Short communication

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

L. Mark Elbroch*, Connor O'Malley, Michelle Peziol, Howard B. Quigley

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

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 Sànchez-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 Sànchez-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 Sànchez-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 kleptoparatism by scavengers. Cheetahs, for example,

---

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 kleptoparatism 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 worth, AICc values, ΔAICc, Model likelihood, and Akaike weights (w_i).

Model	AICc	ΔAIC	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 + Weight	548.686	43.891	0.000	0.000
PumaID (Rnd) + Canopy + Temp	550.59	45.795	0.000	0.000

weather station 506 in the north of our study area. We believed *temperature* would capture potential variation in scavenging activity due to season, snow cover, and other annual weather patterns; *CanopyCover* (4 categories: 0–25%, 26–50%, 51–75%, 76–100%), measured with a spherical densitometer directly above carcasses, to capture variation across habitat cover classes that might influence the detectability of carcasses by avian scavengers; *Weight* (carcass size in kg) to capture variation in the number of scavengers due to competition over limited resources. We also included *CameraDays*, which we defined as the number of days a carcass was sampled by cameras, to test for variation due to different sampling periods across kills, and individual *PumaID* as a random effect, to account for spatial autocorrelation between kills that might capture localized scavenger communities on the landscape, and thus bias results.

Before model building, we tested for multi-collinearity among covariates; all covariates were correlated at $r < |0.5|$, and all variables were included in our analyses. We calculated Akaike's Information Criterion adjusted for small sample size (AICc), ΔAICc, and Akaike weights (w_i) for each model (Burnham and Anderson, 2002). We assessed top model performance with R^2 values, and reported parameter estimates ($\pm$ SE) for covariates in top models.

3. Results

3.1. Pumas and scavengers

Between April 2012 and December 31, 2015, we marked 15 independent pumas (5 male, 10 female), documented 1022 prey killed by pumas, and deployed motion-triggered cameras at 242 kills of prey weighing on average 135 ($\pm$ 93 SD) kg to assess vertebrate scavenger diversity. We set cameras within 43 ($\pm$ 38 SD) hrs of when kills were made, and recorded scavenger activity for on average 7.0 ($\pm$ 3.7 SD) days. We detected 39 scavenger species (Appendix A; Fig. 1), plus domestic dogs which we did not include in our biodiversity analyses. Red foxes (*Vulpes vulpes*) and black-billed magpies (*Pica hudsonia*) were by far recorded at the most carcasses (Fig. 1). Scavengers represented 10.9% of local birds, 28.3% of local mammals, and 14.9% of all birds and mammals (Appendix A).

3.2. Scavenger diversity

Mean Shannon's Diversity Index *H* was 0.83 ($\pm$ 0.58 SD) across all carcasses. We identified two top models that best fit our data, *H*, and which explained 84% of the AIC weight (Table 1). Neither top model, however, performed well as determined with R^2 values. Our model *CameraDays + Weight* explained 10% of the variation in the data; parameter estimates for *CameraDays* was 0.0538 ($\pm$ 0.0177 SE), and for *Weight*, 0.0003 ($\pm$ 0.0008 SE). Our second top model *CameraDays + Temperature* explained 9% of the variation in the data; parameter estimates for *CameraDays* was 0.0546 ($\pm$ 0.0176 SE), and for *Temperature*, 0.0002 ($\pm$ 0.0084 SE).

4. Discussion

We documented the highest vertebrate scavenger diversity of any study to date, emphasizing 1) the ecological importance of pumas, and potentially other subordinate, apex felids in the production of carrion, 2) the diversity of food-web vectors supported by pumas, and 3) the positive contributions of pumas to ecological stability through predation and their adapted tolerance for kleptoparatism by diverse scavengers. For example, we documented both higher numbers of species and higher representative percentages of local birds and mammals than nine studies of scavengers at hunter offal around the globe (Mateo-Tomás et al., 2015). We also documented > 3 times the scavenger species recorded at wolf and hunter kills in the same ecosystem just north of our study area (Wilmers et al., 2003), however, it remains

possible that our results differed due to methods rather than reflected differences in diversity.

Overall, our analyses indicated scavenger biodiversity was relatively consistent across a range of temperatures, carcass sizes and canopy cover. Scavenger biodiversity was most influenced by the duration of sampling, emphasizing the need for longer sampling periods at carcasses in the future, as well as further research to determine the length of time needed to capture potential biodiversity, much like detection probabilities in camera-trap surveys for rare species (Long et al., 2012). In support for our hypotheses, temperature and carcass weight did influence scavenger diversity, but only minimally. Our sampling, however, was biased towards large carcasses over small, as large carcasses persisted long enough to visit and set up a camera to record scavengers. Therefore, we believe we did not adequately test for the potential effect of carcass size on scavenger diversity. In the case of temperature, our results suggested that there were a similar number of species scavenging puma carcasses across seasons; however, an important next step is to test for species turnover at carcasses to test for differences in scavenger assemblages. Some scavengers exhibit migrations, and others enter periods of dormancy during the coldest months, affecting their presence at carcasses (Fig. 1). Last, we did not find support for our hypothesis that canopy cover would influence species richness, but again, this may be due to an equal number of different species utilizing carcasses under different canopies, rather than identical scavenger assemblages across the landscape.

Carcasses produced by predators are greater utilized by scavengers than other sources of carrion (Selva et al., 2005; Moleón and Sànchez-Zapata, 2015), and evidence suggests that subordinate, apex felids that kill prey larger than themselves play disproportionate roles in providing carrion to natural systems (Hunter et al., 2006; Elbroch and Wittmer, 2012). Thus, we identified six additional felids ecologically-similar to pumas (e.g., stalk-and-ambush, apex predators that weigh > 20 kg, kill prey larger than themselves, and are subordinate to other sympatric predators in competition scenarios) that may also disproportionately provision carrion to their ecological communities: cheetah, clouded leopard (*Neofelis nebulosa*), Eurasian lynx, leopard (*Panthera pardus*), snow leopard (*Panthera uncia*), and sunda clouded leopard (*Neofelis diardi*). As determined with International Union for Conservation of Nature (IUCN) maps (Gerngross, 2016; Iberlince and EU LIFE Programme, 2015; International Snow Leopard Trust and WCS, 2010; IUCN, 2015; IUCN, 2016), the global distribution for all seven functionally-similar species is 57,975,188 km², or 43.0% of terrestrial lands except Antarctica (Fig. 2). According to the IUCN, the snow leopard is endangered, and the leopard, cheetah, sunda clouded leopard, and clouded leopard are vulnerable. The cheetah inhabits just 9% (Durant et al., 2017) and the leopard, 25–37%, (Jacobson et al., 2016) of their historic ranges, due to intense persecution. Yet even following centuries of exploitation, these seven species still cover an area almost half the land mass north of Antarctica; their wide-spread distributions are not only evidence of their ecological plasticity, but may also indicate their importance in diverse ecosystems around the globe. We urge conservation scientists and managers to prioritize the support of functioning populations of subordinate, apex felids, for example through reduced hunting quotas and livestock conflict mitigation measures, as a means of focusing resources to best ensure the production of carrion that promotes biodiversity and ecosystem stability.
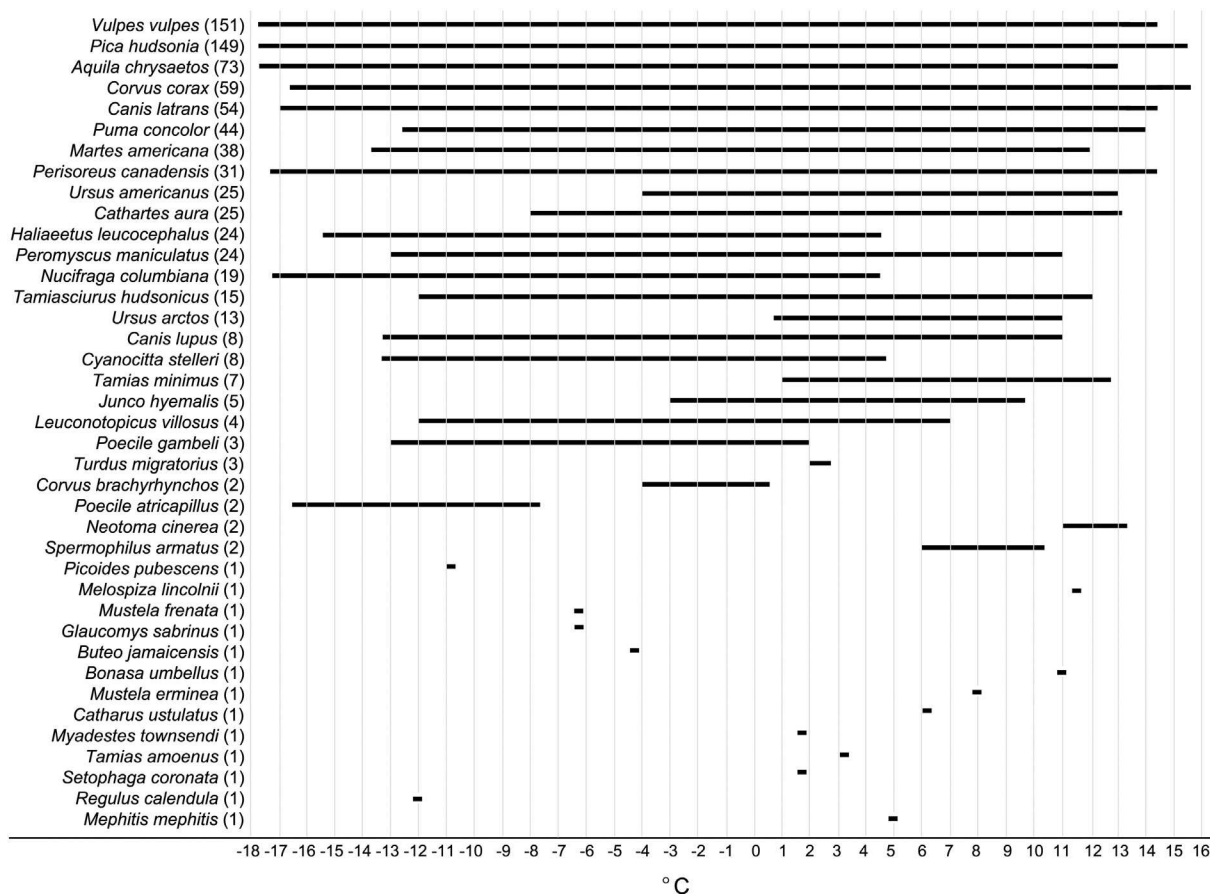
Fig. 1. Species recorded at puma kills in the Greater Yellowstone Ecosystem, ranked in order by the frequency of kills at which they were detected (*n*), and followed by a visual representation of the temperature range for kills at which they were detected (°C).

Fig. 2. The combined global distribution of seven functionally-similar subordinate, apex felids that hunt prey larger than themselves. a: puma (*Puma concolor*), b: cheetah (*Acinonyx jubatus*) compliments of Tobi87, c: leopard (*Panthera pardus*) compliments of Ninara, d: Eurasian lynx (*Lynx lynx*) compliments of Böhringer Friedrich, e: snow leopard (*Panthera uncia*) compliments of Bernard Landgraf, f: clouded leopard (*Neofelis nebulosa*) compliments of Ltshears, g: sunda clouded leopard (*Neofelis diardi*) compliments of Heiko Wittmer and Andrew Marshall. The star denotes the location of our puma study in North America.

Appendix A. Appendix A

	Detected at puma kills
Mammals (Source: Wiki, 2016. https://en.wikipedia.org/wiki/Mammals_of_Grand_Teton_National_Park. Viewed 1 January 2017.)	
Black bear, *Ursus americanus*	1
Grizzly bear, *Ursos arctos*	1
Coyote, *Canis latrans*	1
Gray wolf, *Canis lupus*	1
Red fox, *Vulpes vulpes*	1
Bobcat, *Felis rufus*	
Cougar, *Felis concolor*	1
Raccoon, *Procyon lotor*	
American badger, *Taxidea taxus*	
American marten, *Martes americana*	1
American mink, *Neovison vison*, riparian forests	
North American river otter, *Lontra canadensis*	
Least weasel, *Mustela nivalis*	
Long-tailed weasel, *Mustela frenata*	1
Short-tailed weasel, *Mustela erminea*	1
Wolverine, *Gulo gulo*, alpine	
Striped skunk, *Mephitis mephitis*	1
Elk (wapiti), *Cervus elaphus*	
Mule deer, *Odocoileus hemionus*	
White-tailed deer, *Odocoileus virginianus*	
Moose, *Alces alces*	
Pronghorn, *Antilocapra americana*	
Bison, *Bison bison*	
Mountain goat, *Oreamnos americanus*	
Bighorn sheep, *Ovis canadensis*	
Snowshoe hare, *Lepus americanus*	
White-tailed jackrabbit, *Lepus townsendii*	
American pika, *Ochotona princeps*	
Masked shrew, *Sorex cinereus*	
American water shrew, *Sorex palustris*	
Dwarf shrew, *Sorex nanus*	
Vagrant shrew, *Sorex vagrans*	
Beaver, *Castor canadensis*	
Least chipmunk, *Tamias minimus*	1
Uinta chipmunk, *Tamias umbrinus*	
Yellow-pine chipmunk, *Tamias amoenus*	1
Yellow-bellied marmot, *Marmota flaviventris*	
Golden-mantled ground squirrel, *Spermophilus lateralis*	
Northern flying squirrel, *Glaucomys sabrinus*	1
American red squirrel, *Tamiasciurus hudsonicus*	1
Uinta ground squirrel, *Spermophilus armatus*	1
Northern pocket gopher, *Thomomys talpoides*	
Deer mouse, *Peromyscus maniculatus*	1
Western jumping mouse, *Zapus princeps*	
Muskrat, *Ondatra zibethicus*	
Western heather vole, *Phenacomys intermedius*	
Long-tailed vole, *Microtus longicaudus*	
Meadow vole, *Microtus pennsylvanicus*	
Montane vole, *Microtus montanus*	
Sagebrush vole, *Lemmiscus curtatus*	
Southern red-backed vole, Myodes gapperi	
Water vole, *Microtus richardsoni*	
Bushy-tailed woodrat, *Neotoma cinerea*	1
North American porcupine, *Erethizon dorsatum*	
Big brown bat, *Eptesicus fuscus*	

Hoary bat, *Lasiurus cinereus*
Little brown bat, *Myotis lucifugus*
Long-eared bat, *Myotis evotis*
Long-legged bat, *Myotis volans*
Silver-haired bat, *Lasionycteris noctivagans*

60 mammals	Total	17
Percent		0.283333333

Birds (Source: Raynes, 2014. Birds of Jackson Hole. Jackosn WY: Grand Teton Association, Wyoming Game and Fish Department.)

Snow goose	
Canada goose	
Trumpeter swan	
Tundra swan	
Wood duck	
Gadwall	
American wigeon	
Mallard	
Blue-winged teal	
Cinnamon teal	
Northern shoveler	
Northern pintail	
Green-winged teal	
Canvasback	
Redhead	
Ring-necked duck	
Lesser scaup	
Harlequin duck	
Bufflehead	
Common goldeneye	
Barrow's goldeneye	
Hooded merganser	
Red-breasted merganser	
Common merganser	
Ruddy duck	
Gray partridge	
Ruffed grouse	1
Greater sage-grouse	
Dusky grouse	
Sharp-tailed grouse	
Common loon	
Pied-billed grebe	
Eared grebe	
Western grebe	
Clark's grebe	
American white pelican	
Double-crested cormorant	
Great blue heron	
Great egret	
Snowy egret	
White-faced ibis	
Turkey vulture	1
Osprey	
Bald eagle	1
Northern harrier	
Sharp-shinned hawk	
Cooper's hawk	
Northern goshawk	
Swainson's hawk	
Red-tailed hawk	1
Ferruginous hawk	
Rough-legged hawk	
Golden eagle	1
American kestrel	
Merlin	
Peregrine falcon	
Prairie falcon	

Virginia rail	
Sora	
American coot	
Sandhill crane	
Semipalmated plover	
Killdeer	
American avocet	
Spotted sandpiper	
Solitary sandpiper	
Greater yellowlegs	
Willet	
Lesser yellowlegs	
Long-billed curlew	
Semipalmated sandpiper	
Western sandpiper	
Least sandpiper	
Baird's sandpiper	
Long-billed dowitcher	
Wilson's snipe	
Wilson's phalarope	
Franklin's gull	
Ring-billed gull	
California gull	
Caspian tern	
Common tern	
Forster's tern	
Rock dove	
Eurasian collared-dove	
Mourning dove	
Great horned owl	
Northern pygmy-owl	
Great gray owl	
Long-eared owl	
Short-eared owl	
Boreal owl	
Northern saw-whet owl	
Common nighthawk	
White-throated swift	
Black-chinned hummingbird	
Calliope hummingbird	
Broad-tailed hummingbird	
Rufous hummingbird	
Belted kingfisher	
Lewis' woodpecker	
Williamson's sapsucker	
Red-naped sapsucker	
Downy woodpecker	1
Hairy woodpecker	1
American three-toed woodpecker	
Black-backed woodpecker	
Northern flicker	
Olive-sided flycatcher	
Western wood-pewee	
Willow flycatcher	
Least flycatcher	
Hammond's flycatcher	
Dusky flycatcher	
Cordilleran flycatcher	
Eastern kingbird	
Loggerhead shrike	
Northern shrike	
Plumbeous vireo	
Warbling vireo	
Gray jay	1
Steller's jay	1
Clark's nutcracker	1

Black-billed magpie	1
American row	1
Common raven	1
Horned lark	
Tree swallow	
Violet-green swallow	
Northern rough-winged swallow	
Bank swallow	
Cliff swallow	
Barn swallow	
Black-capped chickadee	1
Mountain chickadee	1
Red-breasted nuthatch	
White-breasted nuthatch	
Brown creeper	
Rock wren	
House wren	
Marsh wren	
American dipper	
Golden-crowned kinglet	
Ruby-crowned kinglet	1
Mountain bluebird	
Townsend's solitaire	1
Swainson's thrush	1
Hermit thrush	
American robin	1
Gray catbird	
Sage thrasher	
European starling	
American pipit	
Bohemian waxwing	
Cedar waxwing	
Orange-crowned warbler	
Yellow warbler	
Yellow-rumped warbler	1
Townsend's warbler	
American redstart	
Northern waterthrush	
MacGillivray's warbler	
Common yellowthroat	
Wilson's warbler	
Western tanager	
Green-tailed towhee	
Spotted towhee	
American tree sparrow	
Chipping sparrow	
Clay-colored sparrow	
Brewer's sparrow	
Vesper sparrow	
Savannah sparrow	
Fox sparrow	
Song sparrow	
Lincoln's sparrow	1
White-crowned sparrow	
Dark-eyed junco	1
Snow bunting	
Black-headed grosbeak	
Lazuli bunting	
Bobolink	
Red-winged blackbird	
Western meadowlark	
Yellow-headed blackbird	
Brewer's blackbird	
Common grackle	
Brown-headed cowbird	
Bullock's oriole	

Gray-crowned rosy-finch
Black rosy-finch
Pine grosbeak
Cassin's finch
House finch
Red crossbill
White-winged crossbill
Common redpoll
Pine siskin
American goldfinch
Evening grosbeak
House sparrow

201 mammals	Total	22
Percent		0.109452736
Total percent		0.14942529

References

Allen, M.L., Elbroch, L.M., Wilmers, C.C., et al., 2015. The comparative influences of large carnivores on the acquisition of carrion by scavengers. Am. Nat. 185, 822–833.

Arnold, T.W., 2010. Uninformative parameters and model selection using Akaike's information criterion. J. Wildl. Manag. 74, 1175–1178.

Beausoleil, R.A., Koehler, G.M., Maletzke, B.T., et al., 2013. Research to regulation: cougar social behavior as a guide for management. Wildl. Soc. Bull. 37, 680–688.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multi-model Inference: A Practical Information-Theoretic Approach. Springer, New York, NY.

Carbone, C., Teacher, A., Rowcliffe, J.M., 2007. The costs of carnivory. PLoS Biol. 5, e22.

Cortés-Avizanda, A., Selva, N., Carrete, M., et al., 2009. Effects of carrion resources on herbivore spatial distribution are mediated by facultative scavengers. Basic Appl. Ecol. 10, 265–272.

DeVault, T.L., Rhodes, O.E., Shivik, J.A., 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos 102, 225–234.

Durant, S.M., Mitchell, N., Groom, R., et al., 2017. The global decline of cheetah Acinonyx Jubatus and what it means for conservation. Proc. Natl. Acad. Sci. 114, 528–533.

Elbroch, L.M., Wittmer, H.U., 2012. Table scraps: intra-trophic food provisioning by pumas in Patagonia. Biol. Lett. 8, 776–779.

Elbroch, L.M., Lendrum, P., Newby, J., et al., 2013. Seasonal foraging ecology of non-migratory cougars in a system with migrating prey. PLoS One 8, e83375.

Elbroch, L.M., Allen, M.L., Lowrey, B.H., et al., 2014. The difference between killing and eating: ecological shortcomings of puma energetic models. Ecosphere 5, 53.

Gerngross, P., 2016. The IUCN Red List of Threatened Species. Version 2016-3. http://www.iucnredlist.org. Downloaded on 11 December 2016.

Hunter, J.S., Durant, S.M., Caro, T.M., 2006. Patterns of scavenger arrival at cheetah kills in Serengeti National Park Tanzania. Afr. J. Ecol. 45, 275–281.

Iberlince and EU LIFE Programme, 2015. The IUCN Red List of Threatened Species. Version 2016–3. http://www.iucnredlist.org. Downloaded on 11 December 2016.

Inger, R., Cox, D.T.C., Per, E., et al., 2016. Ecological role of vertebrate scavengers in urban ecosystems in the UK. Ecol. Evol. 6, 7015–7023.

International Snow Leopard Trust and Wildlife Conservation Society, 2010. The IUCN Red List of Threatened Species. Version 2016–3. http://www.iucnredlist.org. Downloaded on 11 December 2016.

International Union for Conservation of Nature, 2015. The IUCN Red List of Threatened Species. Version 2016–3. http://www.iucnredlist.org. Downloaded on 11 December 2016.

International Union for Conservation of Nature, 2016. The IUCN Red List of Threatened Species. Version 2016–3. http://www.iucnredlist.org. Downloaded on 11 December 2016.

Jacobson, A.J., Gerngross, P., Lemeris, J.R., et al., 2016. Leopard (Panthera pardus) status, distribution, and the research efforts across its range. PeerJ 4, e197.

Krebs, C.J., 1999. Ecological Methodology. Addison Wesley Longman, California.

Krofel, M., Kos, I., Jerina, K., 2012. The noble cats and the big bad scavengers: effects of dominant scavengers on solitary predators. Behav. Ecol. Sociobiol. 66, 1297–1304.

Long, R.A., MacKay, P., Ray, J., et al., 2012. Noninvasive Survey Methods for Carnivores. Island Press, Washington, DC.

Mateo-Tomás, P., Olea, P., Moleón, M., et al., 2015. From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. Divers. Distrib. 21, 913–924.

Moleón, M., Sànchez-Zapata, J.A., 2015. The living dead: time to integrate scavenging into ecological teaching. Bioscience 65, 1003–1010.

Moleón, M., Sànchez-Zapata, J.A., Selva, N., et al., 2014. Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. Biol. Rev. 89, 1042–1054.

Oro, D., Genovart, M., Tavecchia, G., et al., 2013. Ecological and evolutionary implications of food subsidies from humans. Ecol. Lett. 16, 1501–1514.

Raynes, B., 2014. Birds of Jackson Hole. Grand Teton Association, Wyoming Game and Fish Department, Jackson, WY.

Ripple, W.J., Estes, J.A., Beschta, R.L., et al., 2014. Status and ecological effects of the world's largest carnivores. Science 343, 1241484.

Ruth, T.K., Murphy, K., 2010. Competition with other carnivores for prey. In: Hornocker, M., Negri, S. (Eds.), Cougar: Ecology and Conservation. University of Chicago Press, Chicago, IL.

Scantlebury, D.M., Mills, M.G.L., Wilson, R.P., et al., 2014. Flexible energetics of cheetah hunting strategies provide resistance against kleptoparasitism. Science 346, 79–81.

Selva, N., Jędrzejewska, B., Jędrzejewski, W., et al., 2005. Factors affecting carcass use by a guild of scavengers in European temperate woodland. Can. J. Zool. 83, 1590–1601.

Sikes, R.S., Gannon, W.L., Animal Care and Use Committee of the American Society of Mammalogists, 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. J. Mammal. 92, 235–253.

Wallach, A.D., Izhaki, I., Toms, J.D., et al., 2015. What is an apex predator? Oikos 124, 1453–1461.

Wiki, 2016. https://en.wikipedia.org/wiki/Mammals_of_Grand_Teton_National_Park Viewed 1 January 2017.

Wilmers, C.C., Crabtree, R.L., Smith, D.W., et al., 2003. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. J. Anim. Ecol. 72, 909–916.

Wilson, E.E., Wolkovich, E.M., 2011. Scavenging: how carnivores and carrion structure communities. Trends Ecol. Evol. 26, 129–135.