

Note

Free Lunch, May Contain Lead: Scavenging Shot Small Mammals

MICHAEL McTEE,¹ *MPG Ranch, 19400 Lower Woodbuck Rd, Florence, MT 59833, USA*

BRIAN HILLER, *Bemidji State University, 1500 Birchmont Drive NE, Bemidji, MN 56601, USA*

PHILIP RAMSEY, *MPG Ranch, 19400 Lower Woodbuck Rd, Florence, MN 59833, USA*

ABSTRACT Scavengers are subsidized by the remains of hunting worldwide. Although most studies focus on carcasses of large mammals, small mammals that have been shot likely provide a significant food subsidy as well, particularly in parts of the western United States. Millions of small mammals are estimated to be shot each year for damage control and recreation, many being left in the field. Despite this prevalence of carrion, and the potential for scavengers to ingest residual lead from bullet fragments, the fate of these carcasses is largely unknown. We deployed remote cameras to observe which scavengers consumed shot ground squirrels (*Uroditellus* spp.) and black-tailed prairie dogs (*Cynomys ludovicianus*) in 8 locations across Montana, USA. At least 5 species of mammals and 9 species of birds scavenged, including burrowing owls (*Athene cunicularia*). Scavengers fully consumed 66% of carcasses and partially consumed 9%. Carcasses lasted an average of 24.5 hours before the first scavenger arrived. Of carcasses that were scavenged, mammals ate 16% and birds ate 84%, with corvids and raptors consuming an equal number of carcasses. Common ravens (*Corvus corax*) and black-billed magpies (*Pica hudsonia*) visited the most carcasses and often arrived first. Scavengers consumed only 9% of the carcasses that were partially concealed by being inside a burrow. Overall, our results indicate that a diverse scavenger community consumes shot ground squirrels and black-tailed prairie dogs, and consequently, may be exposed to lead from bullet fragments. © 2019 The Wildlife Society.

KEY WORDS ammunition, bullet, ground squirrel, lead, Montana, nonlead, prairie dog, raptor, scavenger, small mammal.

In many locations worldwide, humans subsidize scavengers with carcass remains (Mateo-Tomás et al. 2015, Lafferty et al. 2016, Gomo et al. 2017). These food subsidies often occur predictably in time and space (e.g., during and following hunting seasons) and have the potential to improve the body condition and overall survival of the scavengers (Haroldson et al. 2004, Mateo-Tomás et al. 2015). Consequently, facultative scavengers may become more prevalent and increase their overall predation on prey (Moleón et al. 2014). Alternatively, food subsidies may divert predators from prey (Moleón et al. 2014). Despite these important ecological interactions, information regarding the habits of scavengers feeding on carrion left by humans in terrestrial ecosystems is scarce (Mateo-Tomás et al. 2015). Of the research that exists, most focuses on carrion left from the hunting of large mammals (Mateo-Tomás et al. 2015), but shot small mammals likely represent a significant food subsidy to scavengers too.

It is estimated that humans shoot and kill millions of small mammals each year for damage control and recreation (Reeve

and Vosburgh 2005). These animals are often excluded from wanton waste laws that require the animals to be recovered; therefore, carcasses often remain in the field where they are available to scavengers. Ground squirrels (*Uroditellus* spp.) and prairie dogs (*Cynomys* spp.) comprise a large part of the small mammals that are shot in the western United States. Shooters can kill hundreds in a day (Vosburgh and Irby 1998), thus creating a pulse of high-quality food in a spatially discrete area. Scavengers can access these carcasses without exerting the energy normally required to hunt. But compared to the carcasses of large mammals that may remain in the field for weeks or longer (Lafferty et al. 2016), the carcasses of small mammals are small enough to be eaten whole or carried away. This creates an incentive for scavengers to find these carcasses as soon as they become available. In studies that monitored moose (*Alces alces*) carcasses, corvids were often the first scavengers to arrive (Lafferty et al. 2016, Gomo et al. 2017). Similarly, some scientific and anecdotal evidence suggests that corvids and raptors respond to the sounds of gun shots and eat shot small mammals left in the field (Chesser 1979, White 2005). Although scavengers may be receiving a caloric benefit from consuming these carcasses, if the small mammals were shot with lead bullets, residual particles of lead could poison scavengers (Pattee et al. 1981, Haig et al. 2014).

Received: 26 February 2019; Accepted: 1 May 2019

¹E-mail: mmctee@mpgranch.com

Hunting ammunition has been linked to elevated blood lead levels in many species of raptors (Haig et al. 2014). When a lead bullet penetrates an animal, particles of the bullet can fragment and be left in the carcass (Haig et al. 2014). Many of the bullets that are used to control small mammals are designed to fragment to cause maximum tissue damage. Previous research reported that most Columbian ground squirrels (*Urocitellus columbianus*) shot with lead bullets contained residual lead, and in some cases, contained hundreds of bullet fragments (McTee et al. 2017). When ingested, these small fragments are eroded and potentially absorbed from the gastrointestinal tract into blood more readily than larger fragments, which makes the scavengers more likely to suffer adverse effects from lead exposure (Bartrop and Meek 1979). Lead poisoning is a conservation concern for avian scavengers (Haig et al. 2014), causing a range of symptoms, including sublethal effects that may affect behavior and physiological function (e.g., anemia, body condition, flight height, blindness), potentially resulting in death (Church et al. 2006, Finkelstein et al. 2012, Ecke et al. 2017).

Although small mammals that have been shot often contain fragments of lead that pose a threat to scavengers, the fate of these carcasses is largely unknown (Knopper et al. 2006, Pauli and Buskirk 2007, Herring et al. 2016, McTee et al. 2017). To our knowledge, only Stephens et al. (2005) investigated whether scavengers consume shot small mammals, yet the researchers failed to detect scavenging. However, it is likely that scavengers prey upon injured or dead animals, as seen in areas where anticoagulant rodenticides are used (López-Perea and Mateo 2018). To improve our understanding of how small mammals that have been shot are scavenged, we installed remote cameras near the carcasses of ground squirrels and black-tailed prairie dogs (*Cynomys ludovicianus* [prairie dogs]). The animals were shot for damage control at ranches and private properties across Montana, USA. We designed the study to produce descriptive results that would allow us to explore what species consume small mammals that have been shot and how the timing of scavenging varies among locations, carcass species, and scavengers. We predicted that many endemic scavengers would opportunistically consume carcasses, but corvids would arrive first and thus have greater access to carcasses than other scavengers.

STUDY AREA

We conducted the study on 8 ranches and private properties across Montana where shooters frequently controlled ground squirrels and prairie dogs to reduce agricultural and pasture damage (Fig. 1; Table 1). We deployed remote cameras between April and June 2018 in areas that ranged in size from 5 ha to 800 ha. We limited the study to private properties to help prevent the cameras from being stolen or vandalized. Ground squirrels, primarily Columbian and Richardson's (*Urocitellus richardsonii*), were present in 5 locations in western Montana where broad mountain valleys dominated the landscape and elevations ranged between 975 m to 1,550 m. Sampling in ground squirrel colonies

may have coincided with raptor migration. Prairie dogs were present in 3 locations in eastern Montana where the landscape consisted of badlands and grasslands with elevations ranging between 700 m and 1,000 m. Ground squirrel and prairie dog colonies were in or near agricultural fields or cattle pastures often consisted of grasses and fauna associated with grassland and riparian areas. On larger ranches, we often set up cameras in separate colonies, with the maximum distance between colonies being 5 km. Locations near Sheridan, Montana were in the same valley but had different landowners, consisted of dissimilar vegetation communities, and were ≥ 7 km apart, so we treated them as independent locations.

METHODS

We timed our sampling to occur immediately after planned shooting with lead and nonlead bullets, which complied with all state and federal laws, and was approved by Bemidji State University (protocol number BSU-2018-1). We also followed guidelines presented by Sikes (2016) regarding the care and use of animals.

We deployed 83 cameras near 89 carcasses. At each location, we began placing cameras within 2 hours after shooting and finished within 3 hours after starting. We located carcasses opportunistically and a small number may have been present from prior shooting. We did not place carcasses in front of cameras or identify each ground squirrel to species. In each of the 8 locations, we monitored between 4 to 22 carcasses (Table 1). We used Browning Spec Ops Platinum and Advantage cameras (Prometheus Group, Birmingham, Alabama, USA). We programmed the cameras to take 12-megapixel pictures when triggered by motion with 5-second delays between pictures. We tied and then taped each camera 0.5–1.0 m off the ground on a wooden stake placed 3–5 m from the carcass. We pounded a second stake diagonally in the ground to serve as a cross brace for the first stake and taped the stakes together. At each location except Miles City, we deployed a camera where no carcass was present to determine whether cameras attracted scavengers. We left cameras in the field for ≥ 2

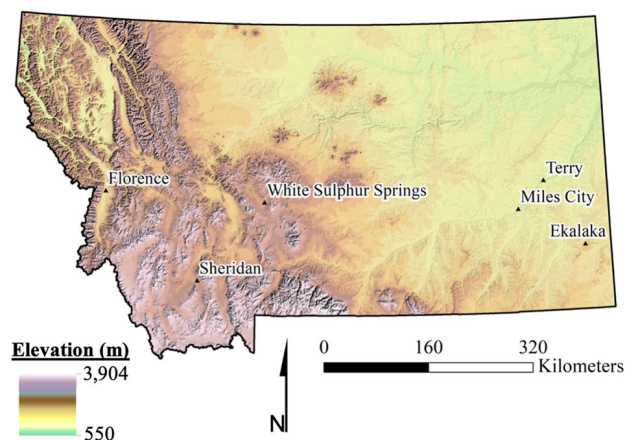


Figure 1. The closest towns to the sampling locations for scavenged small mammals that had been shot across Montana, USA, spring 2018. Three locations were sampled near Sheridan.

Table 1. Descriptions of sampling locations where remote cameras photographed scavengers visiting shot ground squirrels and black-tailed prairie dogs. Sampling occurred in Montana, USA, spring 2018. The sample size represents the number of carcasses observed for each location. The density of carcasses (carcasses/km²) may be an underestimate because small mammals were sometimes shot on neighboring ranches. We set up cameras within 3 hours of each other at each location.

Location	Date sampled	Hours in field (\bar{x})	Carcasses/km ² ($\bar{x} \pm SD$) ^a	<i>n</i>	Landscape
Ground squirrels					
Sheridan 1	11 Apr 2018	94	7.8 ± 0.5	8	Agricultural field
Sheridan 2	11 Apr 2018	93	5.0 ± 0.0	5	Mixed grasses near agricultural field
Sheridan 3	11 Apr 2018	98	10.0 ± 0.0	9	Mixed grasses near riparian area
Florence	24 Apr 2018	144	4.0 ± 0.0	4	Mixed grasses near riparian area
White Sulphur Springs	16-17 May 2018	68, 39	4.4 ± 1.6	15, 3	Cattle pasture and agricultural field
Prairie dogs					
Miles City	7 Jun 2018	64	6.0 ± 0.0	6	Cattle pasture
Terry	8 Jun 2018	38	8.8 ± 1.5	17	Cattle pasture
Ekalaka	10 Jun 2018	64	6.8 ± 2.2	22	Cattle pasture and agricultural field

^a We calculated the density of carcasses around each individual carcass and used those values to calculate the mean and standard deviation per location.

nights and ≥ 38 hours. The length of camera deployment was often unequal among locations and was determined by logistical constraints and the need to minimize the disruption of normal farming and ranching operations. When we added the amount of time that all cameras were left in the field, the sum approximately equaled 6,000 hours of potential observation. We recorded carcasses as being located in or out of a burrow. When carcasses were in burrows, we included only those that were within 0.3 m of the surface and were visible. In cases where carcasses were within 2 m of each other, we used a single camera and observed each carcass independently. While retrieving the cameras, we recorded whether the carcasses were partially scavenged, fully scavenged, or not scavenged at all.

We first classified pictures by documenting all species that were photographed scavenging. We then calculated the elapsed time until each carcass was first scavenged and until the carcass was fully scavenged. When a scavenger removed a carcass from the view of the camera, we considered the carcass fully scavenged. We recorded whether scavenging occurred at day or night. In some instances, carcasses were absent when we retrieved the cameras, yet the camera did not photograph the final scavenger. This happened either because the camera malfunctioned or cattle pushed the camera setup to the ground. We classified these carcasses as scavenged, but did not calculate the elapsed time until the carcass was fully scavenged. In 2 instances, pictures were taken before and after a carcass had been scavenged, yet the picture of the scavenger feeding was not recorded. The length of time between pictures was < 6.5 hours, so we used the midpoint between pictures to estimate the elapsed time until fully scavenged. The resulting data from these 2 instances were within the range of values of the rest of the dataset. For each of the 8 locations, we calculated the percent of carcasses that each scavenger fully consumed or carried away. We also calculated the number of carcasses visited by each scavenger and the average amount of time until they first scavenged.

We compared the elapsed time until scavenging by corvids, raptors, and mammals using a gamma generalized linear model (GLM). We reran the model and included location as a random factor to determine whether location

influenced overall trends. We used gamma GLMs because they accommodate continuous data with unequal variances (Faraway 2006). We compared the time that ground squirrels and prairie dogs were first scavenged with an unequal-variance *t*-test after the data had been log transformed. For descriptive purposes, we counted the number of carcasses within 1 km² of each carcass to calculate the mean and standard deviation of carcass density (Table 1). We did not include carcass density in our analysis because in 3 out of the 8 locations, we observed small mammals being shot on neighboring ranches. These activities increased the density of carcasses to an unknown extent that we could not account for in our analysis. We performed statistical analyses in RStudio (version 1.0.143, www.r-project.org, accessed 7 Sep 2018).

RESULTS

Scavengers fully consumed 66% of carcasses and partially consumed 9% of them. Ground squirrel carcasses were fully scavenged 56–100% of the time and 44–100% of prairie dog carcasses were scavenged, depending on location. Because of camera malfunction or interference by cows, pictures were not captured for 24% of carcasses that were fully scavenged by unknown animals. When considering only carcasses that were observed being fully scavenged, birds consumed 84%, whereas mammals consumed 16%. Mammals scavenged only at night. Corvids and raptors comprised all avian scavenging and consumed an equal number of carcasses. Qualitatively, the composition of scavengers differed between locations (Fig. 2). We observed higher relative abundances of raptors in Miles City, Florence, and Sheridan 1, whereas corvids dominated the scavenging community in White Sulphur Springs and Sheridan 2. American crows (*Corvus brachyrhynchos*) appeared at only 2.5% of the carcasses. Badgers (*Taxidea taxus*) and canids (i.e., coyotes and red foxes [*Vulpes vulpes*]) scavenged at 25% and 38% of the locations, respectively. One of 11 carcasses in burrows (9%) was scavenged, this was a prairie dog carcass that was eaten by a turkey vulture (*Cathartes aura*) that stuck its head and neck into a burrow. We did not see strong evidence that cameras attracted scavengers because the 7 cameras

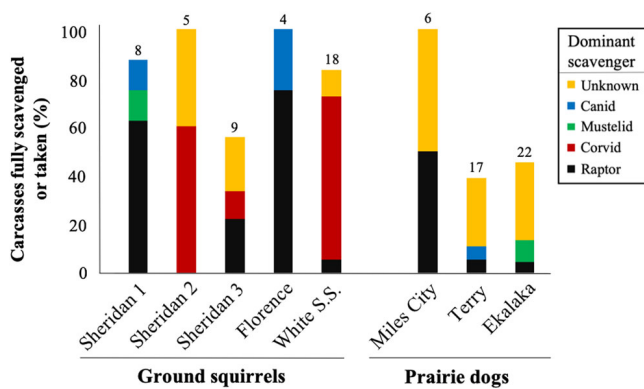


Figure 2. Percent of carcasses that were fully scavenged or taken by the time cameras were retrieved (38–144 hr). We deployed remote cameras to document the scavengers that consumed shot ground squirrels and black-tailed prairie dogs across Montana, USA, spring 2018. Each bar shows the relative abundance of the dominant scavenger groups that we observed eating carcasses. Some instances of scavenging were not photographed because of camera malfunction or cattle interference, so the identity of many scavengers were unknown. Sample sizes are given above each bar. Observations within a location may not be independent of each another because scavenging behavior could attract additional scavengers. White S.S. = White Sulphur Springs.

deployed without a carcass nearby recorded only 1 scavenger, which was a black-billed magpie [*Pica hudsonia*].

Carcasses were in the field for a mean of 16.1 ± 17.6 (SD) hours before the first scavenger arrived. Scavengers arrived sooner to ground squirrel carcasses than prairie dog carcasses ($t = 316.8$, $P < 0.001$). Observationally, the elapsed time until the first scavenger arrived varied among locations (Fig. 3A), with the fastest appearance being at the White Sulphur Springs and Florence study areas. At these locations, the first scavengers arrived in an average of 2.8 hours and 4.8 hours, respectively. In 21% of the cases where we observed the first scavenger, that scavenger took the carcass and left; the scavenger in these cases was usually a buteo, canid, or badger. Carcasses that were fully scavenged lasted an average of 24.5 hours in the field. Ground squirrels were fully scavenged in an average of 19.3 hours compared to 32.9 hours for prairie dogs ($t = 7.2$; $P < 0.001$). The elapsed time until carcasses were fully consumed among

locations qualitatively followed the same trends as observed with the elapsed time until the first scavenger arrived (Fig. 3B). At all locations near Sheridan, a snowstorm covered carcasses for approximately 1 day, possibly delaying scavenging.

Black-billed magpies and common ravens (*Corvus corax*) were observed most often and visited 16.3% and 22.5% of the carcasses, respectively (Table 2). Corvids arrived at carcasses sooner than raptors and mammals when location was omitted from the model ($Z = 5.8$, $P < 0.001$; $Z = 4.2$, $P < 0.001$, respectively). However, when the model included location as a random factor, the differences did not persist. At White Sulphur Springs, common ravens showed evidence of local enhancement where their presence attracted more common ravens. We observed an average of 3.5 individual common ravens at each carcass, with 1 carcass having 11 individuals. The potential for local enhancement means that, within a location, scavenger behavior might not be independent among carcasses. At Sheridan 1, we observed ≥ 5 different hawks feeding on a single ground squirrel carcass on at least 10 occasions over 7 hours. In many instances, they arrived within 30 minutes of each other, often sooner. They fed individually, except for when 2 Swainson's hawks (*Buteo swainsoni*) appeared to copulate on the carcass. The other hawks included a red-tailed hawk (*Buteo jamaicensis*), an adult male northern harrier (*Circus cyaneus*), a juvenile northern harrier, and likely a third northern harrier that was female, based on partial identification and the presence of another bird of that description visiting a nearby carcass.

Golden eagles (*Aquila chrysaetos*) only appeared after corvids had arrived and were seen only at White Sulphur Springs. Raptors other than golden eagles appeared sporadically, and on average, first appeared ≥ 1 day after a camera was deployed (Table 2). However, there were instances of earlier arrivals. For example, a turkey vulture, northern harrier, and red-tailed hawk all arrived in ≤ 5 hours. Northern harriers visited more carcasses than other raptors and burrowing owls (*Athene cunicularia*) were the rarest, scavenging only 2.5% of the carcasses, although they

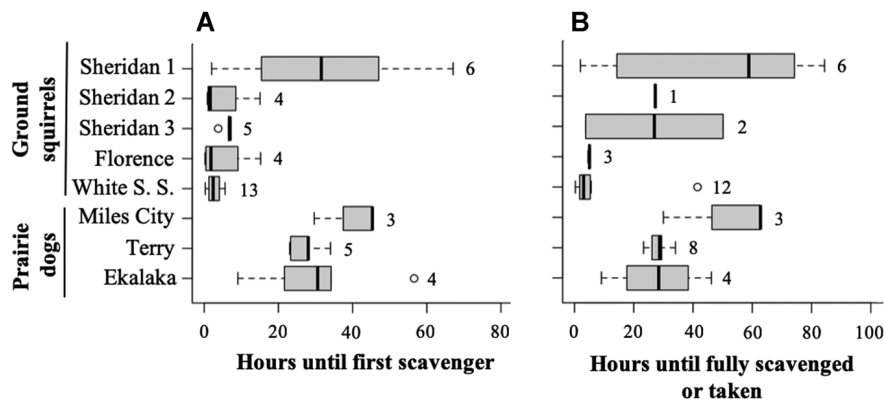


Figure 3. The hours until the carcasses of shot ground squirrels and black-tailed prairie dogs were A) first scavenged and B) fully scavenged or taken. Sample sizes are to the right of each box. Data are based on pictures from remote cameras that photographed scavengers consuming or taking carcasses across Montana, USA, spring 2018. Observations within a location may not be independent of each another because scavenging behavior could attract additional scavengers. White S.S. = White Sulphur Springs.

Table 2. Eighty occurrences of scavenging species that visited shot ground squirrels and black-tailed prairie dogs obtained from pictures taken with remote cameras in the spring of 2018 in Montana, USA. We excluded cameras that stopped taking photographs or were disturbed by cattle. Observations within a location may not be independent of one another because scavenging behavior could attract additional scavengers.

Species	% visited	Hours until first visit		
		\bar{x}	SD	Min.
Birds				
Black-billed magpie	16.3	4.4	3.9	0.9
American crow	2.5	23.2	8.2	0.3
Common raven	22.5	7.1	0.2	23.0
Turkey vulture	7.5	28.5	15.7	0.2
Northern harrier	10.0	40.5	30.2	2.0
Red-tailed hawk	5.0	28.7	32.6	5.1
Swainson's hawk	3.8	54.4	32.4	17.5
Golden eagle	3.8	4.2	2.2	1.7
Burrowing owl	2.5	45.7	15.3	34.9
Mammals				
Badger	3.8	18.0	11.2	9.2
Red fox	1.3	84.4		84.4
Coyote	1.3	34.0		34.0
Ground squirrel ^a	7.5	36.5	50.6	0.7
Unidentified rodents	3.8	46.4	35.0	13.4

^a Ground squirrels were not present near prairie dog colonies, so the percent of carcasses visited by ground squirrels reflects only the locations where they lived ($n = 41$).

appeared at 7.5% of them. Badgers and canids collectively visited < 6.4% of the carcasses. Living ground squirrels were often present near carcasses but only scavenged occasionally. We observed herbivores (i.e., moose, white-tailed deer [*Odocoileus virginianus*], cows) approaching and smelling carcasses. At the Ekalaka location, a long-tailed weasel (*Mustela frenata*) was photographed several meters away from the carcass, but it did not scavenge.

DISCUSSION

Similar to carcasses from big game hunting, shot ground squirrels and prairie dogs were consumed by a diverse suite of scavengers (Mateo-Tomás et al. 2015, Lafferty et al. 2016, Gomo et al. 2017). We observed 14 different species of scavengers across 8 locations in Montana (Table 2; Fig. 4). Scavengers ate most carcasses that were left in the field but consumed only 9% of carcasses that we monitored in burrows. Ground squirrels and prairie dogs frequently re-enter or fall into burrows after being shot, so many of those carcasses may not be scavenged. Carcasses lasted an average of 24.5 hours, with the fastest arrival times of scavengers being for black-billed magpies and common ravens (Table 2). This demonstrates the ability of corvids to rapidly exploit temporary resources, as seen elsewhere (Lafferty et al. 2016, Gomo et al. 2017). Birds consumed 84% of carcasses that we observed being scavenged, with raptors and common ravens scavenging the same number (Fig. 2). This corroborates previous work showing that birds, on a global scale, scavenge more often than mammals (Mateo-Tomás et al. 2015). Raptors scavenged sporadically, possibly indicating that they opportunistically took carcasses when hunting. We observed at least 5 different hawks feeding intermittently on a single carcass, and burrowing

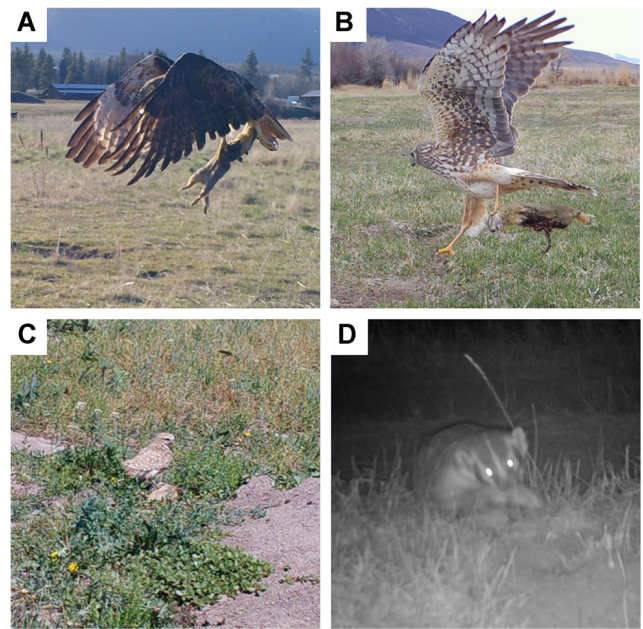


Figure 4. Pictures of species that scavenged shot ground squirrels and black-tailed prairie dogs captured by remote cameras deployed across Montana, USA, spring 2018. A) Red-tailed hawks, B) northern harriers, and other buteos frequently flew away with carcasses. C) Burrowing owls visited several prairie dog carcasses. D) Badgers and canids were observed scavenging only at night.

owls scavenging (Table 2; Fig. 4), which to our knowledge has not previously been documented. Overall, our results show that a diverse scavenger community consumes the carcasses of shot small mammals, and consequently, may be exposed to lead from bullet fragments.

Game cameras can introduce biases and limitations to a study. In our study, nearly a quarter of the carcasses that had been scavenged were scavenged without a picture being taken because of cattle disrupting the camera setups and camera malfunction. In some instances, pictures ceased to be taken for unknown reasons, while at other times, cameras failed to detect the scavenger. Failure to detect motion may have biased our results and caused an underestimation of species that have lower detection probabilities. These species may include those that seize carcasses and leave, such as buteos, canids, and badgers. This contrasts with corvids, turkey vultures, and burrowing owls, which often scavenged in front of the camera and would potentially be more likely to trigger the camera.

The presence of cameras may have attracted or deterred scavengers. At the Miles City location, a coyote (*Canis latrans*) that walked beyond the carcass appeared frightened by the camera and did not scavenge. In a similar study, wolves (*Canis lupus*) scavenging moose remains were startled by the flash of a camera (Lafferty et al. 2016). When practical, setting up a camera to film the carcass from a distance may yield observations of deterrence. Conversely, we did not see evidence that cameras attracted scavengers. Cameras that were placed without a carcass nearby collectively took only 1 picture of a scavenger (black-billed magpie). We also never observed bird feces on the cameras

or stakes that would have indicated that birds were attracted to camera setups to use them as perches. Despite these potential biases, our results captured a wide breadth of the scavenger community that likely would not have been documented with direct observations, which present their own challenges, including sampling bias and logistical constraints (Caravaggi et al. 2017).

The small body size of shot small mammals means that they can be more rapidly scavenged than the carcasses of large mammals. In some cases, small mammals are eaten whole. This creates an incentive for scavengers to find carcasses before competitors. Consistent with studies from other parts of the world, corvids tended to arrive first and they visited the most carcasses (Table 2; Lafferty et al. 2016, Gomo et al. 2017). In the case of common ravens, their ability to rapidly find carrion likely results from their communicating with one another and their ability to associate with predators and possibly hunters and shooters (Marzluff et al. 1996, White 2005). For example, one study reported that common ravens associated with wolves to immediately discover wolf kills and later scavenge (Stahler et al. 2002). Afterward, the number of common ravens increased because of local enhancement where their presence attracted more common ravens.

Our data suggest a similar association may occur between common ravens and shooters. At White Sulphur Springs, common ravens visited all observed carcasses that were not in burrows. This occurred despite us observing multiple species of buteos actively hunting the area, presumably for ground squirrels. Common ravens first visited carcasses an average of 2.8 hours after deployment, with the earliest arrival being in 0.3 hours (Table 2). The presence of ravens may have also attracted more common ravens. This contrasts with other locations where > 1 common raven at a carcass was unusual. In instances where local enhancement occurred, observations of scavenging among carcasses may not have been independent at each location. This is likely an inherent factor in studies that monitor pulses of carrion in spatially discrete areas.

Gunshots may have attracted birds, which has been observed with common ravens (White 2005). Although common ravens may be the primary beneficiaries from this attraction, it could transfer to raptors living in areas where shooters provide a significant amount of carrion. In 2 instances, we observed a turkey vulture and red-tailed hawk scavenging carcasses during and immediately after shooting, respectively. This behavior has been observed elsewhere with ferruginous hawks (*Buteo regalis*; Chesser 1979). Also, like common ravens, raptors may have exhibited local enhancement. All 3 observations of golden eagles were at the White Sulphur Springs location after common ravens had arrived at the carcass. Similarly, we observed repeated scavenging on a single ground squirrel carcass by ≥ 5 raptors at Sheridan 1. Because we sampled this site in mid-April, these birds could have been using the area as a stopover during migration, they could have been residents, or they could have been on their summering grounds (Preston and Beane 2009, Bechard et al. 2010, Smith et al. 2011).

Millions of small mammals are estimated to be shot each year (Reeve and Vosburgh 2005), but based on our observations and results, it is likely that many are not scavenged. We found fewer carcasses in the field than shooters reported because animals often re-entered or fell down burrows after being shot. For scavengers that rely on visual cues to find prey, such as many raptors, carcasses in burrows may not be located. The primary scavengers of these carcasses might be those with a strong sense of smell, such as canids, badgers, and turkey vultures. Indeed, the only scavenger to consume a carcass in a burrow was a turkey vulture. Longer observation periods may have resulted in more carcasses being scavenged in burrows and on the surface. At the Terry location, however, the hot weather rapidly desiccated carcasses and flies consumed fresh tissue. Environmental conditions like these may limit the duration that carcasses would be fresh and available. Moreover, we found completely desiccated carcasses, skulls, and bones in prairie dog colonies. These carcasses were likely either scavenged within the colony by unknown species, or not scavenged at all. Lower occurrences of scavenging, as seen to some extent in Terry and Ekalaka, may have been influenced by multiple factors. First, the densities of scavengers could have been too low for them to use all available carrion. A similar occurrence was seen in Alaska, USA, with a high density of moose remains (Lafferty et al. 2016). In our study, however, the biomass of shot small mammals would be considerably lower, so the landscape being saturated with carcasses seems unlikely. Alternatively, facultative scavengers could have been focusing on prey species other than prairie dogs. This may have occurred at the Thunder Basin National Grassland in Wyoming, USA, where researchers in the field never witnessed raptors scavenging shot prairie dogs despite the prevalence of shooting and abundance of raptors (Stephens et al. 2005). They concluded that the lack of scavenging could have been a result of lower prairie dog numbers due to a recent outbreak of sylvatic plague. Consequently, raptors may have targeted lagomorphs instead, which were abundant.

Our study raises additional uncertainties regarding the relationship between scavengers and shot small mammals. We observed a diverse scavenger community consuming carcasses to varying degrees; however, it is unclear to what extent shot small mammals comprise the diet of those scavengers. In some cases, such as when raptors live in areas with no human presence, shot small mammals would be infrequently scavenged because their availability would be low. Conversely, resident scavengers living in areas with frequent shooting may specialize on shot small mammals. In these cases, carcasses could constitute a significant portion of their diet, and for birds, possibly the diets of their nestlings (Herring et al. 2016). Additionally, it is uncertain how the consumption of these carcasses influence predator-prey relationships and even disease transmission. Fleas carrying sylvatic plague could infect a scavenger or travel with it to a new prairie dog colony or elsewhere. Additionally, repeating the study in different land cover

types may yield new scavenger species. Sampling near forests, for example, could generate observations of black bears (*Ursus americanus*), accipiters, and other wildlife not detected in this study. Similarly, we did not sample within the core range of grizzly bears (*U. arctos*), but because they prey on ground squirrels (Foresman 2012), they may opportunistically scavenge ones that have been shot.

Even though shot small mammals provide a food subsidy to scavengers, the carcasses may contain fragments of lead bullets. Lead exposure is a primary concern for the conservation of raptors because it impairs their health, performance, and sometimes survival (Haig et al. 2014, Ecke et al. 2017). Elevated blood lead levels have been observed in most of the avian species observed scavenging in this study (Fisher et al. 2006). These elevated blood lead levels have been linked to fragments of lead bullets and lead shot, both being left in offal piles or unrecovered animals (Clark and Scheuhammer 2003, Church et al. 2006, Martin et al. 2008, Haig et al. 2014). A portion of this lead has the potential to be absorbed into the circulatory system where it can cause various toxicological effects (Haig et al. 2014). Previous work demonstrated that small mammals shot with lead often contain bullet fragments (McTee et al. 2017), and combined with this study, indicates that a diverse scavenger community is exposed to lead by consuming shot small mammals. To our knowledge, this study documents the first evidence of burrowing owls scavenging shot prairie dogs, although others have found burrowing owls to be opportunistic feeders (Poulin et al. 2011). We observed burrowing owls scavenging only 2.5% of carcasses, but they were present at 7.5% of carcasses and could have scavenged without a picture being taken. Our findings suggest that burrowing owls might be exposed to lead if they live in areas where small mammals are shot. Despite this risk, previous research showed no differences in the lead concentrations of feathers collected from burrowing owls caught in prairie dog colonies where shooting did or did not occur (Stephens et al. 2005). An additional concern is that nestlings, those of burrowing owls and other raptors, are being exposed to lead, which could hinder their growth rate (Herring et al. 2016). To better understand this threat, researchers could test the blood lead levels of scavengers living in areas where humans often shoot small mammals.

MANAGEMENT IMPLICATIONS

Shot small mammals provide a pulse of carrion for scavengers in a spatially discrete area. The varying times that it took for scavengers to discover carcasses suggests that scavengers feed on shot small mammals opportunistically, but perhaps some also associate shooting activities with available carrion. These carcasses likely provide a significant food subsidy to scavengers, but the carcasses may expose scavengers to lead. This hazard may be lessened if carcasses are removed from the field, although this would reduce the availability of carrion to scavengers. Alternatively, shooters could use non-lead ammunition while continuing to provide carrion to scavengers.

ACKNOWLEDGMENTS

We are grateful to C. W. Casper for creating Figure 1 and A. B. Ramsey and K. R. Stone who gave us helpful feedback regarding our study design. We thank the following people for helping coordinate efforts: B. K. Beach, A. M. Buckingham, L. S. Bullington, C. A. Daubel, D. A. Delisi, J. A. Harding, P. G. and R. P. Haughian, M. A. Henning, M. R. Matchett, L. G. Miller, J. J. Moser, D. J. and M. J. Rinella. We appreciate the comments provided by 2 anonymous reviewers and A. J. Kuenzi that helped improve this paper.

LITERATURE CITED

- Barltrop, D., and F. Meek. 1979. Effect of particle size on lead absorption from the gut. *Archives of Environmental Health: An International Journal* 34:280–285.
- Bechard, M. J., C. S. Houston, J. H. Saransola, and A. S. England. 2010. Swainson's hawk (*Buteo swainsoni*). Account 265 in A. F. Poole, editor. *The birds of North America*. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Caravaggi, A., P. B. Banks, A. C. Burton, C. M. V. Finlay, P. M. Haswell, M. W. Hayward, M. J. Rowcliffe, and M. D. Wood. 2017. A review of camera trapping for conservation behaviour research. *Remote Sensing in Ecology and Conservation* 3:109–122.
- Chesser, R. K. 1979. Opportunistic feeding on man-killed prey by ferruginous hawks. *Wilson Bulletin* 91:330–331.
- Church, M. E., R. Gwiazda, R. W. Risebrough, K. Sorenson, C. P. Chamberlain, S. Farry, W. Heinrich, B. A. Rideout, and D. R. Smith. 2006. Ammunition is the principal source of lead accumulated by California condors re-introduced to the wild. *Environmental Science & Technology* 40:6143–50.
- Clark, A. J., and A. M. Scheuhammer. 2003. Lead poisoning in upland-foraging birds of prey in Canada. *Ecotoxicology* 12:23–30.
- Ecke, F., N. J. Singh, J. M. Arnemo, A. Bignert, B. Helander, Å. M. M. Berglund, H. Borg, C. Bröjer, K. Holm, M. Lanzone, T. Miller, Å. Nordström, J. Räikkönen, I. Rodushkin, E. Ågren, and B. Hörnfeldt. 2017. Sublethal lead exposure alters movement behavior in free-ranging golden eagles. *Environmental Science & Technology* 51:5729–5736.
- Faraway, J. J. 2006. *Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models*. Chapman & Hall/CRC, Boca Raton, Florida, USA.
- Finkelstein, M. E., D. F. Doak, D. George, J. Burnett, J. Brandt, M. Church, J. Grantham, and D. R. Smith. 2012. Lead poisoning and the deceptive recovery of the critically endangered California condor. *Proceedings of the National Academy of Sciences of the United States of America* 109:11449–54.
- Fisher, I. J., D. J. Pain, and V. G. Thomas. 2006. A review of lead poisoning from ammunition sources in terrestrial birds. *Biological Conservation* 131:421–432.
- Foresman, K. 2012. *Mammals of Montana*. Second edition. Mountain Press Publishing Company, Missoula, Montana, USA.
- Gomo, G., J. Mattisson, B. R. Hagen, P. F. Moa, and T. Willebrand. 2017. Scavenging on a pulsed resource: quality matters for corvids but density for mammals. *BMC Ecology* 17:22.
- Haig, S. M., J. D'Elia, C. Eagles-Smith, J. M. Fair, J. Gervais, G. Herring, J. W. Rivers, and J. H. Schulz. 2014. The persistent problem of lead poisoning in birds from ammunition and fishing tackle. *The Condor* 116:408–428.
- Haroldson, M. A., C. C. Schwartz, S. Cherry, and D. S. Moody. 2004. Possible effects of elk harvest on fall distribution of grizzly bears in the Greater Yellowstone Ecosystem. *Journal of Wildlife Management* 68:129–137.
- Herring, G., C. A. Eagles-Smith, M. T. Wagner, C. Sanders-Reed, L. Bervoets, M. Eens, and M. Ortiz-Santaliestra. 2016. Ground squirrel shooting and potential lead exposure in breeding avian scavengers. *PLOS ONE* 11:e0167926.
- Knopper, L. D., P. Mineau, A. M. Scheuhammer, D. E. Bond, and D. T. McKinnon. 2006. Carcasses of shot Richardson's ground squirrels may

- pose lead hazards to scavenging hawks. *Journal of Wildlife Management* 70:295–299.
- Lafferty, D. J. R., Z. G. Loman, K. S. White, A. T. Morzillo, and J. L. Belant. 2016. Moose (*Alces alces*) hunters subsidize the scavenger community in Alaska. *Polar Biology* 39:639–647.
- López-Perea, J. J., and R. Mateo. 2018. Secondary exposure to anticoagulant rodenticides and effects on predators. Pages 159–193 in N. W. van den Brink, J. E. Elliot, R. F. Shore, and B. A. Rattner, editors. *Anticoagulant rodenticides and wildlife*. First edition. Springer, Cham, Switzerland.
- Martin, P. A., D. Campbell, K. Hughes, and T. McDaniel. 2008. Lead in the tissues of terrestrial raptors in southern Ontario, Canada, 1995–2001. *Science of The Total Environment* 391:96–103.
- Marzluff, J. M., B. Heinrich, and C. S. Marzluff. 1996. Raven roosts are mobile information centres. *Animal Behaviour* 51:89–103.
- Mateo-Tomás, P., P. P. Olea, M. Moleón, J. Vicente, F. Botella, N. Selva, J. Viñuela, and J. A. Sánchez-Zapata. 2015. From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. *Diversity and Distributions* 21:913–924.
- McTee, M., M. Young, A. Umansky, and P. Ramsey. 2017. Better bullets to shoot small mammals without poisoning scavengers. *Wildlife Society Bulletin* 41:736–742.
- 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.
- Pattee, O. H., S. N. Wiemeyer, B. M. Mulhern, L. Sileo, and J. W. Carpenter. 1981. Experimental lead-shot poisoning in bald eagles. *Journal of Wildlife Management* 45:806–810.
- Pauli, J. N., and S. W. Buskirk. 2007. Recreational shooting of prairie dogs: a portal for lead entering wildlife food chains. *Journal of Wildlife Management* 71:103–108.
- Poulin, R. G., L. D. Todd, E. A. Haug, B. A. Millsap, and M. S. Martell. 2011. Burrowing owl (*Athene cunicularia*), version 2.0. Account 61 in A. F. Poole, editor. *The birds of North America*. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Preston, C. R., and R. D. Beane. 2009. Red-tailed Hawk (*Buteo jamaicensis*). Account 52 in A. F. Poole, editor. *The birds of North America*. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Reeve, A. F., and T. C. Vosburgh. 2005. Recreational shooting of prairie dogs. Pages 139–156 in J. L. Hoogland, editor. *Conservation of the black-tailed prairie dog*. Island Press, Washington, D.C., USA.
- Sikes, R. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* 97:663–688.
- Smith, K. G., S. R. Wittenberg, R. B. Macwhirter, and K. L. Bildstein. 2011. Hen/northern harrier (*Circus cyaneus/hudsonius*). Account 210 in A. F. Poole, editor. *The birds of North America*. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Stahler, D., B. Heinrich, and D. Smith. 2002. Common ravens, *Corvus corax*, preferentially associate with grey wolves, *Canis lupus*, as a foraging strategy in winter. *Animal Behaviour* 64:283–290.
- Stephens, R. M., A. S. Johnson, R. Plumb, K. K. Dickerson, M. C. McKinstry, and S. H. Anderson. 2005. Secondary lead poisoning in golden eagles and ferruginous hawk chicks consuming shot black-tailed prairie dogs, Thunder Basin National Grassland, Wyoming. U.S. Fish and Wildlife Service, Washington, D.C., USA.
- Vosburgh, T. C., and L. R. Irby. 1998. Effects of recreational shooting on prairie dog colonies. *Journal of Wildlife Management* 62:363–372.
- White, C. 2005. Hunters ring dinner bell for ravens: experimental evidence of a unique foraging strategy. *Ecology* 86:1057–1060.

Associate Editor: Amy Kuenzi.