and a Gaussian distribution with a log link for mean feeding-bout duration.

Following these GLM analyses, we performed post hoc Akaike information criterion (AIC; Akaike 1974) analyses to determine the likely cause of the observed increased scavenging of small carnivores at puma kills. We used the GLM analyses as described above, using each aspect of carrion acquisition as our dependent variable. For our predictor variables we used models for just pumas and for the mesocarnivore and avian classes combined and then compared the AIC weights of the models to determine the top model.

Results

Between May 2011 and November 2012, we recorded 10,775 videos of animal activity at puma kills and 9,663 videos of animal activity at puma control carcasses. From GPS data, pumas stayed within 150 m of 58 black-tailed deer kills we monitored for a mean of 75.1 (± 5.9 SE) h. We set up cameras at puma kills a mean of 39.8 (± 2.9 SE) h after the puma made the kill, and we set up the paired carcasses and cameras within a mean of 1.5 (± 0.2 SE) h after the camera was set up at the puma kill.

Between January 2010 and November 2012, we recorded 3,039 videos of animal activity at carcasses where black bears were present and 9,038 videos of animal activity at carcasses where black bears were absent. Black bears detected carcasses a mean of 48.5 (± 12.1 SE) h after they were placed in the landscape. Black bears had a mean total feeding time of 105.9 (± 25.6 SE) min and a mean feeding-bout duration of 4.8 (± 0.9 SE) min.

Effects of Pumas on Scavengers

Pumas had mixed effects on the three aspects of acquisition of carrion by specific scavenger classes and species at their kills (table 2). Pumas did not limit large carnivores overall, but among large carnivores, pumas significantly limited the presence of domestic dogs ($z_{114} = -2.40$, $P = .0166$) and marginally limited the presence of coyotes and the mean

Table 1: Species for each scavenger class

Scavenger class	Scavenger species
Large carnivore	Black bear (<i>Ursus americanus</i>), coyote (<i>Canis latrans</i>), domestic dog (<i>Canis familiaris</i>), puma (<i>Puma concolor</i>)
Mesocarnivore	Bobcat (<i>Lynx rufus</i>), fisher (<i>Martes pennanti</i>), gray fox (<i>Urocyon cinereoargenteus</i>), raccoon (<i>Procyon lotor</i>)
Small carnivore	Ringtail (<i>Bassariscus astutus</i>), striped skunk (<i>Mephitis mephitis</i>), western spotted skunk (<i>Spirogale gracilis</i>)
Avian	Bald eagle (<i>Haliaeetus leucocephalus</i>), common raven (<i>Corvus corax</i>), golden eagle (<i>Aquila chrysaetos</i>), great horned owl (<i>Bubo virginianus</i>), northern goshawk (<i>Accipiter gentilis</i>), red-tailed hawk (<i>Buteo jamaicensis</i>), turkey vulture (<i>Cathartes aura</i>)

Note: Species composition for each of the four scavenger classes we tested for influences from pumas and black bears. Scavenger species were grouped into classes on the basis of their mass.

Table 2: Effects of pumas on three aspects of carrion acquisition by scavengers (presence, total feeding time, and mean feeding-bout duration)

Scavenger	Presence (%)			Mean total feeding time in minutes (95% CI)			Mean feeding-bout duration in minutes (95% CI)			P
	Kill	Control	P	Kill	Control	P	Kill	Control	P	
Class:										
Large carnivore	79.3	82.8	.4052	136.1 (90.3–181.8)	127.3 (72.4–182.3)	.6564	7.90 (5.84–9.96)	8.99 (6.98–10.99)	.6481	
Mesocarnivore	44.8	60.3	.0845	58.8 (29.7–87.8)	135.1 (93.3–177.0)	.0021	2.33 (1.73–2.93)	3.77 (3.01–4.54)	.0046	
Small carnivore	25.9	22.4	.3213	47.0 (7.7–86.3)	26.8 (5.6–48.0)	.4589	3.89 (.84–6.95)	1.53 (1.10–1.95)	.2293	
Avian	37.9	36.2	.7972	50.4 (43.6–57.2)	152.9 (65.9–239.8)	.0132	3.28 (2.05–4.52)	5.56 (3.81–7.31)	.0366	
Species:										
Black bear	72.4	62.1	.3852	145.9 (98.5–193.2)	151.8 (81.2–222.3)	.5134	8.91 (6.64–11.18)	13.78 (9.24–18.33)	.0868	
Bobcat	8.6	15.5	.4126	7.8 (–1.7 to 17.3)	37.7 (–34.0 to 109.3)	.0386	1.68 (.76–2.59)	1.22 (.93–1.51)	.8432	
Common raven	22.4	27.6	.7715	29.1 (4.6–53.5)	47.9 (21.9–73.8)	.7557	3.07 (1.40–4.73)	4.00 (2.49–5.51)	.6084	
Coyote	25.9	36.2	.0796	8.0 (1.9–14.1)	16.5 (6.6–26.3)	.2533	1.46 (1.01–1.92)	2.71 (1.59–3.82)	.4544	
Domestic dog	1.7	13.8	.0166	7.0 (7.0–7.0)	28.0 (–.3 to 56.3)	.6344	1.40 (1.40–1.40)	3.67 (1.04–6.30)	.9571	
Fisher	17.2	22.4	.4637	8.3 (2–16.5)	82.3 (–.2 to 164.9)	.0004	1.95 (.47–3.43)	3.33 (2.12–4.55)	.2379	
Gray fox	37.9	48.3	.1454	81.4 (11.0–151.9)	96.3 (48.8–143.9)	.0075	2.29 (1.68–2.89)	3.90 (2.98–4.82)	.0123	
Ringtail	15.5	6.9	.0680	51.0 (–20.2 to 122.2)	36.5 (–1.6 to 74.6)	.1299	2.96 (1.73–4.19)	2.17 (1.16–3.18)	.6861	
Spotted skunk	17.2	13.8	.2564	45.0 (–26.1 to 116.1)	20.2 (–3.8 to 44.2)	.0313	3.95 (–.68 to 8.58)	1.28 (.90–1.65)	.0082	
Turkey vulture	19.0	22.4	.4568	66.5 (27.8–105.1)	178.8 (57.3–300.2)	.2818	4.40 (2.12–6.68)	8.32 (4.20–12.43)	.3228	

Note: We report the effects on scavenger classes and species for each variable at puma kills and control carcasses. We report the percentage of carcasses where a scavenger was present and the mean and 95% confidence intervals (CI) for total feeding time and mean feeding-bout duration. We also report the P value from our generalized linear models, with statistically significant P values indicated by boldface.

feeding-bout duration of black bears (table 2). Pumas also marginally limited the presence of mesocarnivores (table 2) while significantly decreasing both their total feeding time ($t_{60} = -3.22, P = .0021$) and their mean feeding-bout duration ($t_{60} = -2.95, P = .0046$). Among mesocarnivores, pumas significantly limited the total feeding times of three species, bobcat ($t_{13} = -3.53, P = .0386$), fisher ($t_{22} = -4.85, P = .0004$), and gray fox ($t_{49} = -2.82, P = .0075$), while also significantly decreasing the mean feeding-bout duration of gray foxes ($t_{49} = -2.63, P = .0123$). Finally, pumas significantly decreased the total feeding time of avian scavengers ($t_{42} = -2.60, P = .0132$) as well as their mean feeding-bout duration ($t_{42} = -2.17, P = .0366$).

Pumas apparently had positive effects on the acquisition of carrion by small carnivores. For example, small-carnivore total feeding time was 75% longer at puma kills than at control carcasses, and their mean feeding-bout duration was 2.6 times longer at puma kills than at control carcasses. Among small carnivores, ringtails marginally increased their presence at puma kills (table 2), while spotted skunks significantly increased their total feeding time ($z_{17} = 2.61, P = .0313$) and mean feeding-bout duration ($z_{17} = 3.49, P = .0082$). Using a post hoc AIC analyses, we found that the

combined effect of the presence of mesocarnivore and avian classes was more important than the presence of pumas on small-carnivore presence ($wAIC$ [AIC weight] = 1.00 vs. $wAIC = 0.00$). Total feeding times of mesocarnivores and avian scavengers were slightly better than puma presence at explaining small-carnivore total feeding time ($wAIC = 0.58$ vs. $wAIC = 0.42$), while presence of pumas was much better than the combined mean feeding-bout durations of mesocarnivores and birds at explaining the mean feeding-bout duration of small carnivores ($wAIC = 0.81$ vs. $wAIC = 0.19$). This suggests that pumas may initiate a cascading effect among scavenger classes by limiting the presence and total feeding times of mesocarnivore and avian scavengers and thus allowing small carnivores to increase access to carrion at their kills (fig. 2).

Effects of Black Bears on Scavengers

Overall, black bears had a strong limiting influence on the acquisition of carrion by scavengers. In most cases, the limitations exhibited by black bears were of a larger magnitude than those of pumas (table 3), but they did not significantly limit the feeding-bout duration of any class or

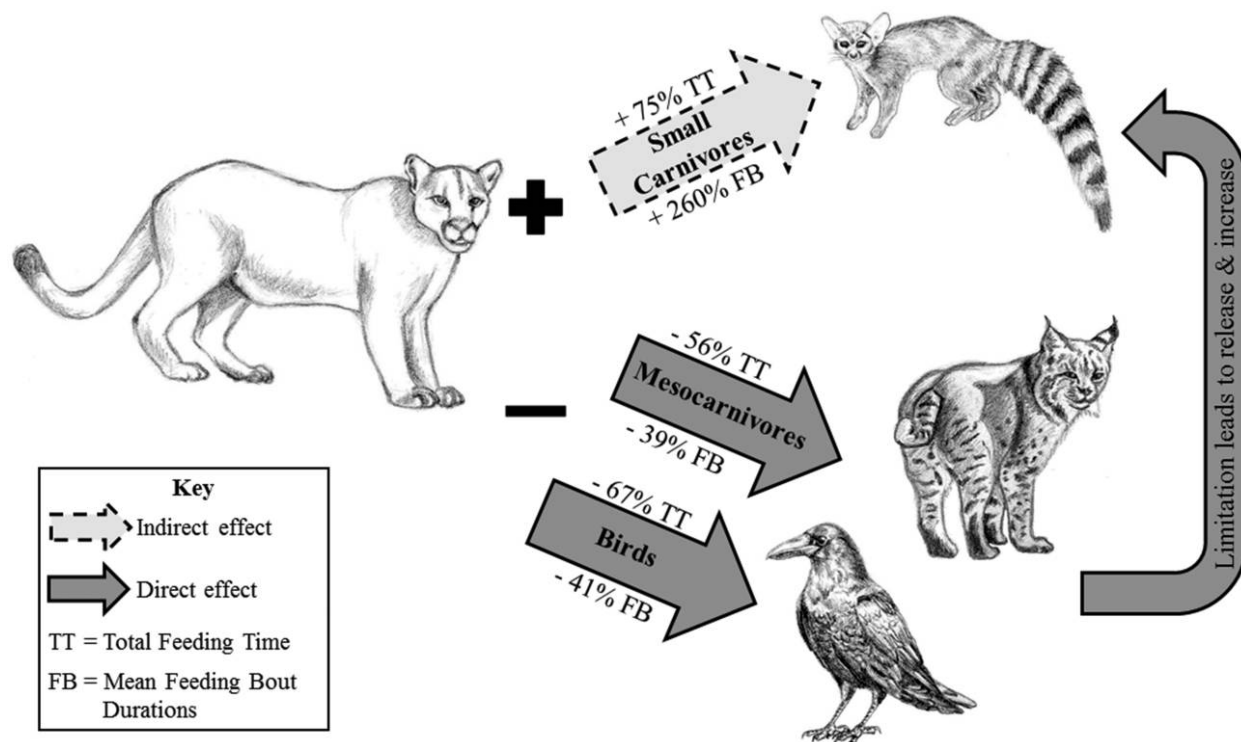


Figure 2: Potential cascading effects initiated by pumas at their kills. Pumas limited the total feeding times and mean feeding-bout durations of mesocarnivores and birds. By reducing carrion acquisition by these classes, pumas apparently allowed small carnivores to increase their acquisition of carrion. Drawings provided courtesy of Yiwei Wang.

Table 3: Effects of black bears on three aspects of carrion acquisition by scavengers (presence, total feeding time, and mean feeding-bout duration)

Scavenger	Presence (%)		Mean total feeding time in minutes (95% CI)		Mean feeding-bout duration in minutes (95% CI)		P		
	Present	Absent	Present	Absent	Present	Absent			
Class:									
Large carnivore	18.2	63.0	.0021	10.0 (-8 to 20.8)	49.7 (23.8-75.5)	1.55 (.80-2.30)	3.82 (2.14-5.51)	.0173	.2584
Mesocarnivore	27.3	84.8	< .0001	6.1 (3.1-9.1)	269.1 (167.1-371.2)	1.13 (.91-1.35)	4.81 (3.73-5.90)	< .0001	.1441
Small carnivore	6.1	17.4	.8805	1.0 (1.0-1.0)	15.0 (.0-30.0)	1.00 (1.00-1.00)	1.74 (1.05-2.43)	.0134	.8893
Avian	60.6	65.2	.1714	50.4 (26.5-74.3)	180.8 (109.6-252.0)	3.13 (2.04-4.22)	6.45 (3.57-9.34)	.0003	.5284
Species:									
Bobcat	6.1	28.3	.0397	11.0 (-8.6 to 30.6)	217.8 (108.2-327.4)	1.55 (.47-2.63)	3.98 (2.70-5.27)	.0128	.3965
Common raven	33.3	43.5	.2477	8.3 (3.3-13.2)	94.3 (19.1-169.5)	1.89 (.48-3.30)	3.18 (1.24-5.12)	.0043	.2482
Coyote	18.2	41.3	.5106	9.7 (-1.3 to 20.6)	36.6 (20.4-52.7)	1.55 (.80-2.30)	2.90 (1.54-4.27)	.3144	.7662
Domestic dog	3.0	19.6	.2077	1.0 (1.0-1.0)	27.1 (-4.0 to 58.2)	1.00 (1.00-1.00)	3.52 (1.34-5.69)	.0799	.0988
Fisher	9.1	32.6	.1312	8.0 (3.1-12.9)	144.7 (20.4-269.0)	2.22 (.70-3.75)	4.34 (2.65-6.04)	.0603	.7114
Golden eagle	12.1	13.0	.2409	11.0 (-4.2 to 26.2)	177.3 (57.1-297.6)	3.20 (.40-5.99)	10.18 (3.09-17.27)	.3102	.4531
Gray fox	15.2	60.9	.0021	12.4 (3.4-21.4)	171.2 (66.9-275.4)	1.03 (.97-1.10)	4.81 (3.25-6.37)	.0016	.2020
Ringtail	.0	6.5	.9971	...	7.3 (-2.3 to 17.0)	...	1.63 (1.01-2.25)
Spotted skunk	.0	10.9	.9980	...	19.4 (-4.1 to 42.9)	...	1.92 (.84-3.00)
Turkey vulture	51.5	21.7	.0440	65.2 (30.6-99.9)	222.7 (110.0-335.4)	3.95 (2.42-5.48)	9.39 (3.42-15.36)	.0063	.0086

Note: We report the effects on scavenger classes and species for each variable at carcasses where black bears were present and absent. We report the percent of carcasses where a scavenger was present and the mean and 95% confidence intervals (CI) for total feeding time and mean feeding-bout duration. We also report the P value from our generalized linear models, with statistically significant P values indicated by boldface.

species. Black bears exhibited the largest limitation on carrion acquisition for mesocarnivores. For example, mesocarnivores fed 44 times longer at carcasses where black bears were absent than at those where bears were present. Black bears significantly limited mesocarnivore total feeding time ($t_{47} = -9.06$, $P < .0001$) and presence ($z_{114} = -4.11$, $P < .0001$). Among mesocarnivores, black bears significantly limited bobcat total feeding time ($t_{14} = -4.29$, $P = .0128$) and presence ($z_{77} = -2.06$, $P = .0397$) as well as gray fox total feeding time ($t_{32} = -3.46$, $P = .0016$) and presence ($z_{77} = -3.08$, $P = .0021$).

Black bears significantly limited the acquisition of carrion by large carnivores by limiting both their presence ($z_{77} = -3.08$, $P = .0021$) and their total feeding time ($t_{34} = -2.52$, $P = .0173$). Black bears also significantly limited the total feeding time of small carnivores ($t_9 = -3.74$, $P = .0134$) and completely excluded ringtails and spotted skunks from carcasses where they were present. Black bears significantly limited the total feeding time of the avian class ($t_{48} = -3.97$, $P = .0003$) and two avian species: common ravens ($t_{30} = -3.22$, $P = .0043$) and turkey vultures ($t_{22} = -3.21$, $P = .0063$). Among scavengers, the only exception to limitation was the presence of turkey vultures, which were present at significantly more carcasses where black bears were also present ($z_{77} = 2.01$, $P = .0440$).

Effects of Black Bears on Pumas

Black bears affected puma carrion acquisition by limiting their presence, total feeding time, and feeding-bout duration. In particular, pumas scavenged at 15.2% of carcasses where black bears were absent but did not scavenge at any of the carcasses where black bears were present. At carcasses where black bears were absent, total feeding time for scavenging pumas was 53.9 (95% confidence interval [CI] = -25.3 to 133.0) min, and their mean feeding-bout duration was 11.1 (95% CI = -2.1 to 24.3) min.

Black bears also affected puma feeding behaviors at their own kills, affecting how quickly pumas abandoned their kills as well as their total feeding time and mean feeding-bout duration. After the arrival of a black bear, pumas did not return to 72.4% of their kills and returned only once to another 13.8%. Before black bear arrival, pumas fed for a total feeding time of 106.5 (95% CI = 66.2–146.9) min, and after bear arrival, they fed for 16.8 (95% CI = 3.3–30.2) min, resulting in a significant limitation ($t_{33} = -4.46$, $P < .0001$). Black bears did not significantly limit puma mean feeding-bout duration ($t_{33} = -1.07$, $P = .2943$). Black bears fed for a total mean feeding time of 145.9 (95% CI = 98.5–193.2) min at puma kills, suggesting that pumas could still have fed on the carcasses they abandoned after the arrival of black bears. The usurpation of puma kills was not without risk, as in one instance a

puma killed a subadult black bear that had been feeding on its kill.

Discussion

Many species are facultative scavengers to some degree, and, in some food webs, there is a greater amount of energy transferred through the scavenging of carrion than through direct predation (Wilson and Wolkovich 2011). Thus, the importance of carrion resources in driving and structuring ecological communities is increasingly being recognized (DeVault et al. 2003; Wilmers et al. 2003a; Wilson and Wolkovich 2011; Cortés-Avizanda et al. 2012; Moleón et al. 2014). Given the importance of carrion, any variables influencing access to these resources are likely to affect scavenger population dynamics, the composition of facultative scavengers in ecological communities, and potentially ecosystem function (Angerbjörn et al. 1991; Watson et al. 1992; Selva and Fortuna 2007; Wilson and Wolkovich 2011; Moleón et al. 2014). Despite low sample sizes for some scavenger species (e.g., we recorded only 14 bobcats and 13 ringtails at our 58 active puma kills and 58 matching control carcasses), we found that pumas and black bears both affected aspects of carrion acquisition by other scavengers. General trends suggested that pumas varied in their effects on scavenger classes, while black bears limited all scavengers and were generally more effective at monopolizing carcasses than pumas.

Pumas provided carrion through their kills to diverse vertebrate scavengers and had species-specific effects on scavengers. While pumas did not limit other large carnivores within their communities, they limited the total feeding times and mean feeding-bout durations of both mesocarnivores and birds. This suggests that pumas are effective at excluding smaller, subordinate competitors but not dominant competitors. In the case of these subordinate scavengers, most of their feeding is likely occurring while pumas are absent from their kill or after they abandon it, rather than through direct usurpation. Since energy intake of scavengers from carrion can influence fitness and reproductive ability (e.g., Angerbjörn et al. 1991; Watson et al. 1992), these interactions with pumas may very well affect the population dynamics of scavengers.

We also observed a surprising trend, where the limitation by pumas of carrion acquisition by mesocarnivores and avian scavengers apparently led to an increase in all three aspects of carrion acquisition by small carnivores at their kills. This suggests a cascading pattern in the acquisition of carrion among scavengers and may provide an alternate explanation for observed intraguild cascades among carnivores (e.g., Levi and Wilmers 2012). The cascading patterns initiated by large carnivores, intraguild or otherwise, may include how large carnivores increase small-

carnivore acquisition of carrion, in conjunction with other resources (e.g., Hardin 1960).

The effects on carrion acquisition attributable to black bears were less intricate than those of pumas but, surprisingly, were of a greater magnitude. Black bears monopolized carrion resources they found and had the largest limitations on the total feeding times of all scavengers. Given that black bears are unlikely to provide significant amounts of carrion to other scavengers through their own kills (*sensu* Svoboda et al. 2011), this result suggests that black bears were an important limitation on other scavengers. Black bears limited all three aspects of carrion acquisition for every scavenger class and for nearly every scavenger species (the presence of turkey vultures was higher at carcasses where black bears were present, while black bears completely excluded ringtails and spotted skunks), although none of the effects on mean feeding-bout duration were significant. The high magnitude of their effects suggests that black bears, like other dominant scavengers (Cortés-Avizanda et al. 2010, 2012), act as a major limitation on energy transfer with regard to carrion resources in ecological communities. We thus hypothesize that black bears are dominant over other scavengers because of their ability to eat large quantities of food quickly rather than because they use their large size to actively exclude other scavengers.

Black bears also affected pumas at their kills, supporting the growing body of evidence that solitary felids are negatively affected by dominant scavengers that can usurp their kills (Murphy et al. 1998; Hunter et al. 2006; Krofel et al. 2012; Allen et al. 2013; Elbroch and Wittmer 2013). Pumas abandoned 72.4% of their kills once black bears arrived, a behavior similar to that of cheetahs (*Acinonyx jubatus*), which limit risk by abandoning their kills after the arrival of dominant scavengers (Hunter et al. 2006). The abandonment of kills likely limits the energetic intake of pumas and could force pumas to kill more often to meet their energetic requirements (Murphy et al. 1998; Elbroch and Wittmer 2013; Allen et al. 2014a; Elbroch et al. 2014). Facultative scavengers are not generally believed to affect population dynamics of species they consume during scavenging (Wilson and Wolkovich 2011). However, if black bears are causing pumas to increase their kill rates, they may be indirectly affecting prey populations in ways that could have wider repercussions for the ecological community (*sensu* Elbroch and Wittmer 2013).

Pumas and black bears clearly have important but different effects on the acquisition of carrion by scavengers. Pumas were a source of carrion for scavengers across different trophic levels and also may have initiated a cascading pattern of energy availability through their limitation of mesocarnivores, which increased access for smaller carnivores. The influences of pumas on how energy in carrion resources is distributed may constitute keystone ef-

fects, in that they enhance biodiversity (Elbroch and Wittmer 2012). Changes in puma abundances may therefore have unexpected and important effects on ecological communities. In contrast, black bears were a dominant scavenger that greatly limited the ability of all other scavengers to take advantage of carrion resources. Further, black bears limited access of pumas at their own kills. Our results thus provide evidence that black bears directly affect the scavenger community and suggest that black bears may also have important indirect effects on other aspects of the ecological community, including ungulate populations, through their effects on top predators. More generally, our results highlight the complexity of possible interactions, including competition among scavengers and large carnivores at ungulate carcasses, and the potential effects of this competition on the structure and dynamics of ecological communities.

Acknowledgments

All capture methods were approved by the independent Institutional Animal Care and Use Committee at the University of California, Davis, and the Wildlife Investigations Lab of the California Department of Fish and Wildlife. The California Department of Fish and Wildlife and the University of California at Davis generously provided funding for the project. We thank D. Casady, K. Cripe, B. Evans, J. Golla, B. Millsap, C. Wiley, and many field technicians for their help on the project. Two anonymous reviewers provided helpful comments on a previous draft of the manuscript.

Literature Cited

- Akaike, H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19:716–723.
- Allen, M. L., L. M. Elbroch, D. S. Casady, and H. U. Wittmer. 2014a. Seasonal variation in the feeding ecology of pumas (*Puma concolor*) in northern California. *Canadian Journal of Zoology* 92: 397–403.
- . 2015. The feeding and spatial ecology of mountain lions in Mendocino National Forest, California. *California Fish and Game* 101:51–65.
- Allen, M. L., L. M. Elbroch, C. C. Wilmers, and H. U. Wittmer. 2014b. Trophic facilitation or limitation? comparative effects of pumas and black bears on the scavenger community. *PLoS ONE* 9:e102257. doi:10.1371/journal.pone.0102257.
- . 2015. Data from: The comparative effects of large carnivores on the acquisition of carrion by scavengers. *American Naturalist*, Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.dh2vr>.
- Allen, M. L., L. M. Elbroch, and H. U. Wittmer. 2013. Encounter competition between a cougar, *Puma concolor*, and a western spotted skunk, *Spilogale gracilis*. *Canadian Field-Naturalist* 127:64–66.

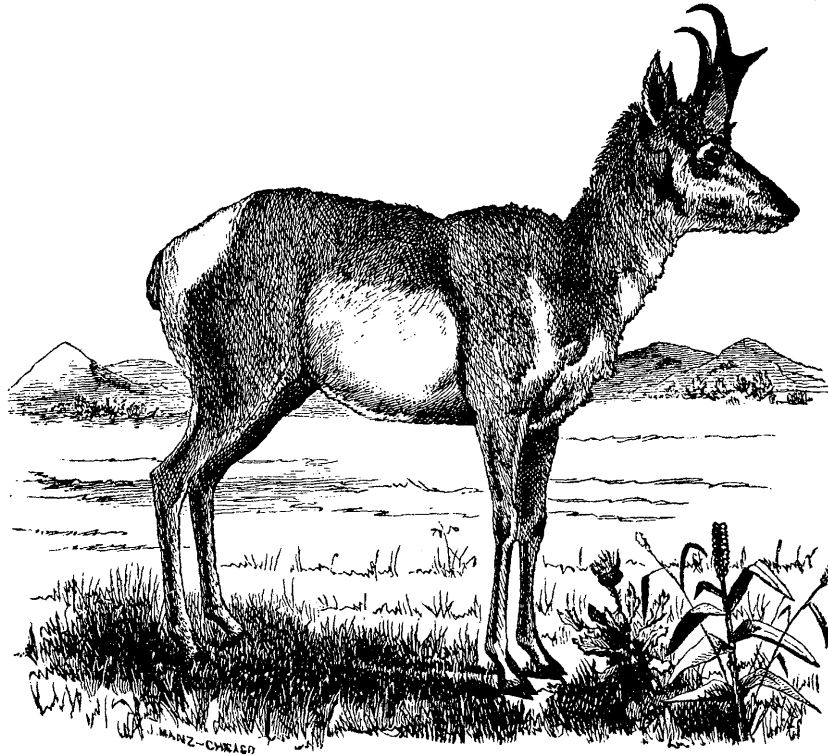
- Angerbjörn, A., B. Arvidson, E. Norén, and L. Strömberg. 1991. The effect of winter food on reproduction in the arctic fox. *Journal of Animal Ecology* 60:705–714.
- Atwood, T. C., E. M. Gese, and K. E. Kunkel. 2007. Comparative patterns of predation by cougars and recolonizing wolves in Montana's Madison Range. *Journal of Wildlife Management* 71:1098–1106.
- Bauer, J. W., K. A. Logan, L. L. Sweanor, and W. M. Boyce. 2005. Scavenging behavior in puma. *Southwestern Naturalist* 50:466–471.
- Bischoff-Mattson, Z., and D. Mattson. 2009. Effects of simulated mountain lion caching on decomposition of ungulate carcasses. *Western North American Naturalist* 69:343–350.
- Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. *Theoretical Population Biology* 9:129–136.
- Cortés-Avizanda, A., M. Carrete, and J. A. Donazar. 2010. Managing supplementary feeding for avian scavengers: guidelines for optimal design using ecological criteria. *Biological Conservation* 143:1707–1715.
- Cortés-Avizanda, A., R. Jovani, M. Carrete, and J. A. Donazar. 2012. Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: a field experiment. *Ecology* 93:2570–2579.
- Courchamp, F., M. Langlais, and G. Sugihara. 1999. Cats protecting birds: modelling the mesopredator release effect. *Journal of Animal Ecology* 68:282–292.
- DeVault, T. L., O. E. Rhodes Jr., and J. A. Shivik. 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* 102:225–234.
- Elbroch, L. M., M. L. Allen, B. H. Lowery, and H. U. Wittmer. 2014. The difference between killing and eating: ecological shortcomings of puma energetic models. *Ecosphere* 5:53.
- Elbroch, L. M., and H. U. Wittmer. 2012. Table scraps: inter-trophic provisioning by pumas in Patagonia. *Biology Letters* 8:776–779.
- . 2013. Nuisance ecology: do scavenging condors exact foraging costs on pumas in Patagonia? *PLoS ONE* 8:e53595. doi:10.1371/journal.pone.0053595.
- Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. *Science* 185:1058–1060.
- Forrester, T. D. 2014. Effects of predation and forage availability on the survival of black-tailed deer (*Odocoileus hemionus columbianus*) in the Mendocino National Forest, California. PhD diss. University of California, Davis.
- Hardin, G. 1960. The competitive exclusion principle. *Science* 131:1292–1297.
- Hertel, F. 1994. Diversity in body size and feeding morphology within past and present vulture assemblages. *Ecology* 75:1074–1084.
- Houston, D. C. 1995. The adaptations of scavengers. Pages 263–286 in A. R. E. Sinclair and M. Norton-Griffiths, eds. *Serengeti: dynamics of an ecosystem*. University of Chicago Press, Chicago.
- Hunter, J. S., S. M. Durant, and T. M. Caro. 2006. Patterns of scavenger arrival at cheetah kills in Serengeti National Park, Tanzania. *African Journal of Ecology* 45:275–281.
- Knopff, K. H., A. A. Knopff, and M. S. Boyce. 2010. Scavenging makes cougars susceptible to snaring at wolf bait stations. *Journal of Wildlife Management* 74:644–653.
- Krofel, M., I. Kos, and K. Jerina. 2012. The noble cats and the big bad scavengers: effects of dominant scavengers on solitary predators. *Behavioral Ecology and Sociobiology* 66:1297–1304.
- Larivière, S. 2001. *Ursus americanus*. *Mammalian Species* 647:1–11.
- Levi, T., and C. C. Wilmers. 2012. Wolves-coyotes-foxes: a cascade among carnivores. *Ecology* 93:921–929.
- Moleón, M., J. A. Sánchez-Zapata, N. Selva, J. A. Donazar, and N. Owen-Smith. 2014. Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. *Biological Reviews* 89:1042–1054.
- Murphy, K. M., G. S. Felzien, M. G. Hornocker, and T. K. Ruth. 1998. Encounter competition between bears and cougars: some ecological implications. *Ursus* 10:55–60.
- Murphy, K., and T. K. Ruth. 2010. Diet and prey selection of a perfect predator. Pages 118–137 in M. Hornocker and S. Negri, eds. *Cougar: ecology and conservation*. University of Chicago Press, Chicago.
- Pelton, M. R. 1982. Black bear. Pages 504–514 in J. A. Chapman and G. A. Feldhamer, eds. *Wild mammals of North America: biology, management, and economics*. Johns Hopkins University Press, Baltimore.
- Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Liliberte, and J. S. Brashares. 2009. The rise of the mesopredator. *BioScience* 59:779–791.
- R Development Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? *Bioscience* 54:755–766.
- Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, et al. 2014. Status and ecological effects of the world's largest carnivores. *Science* 343:1241484.
- Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation* 102:227–234.
- Rogers, C. M., and M. J. Caro. 1998. Song sparrows, top carnivores and nest predation: a test of the mesopredator release hypothesis. *Oecologia (Berlin)* 116:227–233.
- Root, R. B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological Monographs* 37:317–350.
- Ruth, T. K., and K. Murphy. 2010. Competition with other carnivores for prey. Pages 163–172 in M. Hornocker and S. Negri, eds. *Cougar: ecology and conservation*. University of Chicago Press, Chicago.
- Sargeant, A. B., S. H. Allen, and J. O. Hastings. 1987. Spatial relationships between sympatric coyotes and red foxes in North Dakota. *Journal of Wildlife Management* 51:285–293.
- Selva, N., and M. A. Fortuna. 2007. The nested structure of a scavenger community. *Proceedings of the Royal Society B: Biological Sciences* 274:1101–1108.
- Selva, N., B. Jedrzejewska, W. Jedrzejewski, and A. Wajrak. 2003. Scavenging on European bison carcasses in Białowieża Primeval Forest (eastern Poland). *Ecoscience* 10:303–311.
- Svoboda, N. J., J. L. Belant, D. E. Beyer, J. F. Duquette, H. K. Sticker, C. A. Albright. 2011. American black bear predation of an adult white-tailed deer. *Ursus* 22:91–94.
- Watson, J., S. R. Rae, and R. Stillman. 1992. Nesting density and breeding success of golden eagles in relation to food supply in Scotland. *Journal of Animal Ecology* 61:543–550.
- Wilmers, C. C., R. L. Crabtree, D. W. Smith, K. M. Murphy, and W. M. Getz. 2003a. Trophic facilitation by introduced top pred-

ators: grey wolf subsidies to scavengers in Yellowstone National Park. *Journal of Animal Ecology* 72:909–916.

Wilmsers, C. C., D. R. Stahler, R. L. Crabtree, D. W. Smith, and W. M. Getz. 2003*b*. Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. *Ecology Letters* 6:996–1003.

Wilson, E. E., and E. M. Wolkovich. 2011. Scavenging: how carnivores and carrion structure communities. *Trends in Ecology and Evolution* 26:129–135.

Natural History Editor: Mark A. McPeck



“The American antelope... was first made known to the scientific world through Lewis and Clark, who found it in 1804 on the Upper Missouri. . . . They are exceptionally gregarious in their habits, although the immense bands of thousands in which they formerly assembled are now broken up by the advancement of civilization, which has absolutely expelled them from those regions where they were met with in great numbers a quarter of a century since. Then they were most abundant in California, where they sometimes almost literally covered the plains and the foot-hills west of the Sierras, and where now a solitary wanderer is rarely heard of.” From “The American Antelope, or Prong Buck” by J. D. Caton (*The American Naturalist*, 1876, 10:193–205).