
Carrion Ecology, Evolution, and Their Applications

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Ecological Role of Vertebrate Scavengers

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6.1 Introduction

Scavenging, or the consumption of dead animal matter, has been documented for a wide array of vertebrate taxa by naturalists and researchers for centuries. Yet, until recently, the importance of scavenging-derived nutrients to many vertebrate species has been largely unknown (DeVault et al. 2003; Beasley et al. 2012b; Barton et al. 2013). As a result, the role vertebrate scavenging plays in food-web dynamics relative to that of microbes and invertebrates has been greatly underestimated (Wilson and Wolkovich 2011) and has thus become an important area of research. Indeed, in some ecosystems, vertebrates have been documented to assimilate as much as 90% of the available carrion (Houston 1986; DeVault et al. 2011). Such substantive acquisition of carrion resources by vertebrates challenges the traditional paradigm of microbial and invertebrate dominance of nutrient recycling in food-web theory and suggests that intensive interkingdom competition exists for access to carrion nutrients.

The lack of quantitative measures of vertebrate scavenging behavior, particularly among facultative scavengers, largely stems from human aversion to decomposing matter and difficulties in assessing foraging behavior for many species (DeVault et al. 2003). However, advances in technology and an increased awareness of the ecological (Bump et al. 2009; Ogada et al. 2012; Barton et al. 2013) and economic (Markandya et al. 2008) importance of scavenging by vertebrates have sparked an abundance of scavenging research during the past decade. These studies have greatly advanced our understanding of the importance of scavenging to both individual species and as an ecosystem service, but we are only

beginning to appreciate the complexity of energy recycling via scavenging pathways and the cascading impacts anthropogenic activities can have on the disruption of these processes.

This chapter highlights the growing body of evidence supporting the importance of scavenging-derived nutrients to a multitude of vertebrate scavengers in both terrestrial and aquatic ecosystems, as well as the complex interactions among microbes, invertebrates, and vertebrates for access to carrion resources. The role of carrion in structuring vertebrate scavenging communities and the subsequent ecosystem services provided by this pervasive feeding strategy will also be discussed, drawing examples from the literature to highlight advancements along this front and where additional research is particularly needed. The chapter will conclude with a discussion of the documented and potential effects of various anthropogenic activities (e.g., climate change, habitat loss and fragmentation, loss of apex predators, and pollution) on vertebrate scavengers and the important ecosystem services scavengers provide.

6.2 Evolution of Vertebrate Scavengers

Species that scavenge can be separated into two unequal groups: those that rely on carrion for survival and reproduction ("obligate scavengers") and those species that will scavenge, but do not depend solely on carrion for their survival or reproduction ("facultative scavengers"). Vultures (families: Accipitridae and Cathartidae) feed extensively and in some cases exclusively on carrion, and these birds are believed to be the only obligate vertebrate scavengers (DeVault et al. 2003), although some benthic scavengers (e.g., hagfish: family Myxinidae) rely on necrophagy for a large portion of their diet and may indeed be obligate scavengers (Smith and Baco 2003; Beasley et al. 2012b). Although interesting for their adaptations to carrion-feeding and monopolization, obligate scavenging species are greatly outnumbered by a diverse assemblage of facultative scavengers. For example, most carnivorous species fall among the ranks of facultative scavengers; even species we recognize primarily as predators are regularly documented consuming carrion as part of their food habits, including the bobcat (*Lynx rufus*; Platt et al. 2010), barred owl (*Strix varia*; Kapfer et al. 2011), and many snake species (DeVault and Krochmal 2002). However, facultative scavengers are a more diverse group than just carnivores, as scavenging activity appears to be pervasive across the animal kingdom (DeVault et al. 2003) (Figure 6.1). In fact, a surprising array of animals will forage on carrion, including the hippopotamus (*Hippopotamus amphibius*; Dudley 1996), white-tailed deer (*Odocoileus virginianus*; Rooney and Waller 2003; Olson et al. 2012), pileated woodpecker (*Dryocopus pileatus*; Servín et al. 2001), and various lizards (Huijbérs et al. 2013).

Acquisition of carrion by scavengers has been described as a function of their ability to detect carcasses, and thus obligate scavengers are primarily limited by the efficiency with which they can locate meals (Ruxton and Houston 2004; Shivik 2006). Consequently, obligate vertebrate scavengers are all large, soaring birds in terrestrial ecosystems (Houston 1986; Shivik 2006). Because of this specialization, Ruxton and Houston (2004) proposed that obligate scavenging differs from other trophic relationships such as predation and herbivory. They conclude that the evolutionary costs of being a predator are in large part related to the energetic and physical demands associated with handling prey (Ruxton and Houston 2004). Herbivores, in contrast, expend much of their energy processing and overcoming the chemical defenses of the plants that they eat (Freeland and Janzen 1974).

In addition to efficient locomotion, obligate scavenging birds exhibit spectacular adaptations to a life-style dependent on carrion. Diminished feather coverage on the head presumably helps protect against fouling (Houston 1979). Vultures also exhibit highly acidic guts, which maintain the dual benefits of speeding digestion during foraging bouts and also presumably of protecting against virulent pathogens encountered at carrion (Houston and Cooper 1975). Excellent visual and olfactory perception and extreme efficiency of travel via soaring all increase scavenging efficiency, as these animals have adapted to scale-up their search area to overcome the fine-scale spatial and temporal unpredictability of most carrion (Wilmers et al. 2003b; Ruxton and Houston 2004). The temporal unpredictability of carrion has also seemed to select for larger body sizes that can sustain some periods of time without food (Ruxton and Houston 2004). Similarly, hagfish are highly mobile marine scavengers that are able to survive a year or more between meals and have evolved sensitive chemoreceptive abilities, which allow them to



FIGURE 6.1 (See color insert.) Although few vertebrates are considered obligate scavengers, most species appear to utilize carrion resources facultatively. Results of experimental scavenging trials showing coyote, *Canis latrans* (top left) and black vulture, *Coragyps atratus* (top right) scavenging of a feral pig—*Sus scrofa*—carcass, scavenging of a cane toad—*Rhinella marina*—carcass in Hawaii by an invasive small Asian mongoose—*Herpestes javanicus* (bottom left), and scavenging of a rat carcass by a gray fox—*Urocyon cinereoargenteus* (bottom right).

detect distant carrion resources in benthic ecosystems (Smith 1985). In combination, these traits are the hallmark of the group of organisms best adapted to scavenging as a way of life.

Outside of this specialized group, the highly diverse assemblage of facultative scavengers varies in how frequently each species engages in scavenging activity. These animals do not require carrion for survival or reproduction in general, and so differences in scavenging frequency are likely driven by a number of factors specific to particular phylogenies, populations, and individuals. For example, variance in the frequency of scavenging by facultative scavengers can be related to the relative ability of each species to tolerate microbes and the microbial by-products of decomposition associated with carrion (Janzen 1977; Shivik 2006). Moreover, facultative scavengers that utilize carrion frequently must also possess the ability to detect and acquire carrion resources (Ruxton and Houston 2003) either by superior perceptive ability or travel efficiency. Indeed, there has been a discussion in the literature surrounding the idea that efficient distance running in early humans may have evolved to allow our ancestors to capitalize on non-predator killed carcasses to supply their diets with protein (e.g., Bramble and Lieberman 2004; Ruxton and Wilkinson 2011). Alternatively, a facultative scavenging species may be able to consume a disproportionate amount of carrion resources simply by occurring in very high abundances relative to other species on the landscape (DeVault et al. 2011; Ruxton and Wilkinson 2012). All of these factors interact to form scavenger guilds at carcasses and across landscapes, but disentangling how each factor affects guild formation represents a challenge in scavenging ecology. What is clear is that there are substantial benefits to vertebrates for participating in scavenging behavior.

The benefits associated with feeding on carrion might be apparent for the obligate scavengers as they require carrion for survival and reproduction. However, the benefits of scavenging may also be substantial for the facultative scavengers. The food resources provided by carrion are a critical subsidy for many vertebrates, particularly in temperate climates during colder seasons when carcasses are less susceptible to decomposition (Gese et al. 1996; Fuglei et al. 2003; Selva et al. 2005; Blázquez et al. 2009;

Killengreen et al. 2012). In fact, grizzly bears (*Ursus arctos*) eliminate much of their annual energy debt by utilizing carrion after they emerge from hibernation (Green et al. 1997; Mattson 1997). Carrion use may also enhance the survival of certain individuals of a species at times of the year when other food resources are generally less abundant. Juveniles or low-dominance individuals may be outcompeted for preferred resources in the presence of larger, more experienced, or more dominant individuals, but may subsist in part by using carrion resources (Gese et al. 1996; Bennetts and McClelland 1997; Shivik and Clark 1999). However, the degree to which facultative scavengers actually require carrion resources is difficult to address in natural systems. This certainly represents a growth edge for discovery in scavenging ecology.

6.3 Interkingdom Competition among Vertebrates, Invertebrates, and Microbes

Because carcasses represent a rich source of nutrients to any organism that can utilize the resource, there is a race for organisms to find and consume carrion before other organisms can monopolize it (Janzen 1977). This race can lead to sometimes intense competition among microbes, invertebrates, and vertebrate scavengers for the resources sequestered in a carcass (DeVault et al. 2003). Competition among these groups is shaped by factors associated with the carcass itself, but also by factors associated with the environment surrounding the carcass (Payne 1965; DeVault et al. 2004b).

During the successive stages of decomposition, the competitive landscape at a carcass shifts as the process of degradation occurs (DeVault et al. 2003; Carter et al. 2007). The first organisms to compete at a carcass are the endogenous microbes that existed in and on the animal before it died (Putman 1978a; Carter et al. 2007). As the microbial community begins to break down the carcass, they compete with one another for space and nutrients, but also begin producing odiferous byproducts of their metabolism (Janzen 1977; Brown et al. 2009). The production of these volatile compounds signals the availability of a carcass to species of invertebrates, which are able to detect even minute quantities of volatiles from a volume of air (Paczkowski et al. 2012). Upon the arrival of the first invertebrate scavengers, competition for the resources in a carcass shifts from interactions among microbes to include interactions between microbes and invertebrates (Scott 1998; Burkepile et al. 2006; Rozen et al. 2008) and interactions among invertebrates (Denno and Cothran 1976; Hanski and Kuusela 1980). Degradation of a carcass during invertebrate feeding, primarily due to the action of their larvae, dramatically increases the rate of carcass attenuation (Payne 1965; Putman 1978b; Carter et al. 2007). However, during the early phases of carcass decay, the volatile compounds produced during microbial metabolism may also alert vertebrate scavengers to the potential for a meal (Smith and Paselk 1986; DeVault et al. 2003).

Competition among vertebrates for carcasses is often spectacular and has received much attention, particularly among scavenging birds (Kruuk 1967; Wallace and Temple 1987) and African mammals (Kruuk 1972; Houston 1979). However, competition for carcasses also occurs among microbes, invertebrates, and vertebrates at this stage in carcass decomposition, and interkingdom competition for carrion has had profound effects on the evolution and ecology of scavengers. For example, microbes involved in this competition use chemicals to ward off crustaceans in marine ecosystems (Burkepile et al. 2006), and some species of burying beetle (e.g., *Nicrophorus vespilloides* [Coleoptera: Silphidae]) produce an antimicrobial compound to protect carrion used in reproduction from decomposition by microbes (Rozen et al. 2008). Vertebrate scavenging may ultimately supersede some of these other mechanisms of retaining or monopolizing a carcass, because carcasses consumed by vertebrates may act as ecological sinks for some invertebrate species when the entire local population is consumed. Janzen (1977) was the first to discuss the idea of interkingdom competition for carcasses in detail, and much interesting work has added to our knowledge base since then.

Factors outside the carcass itself also affect competition for carrion resources. For example, vertebrate scavengers appear to be disadvantaged when humidity and temperature favor microbial and invertebrate reproduction (between 21°C and 38°C, Vass 2001; Zhou and Byard 2011). In a study by DeVault et al. (2004b), it was found that at temperatures above 20°C vertebrates were able to detect and consume only

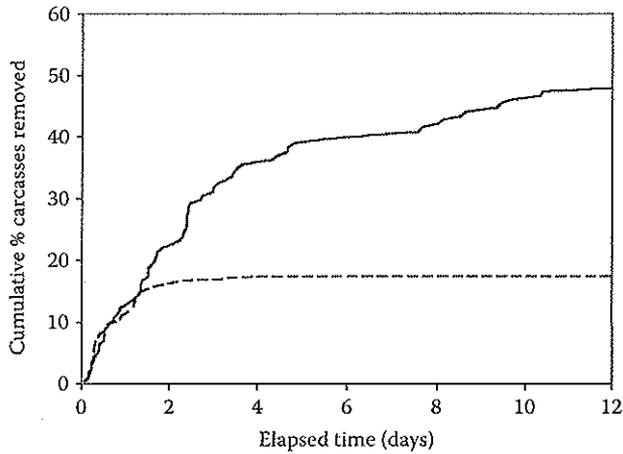


FIGURE 6.2 The competition for carrion between vertebrate scavengers and decomposers is heavily influenced by ambient air temperature. Here, the cumulative percentage of carcasses removed by vertebrates as a function of time during cool (5.8–17.0°C; solid line) and warm weather (22.6–27.8°C; dashed line) is shown for experimental rodent carcasses from South Carolina, USA. (Modified from DeVault, T.L., I.L. Brisbin Jr, and O.E. Rhodes Jr. 2004b. *Canadian Journal of Zoology* 82:502–509.)

19% of small-mammal carcasses, whereas at temperatures below 18°C, vertebrates consumed 49% of carcasses (Figure 6.2). Interestingly, early work by Houston (1986) indicated that the presence of a highly efficient vertebrate scavenger could alter the outcome of interkingdom competition for carrion nutrients. Namely, 71 of 74 carcasses were consumed by vultures at that equatorial study site, despite relatively high temperature and humidity (Houston 1986). Along similar lines, DeVault et al. (2011) found that temperature effects could be mediated by scavenging community composition in a fragmented, agricultural landscape. Specifically, facultative scavenging mammalian mesopredators (i.e., midtrophic level predators) dominated carcass acquisition over invertebrate and microbial competitors, likely due to the elevated abundances of mesopredators in their study landscape (DeVault et al. 2011). Similarly, highly abundant scavengers from one habitat may recruit into adjacent habitats when carcasses are available (Killengreen et al. 2012). Despite the focus on the outcome of interkingdom competition in the context of temperature and community structure, there is evidence to suggest that in some ecosystems the timing of carcass disappearance is similar, regardless of whether carcass assimilation is dominated by vertebrate or invertebrate communities (Sugiura et al. 2013).

Information regarding the influence of habitats on the competition for carrion is more equivocal and is often conflated with climate differences (i.e., temperature and relative humidity). For example, the available literature suggests that carcass decomposition occurs more rapidly in warm, moist habitats when compared with more xeric habitats (see Carter et al. 2007; Parmenter and MacMahon 2009). Competition for carrion can also be affected by fine-scale or microsite differences in habitat. DeVault et al. (2004b) found that carcass acquisition by vertebrate scavengers was higher in lowland hardwood habitats compared with upland conifer habitats within the same study site. Parmenter and MacMahon (2009) extensively investigated microsite effects on decomposition rates of carcasses and found that carcasses located underground in burrows decomposed faster in their semiarid study site during spring and summer months. However, more frequently, carcass burial is negatively correlated with decomposition rates in the forensic literature (Carter et al. 2007). The location of a carcass in relation to habitat attributes on the landscape may allow particular species to colonize more easily. For example, forest openings and other open habitats may facilitate carcass location by vertebrate scavengers that rely largely on vision to find carrion (Houston 1988; Selva et al. 2003). The habitat occupied by a carcass has also been shown to affect the time of appearance for carrion-associated insects on pig carcasses in Europe, although these differences did not translate to an overall shift in the successional pattern of colonization by insects (Matuszewski et al. 2011).

In addition to the effects of habitat type on the competition for carrion, habitat fragmentation appears to affect the balance in interkingdom competition for carcasses. Gibbs and Stanton (2001) demonstrated that the abundance of carrion beetles decreased, taxon richness decreased, and community structure shifted in areas of fragmented versus more contiguous forests in New York, USA. However, they were unable to link these changes in an important group of carrion specialists to carrion abundance or other factors (Gibbs and Stanton 2001). The work of DeVault et al. (2011) may provide such a link. DeVault et al. (2011) discovered that in an agriculturally fragmented habitat, most (88%) small-mammal carcasses were consumed by vertebrates, which was a substantial increase in carrion acquisition by vertebrates over earlier work conducted in more contiguous habitats (i.e., DeVault et al. 2004b). They argued that an increase in mesopredator abundance, primarily raccoons (*Procyon lotor*) and Virginia opossums (*Didelphis virginiana*), accounted for this disparity (DeVault et al. 2011). Moreover, they proposed that the occurrence of a highly efficient suite of vertebrate competitors for the same carcasses used by carrion beetles might explain the declines of carrion beetles that Gibbs and Stanton (2001) reported in similarly fragmented habitats. An interesting area of future research associated with habitat fragmentation might include an assessment of competition for carcasses along the front of northward-expanding vulture populations in North America, an expansion that may be due, at least in part, to greater carcass availability from vehicular-related road-kills (Houston et al. 2011).

6.4 Ecosystem Effects of Carrion Use by Vertebrates

Carrion use by vertebrates has interesting implications for ecosystems. From a physical perspective, the molecules that make up an animal's body become progressively less aggregated after that animal dies (see Chapter 2 for details). The speed and the extent to which these molecules are dispersed are explicitly related to the scavengers that feed on the carcass. Microbial decomposition creates well-defined and well-documented cadaver decomposition islands (CDIs; Johnson 1975) as nutrients released through microbial action are incorporated into the detrital pathway immediately below and near where the carcass decomposes (Moore et al. 2004; Melis et al. 2007). Subsequently, those nutrients are mobilized by the adjacent flora creating localized effects (Towne 2000; Danell et al. 2002; Bump et al. 2009). For large carcasses, elevated nutrient levels coincident with a CDI have been detected in soil and foliar samples for years after the carcass decomposed (Danell et al. 2002; Melis et al. 2007).

The addition of invertebrate scavenging to the effects of microbial action increases the final nutrient dispersion from a carcass farther into the surrounding environment as the arthropods pupate and disperse (Carter et al. 2007). However, in general, vertebrate scavenging represents the widest dispersal of nutrients and energy from carcasses as vertebrate movement scales away to the broader landscape (Payne and Moore 2006; Barton et al. 2013). In this process, vertebrate scavengers diminish the formation of CDIs by scattering and incorporating portions of the carcass into the surrounding ecosystem (Kjorlien et al. 2009; Reeves 2009). Thus, the spatial heterogeneity of resources that carcasses contribute to the landscape depends in part on the identity of the scavengers that feed on them. Carcasses, then, in some instances, can contribute nutrients and energy to initiate resource hot-spots that add to landscape complexity (Payne and Moore 2006; Bump et al. 2009; Parmenter and MacMahon 2009), but in other instances, carrion is effectively recycled among higher trophic levels by scavengers with limited direct inputs to the detrital pathway. We are just beginning to understand the ecological effects that carcasses have on the landscape (Bump et al. 2009), and further work is needed to determine how vertebrate scavengers influence those effects.

In addition to impacting landscape heterogeneity by the disruption of decomposition patterns, scavengers can also shape the structure of vertebrate communities through interactions with predators. In systems in which the predator is smaller than its prey, some portion of each fresh kill often cannot be immediately consumed by the predator. For example, the gleanings from partially consumed, or usurped, predator kills on the African savannah sustain an entire guild of vertebrate scavengers (Hunter et al. 2007), although predator kills are probably not the primary source of carrion in this ecosystem (Houston 1979). Scavenging activity such as this is often grouped with kleptoparasitism in the literature, and it places a limit on the amount of resources the original predator can gain from each kill with

potentially cascading effects (Vucetich et al. 2004). In Isle Royale National Park, USA, raven scavenging of wolf (*Canis lupus*)-killed moose (*Alces alces*) carcasses is apparently extensive enough to make increased pack sizes beneficial, despite the smaller share of each moose that an individual wolf receives when hunting in these larger packs (Vucetich et al. 2004). Eurasian Lynx (*Lynx lynx*) in areas of Europe have been shown to increase their kill rates when the carcasses they cache are scavenged by grizzly bears (*U. arctos*; Krofel et al. 2012). Further, their review of the literature revealed lower but still significant scavenging of felid-killed carcasses from Europe, North America, and Africa (Krofel et al. 2012), indicating that the phenomenon is not restricted to any particular ecosystem. Presumably, scavenging by grizzly bears also increases ungulate kill rates of wolves in Yellowstone National Park, USA (Hebblewhite and Smith 2010). Increased kill rates by top predators may represent a little acknowledged marginal cost to the vertebrate community, directly attributable to scavenging activity. Given the importance of top-down effects in many ecosystems, even a minor alteration to predation rates as driven by vertebrate scavengers may cause a significant flux in community composition.

Another possible effect of vertebrate scavengers on vertebrate communities is related to the fact that many facultative scavengers are also predators (DeVault et al. 2003). Cortés-Avizanda et al. (2009) found that the abundance of prey species (i.e., hares—*Lepus* spp. and squirrels—*Sciurus* spp. in this case) decreased in sectors containing a carcass based on evidence from tracks in snow. An interesting hypothesis emerged, in which the scavengers that are recruited to a carcass may have temporarily played the dual role of increasing predator abundance near each carcass (Cortés-Avizanda et al. 2009). It is unclear from this study whether tracks of the prey species might have declined because incidental predation by facultative scavengers reduced the abundance of prey species near carcasses or because of nonconsumptive effects such as altered behavior by prey species in the vicinity of carcasses due to the presence of predatory scavengers (Cortés-Avizanda et al. 2009). However, the second possibility adds an interesting dimension to the “landscape of fear” hypothesis, in which movements and foraging decisions by prey species are influenced by a perceived risk of predation (Lima and Dill 1990; Blumstein 2006).

Some of the most visible and well-studied effects of vertebrate scavengers on communities can be seen in the interactions of scavengers at carrion. Dominance hierarchies and structural differences within and among species of vultures in the Old World (Kruuk 1967; Houston 1975; Alvarez et al. 1976) and the New World (Wallace and Temple 1987) have established competitive frameworks that delineate resource acquisition at carcasses. Superficially, larger species tend to dominate smaller species for access to carcasses (Petrides 1959; Alvarez et al. 1976), but larger species also facilitate access to carcasses for a variety of less-specialized and smaller species by breaking through the thick hides of larger carrion (Kruuk 1967; Selva et al. 2005; Blázquez et al. 2009).

6.5 Ecosystem Services Provided by Vertebrate Scavengers

Vertebrate scavengers provide various ecosystem services, including cultural (e.g., spiritual value), supporting (nutrient cycling), and regulating services (carcass removal from the landscape) (Millennium Ecosystem Assessment 2003; Wenny et al. 2011; DeVault et al. 2016). In this section, four of the most prominent are highlighted: critical linkages in food webs, nutrient distribution within and among ecosystems, economic benefits related to sanitary measures, and altered disease dynamics. This section documents how vertebrate scavengers, both obligate (e.g., vultures) and facultative (e.g., crows—*Corvus* spp., raccoons), play underappreciated but pivotal roles in maintaining healthy ecosystem function.

6.5.1 Vertebrate Scavengers Provide Critical Linkages in Food Webs

Historically, the prevalence of scavenging activities has been greatly underestimated. However, upon recognition that (1) in most ecosystems, a large number of animals die from causes other than predation and thus become available to scavengers; (2) most carcasses are scavenged by vertebrates before they are completely decomposed by arthropods and bacteria; and (3) almost all carnivorous animals are facultative scavengers, the importance of scavenging in food webs seems unsurprising (DeVault et al. 2003). In fact, Wilson and Wolkovich (2011) estimated that scavenging links are underrepresented in

food-web research by 16-fold. The omission of these connections in ecological models is striking, especially considering the role that the number (Dunne et al. 2002) and strength of trophic connections (weak links, McCann et al. 1998; McCann 2000) are known to play in promoting the persistence and stability of ecological communities and the ecosystem services they deliver. The omission of scavenging activities from food-web models has largely been the result of oversimplification; that is, the treatment of all types of detritus (from low-quality dead plant material to high-quality animal carrion) as a single resource pool (Swift et al. 1979; Wilson and Wolkovich 2011). However, food webs are increasingly recognized as complex and highly interconnected (e.g., Polis 1991; Polis and Strong 1996), and the importance of detritus, especially animal carrion as a distinct resource, is becoming widely accepted (DeVault et al. 2003; Moore et al. 2004; Wilson and Wolkovich 2011; Barton et al. 2013).

Scavenging activities may be especially important for the resiliency of food webs. The stabilizing nature primarily results from the high number of interspecies links from scavenging (scavengers often feed on carrion from many species, making webs more interconnected; Wilson and Wolkovich 2011). Also, the use of carrion as a supplemental food resource during prey shortages for species that are primarily predators might add to the stabilizing nature of scavenging (McCann et al. 1998; DeVault et al. 2003). As ecosystems are increasingly subject to multiple stressors from human activities, it is important to gain a better understanding of the intrinsic properties of food webs that promote stability, and carrion use by vertebrates appears to be one such factor.

6.5.2 Distribution of Nutrients within and among Ecosystems

In addition to acute visual and/or olfactory abilities for detecting carcasses, one of the key attributes of the most successful scavengers is the ability to quickly and efficiently travel great distances in search of carrion, which in many cases is unpredictable and ephemeral (Houston 1979; Ruxton and Houston 2004; Shivik 2006). As a result, obligate scavengers such as vultures generally have very large home ranges (e.g., Houston 1974; DeVault et al. 2004a). These scavengers, as well as some facultative scavengers such as certain bottom-dwelling marine species (Smith 1985; Beasley et al. 2012b), often disperse assimilated carrion across large areas. This dispersion of carrion biomass by vertebrates is especially evident when carrion is initially concentrated spatially. For example, carcasses produced from fishing by-catch (Furness 2003), salmon (*Salmonidae*) die-offs (Hewson 1995), forest fires (Blanchard and Knight 1990), and single large carcasses (e.g., whales—*Cetacea*; Smith and Baco 2003) are often visited by multiple scavengers that range widely and therefore transport the nutrients from those carcasses over large distances. In particular, salmon represent a significant annual pulse of marine-derived nutrients that can be disseminated from aquatic to terrestrial ecosystems through vertebrate scavenging. Movement of salmon carcasses to terrestrial habitats, usually by bears (*Ursus* spp.) or other large mammals, also links terrestrial invertebrate communities to marine-derived nutrients by providing substantial carrion subsidies to ovipositing flies and terrestrial invertebrate scavengers unable to access carrion in aquatic habitats (Meehan et al. 2005). Cross-habitat nutrient transport can produce a variety of important outcomes in recipient systems (e.g., Polis et al. 2004), and scavengers can play a significant role in moving “ecological subsidies” between habitats. For example, the use of ocean-derived carrion by terrestrial mammals (Rose and Polis 1998) and birds (Schlacher et al. 2013) is extensive and may strongly influence dynamics of coastal food webs.

6.5.3 Economic Benefits Related to Sanitary Measures

Traditionally, in Europe, carcasses of free-ranging livestock have been left at the site of death to be consumed by avian scavengers (Donázar et al. 1997; Margalida et al. 2010). The arrangement, which persisted for centuries, was mutually beneficial, as this ecosystem service saved farmers in the European Union €0.97–1.60 million annually (Margalida and Colomer 2012) and provided vultures with a vital food resource (Donázar et al. 1997; Margalida et al. 2011). However, more restrictive sanitary policies enacted in Europe after the emergence of bovine spongiform encephalopathy (“mad cow disease”) in cattle between 1996 and 2000 required that carcasses be disposed of in authorized facilities (Margalida et al. 2010). Because of the resultant food shortages for avian scavengers, several species in the region

experienced decreased breeding success and other demographic problems (Margalida et al. 2010). Recently, however, new guidelines have been enacted that again allow farmers to abandon dead livestock in the field (Margalida et al. 2012). Even so, it is unclear how these new regulations will be applied by various governments and subsequently how vulture populations will respond to any new management scenarios that may emerge (DeVault et al. 2016).

6.6 The Role of Scavengers in Disease Ecology

Large carcasses can serve as incubators for many types of infectious materials. Because many mammalian and avian species often visit single large carcasses (Selva et al. 2003; Jennelle et al. 2009), and scavengers often have large home ranges (discussed earlier), some have suggested that vultures and other wide-ranging vertebrate scavengers might facilitate the spread of pathogens across large areas. For example, vultures might harbor infectious materials on their feet and feathers and introduce them across the landscape as they forage at widely spaced carcasses (Houston and Cooper 1975). Further, VerCauteren et al. (2012) showed that infectious scrapie prions survived passage through the digestive system of American crows (*Corvus brachyrhynchos*) and suggested that crows might spread prion diseases. Also, it has been suggested that scavengers might exacerbate production of anthrax spores by opening carcasses and thus suppressing the ability of anaerobic bacteria residing inside carcasses to antagonize vegetative anthrax cells and thus impede sporulation (Bellan et al. 2013 and references therein).

However, vultures are generally very resistant to diseases, a trait common among many successful scavengers (Shivik 2006). Houston and Cooper (1975) concluded that the digestive tract of griffon vultures is likely to kill most pathogenic bacteria, given that the pH of the stomach ranges from 1 to 2. Thus, as vultures forage, they probably reduce the proliferation of diseases, at least at the local scale, by removing infected carcasses from the landscape (see also Ogada et al. 2012). Also, in experimental work using electrified cage enclosures, Bellan et al. (2013) determined that vertebrate scavenging was not critical for the production of anthrax spores at carcass sites.

It is thus unclear the extent to which scavengers remove infectious materials from the landscape or, alternatively, spread pathogens across large areas. Even so, it seems likely that the identity of the vertebrate species scavenging at carcasses determines, at least in part, whether or not diseases are proliferated or impeded. For example, the near-extirpation of several vulture species in south Asia due to the use of toxic livestock chemicals (Green et al. 2004; Oaks et al. 2004) allowed cattle carcasses to remain in the landscape for longer time periods and thus were made available for consumption by feral dogs and rats, which apparently resulted in population increases in those species (Pain et al. 2003; Prakash et al. 2003). Markandya et al. (2008) estimated that the total costs to human health (including rabies cases from dog bites) that resulted from severe vulture declines totaled over \$34 billion from 1993 to 2006. Also, Ogada et al. (2012) determined that the exclusion of vultures from large animal carcasses in Kenya resulted in a tripling of carcass decomposition times. In addition, the number of mammals scavenging carcasses, the average time spent at carcasses by mammals, and the number of contacts between mammals increased substantially in the absence of vultures. Such increases in inter- and intraspecific interactions due to increased persistence times of carcasses could increase the probability of disease spread within and among species (especially mammals), particularly for some important zoonotic diseases including rabies. Clearly, the role of vertebrate scavengers in disease proliferation is complex, and more research is needed to elucidate factors that influence disease dynamics with regard to scavenging ecology (Jennelle et al. 2009).

6.7 Challenges to Vertebrate Scavengers in Modern Society

There is a growing body of evidence that facultative scavenging is widespread among vertebrates, and resources provided through scavenging are likely critical to many species (DeVault et al. 2003; Fuglei et al. 2003). Consequently, any shift in the availability or distribution of carrion could have a profound impact on the composition of scavenging communities and distribution of carrion resources throughout

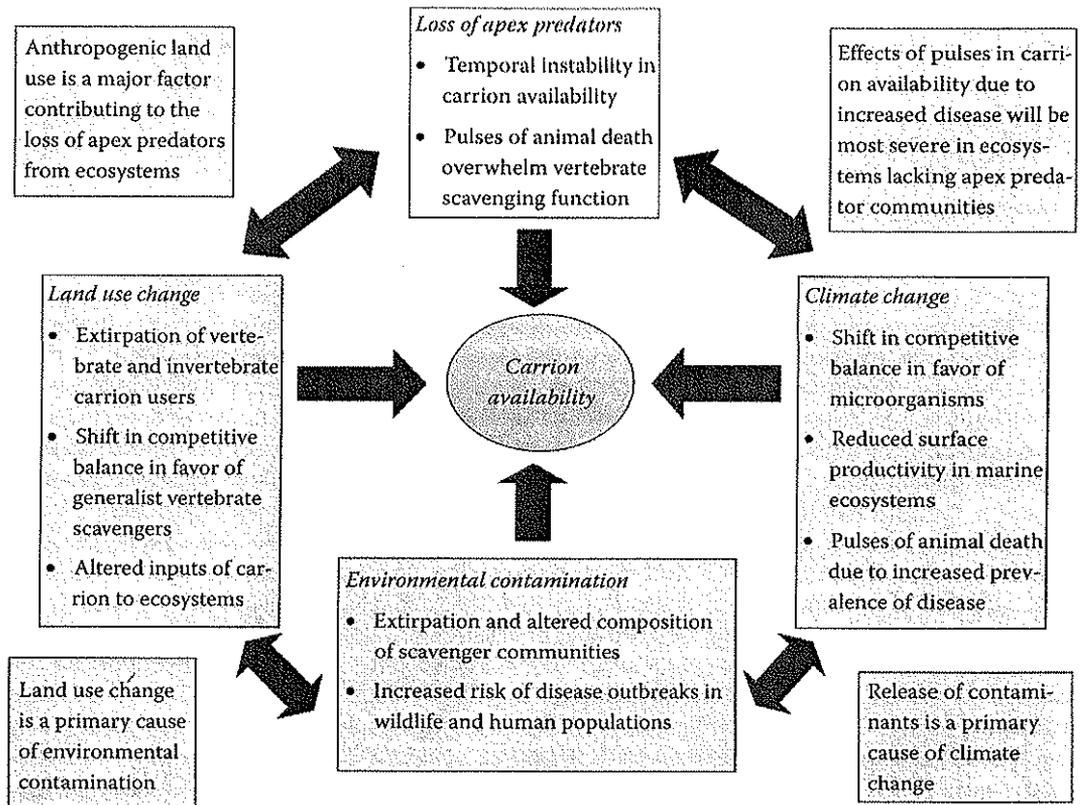


FIGURE 6.3 Generalized diagram illustrating the effects of anthropogenic disturbances on the fate of carrion and the organisms that use these resources. In many instances, ecosystems may face a multitude of human disturbances simultaneously that may interact to exacerbate impacts to scavenger communities. For example, the effects of temporal shifts in carrion availability due to climate change likely will be most severe in ecosystems lacking apex predators as these species play a critical role in the temporal stabilization of carrion resources to facultative scavengers.

food webs. Although numerous factors are involved in modulating carrion availability, climate (DeVault et al. 2004b; Selva et al. 2005; Parmenter and MacMahon 2009), trophic integrity (Wilmers et al. 2003a, b; Wilmers and Post 2006), disease (Wilson and Wolkovich 2011), and habitat availability (DeVault et al. 2011) play integral roles in regulating the fate of carrion, as well as the spatial and temporal distributions of these resources in ecosystems (Figure 6.3). Thus, in light of the numerous anthropogenic threats currently impacting ecosystems across the globe (e.g., climate change, pollution, trophic downgrading, habitat loss and fragmentation, and invasive species), there is a growing need to quantify the potential impacts of such changes to the structure and function of ecosystems.

Scavenging communities, in particular, are highly sensitive to a variety of anthropogenic disturbances to ecosystems due to their reliance on the availability and distribution of carrion resources. Although scavengers face a multitude of challenges due to human activities, below we highlight several that are globally relevant and for which sufficient literature exists to suggest that these activities are having measurable impacts to scavenging dynamics, although this list certainly is not inclusive.

6.7.1 Potential Climate Change Effects on Vertebrates

Competition among vertebrates, invertebrates, and microbes can be influenced by a variety of factors, but is often modulated by abiotic conditions. In particular, acquisition of carrion by vertebrates is highly influenced by temperature, with reduced scavenging efficiency as temperature increases due to increased microbial and invertebrate activity (DeVault et al. 2004b, 2011). As a result, altered temperature and

precipitation patterns due to climate change likely will alter competitive interactions among vertebrates, invertebrates, and microbes, disrupting the flow of energy within and among ecosystems. Slight changes in temperature could have profound impacts on energy flow within ecosystems as carrion decomposition rates roughly double for every 10°C increase in ambient temperature (Vass et al. 1992; Parmenter and MacMahon 2009). Consequently, the availability of carrion to vertebrate scavengers could be reduced by as much as 20%–40% over the next century based on projections from current climate change models (Beasley et al. 2012b). Reduced access to carrion by vertebrates is not trivial as facultative scavengers serve important roles in stabilizing food webs by maintaining energy resources high within food webs of many ecosystems (Rooney et al. 2006). Moreover, in some ecosystems, vertebrates consume as much as 90% of the available carrion biomass and thus a reduction in carrion availability could have a profound effect on the distribution and abundance of vertebrate scavengers, as well as a multitude of other organisms (Houston 1986; DeVault et al. 2011).

In addition to reductions in carrion availability due to increased microbial and invertebrate activity, altered temperature and precipitation patterns resulting from climate change are likely to shift the spatial and temporal distribution of carrion resources through increased incidence and geographic range of many diseases (Patz et al. 1996; Harvell et al. 2002; Wilson and Wolkovich 2011). In particular, vector-borne pathogens are likely to increase in both abundance and geographic range in response to rising temperatures. Although data are not available for many pathogens, such shifts in their distribution have recently been observed for several vector-borne human and livestock diseases including malaria, Lyme disease, tick-borne encephalitis, plague, blue tongue viruses, and African horse sickness (Harvell et al. 2002).

Rather than produce a steady increase in carrion availability, such increases in disease, particularly epidemics, will likely produce pulses of animal death, disrupting the spatial and temporal availability of carrion within ecosystems. As a result, the temporal aggregation of carrion resources may reduce the diversity and evenness of carrion consumption among scavengers (Wilmers et al. 2003b; Cortés-Avizanda et al. 2012). Although the long-term impacts of truncated carrion availability to obligate scavengers are unknown, given that most obligate vertebrate scavengers currently are threatened with extinction (Ogada et al. 2012), any reductions in carrion availability or distribution could contribute to further population declines of these species. Similarly, facultative scavengers that rely on carrion resources for overwinter survival could be negatively impacted by a shift in carrion availability due to increased incidence and aggregation of disease (Fuglei et al. 2003).

Changes in global climate are also expected to substantially alter the availability of carrion resources in marine ecosystems as surface production of organic material could decline by 50% or more (Smith et al. 2008). Such a drastic reduction in productivity undoubtedly will impact a multitude of ecosystem processes, including the availability and distribution of carrion within marine ecosystems. However, the effects of reduced carrion subsidies may be most acute in benthic ecosystems as benthic scavengers are inextricably linked to carrion subsidies provisioned from the euphotic zone, and such reductions in carrion resources may potentially reduce the biodiversity of scavengers in deep-sea environments. Indeed, populations of facultative benthic scavengers already have declined in some regions in response to a decline in food resources from the surface and concurrent increases in water temperature due to increases in global temperatures (Bergmann et al. 2011). In addition to altered marine scavenging communities, changes in ocean surface productivity may also impact terrestrial scavenging communities in coastal areas as many species rely on carrion subsidies washed on shore from marine environments (Schlacher et al. 2013).

6.7.2 Effects of Habitat Loss, Fragmentation, and Urbanization

Habitat loss and fragmentation due to agriculture, urbanization, and other anthropogenic land uses are growing and pervasive issues that can have substantive impacts on the distribution, ecology, and population dynamics of numerous wildlife species across the globe (Foley et al. 2005; Beasley et al. 2011). Although the direct effects of anthropogenic land use on scavenging dynamics are not well defined, the composition and efficiency of vertebrate scavengers appear to be highly altered in landscapes modified by humans. For example, in a highly fragmented agricultural ecosystem in northern Indiana, USA,

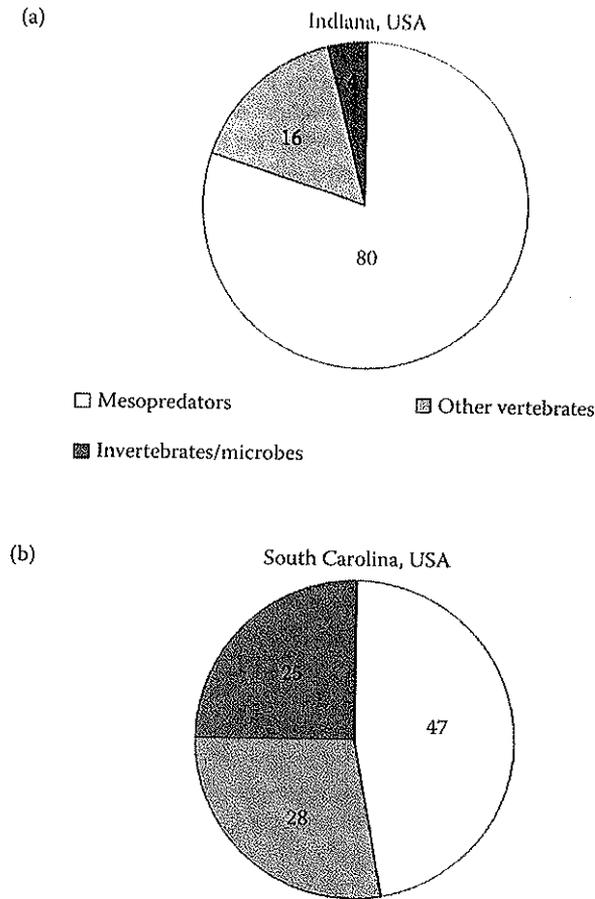


FIGURE 6.4 Results of small-mammal scavenging trials conducted in (a) highly fragmented landscape in northern Indiana, USA and (b) contiguously forested site in South Carolina, USA showing the dominance of carrion acquisition by mesopredators and reduced species diversity of scavengers in ecosystems substantially impacted by anthropogenic activities. (Data from DeVault, T.L., I.L. Brisbin Jr, and O.E. Rhodes Jr. 2004b. *Canadian Journal of Zoology* 82:502–509 and DeVault, T.L. et al. 2011. *Basic and Applied Ecology* 12:268–274.)

DeVault et al. (2011) observed substantially lower species richness of vertebrate scavengers compared to similar studies in more contiguous landscapes (Figure 6.4). Given that human-modified landscapes generally support truncated vertebrate communities comprised of generalist species (Swihart et al. 2003), it is not surprising that fragmented landscapes support impoverished scavenging communities dominated by invasive or generalist species. However, despite the reduced diversity of scavengers, the efficiency of scavenging by these species actually was greatly elevated in the highly fragmented landscape, with nearly 90% of mouse carcasses scavenged compared with 30% in a more contiguously forested site (DeVault et al. 2011). This high frequency of scavenging represents some of the highest efficiencies reported for vertebrate scavengers (Houston 1986; DeVault et al. 2003).

Interestingly, facultative mesopredators comprised 93% of the scavenging events observed by DeVault et al. (2011), and turkey vultures, the only obligate vertebrate scavenger in their study area, failed to acquire a single carcass out of 266 trials. Turkey vultures were observed regularly within the study area and were recorded scavenging on 20%–43% of rabbit and raccoon carcasses, respectively, within the same study sites (Olson et al., unpublished data). Thus, it appears that for small carcasses that can easily be consumed by a single individual, dense populations of mesopredators are able to competitively exclude most other species, including obligate avian scavengers, from these resources. Similarly, Huijbers et al. (2013) also observed highly disparate patterns of carrion removal by vertebrates between

urbanized and rural beaches on the east coast of Australia. In particular, although a similar number of species were detected at both study sites, scavenging communities within rural beaches were dominated by native raptors, whereas urban beach scavengers primarily comprised generalist invasive or feral mammals (Huijbers et al. 2013). Such striking differences in the structure of the scavenging guild in disturbed ecosystems suggest that changes in land use can alter fundamental aspects of scavenging dynamics.

In addition to the direct effects of altered habitat composition and fragmentation on carrion availability, such landscapes often support high densities of generalist species, many of which are efficient scavengers that may monopolize carrion resources in these ecosystems (DeVault et al. 2011). An elevated rate of carrion consumption by mesopredators implies that fewer carrion resources likely are available to invertebrate scavengers and microbes in highly modified landscapes. Although the competitive interaction between mesopredators and invertebrate or microbial scavengers has not been rigorously studied in fragmented ecosystems, the effects of the rapid and nearly complete attenuation of rodent carcasses by mesopredators observed by DeVault et al. (2011) suggest that they are likely not trivial.

6.7.3 Effects of Trophic Downgrading (Loss of Apex Predators)

The loss of apex predators from ecosystems, referred to as trophic downgrading, can have cascading impacts on the composition and function of ecosystems. Over the last few centuries, trophic cascades due to the loss of apex consumers have become pervasive, having now been documented in all of the world's major biomes and in freshwater, marine, and terrestrial ecosystems (Estes et al. 2005). In terms of scavenging, apex predators serve a critical role in modulating the availability of carrion to other vertebrate, invertebrate, and microbial consumers of this resource by reducing or eliminating pulses of death due to starvation and disease epidemics and thus stabilizing the availability of carrion throughout the year (Wilmers et al. 2003a). This stabilization of reliable high-energy food resources may promote biodiversity and undoubtedly facilitates increased survival and reproductive output in some scavenger species (Fuglei et al. 2003; Barton et al. 2013). Predator-killed carrion resources also appear to be used by a more diverse community of vertebrate scavengers than natural or human-provided carrion subsidies (Wilmers et al. 2003a; Selva et al. 2005), although such preferences do not appear to hold for small carrion items (e.g., mice, rats, and rabbits) or in landscapes where apex predators have been extirpated (DeVault et al. 2004b, 2011).

The presence of apex predators within an ecosystem also may indirectly influence carrion availability by regulating the abundance and behavior of mesopredators. In the absence of apex predators, mesopredator populations can reach exorbitant densities (Prugh et al. 2009; Beasley et al. 2011), altering a multitude of ecological processes, including energy flow, by monopolizing carrion resources and greatly reducing the availability of these resources to other scavengers in these ecosystems, including obligate carrion consumers (Olson et al. 2012). Mesopredator release and trophic cascades due to the removal of apex predators are not unique to terrestrial environments, and there are numerous examples from both freshwater and marine ecosystems. For example, overharvesting of apex predatory sharks has led to a significant increase in elasmobranch mesopredators in many regions, particularly the cownose ray (*Rhinoptera bonasus*). In the Chesapeake Bay region alone, there may now be an estimated 40 million cownose rays, more than an order of magnitude increase since the mid-1970s (Myers et al. 2007). Although the effects of increased ray populations to marine scavengers are unknown, increased ray populations have led to the collapse of bay scallop (*Argopecten irradians*) populations and other bivalves within this region, and thus their effects to scavengers are likely profound.

The reintroduction of gray wolves to Yellowstone National Park, USA has served as a unique natural experiment to characterize the role apex predators play in modulating carrion resources to other scavengers in terrestrial ecosystems. Prior to the reintroduction of wolves, the majority of ungulate mortality, and thus carrion availability, occurred in a winter pulse coinciding with peak snow depth, ranging from 0 to >500 kg of carrion per week (Gese et al. 1996). Had wolves been present, Wilmers et al. (2003a) estimated that carrion subsidies would have been relatively stable throughout this period, providing a multitude of scavengers access to high-energy food resources on a consistent basis throughout the winter. Indeed, during November–May, established wolf packs in the northern range of Yellowstone

provide an estimated ~13,000 kg of elk carrion to other scavengers in this ecosystem, accounting for wolf consumption of carcasses (Wilmers et al. 2003b). The temporal distribution of this carrion is consistent throughout the winter and utilized by a much more diverse community of vertebrate scavengers than human hunter-provided carrion that is much more truncated in distribution, both spatially and temporally (Wilmers et al. 2003b).

Although climate change, habitat loss, and trophic downgrading all may play a role in altering the distribution and flow of carrion resources through food webs, each of these effects is integrally linked and when combined may exacerbate or moderate impacts to scavenging dynamics. For example, reduced inter- and intra-annual variability in carrion availability and provisioning of carrion subsidies throughout the winter in terrestrial ecosystems in which apex predators are present likely serve as an important buffer to climate change and other anthropogenic effects for scavengers (Wilmers et al. 2003a; Wilmers and Post 2006). In contrast, habitat loss and fragmentation are usually followed by the extirpation of apex predators and mesopredator release (Estes et al. 2011), which can alter the efficiency and composition of scavenging communities (Olson et al. 2012).

6.7.4 Pollution, Heavy Metals, Veterinary Pharmaceuticals, and Other Anthropogenic Toxicants

Although the aforementioned factors undoubtedly have had a significant impact on vertebrate scavengers, poisoning, whether deliberate or accidental, has probably played the most substantial role in the allocation of protection for this important group of species. Vertebrate scavengers are particularly vulnerable to toxic substances as many species rely on carrion as a significant source of food, numerous individuals and/or species often can feed on a single carcass, and scavenging facilitates feeding above an organism's trophic rank, allowing for increased exposure to toxins that may have bioaccumulated within the tissues of an individual prior to death. For centuries, humans have recognized and exploited these characteristics and the susceptibility of scavengers to toxic substances. For example, the widespread use of carrion laced with strychnine, 1080, and other toxins to control predator populations throughout the last century resulted in the near extirpation of many carnivores where such practices were widely employed (Langley and Yalden 1977; Whitfield et al. 2004). However, such eradication campaigns were often not species-specific, and in addition to mammalian carnivores, numerous other scavengers were killed as collateral damage of these eradication efforts, particularly during the use of 1080, including vultures, eagles, and California condors (*Gymnogyps californianus*). Indeed, in many places, targeted predators often are affected less by poison baiting than nontarget species (Eason and Spurr 1995; Berny 2007; Berny and Gaillet 2008; Márquez et al. 2013).

Although use of toxins to control carnivore populations has been banned or highly regulated throughout much of the world today, such practices continue to be used illegally in some regions to protect livestock and manage game species (Hernández and Margalida 2008, 2009a; Ogada et al. 2012; Márquez et al. 2013) and likely remain the most widespread cause of vulture poisoning worldwide (Donazar 1993; Margalida 2012; Ogada et al. 2012). Today, managers continue to exploit the scavenging tendencies of many vertebrates as a means of controlling invasive species and managing the spread of infectious disease (Slate et al. 2005; Page et al. 2011; Beasley et al. 2012a).

In addition to deliberate poisoning, scavengers can inadvertently be exposed to a multitude of other toxins through consumption of tissues containing pollutants, environmental contaminants, veterinary drugs, or other anthropogenic compounds. In a profound example that highlights the vulnerability of vertebrate scavengers to accidental exposure to toxins, over the last two decades, populations of *Gyps* vultures in Asia have precipitously declined to 3%–5% of their original population size due to accidental poisoning through consumption of livestock treated with diclofenac, a nonsteroidal anti-inflammatory drug (Green et al. 2004; Oaks et al. 2004; Shultz et al. 2004). Although use of diclofenac has been banned in many countries and numerous recovery efforts are underway, some species continue to decline at alarming rates, and full recovery of these species may take centuries (Cuthbert et al. 2011).

Accidental exposure to lead from pellets or bullet fragments also remains a threat to some vertebrate scavengers (Hunt et al. 2006; Kelly et al. 2011; Lambertucci et al. 2011). Indeed, unintentional lead poisoning is the leading cause of death for the California condor and remains one of the factors limiting the

recovery of this species (Cade 2007). Similarly, elevated lead exposure has been documented for a wide range of obligate (e.g., turkey vultures—*Cathartes aura*, Egyptian vultures—*Neophron percnopterus*, and bearded vultures—*Gypaetus barbatus*) and facultative (great horned owls—*Bubo virginianus*, red-tailed hawks—*Buteo jamaicensis*, golden eagles—*Aquila chrysaetos*, and bald eagles—*Haliaeetus leucocephalus*) scavengers across the globe (Clark and Scheuhammer 2003; Hernández and Margalida 2009b; Kelly and Johnson 2011; Kelly et al. 2011). Although exposure to many toxicants can cause direct mortality, particularly in high doses, scavengers often may be exposed to low doses of toxicants that have sublethal effects such as reduced bone mineralization (Gangoso et al. 2009), reduced muscle and fat concentrations (Carpenter et al. 2003), organ damage and internal lesions (Pattee et al. 1981), and reduced hatching success (Steidl et al. 1991). Such effects often go unnoticed and thus are likely underreported in many species (Senthil Kumar et al. 2003).

6.8 Conclusions and Perspectives

Despite the fact that there are few obligate vertebrate scavengers, carrion use by vertebrates has evolved as a pervasive foraging strategy among most vertebrate taxa (DeVault et al. 2003). Yet, we have only begun to recognize and appreciate the important role vertebrate scavengers play in maintaining the stability and structure of food webs (Wilson and Wolkovich 2011). Indeed, in some ecosystems, vertebrates may assimilate as much or more carrion biomass than invertebrates or microbes (Houston 1986; DeVault et al. 2011), maintaining carrion-derived energy resources higher within food webs. Scavenging itself is also an activity that spans trophic levels and can link species through feeding relationships that otherwise would not be associated in food webs. Thus, effects of vertebrate scavengers should not be overlooked in nutrient cycling models or by researchers studying invertebrate and microbial decomposers.

As highlighted, carrion removal by vertebrates is not only important in maintaining biodiversity, but scavenging guilds also play an important role in provisioning numerous ecosystem services, including the regulation of some diseases (Markandya et al. 2008). Current anthropogenic activities threaten the stability and persistence of many of these communities, which in turn may diminish the important ecosystem services provided by carrion consumers. Such activities may not only affect vertebrate scavengers, but also directly impact invertebrate and microbial decomposers by altering carrion availability and may indirectly impact these species by disrupting competitive interactions among vertebrates, microbes, and invertebrates.

Despite the numerous advancements achieved in food-web research over the last few decades, the importance of carrion to the survival and reproduction of facultative scavengers remains unknown for many species. Moreover, the impact of changes in carrion availability on ecosystem-level dynamics and interkingdom competitive interactions remains an important area of research. In particular, a comprehensive evaluation of the fate of carrion, and the nutrients sequestered therein, in response to various biotic and abiotic alterations to ecosystems to due anthropogenic activities, remains an area of critical need in scavenging research.

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