



Short communication

Vertebrate diversity benefiting from carrion provided by pumas and other subordinate, apex felids



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ABSTRACT

Carrion promotes biodiversity and ecosystem stability, and large carnivores provide this resource throughout the year. In particular, apex felids subordinate to other carnivores contribute more carrion to ecological communities than other predators. We measured vertebrate scavenger diversity at puma (*Puma concolor*) kills in the Greater Yellowstone Ecosystem, and utilized a model-comparison approach to determine what variables influenced scavenger diversity (Shannon's *H*) at carcasses. We documented the highest vertebrate scavenger diversity of any study to date (39 birds and mammals). Scavengers represented 10.9% of local birds and 28.3% of local mammals, emphasizing the diversity of food-web vectors supported by pumas, and the positive contributions of pumas and potentially other subordinate, apex felids to ecological stability. Scavenger diversity at carcasses was most influenced by the length of time the carcass was sampled, and the biological variables, *temperature* and *prey weight*. Nevertheless, diversity was relatively consistent across carcasses. We also identified six additional stalk-and-ambush carnivores weighing > 20 kg, that feed on prey larger than themselves, and are subordinate to other predators. Together with pumas, these seven felids may provide distinctive ecological functions through their disproportionate production of carrion and subsequent contributions to biodiversity. We urge conservation managers to increase support for these species, as a means of prioritizing resources to best ensure the persistence of carrion in natural systems.

1. Introduction

There is increasing recognition for the importance of carrion in supporting biodiversity and structuring ecosystems (Wilson and Wolkovich, 2011; Moleón and Sánchez-Zapata, 2015; Inger et al., 2016). Animals that eat carrion facilitate energy transfer between trophic levels and increase linkages in food webs, promoting ecosystem stability (DeVault et al., 2003; Wilson and Wolkovich, 2011; Moleón et al., 2014). Vertebrate scavengers, in particular, are essential vectors in spreading nutrients and other benefits of carrion across diverse terrestrial and aquatic ecosystems (Wilson and Wolkovich, 2011; Moleón and Sánchez-Zapata, 2015). Scavengers are also often predators themselves (Moleón et al., 2014), and competition over carrion and predator-prey dynamics near carcasses influences the heterogeneity of species assemblages across ecosystems (Cortés-Avizanda et al., 2009; Allen et al., 2015).

Carrion comes in all shapes and sizes, but large carcasses are particularly important, in that they support a greater diversity of scavengers (Selva et al., 2005; Moleón and Sánchez-Zapata, 2015), and therefore disproportionately contribute more to ecosystem function

than smaller carcasses. Large carnivores that provide large carcasses, however, are in sharp decline (Ripple et al., 2014; Mateo-Tomás et al., 2015). Current human populations now produce exponentially more animal waste and carrion than native predators (Oro et al., 2013); carrion produced by people, however, generally occurs infrequently in pulses (e.g., hunters, Wilmers et al., 2003; Mateo-Tomás et al., 2015) or in limited areas (e.g., landfills, Oro et al., 2013; cities, Inger et al., 2016).

Research suggests that felids (Family Felidae) that are apex predators (Wallach et al., 2015) and subordinate to other carnivores in competition over resources, contribute more carrion to ecological communities than other top predators (cheetahs, *Acinonyx jubatus*, in central Africa, Hunter et al., 2006; pumas, *Puma concolor*, in Chilean Patagonia, Elbroch and Wittmer, 2012). Felids are stalk-and-ambush predators and expend less energy in obtaining prey than coursing predators, like wild dogs (*Lycaon pictus*) or wolves (*Canis lupus*) (Scantlebury et al., 2014). Therefore, felids do not suffer the energetic costs that coursing predators do when they lose their kills. Recent research suggests that subordinate, apex felids have adapted to contend with the costs of kleptoparasitism by scavengers. Cheetahs, for example,

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are an apex predator found across Africa and Iran that can withstand losses of 25–35% of their kills with little need for compensatory killing (Scantlebury et al., 2014).

The puma is a widespread, apex predator found throughout the Americas and a species subordinate to a range of predators across its range (Ruth and Murphy, 2010). Pumas kill 10.10 ± 4.10 SD kg of prey/day and abandon 3.9 ± 2.6 kg of prey/day (Elbroch et al., 2014); based upon an average density of 1.7 resident pumas per 100 km² (Beausoleil et al., 2013), pumas conservatively contribute 1,507,348 kg of meat per day across their 22,735,268 km² range in North and South America (IUCN, 2015). Pumas lose or abandon on average 39% of their prey to competitors and scavengers (Elbroch et al., 2014), and like cheetahs, are likely tolerant of some level of kleptoparasitism of their kills. In fact, pumas tolerate scavengers even while they are still feeding, and the presence of a puma at a carcass increases opportunities for smaller carnivores to feed as compared with other large carnivores that exclude them (Allen et al., 2015).

Here, we measured vertebrate scavenger diversity at puma kills in the Greater Yellowstone Ecosystem (GYE) with motion-triggered video cameras. As a specific test of how subordinate, apex predators might support biodiversity through carrion production, we compared mammalian and avian scavenger diversity documented at kills to local species assemblages to see what proportion of resident vertebrates benefited from puma kills. Based upon previous research (Selva et al., 2005; Hunter et al., 2006), we hypothesized that scavenger diversity recorded at puma kills would vary with temperature, carcass size, and canopy cover. We also assessed the global distributions of subordinate, apex felids as a means of assessing the potential contributions of ecologically-similar species to pumas around the world. Solitary felids > 20 kg that feed on prey larger than themselves (Carbone et al., 2007) and are subordinate to other predators may provide distinctive ecological functions through their disproportionate production of carrion and subsequent contributions to ecosystem stability (e.g., cheetahs, Hunter et al., 2006; Eurasian lynx, *Lynx lynx*, Krofel et al., 2012).

2. Methods

2.1. Study area

Our puma study spanned 2300 km² of the GYE north of Jackson, Wyoming (Fig. 2). Elevations ranged from 1800 m to > 3600 m. The area was characterized by short, cool summers during which prey were widely dispersed and long winters with frequent snowstorms during which elk (*Cervus elaphus*) formed large aggregations at lower elevations. Further details about the study area, including plant communities and mammal assemblages, are found in Elbroch et al. (2013).

2.2. Puma capture and collar programming

We captured pumas during winter months from 2012 to 2015, when we employed trailing hounds to force pumas to retreat to a tree where we could safely capture them. Pumas were fitted with a GPS collar (Lotek Globalstar S or Iridium M, Newmarket, Ontario; Vectronics Globalstar GPS Plus, Berlin, Germany). Our capture protocols adhered to the guidelines outlined by the American Society of Mammalogists (Sikes et al., 2011) and were reviewed by the Jackson Institutional Animal Care and Use Committee (Protocol 027-10EGDBS-060210); additional capture details can be found in Elbroch et al. (2013). GPS collars were programmed to acquire location data every two hours.

2.3. Locating and monitoring puma kills

GPS data acquired by puma collars were uploaded to Globalstar satellites six times per day or once per day to Iridium satellites. Upon retrieval, we displayed location data in ArcGIS 10.0. (ESRI, Redlands, CA), and following protocols for studying puma foraging (Elbroch et al.,

2014), identified aggregated GPS points in which ≥ 2 locations spanning ≥ 4 h of time were within 150 m of each other. Researchers transferred puma location data to handheld GPS units to guide them in the field, and we systematically searched aggregated locations to locate prey remains. The state of prey remains, presence and location of bite marks, hemorrhaging at wound sites, and body parts consumed were used to determine whether the puma had killed the animal or was scavenging. If we judged that there was sufficient meat remaining to draw scavengers (e.g., the carcass was cached by the puma, indicating it would likely return, or there was enough meat to cover the long bones of the legs), we placed paired motion-triggered video cameras (Bushnell Outdoor Products, Overland Park, KS) to document scavenger diversity at the carcass; we programmed cameras to record 60s videos with 30s delay between triggers, and only included those species that clearly fed from the carcass as scavengers in our analyses, or in the case of passerines, that may have fed upon insects upon the carcass (it was sometimes difficult to differentiate whether they were eating meat or something on the meat); we did not include species that were recorded by cameras but did not feed from the carcass. Cameras monitored carcasses for variable lengths of time, primarily dependent upon animal activity that could quickly fill the camera's memory, or in winter, extreme temperatures that limited battery life.

2.4. Scavenger diversity

We compared mammal and avian scavengers detected at carcasses with species known to inhabit the area. Then we quantified the percent of local mammals and birds that scavenged puma kills, which were descriptive statistics that we could directly compare to scavenger studies compiled and reported in Mateo-Tomás et al. (2015). We included 201 of 304 bird species listed in the “Birds of Jackson Hole” (Raynes, 2014) (Appendix A), which presented species occurrence in four seasons (spring, summer, fall, winter) and five categories: abundant, common, occasional, rare (defined as “not occurring every year; unexpected as to season or range”), and accidental (defined as “rarely seen”); we did not include 103 birds because they were listed as rare or accidental in all four seasons (e.g., a species was included if it were rare in 1–3 seasons, but at least occasional in one season). We included all 60 mammal species listed for Grand Teton National Park (Wiki, 2016).

Using generalized linear and generalized linear mixed models, and a Poisson distribution, we built and tested 12 simple a priori models (Table 1) to test what biological factors best fit our selection parameter, scavenger biodiversity at kills (Shannon's Diversity Index *H*; Krebs, 1999), and to mitigate the inclusion of uninformative parameters (Arnold, 2010). Based upon previous research (Selva et al., 2005; Hunter et al., 2006) we included three biological variables that influence scavenger diversity at carrion resources: *Temperature*, which we defined as the mean temperature during sampling by cameras at each carcass, as quantified with hourly temperatures recorded by SNOTEL

Table 1

Model comparisons ranked from best fit to worst, AICc values, Δ AICc, Model likelihood, and Akaike weights (w_i).

Model	AICc	Δ AICc	Likelihood	w_i
CamDays + Weight	504.795	0	1.000	0.433
CamDays + Temp	504.906	0.111	0.946	0.410
CamDays + Temp + Weight	506.833	2.038	0.361	0.156
PumaID (Rnd) + Weight + CamDays	529.897	25.102	0.000	0.000
PumaID (Rnd) + Weight	534.495	29.700	0.000	0.000
PumaID (Rnd) + Temp	534.878	30.083	0.000	0.000
PumaID (Rnd) + Temp + Weight	536.694	31.899	0.000	0.000
PumaID (Rnd) + Canopy	546.253	41.458	0.000	0.000
PumaID (Rnd) + Canopy + Weight	547.876	43.081	0.000	0.000
PumaID (Rnd) + Canopy + Temp	548.686	43.891	0.000	0.000
+ Weight				
PumaID (Rnd) + Canopy + Temp	550.59	45.795	0.000	0.000

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