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Anthropogenic Impacts on Wildlife Mortality and Vertebrate Scavenging Communities

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Anthropogenic impacts on wildlife mortality

and vertebrate scavenging communities

By

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Roads cause substantial wildlife mortality, but there is currently limited understanding of the relative magnitude of this mortality source. There are also substantial gaps in knowledge concerning the ecological ramifications of carrion introduced to the environment from vehicle collisions and in particular how vertebrate scavengers may consume carrion resulting from vehicle collisions. Although a variety of factors influence scavenger use of carcasses, the mechanisms influencing competition for this resource between obligate and facultative scavengers have not been thoroughly explored.

I conducted a global synthesis of mortality of terrestrial vertebrates documenting 42,755 mortalities of known cause from 120,657 individuals representing 305 vertebrate species. Overall, 28% of mortalities were directly caused by humans and 72% were from natural sources. Vehicle collisions accounted for 4% of mortality overall. Larger birds were more likely than smaller birds to die from vehicle collisions and vehicle mortality of mammals increased over time.

There was no difference in proportion of rabbit carcasses scavenged or scavenger arrival time between those placed along roads, power line clearings, and forests. No species arrived at roads quicker than other treatments. Turkey vultures (*Cathartes aura*) and coyotes (*Canis latrans*) scavenged equally across treatments, whereas gray foxes (*Urocyon cinereoargenteus*) scavenged along roads and power lines, but not in forests. Scavenger use of carrion near roads likely relates to factors besides carrion availability, such as traffic avoidance and predation risk. Because some scavengers make substantial use of carrion on roads, this resource could be an important mechanism by which human activities impact wildlife.

Scavenging by facultative scavengers did not increase in the absence of competition with vultures. I found no difference in scavenger presence between control carcasses and those from which vultures were excluded. Facultative scavengers did not functionally replace vultures during summer in this study. These results suggest that under the conditions of this study, facultative scavengers would not compensate for loss of vultures. Carcasses would persist longer in the environment and consumption of carrion would likely shift from vertebrates to decomposers. Such changes could have substantial implications for disease transmission, nutrient cycling, and ecosystem functioning.

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CHAPTER I

GENERAL INTRODUCTION

Introduction

Humans influence every ecosystem on Earth's surface and directly dominate many of them (Vitousek et al. 1997). Mechanisms by which humans impact the environment include land transformations, altering biogeochemical cycles, and causing extinctions of wildlife (Vitousek et al. 1997, Waters et al. 2016). Construction of roads can also be an important factor by which humans influence the environment because their presence institutes a suite of ecological consequences (Forman and Alexander 1998, Trombulak and Frissell 2000).

Roads are pervasive across much of the Earth's surface. The ecological effects of a road, which include direct mortality of wildlife, altering hydrology, and introducing noise, chemical and light pollution (Trombulak and Frissell 2000), can extend more than a kilometer from the road itself (Forman and Deblinger 2000). For example, the 6.2 million km of roads in the United States are estimated to impact 20% of the nation's land (Forman and Alexander 1998, Forman 2000). The contribution of roads to environmental changes is so prevalent that a scientific field termed "road ecology" has emerged to better understand and mitigate these impacts (Coffin 2007).

One of the most widely recognized ways that roads can impact wildlife is through direct mortality, which has been the subject of considerable research. Studies have linked mortality from roads to changes in species population demographics (Gibbs and Steen 2005), decreased genetic diversity (Jackson and Fahrig 2011), and have raised concerns that this magnitude of mortality may not be sustainable (e.g. Gibbs and Shriver 2005, Glista et al. 2008). However, many of these studies are based on road surveys of mortality, which does not provide insight into other mortality sources. As such, it has not been possible to understand the magnitude of road mortality in relationship to other mortality factors influencing a population. To determine this, radio telemetry is needed to track the fates of animals, as this technique can provide unbiased estimates of mortality sources (Kays et al. 2015).

An aspect of road mortality that has received less consideration is the fate of animal carcasses on roads. The influx of carrion into the environment resulting from vehicle collisions could have substantial ecological ramifications, as most carnivores are facultative scavengers that consume carrion to some extent (DeVault et al. 2003). Furthermore, they may scavenge more frequently when carrion availability increases (Van Dijk et al. 2008). Scavengers may use roads due to reliable presence of carrion, but might also use roads for other purposes and encounter carrion opportunistically. As a result, the ecological drivers of scavenger use of carrion resulting from vehicle collisions is unclear. Additionally, the habitat around a road that runs through a forest differs in vegetation structure and canopy cover from that of the forest interior, which may alter dynamics between scavenger species in these areas. Habitat can influence competition for carrion through altering carrion detection rates and scavenger predation risk (Storch et al.

1990, Selva et al. 2003, Selva et al. 2005). Examining how consumption patterns of scavenging species differ between carcasses alongside roads and in forest interior is essential to understanding the degree to which carrion from vehicle collisions may subsidize populations of scavenger species. Furthermore, examining carrion use between roads, linear features without presence of carrion, and forest interior sites would provide additional information on mechanisms influencing scavenger consumption of carrion near roads.

Interactions between scavenger species also influence consumption patterns of carrion. Since many carnivores are facultative scavengers, an array of species are potentially in competition for this resource (DeVault et al. 2003). Scavengers frequently rely on exploitation competition by detecting and consuming carrion before competitors are able to do so. Obligate avian scavengers such as vultures can often detect carrion more rapidly than mammals due to enhanced senses of sight and smell, and because soaring flight enables vulture to rapidly traverse large areas (Ruxton and Houston 2004). However, in other scenarios mammals may use physical dominance or abundance in numbers to deter avian scavengers from carrion (Butler and du Toit 2002, DeVault et al. 2011). Studying carcass consumption by mammals in the absence of vultures is necessary to understand the extent to which vultures preclude mammals from scavenging. Such effects on mammals have substantial conservation implications, as vultures are the most endangered avian functional group (Şekercioğlu 2006), and their declines in some regions have been linked to large increases in feral mammal populations (Markandya et al. 2008).

I conducted a global synthesis of cause-specific mortality of terrestrial vertebrates to determine the relative magnitude of vehicle collisions as a mortality source. I also examined traits that best explained vulnerability to different sources of mortality. To examine use of carrion along linear features by vertebrate scavengers, I placed rabbit carcasses alongside roads, along power line clearings and in the forest interior. I used motion-activated cameras to record scavenging behavior and compare both the presence of scavenger species at carcasses and carcass detection time among treatments. Lastly, I placed cages over rabbit carcasses during daylight hours to exclude scavenging by vultures. I used motion-activated cameras to compare the presence of mammalian scavengers and consumption time of carcasses with and without vultures present. These results lend further insight into how mortality from vehicle collisions may influence wildlife populations and into factors influencing carcass use by vertebrate scavengers.

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CHAPTER II

CAUSE-SPECIFIC MORTALITY OF THE WORLD'S TERRESTRIAL VERTEBRATES

Introduction

Human activities impact an estimated 75% of Earth's land surface (Venter et al. 2016). There is growing consensus that human impacts are so pervasive they have shifted the planet into a new geological epoch termed the "Anthropocene" (Waters et al. 2016). In addition to changes in atmospheric composition and the spread of invasive species, widespread faunal extinctions are a defining trait of this epoch (Waters et al. 2016). From 1980 to 2004, 662 amphibian, 223 bird, and 156 mammal species moved one category closer to extinction on the International Union for Conservation of Nature Red List (Hoffmann et al. 2010). Extinction rates of vertebrates during the last century are up to 100 times greater than background levels (Ceballos et al. 2015) and overall, an estimated 41% of amphibian, 25% of mammal and 13% of bird species (Hoffmann et al. 2010) are threatened with extinction.

Illegal killing is one of the largest threats to mammals (Cardillo et al. 2005) and billions of vertebrates die each year collectively from collisions with buildings, power lines, and vehicles (Forman and Alexander 1998, Loss et al. 2015). Mammals are frequently killed when they are deemed a threat to people or their property (Treves and

Karanth 2003). Other animals are killed by indirect human causes such as the introduction of invasive species and habitat loss (Loss et al. 2013). Although it is often assumed that humans are directly responsible for a substantial proportion of wildlife mortality, there has been no systematic examination of mortality sources for animals worldwide to compare the magnitude of anthropic and natural mortality.

Using telemetry to track the fate of animals offers the best insights into the relative magnitude of anthropic mortality because it provides unbiased estimates of mortality causes (Kays et al. 2015). In a mortality study of adult medium and large-sized North American mammals using telemetry studies that monitored mortality of 1,874 individuals, Collins and Kays (2011) found that legal harvest and vehicle collisions collectively accounted for nearly half of all mortality. However, an understanding of mortality sources for other animal classes and for locations beyond North America is currently lacking. I addressed this gap in knowledge by conducting a comprehensive global synthesis of cause-specific mortality of terrestrial vertebrates. This analysis expands on the work of Collins and Kays (2011) by (1) increasing the geographic scope to the entire world, (2) increasing the taxonomic scope to all terrestrial vertebrates, and (3) increasing the demographic scope to juveniles in addition to adults.

Methods

I searched the following databases for studies of cause-specific mortality: JSTOR, BioOne, EBSCO Host, Google Scholar, Web of Science, ProQuest Dissertations and Theses, and SCOPUS. I searched entire documents for the terms 'cause-specific mortality', or 'telemetry' AND 'survival' or 'telemetry' AND 'mortality.' I excluded studies of captive-reared, rehabilitated, or translocated individuals, as these may not be representative of mortality of natural populations (Frair et al. 2007). To ensure the same individuals were not represented multiple times in the data set, I excluded duplicates in which the same animals were used in multiple studies (i.e. the same species monitored in the same location over the same time period). The date range of studies in the analysis started at 1970, roughly the date when radio telemetry became common, and continued through February 2018.

For each study, I documented the species and age class (adult or juvenile) of study animals and classified mortalities as anthropic or natural, with categories within these divisions. Categories of anthropic mortality were legal harvest, illegal harvest, vehicle collision, or other. Categories of natural mortalities were predation, disease, starvation, accident, or other. For birds I included an additional category of collisions with human-made structures (e.g. buildings, power lines, wind turbines) within anthropic mortality sources and for mammals I included a category for management removal within anthropic mortality sources. For reptiles, the categories were vehicle collision, predation, total anthropic and total natural because all other mortality sources were infrequent, each comprising less than 2% of total identified mortality.

I defined harvest policies for each study site as protected or unprotected. I defined protected sites as those that ban harvest of all species year round, whereas unprotected sites permit take of at least one species for some period during the year. I also determined the midpoint of the time period over which the study took place. For each study species, I determined the average adult body mass and diet (carnivore, omnivore, or herbivore) using the databases PanTHERIA (Jones et al. 2009) for mammals and EltonTraits 1.0

(Wilman et al. 2014) for birds. I used handbooks and field guides to derive these traits for reptiles and amphibians.

I used linear mixed effects models to determine the best set of predictor variables for each mortality source using proportions of known mortality from each study. My initial set of models for each taxonomic class included diet, age (juvenile or adult), midpoint of study and protected area status as fixed effects. I included taxonomy as a nested random effect (i.e. Order:Family:Genus:Species; Tucker et al. 2018) and incorporated a Gaussian spatial autocorrelation structure using the geographic coordinates of each study site (Dormann et al. 2007). Because adults and juveniles often vary in their susceptibility to different mortality sources, I did not include studies that did not separate mortalities by age class. I ran another analysis using the same predictors and changed the response variable to magnitude of mortality (i.e. percent of monitored individuals that died). For this analysis, I excluded studies that did not document the number of monitored individuals. I ran another set of models using adults only, including body mass as a predictor and removing age, but keeping all other variables the same. I did not include mass of juveniles as a variable because individuals classified as juveniles within the same species often spanned a range of developmental stages (e.g. fawn, yearling, and subadult for deer), thus a single mass value would not adequately reflect the mass of the animals for which mortalities were documented. I ran models to predict magnitude of mortality for adults as well. I did not run a set of models incorporating age class for reptiles and amphibians because there were very few non-adult mortalities documented.

Because I represent the mortality data as proportions, I performed a logit transformation of the data before analyses (Warton and Hui 2011). I calculated sample size corrected Akaike's information criterion (AIC_c) for each of the candidate models. For each model set I considered the best approximating model as the model with the lowest AIC_c and the difference in AIC_c values between this model and all additive model combinations (represented by Δ_i) was calculated (Burnham and Anderson 2002). Only models with $\Delta_i \leq 2$ were selected for further consideration (Burnham and Anderson 2002). I calculated Akaike weights (w_i) for candidate models to examine the relative weight of evidence for each model. If a best approximating model had a small w_i ($w_{i\text{best}} <$ 0.9), I used multi-model inference to calculate a weighted average of parameter estimates with 85% confidence intervals across competing models (Burnham and Anderson 2002, Arnold 2010).

Results

I compiled 1,114 studies that collectively monitored the fates of 120,657 animals representing 305 vertebrate species (Fig 2.1; a list of data sources is found in Appendix A). From this, I determined 48,791 total mortalities, 42,755 of which had a known cause. Overall, 28% of total mortality was directly human caused, whereas 72% of mortality was the result of natural causes (Fig 2.2). The single largest source of mortality was predation (55%), followed by legal harvest (17%). All other mortality sources, including vehicle collisions, illegal harvest, starvation, accidents, and disease, each accounted for less than 10% of total mortality (Table 2.1). For mammals, there were differences in mortality among age groups, with juveniles having a lower percentage of anthropic mortality (14%) than adults (45%). Trends among reptiles and amphibians were similar, with only 1% of mortalities being anthropic for juveniles, compared to 22% for adults. Anthropic mortality was similar among juvenile and adult birds (17% and 23%, respectively).

Anthropic mortality increased with increasing body mass for mammals, (β = 0.5529; 85% CI = 0.4493, 0.6564), birds (β = 0.5806; 85% CI = 0.3973, 0.7639), and reptiles and amphibians (β = 0.4772; 85% CI = 0.2319, 0.7224). Harvest mortality also increased with increasing body mass for birds (β = 0.3360; 85% CI = 0.1583, 0.5136) and mammals (β = 0.4620; 85% CI = 0.3710, 0.5530). Larger mammals were more likely to be killed than smaller mammals through management removal (β = 0.0312; 85% CI = 0.0115, 0.0509). Larger birds were more likely to die from vehicle mortality (β = 0.2284; 85% CI = 0.2274, 0.2294) and collisions with human-made structures (β = 0.3603; 85% CI = 0.1866, 0.5340) than smaller birds. Among birds, carnivores were more likely than omnivores to die from vehicle mortality (β = 0.2612; 85% CI = 0.0954, 0.4269). Juvenile mammals experienced lower anthropic mortality than adults (β = -0.7619; 85% CI = -0.8394, -0.6845).

The percent of anthropic mortality of mammals (β = -0.4422; 85% CI = -0.6254, -0.2591) and birds (β = -0.5144; 85% CI = -0.8689, -0.1599) was lower in protected areas than unprotected areas. However, protected area status was not a parameter in top models of illegal harvest for mammals and did not significantly influence illegal harvest of birds (β = -0.0027; 85% CI= -0.0192, 0.0138). Protected areas did not influence the magnitude of mortality for mammals (β = -0.0427; 85% CI = -0.1257, 0.0404), birds (β = -0.0253; 85% CI = -0.1449, 0.0943) or reptiles and amphibians (β = -0.0323; 85% CI= -0.1565, 0.0919). Among mammals, vehicle mortality increased over time (β = 0.0026; 85% CI= 0.0011, 0.0041), whereas predation mortality of adults decreased (β = -0.0078; 85% CI= -0.0132, -0.0022). Year was not a significant predictor of magnitude of mortality for any taxa. Results of all models are reported in Appendix B.

Discussion

I found that humans were directly responsible for over one quarter of terrestrial vertebrate mortality worldwide. However, the amount of total anthropic mortality is likely higher than I reported when indirect impacts such as the introduction of invasive species, habitat loss, and poisoning are considered. As a result, human activities may have been the root cause of a mortality assigned to natural sources and several studies explicitly addressed this issue. For example, the largest source of mortality for the endangered Lower Keys marsh rabbit (*Sylvilagus palustris*) was predation by feral cats (Forys and Humphrey 1999), which are estimated to kill billions of birds and mammals annually (Loss et al. 2013). Similarly, predation mortality of Lumhultz's tree kangaroos (*Dendrolagus lumholtzi*) increased after clearcutting removed tree cover and left them vulnerable to predators (Newell 1999). Fishers (*Pekania pennati*) died from seemingly natural causes after exposure to toxicants caused by consuming prey that had ingested rodenticide (Thompson et al. 2014). In cases of poisoning, human impacts underlying the proximate mortality cause may go undiagnosed, particularly when mortality investigations rely on field necropsies (Thompson et al. 2014). Thus the classification of anthropic and natural mortalities does not fully convey the extent of anthropic mortality and likely underestimates the degree to which human activities result in the death of wildlife.

Legal harvest constituted the single greatest source of anthropic mortality to wildlife. Harvest can affect population dynamics (Wright et al. 2006) and cause selection of behavioral traits (Leclerc et al. 2017) even when regulated. Larger bird and mammal species may have been more susceptible to harvest than smaller ones because larger animals provide hunters with more meat per unit effort, leading to increased hunting pressure on these species. Neotropical hunters, for example, show a marked increase in selectivity for prey species larger than 6.5 kg and prey mass explained up to 83% of variation in hunter selectivity (Jerozolimski and Peres 2003). Larger game species in Africa are also more valued by hunters because trophy size generally increases with body mass (Johnson et al. 2010). Larger mammal species were more likely to experience mortality from management removal (i.e. killed in accordance with a depredation permit or in defense of life or property). Among birds and mammals, species with greater body mass experienced increased anthropic mortality, suggesting they are disproportionately killed as a direct result of human activities.

Protected areas that prohibited hunting reduced proportion of anthropic mortality for birds and mammals, but did not influence the amount of mortality of either taxa. This could have resulted from animals leaving the boundaries of protected areas and coming into conflict with humans (Woodroffe and Ginsberg 1998). Additionally, in some areas human populations increase disproportionately along the borders of protected areas, mitigating their effectiveness at preserving biodiversity (Wittemyer et al. 2008). Protected areas also were not successful in preventing illegal harvest of birds or mammals, as protected area status was not a significant predictor of poaching mortality for either taxa. This may result from a higher density of animals in protected areas, which could inadvertently incentivize poaching in such places (Jachmann 2008). These results indicate that protected areas may have the potential to reduce anthropic mortality, but their effectiveness likely varies based on factors such as location and target species.

Larger birds were more likely to die than smaller birds from collisions with vehicles or with human-made structures. The latter included mortality from electrocution, which often impacts larger birds because larger wingspans increase the likelihood of touching multiple parts of a power line simultaneously (Janss 2000). The largest avian species by mass in the dataset were wild turkeys (*Meleagris gallopovo*) and large terrestrial birds are particularly susceptible to collisions with structures due to lack of maneuverability in flight (Bevanger 1998, Shaw et al. 2010). Large predatory birds also have increased vulnerability to many types of collisions because they have reduced vigilance due to being a top predator and may be less aware of structures due to fixation on prey while hunting (Shaw and McKee 2008). This behavior of top predators could also account for the increased vehicle mortality of carnivorous birds. Carnivorous birds may also be more vulnerable to vehicle mortality due to scavenging carrion on roads (Lambertucci et al. 2009, DeVault et al. 2014) or high prey abundance in roadside vegetation (Garland Jr and Bradley 1984, Bautista et al. 2004, Rytwinski and Fahrig 2007).

Most mortality sources did not change significantly over the time period this dataset encompassed, as study year was infrequently a significant predictor of mortality for any source. Percent of mammals dying from vehicle collisions increased over time, which may be a result of the increase in road networks or human population over this time period (Cohen 2003, National Research Council 2005). Predation mortality of adult mammals decreased significantly over time, potentially a result of extirpation of top predators, which decreased prevalence of mortality from predation (Crooks and Soulé 1999, Estes et al. 2011). The overall magnitude of mortality from 1970-2018 did not change significantly for any taxa, indicating that anthropic mortality of wildlife could be largely compensatory. Conversely, wildlife populations may have declined substantially prior to the starting year of the dataset, limiting the potential of this study to fully encompass the extent of anthropic mortality of wildlife (Ceballos et al. 2015).

The high proportions of natural mortality I documented differ from the results of Collins and Kays (2011), likely a consequence of additional taxa, juveniles and increased geographic scope, which resulted in a greater than 22-fold increase in mortality events examined. Considering only adult mammals from North America, the extent of the former study, I also found anthropic and natural mortality roughly equal (55% and 45%, respectively), but I found juvenile mammals had greater natural mortality. Adult mammals were more likely to die from harvest and vehicle collisions, whereas juveniles were more likely to die from predation, indicating that as mammals mature, they experience a shift from predominately natural to predominately anthropic mortality. This is likely driven by hunter selectivity of adults over juveniles (Mysterud et al. 2006), but also could be influenced by greater mobility of adults, which increases their risk of encountering anthropic threats (Schwab and Zandbergen 2011).

My analyses revealed gaps in geographic and taxonomic coverage of cause-specific mortality studies. Studies from North America comprised 85% of the dataset, which could have influenced the mortality estimates, especially for poaching. The illegal trade and consumption of wildlife is widespread across Africa, but less than 2% of the studies were from this continent (Brashares et al. 2011). Rosen and Smith (2010) traced the majority of seized illegal wildlife to Southeast Asia, another area poorly represented in the dataset. In addition to geographical biases, there was a taxonomic bias toward animals that are harvested, particularly from the orders Carnivora and Artiodactyla, which collectively constituted 53% of the studies. In contrast, some orders such as Primates and Chiroptera were entirely absent. Reptiles and amphibians represented less than 7% of studies. Future studies should address these gaps in knowledge to produce a more comprehensive understanding of cause-specific mortality across the globe.

Humans directly cause over one quarter of terrestrial vertebrate mortality worldwide, potentially exerting selective pressures on wildlife populations. Hunter selection of bighorn rams (*Ovis canadensis*) with larger horn sizes, for example, led to increased prevalence of smaller rams with shorter horn lengths (Coltman et al. 2003). This selection may impact population viability, as body size may be correlated with traits that impact survival (Coltman et al. 2001). Hunting might also induce selection of behavioral traits, as hunters have been shown to disproportionately harvest animals that exhibit bolder behavior and have increased movement rates (Ciuti et al. 2012). Hunters can impact population dynamics as well by selecting individuals from different demographic groups more often than natural predators (Wright et al. 2006). Anthropic mortality may affect ecosystem structure and functioning via the extirpation of vertebrates that disperse seeds, consume carcasses, and provide other essential ecosystem services (Şekercioğlu et al. 2016). The magnitude of anthropic mortality of wildlife across the globe is substantial and undoubtedly has ecological ramifications that extend beyond the individual animals that are killed.

Table 2.1 Proportions of mortality causes for each taxa and age class

	Mammal		Birds		Reptiles	
Mortality Source	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile
Legal Harvest	0.28	0.07	0.16	0.14	0.01	0.00
Illegal Harvest	0.05	0.02	0.03	0.01	0.00	0.00
Vehicle	0.07	0.02	0.01	0.01	0.11	0.01
Predation	0.35	0.68	0.68	0.70	0.62	0.95
Accident	0.02	0.01	0.00	0.01	0.02	0.00
Disease	0.04	0.04	0.03	0.01	0.02	0.01
Starvation	0.03	0.07	0.01	0.02	0.00	0.01
Other Human	0.06	0.02	0.03	0.02	0.11	0.00
Other Natural	0.11	0.07	0.04	0.08	0.13	0.03
Total Human	0.45	0.14	0.23	0.17	0.22	0.01
Total Natural	0.55	0.86	0.77	0.83	0.78	0.99

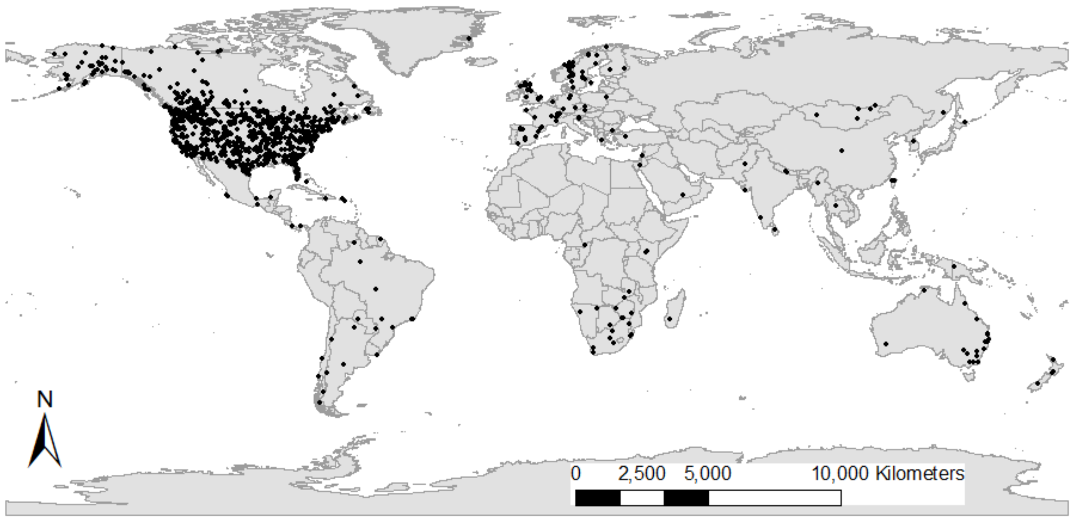

Figure 2.1 Locations of studies of cause-specific mortality of terrestrial vertebrates used for analysis

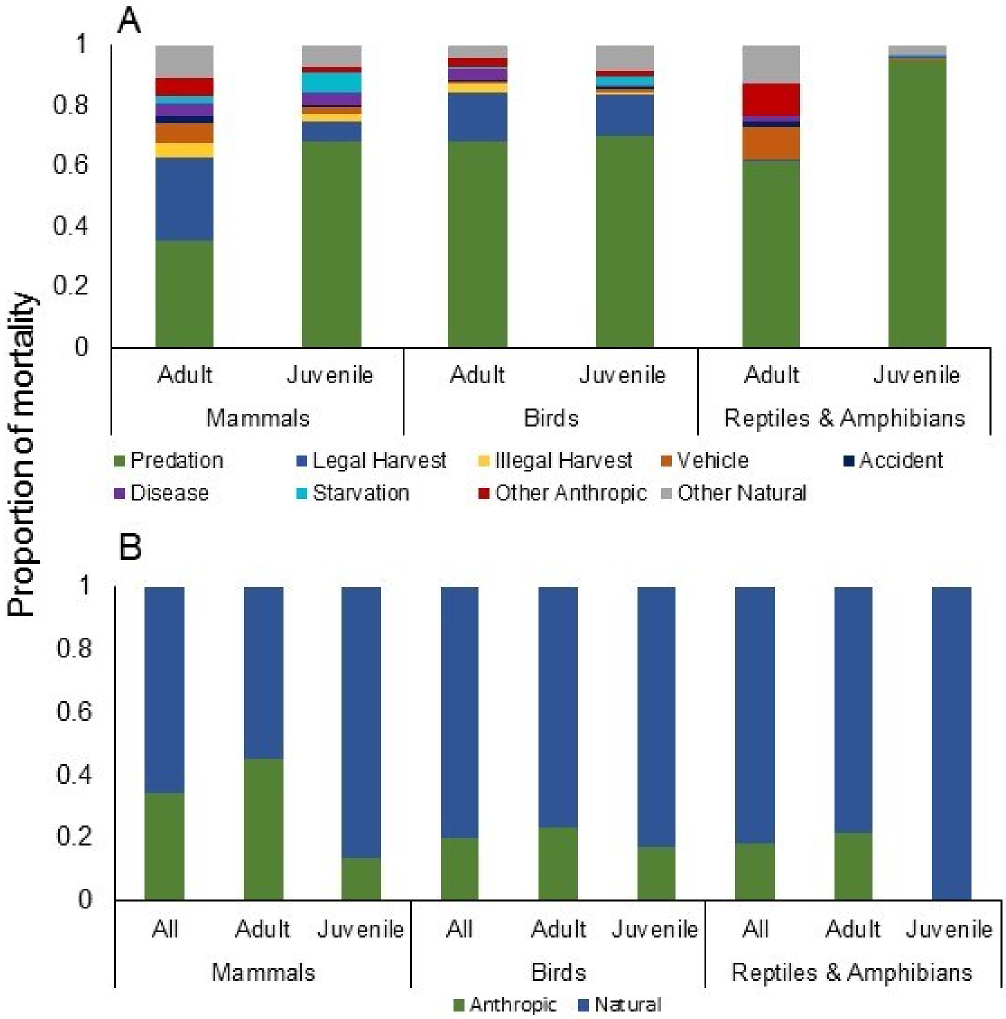

Figure 2.2 Percentage of mortality causes (A) and natural vs. anthropic mortality sources (B) for terrestrial vertebrates.

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CHAPTER III

ROADS DO NOT INCREASE CARRION USE BY A VERTEBRATE SCAVENGING COMMUNITY

Introduction

Human development is increasingly encroaching into natural areas. Roads are an important means by which this occurs as roads fragment habitat (Laurance et al. 2004), facilitate transport of pollutants into the environment (Camponelli et al. 2009), and aid the spread of invasive species (Forys et al. 2002, Brown et al. 2006). There are 6.2 million km of roads in the United States alone, and an estimated 20% of the land is impacted by the presence of roads (Forman 2000, 2003). Roads are directly responsible for nearly 10% of large mammal mortality in North America (Collins and Kays 2011) and each year hundreds of millions of vertebrates die on roads worldwide (Forman and Alexander 1998, Seiler and Helldin 2006, Loss et al. 2014). This mortality can have severe impacts on populations by altering sex ratios (Gibbs and Steen 2005), decreasing genetic diversity (Clark et al. 2010), and jeopardizing population viability (Mumme et al. 2000, Row et al. 2007, Kociolek et al. 2011).

Although considerable research has assessed the effects of roads on wildlife populations, little attention has been focused on the fate of carcasses resulting from vehicle collisions, which result in substantial additions of carrion to the environment. For example, an estimated 500,000 white-tailed deer (*Odocoileus virginianus*) die annually from collisions in the United States (Romin and Bissonette 1996). Assuming an average mass of 45 kg per animal (Cook and Gray 2003), collisions from this species alone represent 22.5 million kg of carrion introduced into the environment each year. The ecological ramifications of this magnitude of carrion could be substantial, as many vertebrates are facultative scavengers (DeVault et al. 2003, Beasley et al. 2015). Scavenging can play an important role in trophic webs because it provides more net energy than predation (Wilson and Wolkovich 2011). Animals may also shift from predation to scavenging when a large amount of carrion becomes available (Van Dijk et al. 2008).

Although scavengers can rapidly remove some carcasses from roads (e.g. Antworth et al. 2005, DeGregorio et al. 2011, Santos et al. 2011, Teixeira et al. 2013), few studies have identified which scavengers are responsible for carcass removal (but see (Lambertucci et al. 2009, Planillo et al. 2015)). As a result, there is currently limited understanding of which scavengers benefit most from this resource. Carrion from vehicle collisions could serve as a food subsidy that increases scavenger populations. Population increases of scavengers may have impacts through increasing human-wildlife conflicts (Lowney 1999, Poessel et al. 2013) and contributing to declines of imperiled fauna (Cypher and Scrivner 1992, Garmestani and Percival 2005). An important step in examining how carrion from vehicle collisions could subsidize scavenger populations is to determine the ecological underpinnings of carrion consumption patterns near roads.

Several factors may influence the degree to which scavengers use carrion resources available on roads. The presence of predators can influence foraging behavior by prohibiting animals from accessing certain habitats due to predation risk (Brown et al. 1999, Laundré et al. 2001). Forested habitats can be less risky for some species because trees provide cover and protection from potential predators (Vásquez et al. 2002, Pickett et al. 2005). In contrast, open areas such as those along roads provide little cover and some species may have higher predation risk in these areas (Vásquez et al. 2002). For example, pine martens (*Martes martes*), which climb trees to escape predators, avoid clear cuts and scavenge most often in forests where they are more adept at avoiding predation (Storch et al. 1990, Selva et al. 2005). The risk of predation in open areas along roads may discourage scavenging by less dominant species and favor carcass consumption by larger and more dominant carnivores. Conversely, some animals may face reduced predation risk near roads due to predator release (Downing et al. 2015).

In addition to minimizing risks, optimal foraging theory predicts that animals should forage to maximize energetic gains, which can be accomplished in part by concentrating foraging in places with reliable food availability (MacArthur and Pianka 1966, Stephens and Krebs 1986). Vultures (Families Cathartidae and Accipitridae, Subfamilies Aegypiinae and Gypaetinae) are obligate scavengers that subsist almost exclusively on carrion (Ruxton and Houston 2004). When vultures forage, they use soaring flight to cover large areas while minimizing energetic costs, which is essential for obligate scavenging (Ruxton and Houston 2004, Shivik 2006). Because they have a limited ability to shift to other food resources, vultures could be expected to heavily use areas that reliably contain carrion to further reduce the energetic costs associated with foraging.

Vultures alter foraging behavior in accordance with resource availability, as access to food is a primary factor influencing home range ecology of birds (Rolando 2002, Kelly et al. 2007). Griffon vultures (*Gyps fulvus*) concentrate activities in areas with high densities of hunter kills (Mateo-Tomás and Olea 2010) and king vultures (*Sarcoramphus papa*) fly along paths used by jaguars (*Panthera onca*) to locate jaguar kills (Schlee 2008). Griffon vultures also arrive sooner at carcasses placed repeatedly in the same location than at carcasses placed in unpredictable locations, indicating that they more frequently visit areas where they have previously encountered carrion (Cortés-Avizanda et al. 2012). Food availability is the greatest predictor of Egyptian vulture (*Neophron percnopterus*) space use and individuals made repeated movements of up to 250 km to cattle pens where food was reliable (López-López et al. 2014). Reliable presence of carrion along roads could thus cause vultures to travel along roads due to increased foraging opportunities (Planillo et al. 2015). However, flying over roads could also benefit vultures through rising thermal drafts from the road surface, which minimize the energy required for flight (Mandel and Bildstein 2007). In Pennsylvania and Maryland, both black vultures (*Coragyps atratus*) and turkey vultures (*Cathartes aura*) foraged mostly in open habitats with roads, but rarely foraged on carcasses along roads (Coleman and Fraser 1989), apparently using roads for thermal drafts rather than foraging.

Similarly, use of roads could offer multiple benefits to mammalian scavengers and road use has been documented in many species ((e.g. James and Stuart-Smith 2000, Frey and Conover 2006, Beatty et al. 2013)). Road clearings may facilitate travel because the vegetation within road clearings typically consists of grasses that are periodically mowed, making movement along roads more energetically efficient than in adjacent habitat. Mammals might select roads for travel because they generally use landscapes in a way that minimizes energy expenditures during movement (Shepard et al. 2013). Wolves (*Canis lupus*), for example, use seismic lines (narrow linear corridors through forests cleared for energy exploration) because they enable quicker movement, allowing wolves to increase encounter rate of prey (McKenzie et al. 2012). Roads might also have a high abundance of rodents because of the altered vegetation (Meunier et al. 1999, McGregor et al. 2008), so increased prey availability could further account for use of roads by mammalian scavengers. The multiple benefits provided by roads to vultures and mammals makes it unclear whether they use roads for scavenging opportunities or for other purposes, and exploit carrion as a byproduct of this use.

I explored the influence of roads on vertebrate scavenging by comparing scavenging of rabbit carcasses placed along road verges, along linear features without roads (i.e. power line clearings), and in the forest interior. I hypothesized linear features influence detection and use of carrion by scavengers. I predicted large predators (i.e. coyotes *Canis latrans*) would use roads most frequently and arrive at them first due to ease of travel and carrion availability from vehicle collisions. I predicted power lines would be used second most frequently by predatory mammals because they would provide the same ease of travel as roads, but would provide less carrion. I predicted that forests would be used least often and have the longest arrival times. I further predicted that avian scavengers (i.e. mainly vultures) would exhibit the same patterns as mammalian predators, with greatest use of roads due to scavenging opportunities and thermals for soaring. For mesocarnivores (e.g. Virginia opossums *Didelphis virginiana*) I predicted greatest use of carrion within forest sites due to reduced exposure to predators.

Methods

Study site

I conducted this study at the Savannah River Site (SRS), a property owned by the US Department of Energy that encompasses 78,000 ha across Aiken, Allendale, and Barnwell Counties in South Carolina, USA (33°19'N, 81°42'W). SRS is dominated by loblolly pine forests (*Pinus taeda*), longleaf pine forests (*Pinus palustris*), and bottomland hardwoods (e.g. *Nyssa* spp., *Quercus* spp.) (White and Gaines 2000). Since 1951, much of SRS has been managed for timber harvest and stands are harvested on a rotating basis (White and Gaines 2000). There are 225 km of primary (i.e. paved) roads and 2250 km of secondary roads on the SRS (Kilgo 2005). I conducted this study December 2016–March 2017; mean monthly temperature ranged from 10.9-14.4 °C and mean daily precipitation was 0.39 cm (NOAA 2017). I chose to carry out the study during winter because scavenging by mammals at SRS is infrequent during summer (Turner et al. 2017, Hill et al. 2018), which would have made it difficult to attain a sample size large enough to test my hypotheses.

Study design

I selected 78 sites in pine (*Pinus* spp.) stands that were greater than 20 years old, which I divided evenly among three treatments: power line clearings, roads, and forest. I chose power line clearings as linear features because they are common on the site and similar in width and vegetation structure to most clearings for roads. All roads were two-lane paved roads and all road and power line sites contained forested habitat on either side. Forest interior sites were located at least 500 m from the forest edge. I separated all sites by at least 500 m and every site was at least 500 m from the next nearest road or power line. The number of sites was determined based on the maximum number of locations available meeting these restrictions, but it was not possible to choose road sites with equal traffic levels and maintain the site selection criteria. Of the road sites, 14 were on public access roads that were heavily trafficked, 9 were not publicly accessible but were frequently traveled by personnel on site, and 3 were not publicly accessible and experienced little traffic. I designated these sites high, medium, and low traffic sites, respectively. I performed four consecutive rounds of 39 trials that lasted three weeks each for 156 total trials. For the first round, I selected 13 sites from each of the three treatments and used the remaining sites in the second round. Proximate sites were not used at the same time so that there was a minimum of 1 km between sites used concurrently. Alternate sites were used in consecutive rounds such that each site was used twice with about three weeks between reuse of sites.

At each site I placed a dark colored rabbit (*Sylvilagus* spp.) carcass weighing ~1300 g obtained from a commercial supplier (RodentPro, Inglefield, IN, USA) and thawed indoors to ambient temperature. I used a cable lock to attach a motion-activated infrared camera (Bushnell Trophy Cam HD Aggressor; Bushnell Corp., Overland Park, KS, USA) to a tree ~3 m from carcasses to record the presence of scavengers. At road and power line sites, there was no tree cover over carcasses so they would be visible from overhead. At road sites, carcasses were placed along verges ~3 m from the road pavement to reduce the risk of animals being struck by a vehicle while scavenging. Cameras took three pictures when motion-activated, with a 1-minute delay between activations. To prevent scavengers from carrying carcasses beyond the field of view, I affixed a non-relaxing cable snare to each carcass and staked it to the ground with a 46-cm steel rebar stake.

I used images from the cameras to identify the scavenger species present at each carcass. I compared whether each carcass was scavenged (i.e. presence/absence of any scavenger) across the three treatments using a generalized linear model with binomial distribution and logit link using R version 3.2.3 (R Core Team 2016). I compared the time between carcass placement and first arrival of any scavenger species between treatments using a generalized linear model with Gaussian distribution and identity link. I also calculated species richness (i.e. number of species present) at each carcass and compared across treatments using a generalized linear model with Poisson distribution and log link. If a species was present at 15 or more carcasses in total, I similarly compared the presence/absence of the species and arrival time of the species across treatments. To examine whether the amount of traffic influenced scavenging behavior, I compared presence/absence of scavenging and time to arrival of the first scavenger as described above between high and medium traffic road sites (sample size of low traffic roads was too small for analysis). A significance level of 0.05 was used for all models. When three-way comparisons were significant, I used a Tukey's HSD test for pairwise comparisons.

I compared species diversity between treatments using the Shannon-Weiner index. I pooled all trials from each treatment using the number of species that were present at each carcass (Table 3.1). This was done because animals frequently attempted to remove carcasses from the snares and number of visits recorded at a carcasses would have depended on the ability to dislocate the carcass and was not an ecologically relevant metric. Thus there was a single species diversity value for each treatment and I bootstrapped these values with 1000 replications to obtain 95% confidence intervals using R version 3.2.3 for this analysis.

Results

After removing trials due to camera failure, the sample size for analysis consisted of 51 forest, 42 power line, and 43 road trials. Across all treatments I documented 17 species scavenging on carcasses, including 11 species in forest, 12 species in power line, and 11 species in road trials (Table 3.1). There was no difference in whether a carcass was scavenged across treatments (Table 3.2); 90 % of forest, 92 % of power line, and 86 % of road trials were scavenged. Mean time to first arrival of a scavenger was shorter at power line sites (5.5 ± 3.2 d) than forest sites (8.1 ± 4.2 d; β = -2.60, *P*-value = 0.013), but no other pairwise comparisons were significant (mean road arrival time = 6.9 ± 4.4 d; Fig 3.1). Mean species richness was 1.5 ± 0.9 for forest, 1.5 ± 0.9 for power line, and 1.3 ± 0.9 for road trials and there were no significant differences between treatments (forest vs. road β = 0.144, *P*-value = 0.698; forest vs. power line β = -0.049, *P*-value = 0.956; power line vs. road β = 0.193, *P*-value = 0.547; Fig 3.2).

Four species met the criteria for further analyses: coyote, turkey vulture, Virginia opossum, and gray fox (*Urocyon cinereoargenteus*). There was no difference in coyote presence or arrival times across treatments (Table 3.3, Table 3.4). Mean coyote arrival times in days were 9.59 ± 4.61 for forest, 10.54 ± 5.60 for power line, and 7.98 ± 5.46 for roads. Turkey vultures scavenged equally across treatments. Mean turkey vulture arrival times in days were 7.96 ± 2.25 for forest, 4.81 ± 2.70 for power line, and 7.37 ± 1.87 for road trials. Turkey vultures arrived at power line carcasses sooner than those at roads (β = -2.56, *P*-value = 0.043) or in the forest (β = -3.15, *P*-value = 0.001). Opossums scavenged at forest sites more often than those at power lines (β = -1.43, *P*-value = 0.017) but no other comparisons were significant. Mean opossum arrival times in days were 10.41 ± 4.89 for forest, 7.21 ± 4.92 for power line, and 9.32 ± 4.34 for road trials and there was no difference across treatments (Table 3.4). Gray foxes never scavenged in the forest and there was no difference in presence (β = 1.18, *P*-value = 0.118) or arrival time (β = 0.20, *P*-value = 0.901) between road and power line treatments. Mean gray fox arrival time in days was 5.97 ± 3.20 for power line and 5.77 ± 2.19 for road trials. There was no difference in whether a carcass was scavenged between the high and medium traffic sites (β = -1.609, *P*-value = 0.208) or arrival time of the first scavenger (β = -0.083, *P*-value = 0.961). Bootstrapped mean species diversity and 95% confidence intervals for forest, road, and power line sites, respectively, was 1.738 [1.572, 1.892], 1.801 [1.610, 1.970], and 1.932 [1.761, 2.096].

Discussion

I did not find support for the prediction that linear features influenced detection of carrion by scavengers. There was no difference in the overall proportion of carcasses scavenged or time to arrival of the first scavenger between the road and other treatments. No species arrived at carcasses near roads sooner than at other treatments. Both coyotes and turkey vultures scavenged equally across all treatments, and opossums scavenged equally between roads and forests. Additionally, species diversity did not differ among treatments. Although the scavenger community overall did not show a substantial response to roads or power lines, exclusive consumption by gray foxes of carrion along linear features indicates that species differ in their use of these features for scavenging compared to forests. Differences in scavenging by species across treatments may have been influenced by resource distribution, sensitivity to vehicle traffic, and habitat and diet flexibility.

In contrast to my expectations, vultures did not scavenge most frequently along roads. Vultures are thought to make considerable use of carrion on roads at the Savannah River Site (SRS) (DeVault et al. 2004b, Kelly et al. 2007), but would only be expected to focus activities on roads if there was a greater chance of encountering food in these locations than in surrounding habitat (Stephens and Krebs 1986). I assumed this behavioral response occurred in the study, but recognize it may not be the case. In Africa, where food was evenly distributed across the landscape, Egyptian vultures exhibited a Brownian movement strategy while foraging (López-López et al. 2013). This seemingly random movement resulted from the uniform distribution of carrion because concentrating activities in a particular area did not increase the probability of foraging success.

Vultures at this site may have access to enough food that they do not need to concentrate on roads. Turkey vulture home ranges have decreased substantially at SRS over the past decade (DeVault et al. 2004b, Holland et al. 2017), which may be due to an increase in carrion availability provided by a growing wild pig population (Beasley et al.

2014). The estimated density of adult wild pigs at SRS is 2.6 pigs/km^2, equivalent to approximately 2000 adults (Keiter et al. 2017). The inclusion of yearlings and piglets makes the total estimated number of individuals at SRS 4000-6000 (Keiter et al. 2017). Management of the wild pig population at SRS involves killing a substantial number of individuals and carcasses are often left in the field, creating a large supply of carrion. However, carcasses are distributed across the site in an unpredictable pattern, so carrion should still be more reliably available along roads than in the forest. Additionally, there is a landfill at SRS and vultures in many locations regularly scavenge at landfills (e.g. Francoeur and Lowney 1997, Al Fazari and McGrady 2016, Tauler-Ametller et al. 2017), further increasing food supply. The abundance of food for vultures at SRS may negate any benefits of concentrating foraging activities in a particular area and may partially account for the lack of increased scavenging along roads.

Traffic on roads could impact scavenging by vultures since they are diurnal and their highest activity levels coincide with times of heavy traffic at SRS. Some birds, including turkey vultures, may not be able to avoid rapidly approaching vehicles, putting them at risk of collision (DeVault et al. 2014, 2015). Both cinereous vultures (*Aegypius monachus*) and Griffon vultures decrease presence near roads as traffic volume increases (Bautista et al. 2004). Andean condors (*Vultur gryphus*) spent more time vigilant when foraging near roads, indicating that they perceived roadside areas to be of higher risk than areas further away from roads (Speziale et al. 2008). I did not detect a difference in scavenging across traffic levels, which may have occurred because there was not enough difference in traffic to impact scavenger behavior. Vultures scavenged equally across road and forest sites, but the risk of vehicle collision may account for lack of increased scavenging near roads.

Opossums overall did not scavenge less frequently in open areas than in the forest. Although they scavenged less frequently along power lines than in the forest, the lack of difference in scavenging between roads and the forest suggest that avoidance of open areas was not a primary driver of scavenging behavior. In Indiana, density of adjoining roads was a significant predictor of opossum density (Beatty et al. 2016) and opossums selected habitat in close proximity to roads throughout much of the year (Beatty et al. 2013). Although coyotes consume opossums (e.g. Schrecengost et al. 2008, Etheredge et al. 2015, Cherry et al. 2016), they may not pose enough of a risk to substantially alter habitat use of opossums at SRS. As generalists, opossums often thrive in anthropogenically modified habitats and these results suggest they have the ability to exploit carrion in both forests and along roads.

Coyotes are also generalists and scavenging by coyotes was ubiquitous across all three treatments with no differences in arrival times. This may have been influenced by the habitat present at our sites, as mature pine stands generally have little undergrowth that would impede movement by coyotes. Additionally, most pine stands on the SRS are routinely subjected to prescribed burns, which would have further reduced the understory vegetation. As a result, movement along roads may have only been marginally more energetically efficient than moving through the forest, resulting in equal use of carcasses across treatments. In habitats with denser understory vegetation, movement might have been substantially more energetically costly, and placing carcasses in such habitats could potentially result in decreased carrion consumption compared to roads.

Gray foxes were the only species that scavenged more frequently on the road than in the forest and there was no difference in arrival time between power line and road treatments. Use of corridors may have been driven by prey availability, as small mammal abundance is an important determinant of gray fox habitat selection (Chamberlain and Leopold 2000) and road verges may have increased rodent densities (Garland Jr and Bradley 1984, Rytwinski and Fahrig 2007, McGregor et al. 2008). The amount of scavenging by gray foxes was more than twice that reported by other studies at SRS due to the focus on linear features. Turner et al. (2017) reported scavenging by gray foxes at 4.3% of rabbit carcasses during winter, whereas I documented gray foxes scavenging at 9.6% of carcasses. The former study examined scavenging in forest interior sites and clear cuts and did not examine use of carrion along linear features. Had I examined forest interior sites exclusively, gray foxes may have never been documented, even though they were the fourth most common scavenger overall. Although species diversity was similar across treatments, the composition of those species was thus different between the linear features and forest sites.

At SRS, space use of gray foxes may be influenced by avoidance of coyotes, as gray foxes have been shown to select core home range areas that do not have high concentrations of coyotes (Chamberlain and Leopold 2005). Furthermore, the mature pine stands in which I placed carcasses are the second most selected habitat by coyotes at SRS (Schrecengost et al. 2009). As a result, any potential protection from predation afforded to gray foxes by vegetative cover in mature pine stands may be offset by increased use of the habitat by potential predators, leading to minimal use of carrion by gray foxes in these habitats. Similarly, gray foxes in Georgia selected roads, but used mature pine stands at random (Deuel et al. 2017). Roads and power lines may have provided efficient travel corridors for gray foxes, allowing them to move through areas of high use by coyotes while minimizing predation risk.

Scavenging patterns were likely influenced by the time of the year in which the study took place, as mammals often scavenge more extensively during cooler seasons (e.g. Selva et al. 2005, Turner et al. 2017). Increase in decomposition rate during warm weather often makes carcasses unpalatable for mammals before they can be detected (DeVault et al. 2003). Coyotes and opossums scavenged frequently in this study, but they seldom scavenge rabbit carcasses during summer at SRS (Turner et al. 2017, Hill et al. 2018). Decomposition of carcasses during warmer temperatures provides olfactory cues used by turkey vultures to detect carrion and slower decomposition rate could diminish their ability to find carcasses (e.g. DeVault et al. 2004a, Grigg et al. 2017). Because black vultures frequently use presence of turkey vultures at carcasses for detection, season may also account for lack of scavenging by black vultures (Turner et al. 2017). Consequently, the patterns of carcass consumption I documented during winter may be much different than what occurs during warmer seasons. Additionally, I did not have data on animal abundance across the habitats in this study. Comparing presence of species at carcasses to their abundance in the habitat may have produced different conclusions and should be a consideration for future studies.

These results indicate that anthropogenic linear features such as roads can result in differences in the scavenger community across small spatial scales (i.e. 500 m apart) within the same habitat, because gray foxes did not scavenge in forests. If roadside habitat offers benefits to a species such as reduced predation risk compared to adjacent habitat, the presence of a road may lead to occurrence of the species in locations it may otherwise avoid. Interactions between species may influence carcass use along linear features and consideration of such interactions is necessary to fully understand the dynamics of scavenger communities.

Although there were not differences in the use of carrion overall across treatments, these results indicate considerable use of carrion along roads by scavengers, as they consumed 86% of roadside carcasses. Consequently, this resource has the ability to influence several aspects of scavengers' ecology. Consuming carcasses along roads could place scavengers at increased risk of vehicle collisions and lead to increases in mortality. Presence of carrion along roads can also be consumed by invasive species and facilitate their range expansions by supplying food (Joseph et al. 2017). Across their geographic ranges, the diet (Van Dijk et al. 2008) and spatial ecology (Haroldson et al. 2004) of scavengers that consume carrion from vehicle collisions could be substantially altered by the presence of this human-provided food subsidy.

Table 3.1 Species documented scavenging rabbit carcasses in pine forests at the Savannah River Site, Aiken SC, December 2016–March 2017.

Species	Forest	Power line	Road	Total
Coyote (*Canis latrans*)	21	18	17	56
Turkey vulture (*Cathartes aura*)	12	17	8	37
Virginia opossum (*Didelphis virginiana*)	21	6	9	36
Gray fox (*Urocyon cinereoargenteus*)	0	4	11	15
Red-shouldered hawk (*Buteo lineatus*)	5	4	1	10
Red-tailed hawk (*Buteo jamaicensis*)	5	4	0	9
Raccoon (*Procyon lotor*)	3	2	3	8
Wild pig (*Sus scrofa*)	1	4	1	6
Bobcat (*Lynx rufus*)	1	1	2	4
Great horned owl (*Bubo virginianus*)	1	1	0	2
American crow (*Corvus brachyrhynchos*)	0	2	0	2
Barred owl (*Strix varia*)	1	0	0	1
Black vulture (*Coragyps atratus*)	0	1	0	1
Southern flying squirrel (*Glaucomys volans*)	1	0	0	1
Striped skunk (*Mephitis mephitis*)	0	0	1	1
Domestic dog (*Canis lupus familiaris*)	0	0	1	1
Red fox (*Vulpes vulpes*)	0	0	1	1
Scavenged	46	39	37	122
Unscavenged	5	3	6	14
Proportion Scavenged	0.90	0.92	0.86	0.90
Mean time to first scavenger arrival (d)	8.1 ± 4.2	5.5 ± 3.2	6.9 ± 4.4	6.9 ± 4.3

Values indicate number of carcasses at which each species was present for each treatment

Table 3.2 Comparisons of rabbit carcasses scavenged by all vertebrates combined across treatments using a generalized linear model with logit link and time to first scavenger arrival using a generalized linear model with identity link.

Metric	Comparison	Estimate	*p*
Carcasses scavenged	Forest vs road	0.400	0.808
	Forest vs power line	-0.346	0.892
	Road vs power line	-0.746	0.574
Time to first scavenger arrival	Forest vs road	1.214	0.395
	Forest vs power line	2.595	0.013
	Road vs power line	1.382	0.328

Carcasses were placed in pine forests >20 yrs old at the Savannah River Site, Aiken, SC, December 2016-March 2017. A significance level of 0.05 was used for all models.

Table 3.3 Presence/absence comparisons of scavenger species at rabbit carcasses analyzed with a generalized linear model with logit link

	Comparison	Coefficient	*p*
Coyote	Forest vs road	0.068	0.986
	Forest vs power line	-0.069	0.985
	Road vs power line	-0.137	0.948
Turkey vulture	Forest vs road	0.504	0.574
	Forest vs power line	-0.586	0.383
	Road vs power line	-1.090	0.076
Opossum	Forest vs road	0.973	0.100
	Forest vs power line	1.435	0.017
	Road vs power line	0.463	0.702
Gray fox*	Road vs power line	1.184	0.118

Carcasses were placed in pine forests >20 yrs old at the Savannah River Site, Aiken, SC, December 2016-March 2017. A significance level of 0.05 was used for all models.
*No comparisons with forest because gray foxes did not scavenge in the forest.

Table 3.4 Comparison of arrival times of scavenger species at rabbit carcasses between treatments analyzed using a generalized linear model with identity link

		Coefficient	*p*
Coyote	Forest vs road	1.616	0.634
	Forest vs power line	-0.945	0.846
	Road vs power line	-2.560	0.344
Turkey vulture	Forest vs road	0.595	0.851
	Forest vs power line	3.154	0.001
	Road vs power line	2.560	0.043
Opossum	Forest vs road	1.095	0.843
	Forest vs power line	3.200	0.342
	Road vs power line	2.105	0.698
Gray fox*	Road vs power line	-0.200	0.899

Carcasses were placed in pine forests >20 yrs old at the Savannah River Site, Aiken, SC, December 2016-March 2017. A significance level of 0.05 was used for all models.
* Some pairwise comparisons not calculated due to small sample sizes.

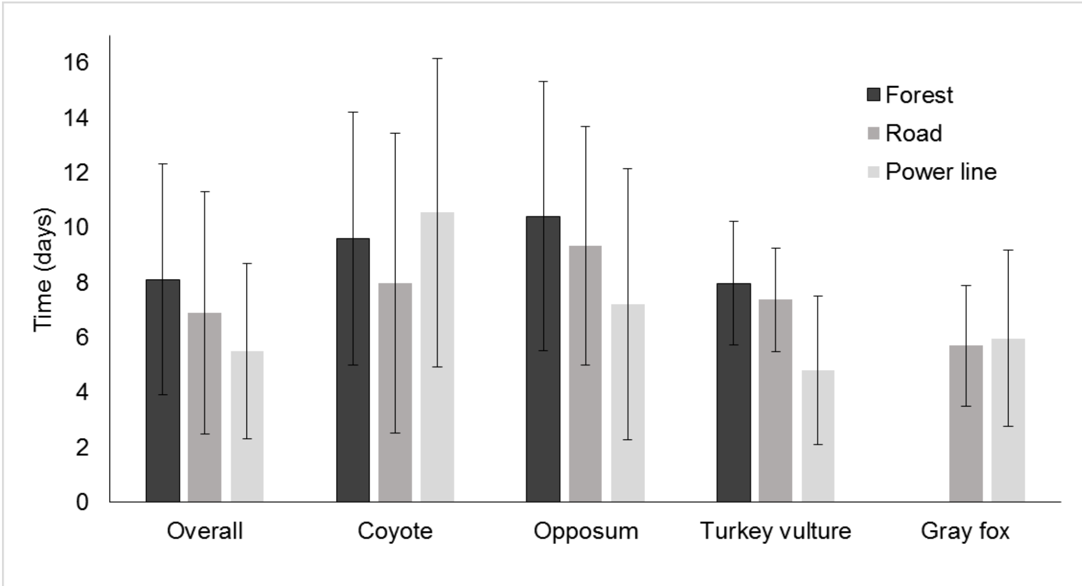

Figure 3.1 Mean arrival time in days with standard deviations of the first scavenger overall and first visit by various species to rabbit carcasses at forest interior, road, and power line sites.

All locations were in pine forests >20 yrs old at the Savannah River Site, Aiken, SC, December 2016-March 2017.

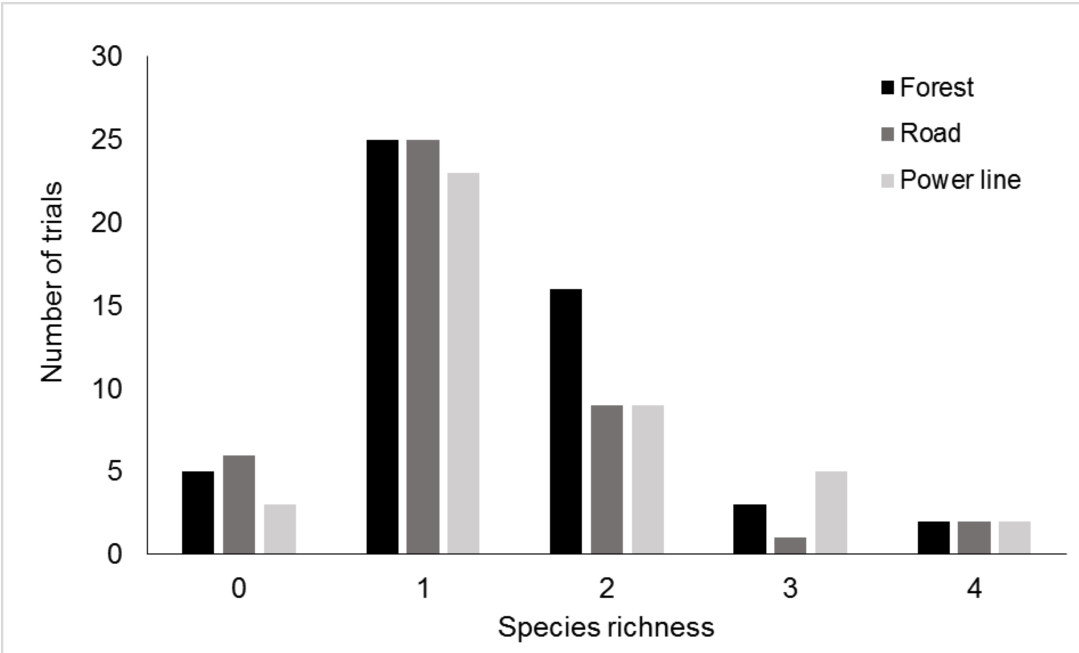

Figure 3.2 Species richness (i.e. number of species) of scavengers foraging on rabbit carcasses placed in forest interior, road and power line sites.

All locations were in pine forests >20 yrs old at the Savannah River Site, Aiken, SC, December 2016-March 2017.

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CHAPTER IV

EFFECTS OF VULTURE EXCLUSION ON CARRION CONSUMPTION BY FACULTATIVE SCAVENGERS

Introduction

The geographic distribution of vultures (Families Cathartidae and Accipitridae, Subfamilies Aegypiinae and Gypaetinae) spans five continents, and throughout their range vultures fulfill an important ecological role through consumption of carrion (Ogada et al. 2012a, DeVault et al. 2016). Scavenging can potentially reduce the spread of disease among wildlife because many pathogenic organisms on carcasses cannot survive passage through the highly acidic vulture digestive system (Houston and Cooper 1975, Beasley et al. 2015). As the dominant consumers of carrion in many environments, vultures can indirectly impact other species because the presence of carrion influences the movement behavior of facultative scavengers and their prey (Wilmers et al. 2003, Cortés-Avizanda et al. 2009). Additionally, an absence of vultures can lead to increases in populations of facultative scavengers due to increased carrion availability (Markandya et al. 2008, Ogada et al. 2012a), and negative ecological impacts as some human commensals (e.g. rats and dogs) can be detrimental to native wildlife (Butler and du Toit 2002, Young et al. 2011).

The ecological functions performed by vultures often translate into direct benefits for humans (DeVault et al. 2016). Consumption of livestock carcasses by vultures precludes the need for people to pay for their removal (Margalida and Colomer 2012). Vultures can also indirectly benefit humans through reduced risk of disease. For example, following the decline of vulture populations in India, populations of feral dogs increased, leading to an increase in cases of humans contracting rabies from feral dog bites (Markandya et al. 2008). The estimated health cost of this increase in rabies transmission from 1992 to 2006 was $34 billion (Markandya et al. 2008). Despite the benefits vultures can provide to people and the environment, vultures are the world's most threatened avian functional group (Şekercioğlu 2006). Populations of vultures are experiencing continent-wide declines in Asia and Africa due to threats such as poisoning, poaching and collisions with power lines (Oaks et al. 2004, Ogada et al. 2012a, Ogada et al. 2016). Some populations have declined more than 90% in 20 years (Prakash et al. 2003) and 12 of the world's 22 species are now listed as endangered or critically endangered by the International Union for Conservation of Nature (Buechley and Şekercioğlu 2016).

The ecological implications of declines in vulture diversity and abundance could be extensive because vultures consume a substantial amount of carrion. Vultures in Serengeti National Park, Tanzania, consumed an estimated 14 million kilograms of meat annually, exceeding that of all mammalian carnivores combined (Houston 1979). New World vultures in Central and South America may also consume more carrion than mammalian carnivores due to their proficiency at locating carrion in Neotropical forests (Houston 1994). Assuming a mean consumption rate of 0.3 kg d^{-1} of carrion for turkey vultures (*Cathartes aura*) (Singh and Chakravarthy 2006, Chhangani 2010) and a population size of 2 million in North America (Inzunza et al. 2010), this species alone could potentially remove 219 million kg of carrion from the environment annually.

Carrion is abundant in most environments because many animals die from causes other than predation, making them potentially available as food for scavengers (DeVault et al. 2003, Collins and Kays 2011). Anthropogenic activities such as collisions with automobiles or human-made structures cause millions of animal deaths annually, further contributing to the amount of carrion available (Forman and Alexander 1998, Loss et al. 2015). The removal of obligate avian scavengers and human-induced increases in carrion results in considerable carrion availability that could subsidize populations of facultative mammalian scavengers (Markandya et al. 2008). Determining how such an increase in abundance of mammals might occur requires an understanding of the mechanisms influencing competition between vultures and mammals for carrion.

Competition between avian and mammalian scavengers is common at carcasses, and the outcome of these interactions depends on factors such as carcass detection ability (Houston 1986, Shivik 2006), habitat type (Selva et al. 2003, DeVault et al. 2004a, DeVault et al. 2011, Turner et al. 2017) and scavenger body size (Butler and du Toit 2002). Vultures frequently outcompete mammals for carrion through exploitation competition because flying enables vultures to traverse large areas more efficiently than mammals, often resulting in quicker detection times of carrion (Houston 1979, Ruxton and Houston 2004). This rapid detection can allow vultures to deplete carcasses before mammals can find them, with vultures consuming 90% of carcasses in some areas (Houston 1986), though competition may change seasonally. Groups of avian scavengers can also monopolize carcasses and deter use by mammals. Scavenging ravens (*Corvus* *corax*) can deter wolves from carcasses (Vucetich et al. 2004) and Andean condors (*Vultur gryphus*) can cause pumas to abandon their kills (Elbroch and Wittmer 2013).

Conversely, mammals dominate carrion consumption in some situations. In forested habitats where vultures have a decreased ability to detect carrion visually, mammals may consume more carcasses than vultures (Ogada et al. 2012b, Turner et al. 2017). Nocturnal mammals also commonly deplete carcasses at night when avian scavengers are inactive (Prior and Weatherhead 1991, DeVault and Rhodes 2002, Ogada et al. 2012b). In Australia, for example, 88% of scavenging by mammals occurred at night (Huijbers et al. 2013). Mammal presence can prevent vultures from landing at carcasses (Prior and Weatherhead 1991) and domestic dogs have used physical dominance to exclude vultures from carcasses (Butler and du Toit 2002). In some habitats, the sheer abundance of mammalian carnivores results in mammals consuming most carrion (DeVault et al. 2011).

Ogada et al. (2012b) demonstrated that when vultures were excluded from carcasses in Africa, there was an increase in the number of individual mammals using carcasses and the amount of time mammals spent at carcasses. There was also an increase in the number of contacts between mammals at carcasses in the absence of vultures, indicating an increased risk of disease transmission (Ogada et al. 2012b). Considering the potential effects of vultures on the scavenging behavior of mammals and contact rates between individuals, there is a need to investigate these interactions in other ecosystems with different communities of avian and mammalian scavengers.

In North America, vulture diversity is primarily limited to turkey and black (*Coragyps atratus*) vultures (Fig. 1), but numerous mammalian scavengers spanning several families are widely distributed (DeVault and Rhodes 2002, DeVault et al. 2004a, Turner et al. 2017). With divergent vulture and mammalian scavenging guilds among continents, it remains unclear to what extent vultures prevent mammals from consuming carrion in North America. Although black and turkey vultures are currently abundant in North America, it is possible that scavenging rates of mammals may increase should vulture populations decline and carrion availability subsequently increase, as has happened in India (Markandya et al. 2008). I explored competition for carrion between vultures and mammals by experimentally excluding vultures from carcasses to test the hypothesis that vultures outcompete mammalian scavengers for carrion through exploitation competition. Following Ogada et al. (2012b), I predicted that when vultures were excluded from carcasses, there would be (1) an increase in presence of mammalian scavengers, (2) an increase in mammal species richness at carcasses, and (3) an increase in the persistence time of carcasses.

Methods

Study Site

I conducted this study at the Savannah River Site, a property owned by the US Department of Energy that encompasses 78,000 ha in Aiken County, South Carolina, USA (33°19’N, 81°42’W). The site is dominated by loblolly pine forests (*Pinus taeda*), longleaf pine forests (*P. palustris*), and bottomland hardwoods (e.g. *Nyssa* spp., *Quercus* spp.) (White and Gaines 2000). Since 1951, much of the site has been managed for timber harvest and stands are harvested on a rotating basis (White and Gaines 2000). I conducted this study during June–August 2016; average daily temperature was 27.6°C and average daily rainfall was 0.33 cm during this period (NOAA 2017).

Study Design

I selected 60 sites in pine (*Pinus* spp.) stands that were greater than 20 years old that were within 15 m of a road. Choosing sites along roads facilitated accessing them twice daily (see below). Each site was separated by a minimum distance of 500 m. At these 60 sites, I conducted a total of 130 trials, randomly selecting 65 to serve as controls and excluding vultures from the remaining trials. I carried out six weeks of trials and each trial lasted seven days. During each seven-day period, I ran 20 trials (10 exclusion and 10 control) concurrently. I used separate sites in weeks 1–3 and reused these sites in the same sequence in weeks 4–6 (sites used in week 1 were reused in week 4, etc.). In the sixth and final week, I increased the number of trials to 30 (15 exclusion and 15 control) to redo trials that had failed due to camera malfunction. The 10 additional sites in the last week had also been used in the first and fourth weeks, so there was a minimum of one week between consecutive uses of the same site.

At each site I placed a dark colored rabbit (*Sylvilagus* spp.) carcass weighing ~1300 g that was obtained from a commercial supplier (RodentPro, Inglefield, IN, USA) and thawed to indoor ambient temperature. I used a cable lock to attach a motion-activated infrared camera (Bushnell Trophy Cam HD Aggressor; Bushnell Corp., Overland Park, KS, USA) to a tree ~2 m from carcasses to record the presence of scavengers. Cameras took three pictures when motion-activated, with a 1-minute delay between activations. To prevent scavengers from carrying carcasses beyond the field of view, I wrapped a non-relaxing cable snare around each carcass and staked it to the ground with a 46-cm steel rebar stake.

To exclude vultures, I used a plastic crate that measured 33.0 cm long by 33.0 cm wide by 27.6 cm tall (Fig. 2). I affixed panels of 1.27-cm gauge wire mesh over the handle openings so that vultures could not fit their heads into them. The crate had openings to permit air flow and access by arthropods so that decomposition of exclusion carcasses would not differ from controls. As most mammalian scavengers at the site detect carrion by olfaction (DeVault and Rhodes 2002), and the olfactory cues are produced by decomposers (DeVault et al. 2003), the openings in the crate minimized the chances that scavenger presence would be impacted by a difference in carcass detectability between the control and treatment trials.

To exclude vultures, which are diurnal, each day between 0700 h and 1000 h I placed a crate on top of carcasses receiving the exclusion treatment. I used 30-cm galvanized metal staples to secure the crate in place and placed logs around the perimeter to prevent vultures from reaching their bills under the crate. Crates were removed daily between 1800 h and 2100 h. Crates were only on carcasses during daylight hours, which prohibited diurnal scavenging. However, I believe this had minimal impact on scavenging rates by facultative scavengers as these species primarily scavenge at night (DeVault and Rhodes 2002, DeVault et al. 2011, Huijbers et al. 2013). Previous research at SRS indicated that 91% of mammal visits to rabbit carcasses occurred between 1800 h and 0900 h (Turner et al. 2017).

Because the design excluded diurnal scavenging, it also incidentally excluded most facultative avian scavengers. However, visits to control carcasses by these species were rare, consisting of one visit each by an American crow (*Corvus brachyrhynchos*) and a red-tailed hawk (*Buteo jamaicensis*) (see Results). In both cases the bird was displaced by a vulture that consumed the majority of the carcass and scavenging by these species likely had a negligible impact on carcass consumption. I removed these species from this analysis because they could not access the exclusion carcasses, but maintained these two trials in analysis. I visited control carcasses twice daily to standardize human presence between the treatment and control trials. For each carcass I documented the date when there appeared to be no edible flesh remaining on the carcass and considered the carcass fully scavenged at that time.

From the photographs, I identified scavenger species at each carcass and examined whether non-avian scavengers were present. Results are expressed as the number of carcasses at which the species was present. I compared the presence/absence of all non-avian scavengers combined between the treatment and control using a generalized linear model with binomial distribution and logit link using R version 3.2.3 (R Core Team 2016). I also calculated species richness of non-avian scavengers at each carcass and compared this variable between the control and treatment using a generalized linear model with a quasi-Poisson distribution (to account for overdispersion of data) and log link. To compare the carcass detection time, I calculated time between carcass placement and when an animal was first observed at the carcass for vultures at control carcasses, mammals at control carcasses, and mammals at exclusion carcasses. Treatments were compared using a generalized linear model with normal distribution and identity link. I used the Kaplan-Meier procedure to compare the time to carcass depletion between the treatment and control using the R package 'survival' (Therneau 2015). I chose this procedure because there was a single binary predictor. I right-censored trials in which the carcass had not been fully consumed at the end of seven days. A p-value of 0.05 was used to determine statistical significance for all analyses.

Results

Of the 130 trials, 110 produced usable data (53 control and 57 exclusion). I censored trials due to camera failure (*n* = 15) and failure to prevent vultures from accessing exclusion carcasses (*n* = 4). The latter happened when vultures arrived at the carcass when the crate was absent or when vultures were able to pull the carcass from under the crate and consume it. I also censored one exclusion trial when the carcass was consumed by a red-tailed hawk while the crate was not positioned on the carcass. At exclusion sites, there were 122 detections of mammals (i.e. a mammal in at least one of the three pictures taken when the camera was triggered, including multiple detections of the same species at a carcass and those that did not scavenge) at night when the crate was not positioned over the carcass and only two detections during daylight when the crate was over the carcass. Thus, the use of crates during daylight hours effectively excluded vultures while only minimally impacting carcass accessibility by mammals.

Turkey and black vultures scavenged at 50 and 10 control carcasses, respectively. Mammals recorded scavenging at control carcasses were coyote (*Canis latrans*, *n* = 1), Virginia opossum (*Didelphis virginiana*, *n* = 2), and wild pig (*Sus scrofa*, *n* = 1). Scavengers recorded at exclusion carcasses (at night when crates were removed) were coyote (*n* = 3), opossum (*n* = 6), wild pig (*n* = 1), and American alligator (*Alligator mississippiensis*, *n* = 2). More than 1 species was detected at 13 carcasses (Table 1).

Facultative scavengers scavenged at 9% of control carcasses and 19% of exclusion carcasses. Fifty control carcasses were consumed by scavengers and 3 were not scavenged. By contrast, only 11 exclusion carcasses were scavenged, whereas 46 were not scavenged.

Vultures arrived at control carcasses on average 1.96 ± 0.83 days after placement. Mammals arrived at exclusion carcasses on average 3.02 ± 2.34 days after placement and at control carcasses on average 3.20 ± 1.91 days after placement. Vultures at control carcasses arrived sooner than mammals at exclusion carcasses (β = -1.0755, *P*-value = 0.004). Control carcasses were scavenged more quickly than exclusion carcasses (χ^2 = 86.3, *P*-value < 0.001, Fig. 3). Compared to control carcasses, there was a 1.1- and 8.5-fold increase in the percentage of available exclusion carcasses at the end of 2 and 4 days, respectively. At the end of the trials (7 days), there was a 10.1-fold increase in the number of available exclusion carcasses compared to control carcasses. Treatment was not a significant predictor of non-avian scavenger presence (β = 1.0748, *P*-value = 0.083) or non-avian scavenger species richness (β = 0.6204, *P*-value = 0.203, Fig. 4).

Discussion

Mammals did not scavenge more frequently in the absence of vulture competition and I found no support for the hypothesis that vultures would outcompete mammals for carrion through exploitation competition. Similarly, the prediction that there would be an increase in the presence and species richness of non-avian scavengers when vultures were excluded were not supported by my findings. However, the predicted increase in carcass persistence did occur because when vultures could not access a carcass, it was unlikely to be scavenged by vertebrates.

The increase in carcass persistence indicates that under the environmental conditions in this study, mammals were unable to functionally replace vultures as scavengers. In Spain, ungulate carcasses persisted longer in areas without vultures (Morales-Reyes et al. 2017) and Ogada et al. (2012b) also documented an increase in ungulate carcass persistence when vultures were experimentally excluded in Africa. Facultative scavengers may not be able to compensate for the loss of dominant scavengers even when the dominant scavengers are not vultures. Facultative avian scavengers consume most carrion in Australia, and fish carcasses lasted longer in urban areas with lower avian scavenger abundance (Huijbers et al. 2015). In an agricultural landscape where raccoons (*Procyon lotor*) were the dominant scavenger (DeVault et al. 2011), rodent carcasses persisted longer when raccoons were removed (Olson et al. 2012). Scavenging by mammals increased following reductions in dominant scavenger abundance in each of these studies, but not at a high enough rate to remove carcasses as efficiently as the dominant scavengers.

A notable difference in this study was that there was not a significant increase in mammal scavenging when vultures were excluded, and thus not even partial compensation of the loss of scavenging by vultures. This pattern was likely influenced by season, as I conducted this study in summer, when the average daily temperature was 27.6°C and maximum temperature exceeded 32.2°C on most days (NOAA 2017). Microbial activity generally increases with warmer temperatures (Putman 1978, Pechal et al. 2013) and bacteria can produce noxious chemicals that deter scavenging by animals when they colonize carcasses (Janzen 1977, Burkepile et al. 2006). This increase in decomposer activity can decrease the time that carcasses are palatable to mammals and mammals generally scavenge less during warmer temperatures (e.g. DeVault et al. 2004a, Selva et al. 2005, Turner et al. 2017). Vultures may be more tolerant than mammals to toxins produced by decomposers, making carcasses available to them for a longer period of time than they are to mammals (Houston and Cooper 1975, Roggenbuck et al. 2014, Chung et al. 2015).

Invertebrate decomposers are also more active during warmer temperatures and can rapidly consume carcasses. At another location in South Carolina, arthropods began to reduce the mass of pig carcasses weighing 1000-1400 g after 2 days and reduced the body mass of carcasses by 90% within 6 days (Payne 1965). Because vultures typically arrived less than 2 days after placement (and sometimes within 1 day), there likely had not been substantial carrion consumption by invertebrates when they detected carcasses. However, invertebrate consumption may have increased considerably by the time that mammals arrived, which was on average more than one day later. When environmental conditions facilitate rapid decomposition of carcasses, the ability of vultures to quickly detect carrion likely makes them more efficient scavengers than mammals and might partially account for the inability of mammals to replace vultures as the dominant scavengers under these conditions. Since the majority of exclusion carcasses were not consumed at the end of the 7-day trials, it is possible that mammals may have scavenged carcasses after monitoring ended. However, the advanced state of decomposition of carcasses after seven days makes it unlikely that they would have been scavenged by mammals (Payne 1965).

Another factor contributing to the lack of scavenging by mammals could be that for some facultative scavengers, carrion is a resource consumed primarily when other resources are scarce (Jędrzejewski and Jędrzejewska 1992, Jędrzejewski et al. 1993, Read and Wilson 2004). At SRS, coyotes predominately consume vegetation such as blackberries (*Rubus* spp.) and wild plums (*Prunus* spp.) in summer and shift to mammalian food items in winter as vegetative food items become scarcer (Schrecengost et al. 2008). The abundance of vegetative food items in summer may lead coyotes to consume less carrion during this time because other foods are available. Similarly, the diet of opossums in summer consists largely of vegetation, but may switch to carrion in the winter when other resources become scarce (Hopkins 1974). For both species, I documented instances in which individuals were present at carcasses before vultures arrived. Thus scavenging by mammals at this study site was not solely dependent on the ability to detect carcasses, but is likely also influenced by the availability of alternative food.

Seasonality can influence vertebrate scavenging at SRS, with a decrease in vulture activity and increase in mammal scavenging during winter (Turner et al. 2017). Therefore mammals may compete more effectively with vultures during cooler seasons and might functionally replace vultures in the removal of carrion under such conditions. However, temperatures are warm for much of the year at this location and mean monthly temperature typically exceeds 21.1°C for 5 months or more each year (NOAA 2017). Furthermore, annual temperature in the region is projected to increase 2.2-2.5°C in the next 50 years (Kunkel et al. 2013). Thus even if mammals are capable of replacing vultures in carrion removal during cooler seasons, were vultures to become extirpated from this area, there would still be a substantial portion of the year in which carrion would mostly not be scavenged by vertebrates.

The degree to which vulture presence influences species richness of mammalian scavengers can vary, either by increasing species richness by alerting other scavengers to the presence of carrion (Sebastián-González et al. 2016), or decreasing species richness by exploiting the resource before other scavengers are able to detect it (Ogada et al. 2012b). The low species richness of non-avian scavengers in this study can be attributed in part to the use of rabbit carcasses, as smaller carcasses generally support fewer scavenger species (Moleón et al. 2015). Vulture presence did not influence scavenger species richness in this study because mammals scavenged infrequently regardless of competition with vultures. There were a few instances in which mammals scavenged on control carcasses after vultures had scavenged it partially. The evisceration of these carcasses may have facilitated mammal detections of carrion by making it more detectable through olfaction, but there was not a large enough sample size to test this. Although most studies on such facilitative effects of scavenger species focused on visual cues provided by vultures to mammals (e.g. Sebastián-González et al. 2016, Kane and Kendall 2017), they may also provide olfactory cues when carcasses are not completely consumed.

An important aspect of this study is that vultures were present, but excluded from scavenging the trial carcasses. This contrasts with studies such as Morales-Reyes et al. (2017) in which vultures were entirely absent from the study area; this difference could be meaningful for facultative scavengers. Although vultures could not scavenge experimental carcasses, they were abundant on the site and thus scavenging on other carrion sources, reducing the total availability of carrion in the area. If vultures were absent altogether, carrion availability would likely increase substantially. Since facultative scavengers may switch from predation to scavenging as carrion becomes more available (Van Dijk et al. 2008), a true absence of vultures may lead to increased mammal scavenging due to increased selection of carrion compared to live prey. I was unable to examine such potential shifts in foraging behavior. Also, detection ability is a major factor influencing scavenging behavior under the environmental conditions of this study (Turner et al. 2017); I am uncertain whether mammals would be able to increase their detection times of carrion enough to substantially increase carrion consumption if vultures were truly absent from the study area.

The spacing of carcasses could have also influenced scavenger detections. Distance between sites was based on the availability of sites that met the habitat requirements and the minimum distance of 500 m between sites could have resulted in spatial dependence in terms of scavenger detection of carcasses. However, the overall infrequent detections of mammals, especially within any set of 20 trials, suggests that the same individuals did not scavenge multiple carcasses as a result of carcass proximity. Additionally, the overall mean detection time at control carcasses of 1.96 d was similar to that of 2.20 d reported in another study of scavenging of rabbit carcasses at SRS during summer (Turner et al. 2017). Therefore, I suggest that the spacing of carcasses did not have a substantial impact on scavenger behavior.

Despite these limitations, this study suggests that a decline in vultures in the study area would likely result in a shift in the cycling of nutrients through food webs. Because mammals are not likely to increase carrion consumption in the absence of competition with vultures, at least during summer months, consumption of this resource would shift from vertebrates to decomposers. This shift could promote increased prevalence of disease-causing bacteria, such as *Mycobacterium bovis*, which are known to colonize several species of mammal carcasses (Gortázar et al. 2008, Naranjo et al. 2008). Some arthropods such as blowflies (Diptera: Calliphoridae) that use carrion can also carry diseases (Maldonado and Centeno 2003). However, some toxic bacteria may not survive the digestive tracts of blowflies (Mumcuoglu et al. 2001), so disease-causing decomposers on carcasses may impose some controls on each other. How the overall presence of these decomposers would be impacted by an increase in carrion remains unclear. Most studies of the role of carrion in disease transmission have used ungulate carcasses (e.g. Gortázar et al. 2008, Jennelle et al. 2009, Bellan et al. 2013) and the potential for toxic microbes on smaller mammal carcasses such as those in this study has been less explored.

The spatial distribution of nutrients provided by carcasses would also be impacted by vulture declines. Nutrients from carcasses are distributed throughout the landscape by vultures, which generally have large home ranges because they are obligate scavengers (DeVault et al. 2004b, Ruxton and Houston 2004, Beasley et al. 2015). Had they scavenged extensively, coyotes might have had a similar impact on nutrient dispersion, as they are known to cache food items (e.g. Windberg et al. 1997) and have an average home range size of 31.85 km^2 at SRS (Schrecengost et al. 2009). However, the lack of scavenging I documented on control carcasses indicates that instead of being dispersed throughout the landscape, nutrients would remain spatially clustered near the carcasses (Melis et al. 2007). Nutrients from carcasses can enter the soil, augmenting plant growth

(Bump et al. 2009). The clustering of nutrients around a carcass due to a lack of vertebrate scavenging may impact surrounding plant communities and by extension the organisms that consume those plants (Carter et al. 2007). Although most studies have focused on how vulture declines impact other scavengers, (e.g. Ogada et al. 2012b, Kane and Kendall 2017, Morales-Reyes et al. 2017), the results indicate that the ecological impacts of vulture loss could extend to lower trophic levels as well.

Table 4.1 Presence of vertebrate scavengers consuming rabbit carcasses at the Savannah River Site, Aiken SC (June–August 2016).

Treatment	Number of Trials	Turkey Vulture	Black Vulture	Coyote	Opossum	Wild Pig	American Alligator
Control	38	X					
	8	X	X				
	1	X		X			
	1	X	X			X	
	1	X			X		
	1	X	X		X		
Exclusion	5				X		
	3			X			
	2						X
	1				X	X	

Figure 4.1 Placement of plastic crate over rabbit carcass.

Crates measured 33.0 cm long, 33.0 cm wide, 27.6 cm tall and had panels of wire affixed over the handle openings. Logs were also placed along the perimeter to prevent vultures from reaching their bills under the edge of the crate and pulling out the carcass.

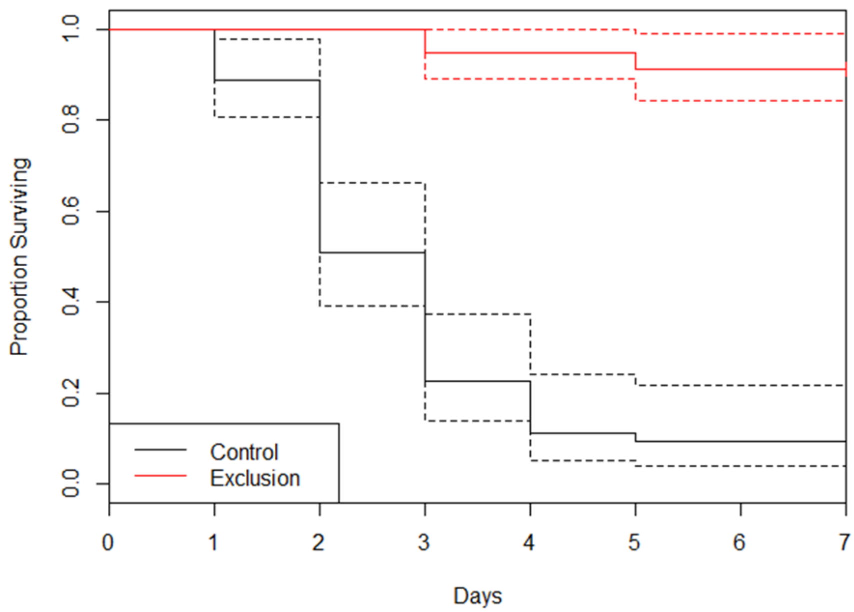

Figure 4.2 Days to complete rabbit carcass consumption by vertebrate scavengers at the Savannah River Site, Aiken SC (June–August 2016) between carcasses from which vultures were excluded and controls.

Survival times were estimated using the Kaplan-Meier procedure. Dashed lines represent 95% confidence intervals.

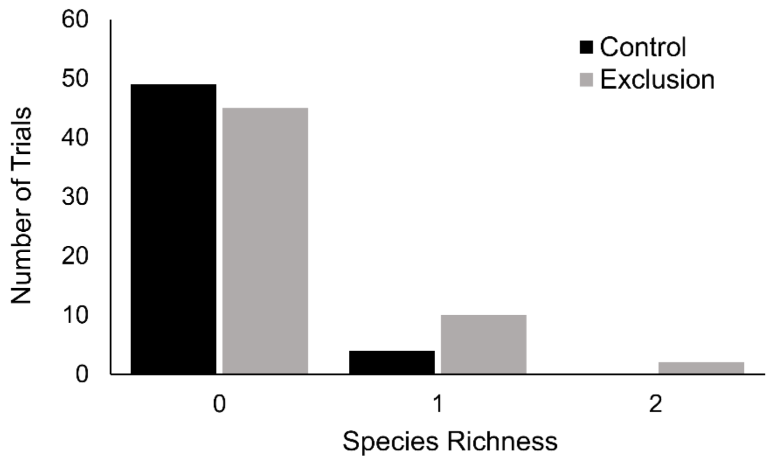

Figure 4.3 Species richness of non-avian scavenger species that visited rabbit carcasses from which vultures were excluded (n = 57) and controls (n = 53) at the Savannah River Site, Aiken SC (June–August 2016)

Generalized linear model with quasi-Poisson distribution and log link indicated no difference in occurrence of non-avian species richness between the exclusion and control carcasses (β = 0.6204, P-value = 0.203).

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APPENDIX A

CAUSE-SPECIFIC MORTALITY STUDIES USED FOR ANALYSIS IN CHAPTER 2

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APPENDIX B

RESULTS OF MODEL SELECTION PROCEDURES FOR CHAPTER 2

Table B.1 Sample size corrected Akaike's information criterion (AIC_c) for models within 2 AIC units of top model, Akaike weights (w_i), and parameters included in models for mortality sources of all mammals (n=21,546 mortalities)

	AICc	w_i	Age	Diet	Protected	Year
Total Human	2290.8	0.73	x	x	x	
	2292.7	0.27	x	x	x	x
Total Natural	2290.8	0.73	x	x	x	
	2292.7	0.27	x	x	x	x
Total Harvest	2057.9	0.58	x	x	x	x
	2058.6	0.42	x	x	x	
Legal Harvest	1724.2	0.37	x	x	x	
	1725.0	0.25	x		x	
	1725.2	0.23	x	x	x	x
	1725.9	0.16	x		x	x
Poached	732.0	0.71	x	x		x
	733.7	0.29	x	x		
Vehicle	403.7	0.46	x			x
	404.8	0.36	x	x		x
	405.6	0.18	x		x	x
Management	-301.3	0.41	x	x	x	
	-300.5	0.27		x	x	
	-299.6	0.18	x		x	
	-299.4	0.15	x	x	x	x
Predation	2320.96	0.51	x	x		
	2321.03	0.49	x	x	x	

Table B.2 Model averaged parameter estimates, standard error, and confidence intervals for mortality sources of all mammals (n=21,546 mortalities)

	Parameter	Estimate	Standard Error	Alpha	Lower CI	Upper CI
Total human	Intercept	0.1123	3.5931	5.1769	-5.0646	5.2893
	Age: Not Adult	-0.7619	0.0538	0.0775	-0.8394	-0.6845
	Diet: Carnivore	0.7760	0.2178	0.3138	0.4622	1.0898
	Diet: Herbivore	-0.3000	0.1939	0.2794	-0.5794	-0.0206
	Protected: Yes	-0.4422	0.1271	0.1832	-0.6254	-0.2591
	Year	0.0003	0.0018	0.0026	-0.0029	0.0023
Total natural	Intercept	-0.1123	3.5931	5.1769	-5.2893	5.0646
	Age: Not Adult	0.7619	0.0538	0.0775	0.6845	0.8394
	Diet: Carnivore	-0.7760	0.2178	0.3138	-1.0898	-0.4622
	Diet: Herbivore	0.3000	0.1939	0.2794	0.0206	0.5794
	Protected: Yes	0.4422	0.1271	0.1832	0.2591	0.6254
	Year	-0.0003	0.0018	0.0026	-0.0023	0.0029
Total harvest	Intercept	4.8235	6.6631	9.5960	-4.7724	14.4195
	Age: Not Adult	-0.5764	0.0455	0.0656	-0.6420	-0.5108
	Diet: Carnivore	0.5909	0.1817	0.2617	0.3292	0.8527
	Diet: Herbivore	-0.0228	0.1629	0.2347	-0.2575	0.2119
	Protected: Yes	-0.3593	0.1124	0.1620	-0.5213	-0.1973
	Year	-0.0029	0.0033	0.0048	-0.0077	0.0019
Legal harvest	Intercept	1.1208	3.9916	5.7493	-4.6285	6.8701
	Age: Not Adult	-0.4199	0.0363	0.0524	-0.4723	-0.3676
	Diet: Carnivore	0.1599	0.1721	0.2479	-0.0880	0.4078
	Diet: Herbivore	0.0116	0.0997	0.1437	-0.1321	0.1553
	Protected: Yes	-0.3374	0.0931	0.1341	-0.4716	-0.2033
	Year	-0.0010	0.0020	0.0029	-0.0039	0.0019
Illegal harvest	Intercept	2.3553	3.1136	4.4842	-2.1288	6.8395
	Age: Not Adult	-0.0816	0.0217	0.0312	-0.1128	-0.0503
	Diet: Carnivore	0.2570	0.0733	0.1056	0.1514	0.3627
	Diet: Herbivore	-0.0117	0.0655	0.0944	-0.1062	0.0827
	Year	-0.0018	0.0016	0.0005	-0.0040	0.0005

Table B.2 (continued)

Vehicle	Intercept	-6.0060	2.1370	3.0792	-9.0852	-2.9268
	Age: Not Adult	-0.0649	0.0176	0.0254	-0.0902	-0.0395
	Year	0.0026	0.0011	0.0015	0.0011	0.0041
	Diet: Carnivore	0.0060	0.0357	0.0515	-0.0456	0.0575
	Diet: Herbivore	-0.0245	0.0452	0.0651	-0.0896	0.0407
	Protected: Yes	-0.0022	0.0175	0.0251	-0.0273	0.0230
Management	Intercept	-1.2020	0.4903	0.7065	-1.9081	-0.4951
	Age: Not Adult	-0.0150	0.0135	0.0195	-0.0345	0.0045
	Diet: Carnivore	-0.0353	0.0346	0.0498	-0.0851	0.0145
	Diet: Herbivore	-0.0634	0.0398	0.0573	-0.1207	-0.0061
	Protected: Yes	0.0594	0.0240	0.0346	0.0248	0.0941
	Year	2.5E-05	0.0002	0.0004	-0.0003	0.0004
Predation	Intercept	-0.0575	0.1965	0.2831	-0.3405	0.2256
	Age: Not Adult	0.5242	0.0496	0.0714	0.4528	0.5956
	Diet: Carnivore	-1.0221	0.2633	0.3379	-1.4015	-0.6427
	Diet: Herbivore	0.2686	0.2345	0.3379	-0.0693	0.6065
	Protected: Yes	0.0949	0.1364	0.1965	-0.1016	0.2913

Table B.3 Sample size corrected Akaike's information criterion (AIC_c) for models within 2 AIC units of top model, Akaike weights (w_i), and parameters included in models of magnitude of all mammal mortality (n=20,482 mortalities of 51,184 individuals)

AICc	w_i	Age	Diet	Protected	Year
713.23	0.31	x	x	x	
713.37	0.29	x	x		
714.00	0.21	x	x	x	x
714.00	0.20	x	x		x

Table B.4 Model averaged parameter estimates, standard error, and confidence intervals for magnitude of all mammal mortality (n=20,482 mortalities of 51,184 individuals)

	Estimate	Standard Error	Alpha	Lower CI	Upper CI
Intercept	1.1328	2.7526	3.9650	-2.8322	5.0978
Age: Not adult	0.2092	0.0287	0.0413	0.1679	0.2506
Diet: Carnivore	0.1524	0.0751	0.1082	0.0442	0.2606
Diet: Herbivore	0.1633	0.0654	0.0942	0.0691	0.2575
Protected: Yes	-0.0427	0.0577	0.0830	-0.1257	0.0404
Year	-0.0008	0.0014	0.0020	-0.0027	0.0012

Table B.5 Sample size corrected Akaike's information criterion (AIC_c) for models within 2 AIC units of top model, Akaike weights (w_i), and parameters included in models for mortality sources of adult mammals (n=12,798 mortalities)

	AICc	w_i	Mass	Diet	Protected	Year
Total Human	1450.1	0.72	x	x	x	
	1452.0	0.28	x	x	x	x
Total Natural	1450.1	0.72	x	x	x	
	1452.0	0.28	x	x	x	x
All Harvest	1394.2	0.53	x	x	x	
	1394.5	0.47	x	x	x	x
Legal	1216.3	0.51	x		x	
	1217.7	0.25	x		x	x
	1217.9	0.24	x	x	x	
Poached	625.0	0.46	x	x		x
	625.4	0.37	x	x		
	627.0	0.17	x	x	x	x
Vehicle	376.5	0.71				x
	378.25	0.29	x			x
Management	-46.00	0.57	x	x		
	-45.41	0.43	x	x	x	
Predation	1474.3	0.58	x	x	x	x
	1475.0	0.42	x	x		x

Table B.6 Model averaged parameter estimates, standard error, and confidence intervals for mortality sources of adult mammals (n=12,798 mortalities)

	Parameter	Estimate	Standard Error	Alpha	Lower CI	Upper CI
Total human	Intercept	-3.2749	4.1765	6.0196	-9.2946	2.7447
	Diet: Carnivore	0.4178	0.1980	0.2855	0.1324	0.7033
	Diet: Herbivore	-0.4793	0.1787	0.2576	-0.7369	-0.2217
	Mass	0.5529	0.0718	0.1036	0.4493	0.6564
	Protected: Yes	-0.4961	0.1310	0.1888	-0.6850	-0.3073
	Year	0.0004	0.0021	0.0030	-0.0026	0.0034
Total natural	Intercept	3.2749	4.1765	6.0196	-2.7557	9.2946
	Diet: Carnivore	-0.4178	0.1980	0.2855	-0.7033	-0.1324
	Diet: Herbivore	0.4793	0.1787	0.2576	0.2217	0.7369
	Mass	-0.5529	0.0718	0.1036	-0.6564	-0.4493
	Protected: Yes	0.4961	0.1310	0.1888	0.3073	0.6850
	Year	-0.0004	0.0021	0.0030	-0.0034	0.0026
Total harvest	Intercept	2.0210	6.9963	10.0785	-8.0575	12.0995
	Diet: Carnivore	0.3600	0.1715	0.2372	0.1188	0.6132
	Diet: Herbivore	-0.1451	0.1571	0.2265	-0.3716	0.0813
	Mass	0.4620	0.0631	0.0910	0.3710	0.5530
	Protected: Yes	-0.4103	0.1244	0.1794	-0.5897	-0.2309
	Year	-0.0023	0.0035	0.0050	-0.0073	0.0027
Legal harvest	Intercept	-0.6705	3.9023	5.6228	-6.2932	4.9523
	Mass	0.2989	0.0532	0.0766	0.2222	0.3755
	Protected: Yes	-0.3690	0.1068	0.1539	-0.5229	-0.2151
	Diet: Carnivore	0.0307	0.0883	0.1272	-0.0965	0.1578
	Diet: Herbivore	-0.0160	0.0700	0.1009	-0.1169	0.0850
	Year	0.0007	0.0019	0.0028	-0.0035	0.0022
Illegal harvest	Intercept	2.0697	4.0286	5.8035	-3.7338	7.8731
	Diet: Carnivore	0.1848	0.0746	0.1075	0.0773	0.2923
	Diet: Herbivore	-0.0403	0.0685	0.0987	-0.1390	0.0584
	Mass	0.1140	0.0269	0.0388	0.0753	0.1528
	Year	-0.0018	0.0020	0.0029	-0.0047	0.0011
	Protected: Yes	0.0028	0.0260	0.0375	-0.0348	0.0403
Vehicle	Intercept	-10.2771	3.0371	4.3780	-14.6551	-5.8991
	Year	0.0047	0.0015	0.0022	0.0025	0.0069
	Mass	0.0037	0.0139	0.0200	-0.0163	0.0237

Table B.6 (continued)

Management	Intercept	-1.2690	0.0573	0.0826	-1.3516	-1.1864
	Diet: Carnivore	0.0191	0.0261	0.0376	-0.0185	0.0566
	Diet: Herbivore	-0.0738	0.0285	0.0411	-0.1149	-0.0327
	Mass	0.0312	0.0137	0.0197	0.0115	0.0509
	Protected: Yes	0.0149	0.0254	0.0366	-0.0217	0.0515
Predation	Intercept	18.0525	7.6887	11.0835	6.9690	29.1359
	Diet: Carnivore	-0.5548	0.2164	0.3120	-0.8668	-0.2429
	Diet: Herbivore	0.5411	0.1959	0.2824	0.2587	0.8235
	Mass	-0.7541	0.0798	0.1150	-0.8691	-0.6391
	Protected: Yes	0.1313	0.1517	0.2185	-0.0873	0.3498
	Year	-0.0078	0.0038	0.0055	-0.0132	-0.0022

Table B.7 Sample size corrected Akaike's information criterion (AIC_c) for models within 2 AIC units of top model, Akaike weights (w_i), and parameters included in models of magnitude of adult mammal mortality (n=12,252 mortalities of 32,865 individuals)

AICc	w_i	Mass	Diet	Protected	Year
414.16	0.28	x	x		x
414.24	0.27	x	x	x	x
414.53	0.23	x	x		
414.54	0.23	x	x	x	

Table B.8 Model averaged parameter estimates, standard error, and confidence intervals for magnitude of adult mammal mortality (n=12,252 mortalities of 32,865 individuals)

	Estimate	Standard error	Alpha	Lower CI	Upper CI
Intercept	3.2289	4.0494	5.8338	-0.1121	0.1802
Diet: Carnivore	0.1793	0.0658	0.0948	0.0847	0.2742
Diet: Herbivore	0.1718	0.0605	0.0872	0.0819	0.2558
Mass	-0.0975	0.0241	0.0347	-0.1313	-0.0622
Protected: Yes	-0.0412	0.0586	0.0844	-0.1257	0.0432
Year	-0.0016	0.0020	0.0029	-0.0045	0.0013

Table B.9 Sample size corrected Akaike's information criterion (AIC_c) for models within 2 AIC units of top model, Akaike weights (w_i), and parameters included in models for mortality sources of all birds (n=14,746 mortalities)

	AICc	w_i	Age	Diet	Protected	Year
Total human	804.2	0.55			x	x
	805.9	0.24			x	
	806.1	0.21	x		x	x
Total natural	804.2	0.55			x	x
	805.9	0.24			x	
	806.1	0.21	x		x	x
All harvest	721.2	0.67	x	x		x
	722.6	0.33	x	x		x
Legal harvest	686.7	0.34		x		x
	686.7	0.33	x	x		x
	688.2	0.16	x	x	x	x
	688.2	0.16		x	x	x
Illegal harvest	296.1	0.46				x
	297.8	0.20	x			x
	297.9	0.28			x	x
	298.1	0.17				
Vehicle	404.4	0.18	x	x		
	404.7	0.16	x	x	x	
	404.8	0.14	x	x		x
	405.2	0.12		x	x	
	405.2	0.12		x		
	405.3	0.11	x	x	x	x
	405.8	0.09		x		x
	406.0	0.08		x	x	x
Collision	407.1	0.38				
	407.9	0.26			x	
	408.4	0.20				x
	408.7	0.17	x			
Predation	866.0	0.30	x			x
	866.2	0.28	x		x	x
	867.4	0.16	x	x		x
	867.5	0.15	x	x	x	x
	868.0	0.11	x		x	

Table B.10 Model averaged parameter estimates, standard error, and confidence intervals for mortality sources of all birds (n=14,746 mortalities)

	Parameter	Estimate	Standard Error	Alpha	Lower CI	Upper CI
Total Human	Intercept	15.9609	13.8391	19.9549	-3.9850	35.9067
	Protected: Yes	-0.5144	0.2457	0.3545	-0.8689	-0.1599
	Year	-0.0085	0.0069	0.0100	-0.0185	0.0014
	Age: Not Adult	-0.0054	0.0268	0.0387	-0.0441	0.0333
Total Natural	Intercept	-15.9609	13.8391	19.459	-35.9067	3.9850
	Protected: Yes	0.5144	0.2457	0.3545	0.1599	0.9026
	Year	0.0085	0.0069	0.0100	-0.0014	0.0011
	Age: Not Adult	0.0054	0.0268	0.0387	-0.0333	0.0350
Total Harvest	Intercept	28.7421	10.4855	15.1292	13.6128	43.8713
	Age: Not Adult	-0.0979	0.0419	0.0605	-0.1583	-0.0374
	Diet: Carnivore	-0.2022	0.1682	0.2447	-0.4449	0.0405
	Diet: Herbivore	0.1580	0.1716	0.2476	-0.0896	0.4056
	Year	-0.0151	0.0052	0.0075	-0.0226	-0.0075
	Protected: Yes	-0.0601	0.1519	0.2190	-0.2791	0.1589
Legal Harvest	Intercept	23.8292	10.1701	14.6741	9.1552	38.5033
	Age: Not Adult	0.0260	0.0361	0.0520	-0.0260	0.0780
	Diet: Carnivore	-0.1327	0.1566	0.0260	-0.3586	0.0933
	Diet: Herbivore	0.2195	0.1599	0.2308	0.0487	0.5102
	Year	-0.0127	0.0051	0.0073	-0.0200	-0.0054
	Protected: Yes	-0.0540	0.1430	0.2062	-0.2601	0.1522
Illegal Harvest	Intercept	7.1283	6.5768	9.4804	-2.3522	16.6087
	Year	-0.0046	0.0033	0.0047	-0.0094	0.0001
	Protected: Yes	-0.0027	0.0114	0.0165	-0.0192	0.0138
	Age: Not Adult	-0.0101	0.0543	0.0783	-0.0884	0.0682
Vehicle	Intercept	0.9012	5.1905	7.4812	-6.5801	8.3824
	Age: Not Adult	-0.0365	0.0411	0.0593	-0.0957	0.0228
	Diet: Carnivore	0.2612	0.1149	0.1658	0.0954	0.4269
	Diet: Herbivore	-0.0233	0.1188	0.1714	-0.1947	0.1480
	Year	-0.0015	0.0026	0.0037	-0.0052	0.0022
	Protected: Yes	-0.0871	0.1312	0.1891	-0.2763	0.1020
Collision	Intercept	-3.0351	3.5824	5.1644	-8.1995	2.1294
	Protected: Yes	-0.0414	0.1012	0.1458	-0.1872	0.1045
	Year	0.0005	0.0018	0.0026	-0.0020	0.0031
	Age: Not Adult	0.0028	0.0121	0.0175	-0.0147	0.0203

Table B.10 (continued)

Predation	Intercept	-22.9962	14.8452	21.4034	-44.3996	-1.5928
	Protected: Yes	0.2127	0.2800	0.4036	-1.909	0.6163
	Age: Not Adult	-0.114	0.0514	0.0742	-0.1856	-0.0372
	Year	0.0118	0.0074	0.0107	0.0011	0.0225
	Diet: Carnivore	-0.7064	0.1662	0.2395	-0.3159	0.1631
	Diet: Herbivore	-0.0118	0.1224	0.1795	-0.1913	0.1677

Table B.11 Sample size corrected Akaike's information criterion (AIC_c) for models within 2 AIC units of top model, Akaike weights (w_i), and parameters included in models of magnitude of all bird mortality (n=13,710 mortalities of 39,213 individuals)

AICc	w_i	Age	Diet	Protected	Year
390.53	0.36	x	x		
390.62	0.34	x	x		x
392.15	0.16	x	x	x	
392.42	0.14	x	x	x	x

Table B.12 Model averaged parameter estimates, standard error, and confidence intervals for magnitude of adult bird mortality (n=13,710 mortalities of 39,213 individuals)

	Estimate	Standard Error	Alpha	Lower CI	Upper CI
Intercept	4.0447	6.5824	9.4871	-5.4424	13.5318
Age: Not Adult	0.1902	0.0456	0.0657	0.145	0.2560
Diet: Carnivore	-0.0460	0.1058	0.1527	-0.1987	0.1067
Diet: Herbivore	0.1743	0.1102	0.1590	0.0152	0.333
Protected: Yes	-0.0253	0.0829	0.1196	-0.1449	0.0943
Year	-0.0022	0.0033	0.0047	-0.0070	0.0025

Table B.13 Sample size corrected Akaike's information criterion (AIC_c) for models within 2 AIC units of top model, Akaike weights (w_i), and parameters included in models for mortality sources of adult birds (n=6,360 mortalities)

	AICc	w_i	Mass	Diet	Protected	Year
Total Human	413.81	0.61	x			
	414.71	0.39	x			x
Total Natural	413.81	0.61	x			
	414.71	0.39	x			x
All Harvest	422.2	0.45	x			x
	422.5	0.39	x			
	424.2	0.17	x	x		x
Legal Harvest	418.2	0.21	x			
	418.3	0.20		x		x
	419.1	0.14	x	x		
	419.2	0.13				
	419.3	0.12		x		x
	419.5	0.11	x			x
	420.1	0.08				x
Illegal Harvest	218.4	0.54	x			x
	219.0	0.24	x		x	x
	220.2	0.22	x	x		x
Vehicle	207.4	0.43	x	x		
Collision	198.6	0.70	x			
	200.3	0.30	x		x	
Predation	463.4	0.27	x	x		x
	463.4	0.26	x			x
	463.6	0.24	x	x		
	463.8	0.22	x			

Table B.14 Model averaged parameter estimates, standard error, and confidence intervals for mortality sources of adult birds (n=6,360 mortalities)

	Parameter	Estimate	Standard Error	Alpha	Lower CI	Upper CI
Total human	Intercept	3.7183	12.0227	17.3517	-13.6334	21.0700
	Mass	0.5806	0.1268	0.1833	0.3973	0.7639
	Year	-0.0032	0.0060	0.0086	-0.0118	0.0055
Total natural	Intercept	-3.7183	12.0227	17.3517	-21.0700	13.6334
	Mass	-0.5806	0.1268	0.1833	-0.7639	-0.3973
	Year	0.0032	0.0060	0.0086	-0.0055	0.0118
Total harvest	Intercept	12.5711	16.7926	24.2290	-11.6578	36.8001
	Mass	0.3360	0.1229	0.1776	0.1583	0.5136
	Year	-0.0074	0.0084	0.0121	-0.00195	0.0046
	Diet: Carnivore	-0.0348	0.1345	0.1942	-0.2290	0.1593
	Diet: Herbivore	0.0068	0.1135	0.1641	-0.1573	0.1708
Legal harvest	Intercept	3.3000	11.3948	16.4456	-13.1456	19.7456
	Mass	0.0914	0.1309	0.1887	-0.0973	0.2802
	Year	-0.0025	0.0057	0.0082	-0.0107	0.0057
	Diet: Carnivore	-0.0099	0.1721	0.2489	-0.2588	0.2390
	Diet: Herbivore	0.1443	0.2373	0.3424	-0.1982	0.4867
Illegal harvest	Intercept	19.2699	8.5003	12.2918	6.9781	31.5617
	Mass	0.2629	0.0599	0.0867	0.1763	0.3496
	Year	-0.0110	0.0042	0.0061	-0.0172	-0.0049
	Protected: Yes	0.0854	0.2725	0.3936	-0.3081	0.4790
	Diet: Carnivore	-0.0454	0.1108	0.1597	-0.2051	0.1144
	Diet: Herbivore	-0.0553	0.1267	0.1826	-0.2379	0.1273
Vehicle	Intercept	-2.5800	0.3084	0.0049	-2.4629	-2.2954
	Diet: Carnivore	0.1891	0.2051	0.0023	0.1868	0.1914
	Diet: Herbivore	-0.1535	0.1981	0.0022	-0.1557	-0.1513
	Mass	0.2284	0.0920	0.0010	0.2274	0.2294
Collision	Intercept	-2.9165	0.3296	0.4765	-3.3930	-2.4400
	Mass	0.3603	0.1201	0.1737	0.1866	0.5340
	Protected: Yes	0.1142	0.3626	0.5237	-0.4095	0.6379
Predation	Intercept	-12.0770	18.1785	26.2240	-38.3010	14.1470
	Diet: Carnivore	0.0529	0.2371	0.3428	-0.2899	0.3956
	Diet: Herbivore	0.2510	0.3374	0.4868	-0.2359	0.7378
	Mass	-0.6162	0.1634	0.2360	-0.8522	-0.3802
	Year	0.0071	0.0091	0.0131	-0.0060	0.0202

Table B.15 Sample size corrected Akaike's information criterion (AIC_c) for models within 2 AIC units of top model, Akaike weights (w_i), and parameters included in models of magnitude of adult bird mortality (n=7,173 mortalities of 24,459 individuals)

AICc	w_i	Mass	Diet	Protected	Year
192.5	0.37		x		
193.4	0.24	x			
193.5	0.23	x	x		
193.1	0.16		x		x

Table B.16 Model averaged parameter estimates, standard error, and confidence intervals for magnitude of adult bird mortality (n=7,173 mortalities of 24,459 individuals)

	Estimate	Standard Error	Alpha	Lower CI	Upper CI
Intercept	0.4540	4.1987	6.0640	-5.6101	6.5180
Diet: Carnivore	-0.0856	0.1575	0.2277	-0.3133	0.1421
Diet: Herbivore	0.1067	0.1613	0.2331	-0.1264	0.3399
Mass	0.0603	0.0916	0.1321	-0.0717	0.1924
Year	-0.0005	0.0021	0.0030	-0.0035	0.0025

Table B.17 Sample size corrected Akaike's information criterion (AIC_c) for models within 2 AIC units of top model, Akaike weights (w_i), and parameters included in models for mortality sources of adult reptiles (n=609 mortalities)

	AICc	w_i	Mass	Diet	Protected	Year
Total Human	193.58	0.61	x	x		
	194.48	0.39	x			
Total Natural	193.58	0.61	x	x		
	194.48	0.39	x			
Vehicle	161.35	0.41	x			
	161.47	0.39				
	162.77	0.20	x	x		
Predation	184.10	0.51	x			
	185.29	0.28	x			x
	185.91	0.21	x		x	

Table B.18 Model averaged parameter estimates, standard error, and confidence intervals for mortality sources of adult reptiles and amphibians (n=609 mortalities)

	Parameter	Estimate	Standard Error	Alpha	Lower CI	Upper CI
Total Human	Intercept	-1.7785	0.4420	0.6437	-2.4223	-1.1348
	Diet: Carnivore	-0.0297	0.2221	0.3238	-0.3535	0.2941
	Diet: Herbivore	-0.8156	0.7877	1.1385	-1.9541	0.3228
	Mass	0.4772	0.1687	0.2453	0.2319	0.7224
Total Natural	Intercept	1.7785	0.4420	0.6437	1.1348	2.4223
	Diet: Carnivore	0.0297	0.2221	0.3238	-0.2941	0.3535
	Diet: Herbivore	0.8156	0.7877	1.1385	-0.3228	1.9541
	Mass	-0.4772	0.1687	0.2453	-0.7224	-0.2319
Vehicle	Intercept	-1.5086	0.4616	0.6679	-2.1765	-0.8407
	Mass	0.1524	0.1652	0.2391	-0.0868	0.3915
	Diet: Carnivore	0.0610	0.1675	0.2426	-0.1817	0.3036
	Diet: Herbivore	-0.1293	0.3734	0.5412	-0.6705	0.4119
Predation	Intercept	13.9451	29.4189	42.6235	-28.6784	56.5686
	Mass	-0.4014	0.1423	0.2074	-0.6088	-0.1940
	Year	-0.0064	0.0147	0.0213	-0.0277	0.0149
	Protected: Yes	-0.0483	0.1603	0.2327	-0.2810	0.1844

Table B.19 Sample size corrected Akaike's information criterion (AIC_c) for models within 2 AIC units of top model, Akaike weights (w_i), and parameters included in models of magnitude of adult reptile mortality (n=681 mortalities of 3,107 individuals)

AICc	w_i	Mass	Diet	Protected	Year
82.48	0.71		x		
84.24	0.29		x	x	

Table B.20 Model averaged parameter estimates, standard error, and confidence intervals for magnitude of adult reptile mortality (n=681 mortalities of 3,107 individuals)

	Estimate	Standard Error	Alpha	Lower CI	Upper CI
Intercept	-0.8509	0.1072	0.1562	-1.0071	-0.6947
Diet: Carnivore	0.3524	0.1191	0.1736	0.1788	0.5259
Diet: Herbivore	0.0507	0.2240	0.3265	-0.2758	0.3772
Protected: Yes	-0.0323	0.0856	0.1242	-0.1565	0.0919