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Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems

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MINI- REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems

Travis L. DeVault, Olin E. Rhodes, Jr. and John A. Shivik

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Carion use by terrestrial vertebrates is much more prevalent than conventional theory implies, and, rather than a curiosity of animal behavior, is a key ecological process that must be accounted for. Human aversion to rotted substances and difficulties associated with identifying scavenged material in studies of food habits have contributed to the relative lack of information concerning scavenging behavior in vertebrates. Several lines of evidence, however, suggest that carion resources are more extensively used by vertebrates than has been widely assumed: 1) a substantial number of animals die from causes other than predation and become available to scavengers, 2) a wide variety of vertebrate scavengers, rather than microbes or arthropods, consume most available carcasses, and 3) intense competition exists between vertebrate scavengers and decomposers, especially in warm climates. Although vultures are best adapted to use carion, nearly all vertebrate predators are also scavengers to some extent. The costs and benefits associated with carion use influences the evolution of scavenging behavior in vertebrates, resulting in a continuum of facultative scavengers that use carion to varying degrees. The realized usage of carion by a vertebrate species is influenced by the speed and efficiency with which it forages, its visual and olfactory abilities, and its capacity for detoxifying products of decomposition. A deeper understanding of carion use by facultative scavengers will improve our knowledge of community and ecosystem processes, especially the flow of energy through food webs.

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Carion foraging by vertebrates is a phenomenon frequently noted but infrequently described, and references to it are often indirect and qualitative (Wilton 1986). The obvious reason for the historical lack of scavenging studies is human aversion to decomposing matter. Indeed, the term scavenger connotes a less than noble lifestyle and species that are known to scavenge often suffer from a paucity of basic natural history data. Species such as the gyrfalcon (*Falco rusticolus*) have been given classically biased descriptions in older works, e.g. the "gyrfalcon is noble and this aristocratic bird lives only on warm-blooded living prey, preferably birds, and never eats carrion," although a preponderance of recent evidence demonstrates the actual importance of carrion in falcon diets (Tømmeraa 1989).

Difficulties associated with quantifying scavenged material in animal diets also have contributed to the perceived inconsequential role of scavengers in ecosystems. Common techniques used for studies of food habits often preclude determining whether ingested prey was killed or scavenged. For example, scat analysis does not identify carrion ingested because fecal remnants of killed and scavenged prey are nearly identical. The use of stomach content analysis is limited as well, unless special attention is paid to evidence of carrion consumption (e.g. fly larvae mixed with stomach contents). Carrion is usually omitted from lists of commonly eaten items, and is not reported in some studies because it is either not searched for or not considered important. Natural history and foraging studies are often organismal in their approach and carrion is not a "species" normally studied. Furthermore, in most studies observations typically end with the death of an individual and do not necessarily trace the fate of the animal's carcass.

The subject of decomposition is not without discussion, but fleshy fruits and seeds have received more attention than carrion. Chemical compounds in plants have inspired volumes of research (Rosenthal and Janzen 1979), but other than Houston's (1979, 1985), Putman's (1983), and Shivik's (1999) explorations of the subject, detailed studies of the evolutionary importance of dead animals are lacking. Thus, the phenomenon is viewed as a behavioral curiosity rather than an important ecosystem process. However, decomposers are not the usual primary consumers of carrion; scavengers usually digest carcasses first, keeping energy flows higher in food webs (Putman 1983).

To date, most studies concerning the scavenging behavior of vertebrates have considered the functional roles of scavengers within ecosystems (Putman 1976), rather than cues or constraints governing an individual's ability to scavenge, or the costs and benefits of carrion foraging for facultative scavengers. We believe that new investigations into scavenging behavior of vertebrates will lead to a more accurate definition of the feeding niche of many species, and will provide new

insights into many areas of ecology. In this review, we summarize the current knowledge regarding carrion availability, the extent of carrion use by terrestrial vertebrates, the mechanisms governing competition for carrion among terrestrial vertebrates and decomposers, and the factors affecting the evolution of scavenging behavior and morphology. Additionally, we discuss the manner in which further knowledge of "scavenging ecology" could influence current views on several areas of ecological study, particularly the flow of energy through food webs.

Carrion availability

The issue of carrion availability is paramount to understanding the true role of scavenging in terrestrial communities. A convincing number of studies have demonstrated that vertebrate scavengers consume most available carrion (see below). However, without knowledge of carrion availability, the frequency of scavenging activities, and thus the role of carrion in ecosystems, remains unclear.

Availability of carrion depends on the cause and location of animal mortality. Contrary to widespread belief, vertebrate scavengers consume very few carcasses from predator kills, because predators usually consume entire animals or guard their prey (Houston 1979). Therefore, most scavengers rely on animal deaths due to malnutrition, disease, exposure, parasites, and accidents. Furthermore, the availability of carrion to vertebrate scavengers (and some decomposers) often depends on the accessibility of carcasses (e.g., the location where the animal died).

Studies by Houston (1979, 1986) suggested that the proportion of animal deaths from predation is less than from other causes. Using the food needs of predators, he calculated that only about 30% of all large ungulates die from predation in the African savannah; the rest (roughly 26 million kg annually) become available to scavengers and decomposers through other avenues (Houston 1979). In Neotropical forests, one mammal (of approx. 4 kg) dies from causes other than predation in each 2.5 km² each day (Houston 1986, 1994). Considering smaller carcasses, Putman (1976) calculated that predators generally account for 60% of small mammal mortality annually (using Pearson 1964, Stoddart 1970, Ryszkowski et al. 1971), leaving 40% to scavengers and decomposers. Given the reproductive abilities of most small mammals, the number of such carcasses available to scavengers could be considerable if these figures approach reality (see also Cowles and Phelan 1958).

Empirical data confirm that a substantial number of animals in many ecosystems die from starvation, expo-

sure, and other “natural” causes. However, studies also show that the relative importance of predation and other such mortality factors, and thus the amount of carrion available to scavengers, varies tremendously among ecosystems. For example, Bergerud (1980) reviewed population dynamics in reindeer and caribou (*Rangifer tarandus*) and showed that mortality factors vary widely among populations, primarily due to the presence or absence of effective predators. In unproductive, high arctic ecosystems, herbivores cannot persist in numbers sufficiently high to support an effective predator community; thus most large herbivores die from other causes in these areas (Oksanen and Oksanen 2000). For example, in the Svalbard region of northern Scandinavia, less than 5% of reindeer die from predation (Tyler and Øritsland 1999). Similarly, reindeer on South Georgia Island, which is free from mammalian predators, die primarily from starvation and falling accidents (Leader-Williams 1988). Furthermore, the causes of mortality among species often differ substantially within ecosystems. In the Białowieża Forest in Poland, Jedrzejewski et al. (1993) examined 1090 ungulate carcasses over seven years and reported that predators were responsible for 75% of the mortality observed in red deer (*Cervus elaphus*), 62% in roe deer (*Capreolus capreolus*), 27% in moose (*Alces alces*), and 12% in wild boar (*Sus scrofa*).

Concerning small mammals, many authors have demonstrated the overwhelming importance of predation as a mortality factor (Erlinge 1987, Jedrzejewski and Jedrzejewska 1993, Korpimäki and Krebs 1996, Wirsing et al. 2002). These studies seem to contradict Putman's (1976) calculations. However, in arctic regions predation may, at times, only account for 2–17% of small mammal deaths (Oksanen et al. 1997). Irrespective of the magnitude of predation, it is worth noting that the presence of large numbers of insects whose reproduction is tied to small carrion items provides indirect evidence for the existence of such resources. For instance, burying beetles (genus *Nicrophorus*; ~75 species) are found throughout the northern hemisphere; their presence confirms that at least some small mammals die from other causes in most ecosystems. *Nicrophorus* beetles are obligate carrion breeders – they find and bury small carrion items (primarily mammals 4–100 g in size) on which they raise their young (Milne and Milne 1976, Scott 1998). Smith and Merrick (2001) calculated that 1–2% of the average rodent population was necessary to support the observed *Nicrophorus* populations in Colorado, USA. However, in this region *Nicrophorus* beetles are active only during the warm season (late June through mid-September), when they compete with other insects and vertebrates for small carrion items (Smith and Merrick 2001). Thus, after accounting for rodent deaths during the remainder of the year (especially the winter season) and the number of rodent carcasses consumed by verte-

brate scavengers and other insects, the overall annual non-predator mortality of the rodent population must be much higher than the 1–2% needed to support *Nicrophorus* in this region.

Vertebrate and invertebrate community structure influences the number and type of carcasses available to vertebrates. Houston (1985) showed that Neotropical forests provide a greater food supply to vertebrate scavengers than Afrotropical forests due to the higher biomass and smaller average size (and thus higher average turnover) of herbivorous mammals in Neotropical forests. Also, carcasses remain available to vertebrates in Neotropical forests for longer periods than in Afrotropical forests due to interactions among the invertebrate community. Fly larvae completely consume 2–10 kg carcasses within three days in Afrotropical forests, whereas in Neotropical forests a complex community of ants suppresses maggot infestations on carcasses, thereby extending the availability of carcasses to vertebrates to over 10 days (Houston 1985).

Although animal deaths due to causes other than predation provide a steady supply of carrion in most habitats, scavenging opportunities often occur in seasonal pulses, providing predictable sources of carrion over discrete intervals of time. For example, large-scale die-offs of salmon cohorts produce an abundance of carcasses at regularly spaced intervals (Hewson 1995, Ben-David et al. 1997). In temperate areas, increased snow depths during winter and spring often result in starvation (Green et al. 1997) as well as increased predation by wolves (*Canis lupus*) on ungulates (Clevenger et al. 1992, Huggard 1993), both of which are events that increase carrion availability. Some facultative scavengers may increase their reliance on scavenging during these predictable time periods (Wilton 1986, Huggard 1993). Scavengers also capitalize on non-predictable sources of large-scale mortality, such as disease (Houston 1979) and forest fires (Singer et al. 1989).

Not all carcasses produced in ecosystems may be accessible to vertebrate scavengers. Historically, investigations of animal diets have ignored the potential complications of food accessibility, and simply relied on food abundance as a substitute, mostly because reliable estimates of true availability are difficult to obtain (Litvaitis 2000). As for carrion, there are few data pertaining to the specific locations or microhabitats where those animals not killed by predators die. It seems plausible that many larger animals come to rest in accessible locations and become directly available to scavengers. Conversely, smaller animals such as rodents and small birds may often die in cavities, burrows, and other locations where many vertebrate scavengers cannot access or even detect carrion. However, indirect evidence from diet analyses of turkey vultures (*Cathartes aura*) and black vultures (*Coragyps atratus*), obligate scavengers found throughout temperate and tropical North and South America, provide support for

at least the partial availability of small carcasses to vertebrate scavengers.

Turkey vultures and black vultures are chiefly unable to capture live animals (except for cases of black vultures working together in family groups to prey upon newborn livestock and other helpless animals; Buckley 1999). However, both species are known to consume small mammals. Remains of shrews (*Soricidae*; 2–25 g), moles (*Talpidae*; 40–65 g), cotton rats (*Sigmodon* spp.; 80–120 g), and wood rats (*Neotoma* spp.; 200–400 g) have been found at considerable levels in pellets regurgitated by turkey vultures (Paterson 1984, Hiraldo et al. 1991). Combined pellet analysis of turkey vultures and black vultures revealed remains of Norway rats (*Rattus norvegicus*; 300–540 g; Yahner et al. 1986), white-footed mice (*Peromyscus leucopus*; 16–28 g) and voles (*Clethrionomys gapperi* and *Microtus pennsylvanicus*; 20–50 g; Yahner et al. 1990). Thus, small mammal carrion must be available to vertebrate scavengers at least to some degree. As for carcasses that are not available to avian and other terrestrial scavengers due to inaccessibility, a number of species are well suited to utilizing such resources. Snakes may commonly search out and consume small carcasses that are inaccessible to other scavengers (Shivik and Clark 1997, DeVault and Krochmal 2002), and some species, such as least weasels (*Mustela rixosa*; Mullen and Pitelka 1972) and badgers (*Meles meles*; Roper and Mickevicius 1995), are able to excavate buried carrion.

The appreciable amount of data on cause-specific mortality would seem to indicate that much is known about the prevalence of carrion in ecosystems. Unfortunately, however, the inherent complexity (both spatially and temporally) underlying the causes of mortality and the lack of a clear synthesis inhibits the establishment of general rules and principles. Studies aimed at elucidating trends in carcass availability would be beneficial. It is clear, however, that a sufficient number of carcasses, both large and small, are produced in most ecosystems to influence the behavior, ecology, and evolution of vertebrate scavengers.

Empirical data on scavenging efficiency by vertebrates

Researchers have identified scavenged material in the diet of many carnivorous species, but this has been limited to large prey animals, and the possibility that small animals found in carnivore diets resulted from scavenging rather than predation has been ignored. The scavenged component of carnivore diets is overlooked because most available information concerning their diets is derived from scat and stomach content analyses (Goszczyński 1974, Hersteinsson and Macdonald 1996, Leckie et al. 1998). As a result, most studies consider

food items to have been scavenged only if the animal that the food items came from was too large to have been preyed upon by the study animal (e.g. deer parts found in fox scat). Errington (1935) first recognized this problem and remarked, “a cured ham that some Iowa hunters retrieved from a fox den does not indicate that a fox killed a pig!” Given the large numbers of small carcasses that are likely available to scavengers, and the apparent ability of facultative scavengers to use this resource (see below), it seems plausible that many small food items found in diets of vertebrate carnivores were scavenged rather than preyed upon (Errington 1935, Cowles and Phelan 1958, Mullen and Pitelka 1972).

Although it is difficult to determine the amount of carrion that is scavenged by vertebrates before it decomposes, available research suggests that vertebrates scavenge most available carcasses (Putman 1983). On the Serengeti Plains of Africa, vultures consume most large, conspicuous carcasses, but since researchers may overlook small carcasses, it is nearly impossible to calculate absolute scavenging efficiency (Houston 1979). As an alternative, several researchers have investigated scavenging efficiency using experimentally placed carcasses (Table 1). In Panama and Venezuela, a combined 116 of 120 (97%) brown-feathered domestic chickens placed in forests were scavenged by turkey vultures within 3 days (Houston 1986, 1988). An unknown scavenger took an additional carcass during the night, and the three carcasses that were ignored by scavengers were badly decomposed before they were set out. In Alaska, grizzly bears (*Ursus arctos*), wolves, and ravens (*Corvus corax*) each scavenged at over 50% of 15 experimentally placed large mammal carcasses, and all carcasses were scavenged at least in part by vertebrates (Magoun 1976).

Researchers using small mammals as carrion bait also have observed high levels of scavenging efficiency by vertebrates. To better understand predation and population fluctuations in lemmings (*Lemmus trimucronatus*), Mullen and Pitelka (1972) placed 594 lemming carcasses under the snow in the tundra near Barrow, Alaska during the fall of three consecutive years. Only eight were recovered the following springs. Thus, 99% of the lemming carcasses were removed by scavengers during the winter, particularly arctic foxes (*Alopex lagopus*), red foxes (*Vulpes vulpes*), least weasels, and lemmings. Putman (1976) found that in Oxford, England, scavenging efficiency varied by season and habitat. In winter and spring, 100% of brown house mouse carcasses (*Mus musculus*) were taken by scavengers (mostly red foxes), while in summer and autumn 90% of carcasses placed in forests and 64% of those placed in fields were removed before they completely decomposed. Akopyan (1953, cited in Putman 1976) reported scavenging rates of approximately 60% on ground squirrel carcasses (*Citellus pygmaeus*) in the European steppe, and in the sage-brush desert in Utah,

Table 1. Summary of studies using experimentally-placed carcasses to measure scavenging efficiency of terrestrial vertebrates. In some studies, separate experiments were combined to calculate a single measurement of scavenging efficiency.

Study	Carriion type, <i>n</i>	Habitat type and location	Time frame ^c	Efficiency (%) ^d	Likely primary scavenger
Akopyan 1953 ^a	ground squirrels (<i>Citellus pygmaeus</i>), 300	European steppe	April through July	60	unknown
Balcomb 1986	small birds, 78	agricultural fields in Maryland, USA	5 days in spring	92	unknown
Crawford 1971	small birds, 157	television tower in Florida, USA	1 day in fall	94	great-horned owl (<i>Bubo virginianus</i>), common crow (<i>Corvus brachyrhynchos</i>), fish crow (<i>Corvus ossifragus</i>)
DeVault and Rhodes 2002	house mice (<i>Mus musculus</i>), 48; rats (<i>Rattus norvegicus</i>), 48	forest in South Carolina, USA	14 days in winter	65	raccoon (<i>Procyon lotor</i>), gray fox (<i>Urocyon cinereoargenteus</i>), feral pig (<i>Sus scrofa</i>)
Houston 1986	domestic chickens, 71 ^b	forest in Panama	3 days	100	turkey vulture (<i>Cathartes aura</i>)
Houston 1988	domestic chickens, 46	forest in Venezuela	2 days	100	turkey vulture
Kostecke et al. 2001	small birds, 289	various habitats in South Dakota, USA	5 days in spring	66	striped skunk (<i>Mephitis mephitis</i>)
Linz et al. 1991	blackbirds (Icteridae), 135	wetland in North Dakota, USA	7 days in summer	47	unknown
Linz et al. 1997	small birds, <i>n</i> unspecified	sunflower fields in North and South Dakota, USA	4 days in late summer	88	red fox (<i>Vulpes vulpes</i>), raccoon, coyote (<i>Canis latrans</i>)
Linz et al. 1997	small birds, 20	corn fields in North and South Dakota, USA	4 days in spring	38	red fox, raccoon, coyote
Linz et al. 1997	small birds, 20	forests in North and South Dakota, USA	4 days in spring	25	red fox, raccoon, coyote
Magoun 1976	large mammals, 15	tundra in Alaska, USA	2 summers	100	grizzly bear (<i>Ursus arctos</i>), common raven (<i>Corvus corax</i>)
Mullen and Pitelka 1972	lemmings (<i>Lemmus trimucronatus</i>), 594	tundra in Alaska, USA	fall through spring	99	arctic fox (<i>Alopex lagopus</i>), red fox
Pain 1991	mallards (<i>Anas platyrhynchos</i>), 60	wetland in Camargue, France	8 days in September	100	unknown
Peterson et al. 2001	mallards, 54	agricultural fields in British Columbia, Canada	3 days in winter	96	northwestern crow (<i>Corvus caurinus</i>), bald eagle (<i>Haliaeetus leucocephalus</i>), glaucous-winged gull (<i>Larus glaucescens</i>), various hawks
Putman 1976	house mice, 200	forest and grassland near Oxford, England	33 days in winter and spring	100	red fox
Putman 1976	house mice, 200	forest and grassland near Oxford, England	8 days in summer and fall	78	red fox
Rosene and Lay 1963	northern bobwhite (<i>Colinus virginianus</i>), 30	unspecified habitat in Alabama, USA	4 days in summer	47	mammals
Rosene and Lay 1963	northern bobwhite, 30	unspecified habitat in Texas, USA	4 days in summer	13	mammals
Simonetti et al. 1984	rodents, 24	shrubland in central Chile	14 days in winter	100	didelphid (<i>Marmosa elegans</i>)
Stoddart 1970	jackrabbits (<i>Lepus californicus</i>), 45	desert in Utah, USA	unspecified	60	birds
Tobin and Dolbeer 1990	small birds, 200	fruit orchards in New York, USA	12 days in summer and fall	87	domestic cat (<i>Felis catus</i>), striped skunk, red fox, domestic dog (<i>Canis familiaris</i>)

^a Cited in Putman (1976).

^b 74 carrion baits were actually used, but 3 were badly decomposed when presented.

^c Elapsed time from presentation of carcasses until the conclusion of experiment.

^d Percentage of carrion baits that were consumed, totally or in part, by vertebrate scavengers.

27 of 45 (60%) jackrabbit carcasses (*Lepus californicus*) were scavenged by “birds” (Stoddart 1970). In central Chile, all 24 rodent carcasses (*Octodon degus* and *Abrocoma bennetti*) placed in shrubland patches were removed within two weeks, and half of them within seven days (Simonetti et al. 1984). The mostly likely scavenger at this site was a didelphid (*Marmosa elegans*). DeVault and Rhodes (2002) assessed winter scavenging efficiency on brown-furred Norway rats and house mice in a forested habitat in South Carolina. Vertebrates, primarily raccoons (*Procyon lotor*), gray foxes (*Urocyon cinereoargenteus*), and feral pigs (*Sus scrofa*), removed 65% of the carcasses within 14 days of placement. In this study scavenging efficiency was positively correlated ($R^2 = 0.95$) with ambient air temperature.

Several researchers have assessed scavenging efficiency of small carcasses using birds as carrion bait. In Alabama and Texas (the specific habitats were not specified), 47% and 13% of northern bobwhite carcasses (*Colinus virginianus*) were removed by mammalian scavengers within four days (Rosene and Lay 1963). Crawford (1971) investigated scavenging efficiency of bird carcasses at a television tower in Florida and found that 147 of 157 (94%) carcasses he experimentally placed were “ruined” (disappeared or made unusable for a museum specimen) in only one evening. Crawford attributed the losses to great-horned owls (*Bubo virginianus*) and crows (*Corvus brachyrhynchos* and *C. ossifragus*). Several studies have examined the bias associated with scavenger activities (e.g. removal of dead birds) on bird mortality estimates after exposure to environmental toxicants (Balcomb 1986, Tobin and Dolbeer 1990, Linz et al. 1991, 1997, Pain 1991, Kostecke et al. 2001, Peterson et al. 2001). These studies, using birds as carrion bait, reported scavenging efficiency rates from 25% to 100%, and identified scavengers such as striped skunks (*Mephitis mephitis*), domestic dogs (*Canis familiaris*), red foxes, and several species of scavenging birds.

In summary, a number of studies have demonstrated that in terrestrial habitats vertebrates scavenge the majority of available carcasses, regardless of their size. In the studies reviewed here (Table 1), estimates of scavenging efficiency by vertebrates averaged 75% (range = 13% to 100%; $n = 22$). However, comparisons among studies are tenuous due to differences in methodology. The proportion of carcasses that vertebrates scavenge appears to vary widely, and may be influenced by carcass type and conspicuousness, habitat, climate, and the composition of resident vertebrate and invertebrate communities. Although the studies reviewed here have demonstrated that most carcasses are scavenged by vertebrates, only a few studies have conclusively demonstrated which vertebrate species scavenge experimental carcasses most frequently (Kostecke et al. 2001, Peterson et al. 2001, DeVault and Rhodes 2002) or quantified the total amount of carrion used by individual facultative scavenger species (Gasaway et al. 1991,

Cooper et al. 1999). For individual scavengers, the ratio of food intake from predation versus scavenging may be influenced by social status (Gese et al. 1996a), age (Bennetts and McClelland 1991, Gese et al. 1996b, Bustamante et al. 1997), and health (Cooper et al. 1999). The relative importance of these factors in determining the frequency of carrion use remains largely uninvestigated. Questions also remain concerning the manner in which abiotic factors (e.g. climate) influence scavenging efficiency.

Competition for carrion between vertebrate scavengers and decomposers

In terms of scavenging, vertebrates are spared some negative elements of predator-prey evolutionary dynamics (e.g. the constant evolution of predator adaptations to overcome constantly evolving prey defenses) because dead animals do not develop defenses against scavengers. Natural selection can act through competition among scavenging species, but a predator that consumes carrion avoids the concurrent predator-prey coevolutionary “arms race”. Carcasses do not defend themselves and are relatively easy to handle, but the resource is not without inherent costs. A certain level of competition between vertebrate scavengers and the microbes and arthropods that decompose carrion is to be expected. Microbes use toxins and substrate degradation to monopolize carcasses (Janzen 1977), and this strategy is especially effective in warm climates where their activities are maximized (Putman 1976). Warmer temperatures allow more rapid bacterial and fungal growth, and arthropods steepen carrion decay curves by transporting decomposers to carcasses while insect pupae tunnel and aerate carcasses (Payne 1965, Putman 1978). Payne (1965) demonstrated that when arthropods are experimentally excluded from carcasses, bacteria cannot fully metabolize them; rather, carcasses mummify before they are fully digested.

Decomposers must rapidly discover and colonize carcasses to use the resource maximally (Braack 1987). Microbes are rarely able to colonize all edible materials in a carcass; they instead produce a few objectionable materials, thereby making entire carcasses inedible, unwanted, or toxic to vertebrates (Janzen 1977). *Clostridium perfringens*, *Clostridium botulinum*, *Escherichia coli*, *Staphylococcus aureus*, *Shigella dysenteriae*, *Salmonella typhi* and *Bacillus stearothermophilus* all produce toxins that are dangerous to the mammalian and avian species that are exposed to them. At high concentrations, the wide variety of amines and sulfur compounds characteristic of microbial activity serves as an honest signal, allowing some vertebrate scavengers to immediately identify a piece of meat as being rotten and inedible (Janzen 1977). However, at lower concentrations, low molecular weight compounds such as hydrogen sulfide

and putrescine signal the presence of edible carrion to vertebrates (Stager 1964). Thus, the products of decay are both attractive and repulsive to scavengers, depending upon concentration. The realized usage (a function of both detectability and desirability) of carrion will reach an optimum when the carcass is odoriferous enough to be detected at a distance, but still retains much non-fetid biomass (DeVault and Rhodes 2002). As such, many vertebrate scavengers primarily use odor cues to locate carcasses (Stager 1964, Shivik and Clark 1997, DeVault and Krochmal 2002, DeVault and Rhodes 2002).

Because the products of decomposition are often toxic, the usefulness of a carcass to a vertebrate scavenger declines through time. Also, as bacterial and fungal organisms digest carcasses, compounds useful to vertebrates are metabolized, further degrading the nutritive value. Vertebrate scavengers must out-compete microbes by obtaining carcasses more rapidly, or by detoxifying or otherwise avoiding their chemical defenses (Janzen 1977). To use carrion most efficiently, vertebrate scavengers must assume the fixed costs of developing detoxifying enzymes and associated morphological structures to protect themselves from bacteria and the metabolic cost of the detoxification process itself (Feeny 1973). Interestingly, the realized costs and benefits of eating carrion are equivalent to those of eating plants, except that a herbivore largely coevolves with the plants it eats (the herbivore must constantly counter newly evolved plant chemical defenses), but a scavenger competes not with the carcass itself but with the relatively sessile bacteria and fungi that produce a similar suite of toxic and thus defensive products of metabolism. This interspecific competition is evident because the carrion resource is always recycled, and no one species or taxon completely dominates its use.

The competition for carrion among vertebrates, arthropods, and microbes presents substantial potential for ecological study. When an animal dies, another organism or group of organisms invariably benefits from the death. The key questions, then, involve the factors that mediate the competition between scavengers and decomposers, and the influence that this competition has exerted on the evolution of the taxa that use the resource.

Factors affecting the evolution of scavenging behavior and morphology in vertebrates

Carrion is extremely ephemeral in nature; the temporal patchiness of carrion availability has inhibited evolution towards strict specialization for scavenging behavior in most vertebrates (Houston 1979, Putman 1983, Braack 1987, Heinrich 1988). Due to the rapid decomposition of carcasses, there is typically more live prey

than carrion available to carnivorous vertebrates at any one time. As a result, obligate scavengers are very rare. However, vertebrate carnivores usually consume fresh carrion when it is found – there is no advantage in passing on a free meal. Thus, nearly all carnivorous vertebrates should be considered facultative scavengers.

Although facultative scavenging is common, the propensity to use carrion varies widely among species. Some vertebrates, such as hyenas (*Crocuta crocuta*; Gasaway et al. 1991), red foxes (Henry 1977), and various raptors (Errington and Breckenridge 1938) use carrion frequently, whereas others scavenge only rarely. Nevertheless, even species that are not typically associated with scavenging, such as otters (*Lutra lutra*; O'Sullivan et al. 1992), herons (Ardeidae; Klapste 1991), pileated woodpeckers (*Dryocopus pileatus*; Servin et al. 2001) red phalaropes (*Phalaropus fulicarius*; Wander 1981), ring-necked pheasants (*Phasianus colchicus*; Knox and Buckland 1983), common mergansers (*Mergus merganser*; Rae 1989), hippopotamus (*Hippopotamus amphibius*; Dudley 1996), and a wide variety of snakes (DeVault and Krochmal 2002) occasionally will eat carrion. The realized distribution of vertebrate foraging behaviors for plants, live prey, and carrion is a continuum, with selective pressures operating to shift such foraging strategies as opportunities arise.

Birds are best specialized for carrion use because of the low cost of search efforts in soaring locomotion. Soaring requires less energy than running (Schmidt-Nielson 1972), thus birds may search large areas more efficiently than mammalian or reptilian scavengers (Houston 1979). The only known obligate terrestrial vertebrate scavengers are the Old and New World vultures (for reviews, see Houston 1979, Kirk and Mossman 1998, Buckley 1999). All vultures have the similar characteristics of large wingspans, a soaring habit, keen eyesight, and a reduction of feathers around the head that would otherwise crust with putrefying and potentially toxic material (Houston 2001). Vultures are supremely adapted to a scavenging lifestyle, as evident from their exceptional gliding ability (Houston 1979). They out-compete other vertebrates by simply finding and consuming carrion more rapidly (Kruuk 1967, Pennycuik 1971, Houston 1974, Prior and Weatherhead 1991). Furthermore, New World vultures in the genus *Cathartes*, which largely occupy forested habitats, possess the added advantage of an astonishing olfactory sense used to locate carrion (Bang 1960, Stager 1964). The dominance of vultures for carrion has been demonstrated empirically. Turkey vultures consumed 90–95% of carcasses placed in a Panamanian forest (Houston 1986), and in a similar study, vultures and mammalian scavengers located 63% and 5% of carcasses, respectively (Gomez et al. 1993).

Despite the success of vultures, most carnivorous birds are only facultative scavengers. Obligate scavengers are not widespread among birds because the

morphological and behavioral traits that allow avian scavengers to most effectively utilize carrion resources are in conflict with traits that favor predatory behavior (Houston 1979). For example, the rapid pursuit of prey is best accomplished with narrow wings, whereas efficient locomotion, necessary for locating ephemeral and unpredictable carrion resources, favors broad wings (Houston 1979). However, the high level of scavenging propensity among various species of birds (Hewson 1981, Hiraldo et al. 1991) suggests that even non-soaring flight allows birds to out-compete other vertebrates for carrion in most situations.

No mammals or reptiles have evolved into obligate scavengers, at least in the recent past, because of their relative inability to travel rapidly and efficiently compared to birds. Even the most well adapted mammalian scavengers, such as hyenas, kill the majority of their food (Kruuk 1972, Gasaway et al. 1991, Cooper et al. 1999). However, mammals effectively use carrion resources in some situations. For example, DeVault and Rhodes (2002) demonstrated that mammals consumed most rodent carcasses in dense forests, presumably because birds were limited in their ability to visually detect the carcasses. Similarly, mammalian carnivores can deplete carrion during the night when most birds are inactive (Prior and Weatherhead 1991). Mammals such as bears and wolves may also gain advantage in arctic environments (Magoun 1976) where the lack of thermal uplifts reduces a bird's ability to soar efficiently. Furthermore, although large mammalian carnivores such as bears find fewer carcasses than birds, they are able to monopolize carrion when it is found (Green et al. 1997).

Our understanding of the influence that the spatial and temporal availability of carrion resources has had on the evolution of scavenging behavior is limited to general theory and overall trends. However, the fact that a large proportion of terrestrial vertebrates are facultative scavengers suggests that the benefits of carrion use probably outweigh the adaptive costs associated with scavenging, at least as an occasional energy acquisition strategy. Undoubtedly, as a species increases its dependence upon carrion resources as a primary energy source, the costs of adaptation become more prohibitive, as evidenced by the small percentage of terrestrial vertebrates that depend solely on carrion resources. It is likely that the competitive interaction between decomposers and vertebrates for carrion resources sets the evolutionary price for the development of scavenging as a primary means of energy acquisition, with those adaptations relating to the detection, and possibly detoxification, of carrion resources being the most critical. Further investigation of the relative costs and benefits associated with the use of carrion resources and of the complex relationships between decomposers and vertebrate scavengers should advance our appreciation for the plasticity in scavenging behavior observed in terrestrial vertebrates.

Ecological implications of carrion use by vertebrates

A clearer perspective on carrion use by terrestrial vertebrates will improve our understanding of critical ecological processes, particularly those associated with energy flow and trophic interactions. While many of the elements that influence the spatiotemporal availability and use of carrion in terrestrial environments have been described, at least within the context of a basic conceptual framework, the processes through which carrion resources influence trophic interactions among species or contribute to the stability of terrestrial communities remain unclear. The available data pertaining to the use of carrion by terrestrial vertebrates suggest that most accessible carcasses are scavenged and that many vertebrates do take advantage of carrion resources, even those species primarily thought of as voracious predators. However, little attention has been given to the influence of carrion resources on the flow of energy through food webs and the potential modulating effects that these energy sources might have on interactions among species.

In a manner similar to that of temporal variation in population densities of prey species, the ebb and flow of carrion resources through time may directly influence the strength and nature of species interactions among trophic levels within food webs. The available data suggest that a potentially substantial fraction of the energy sequestered by vertebrates originates from carrion, thus making carrion an integral component of any realistic energy flow model. The use of carrion as a supplemental food resource during prey shortages may have substantial impacts on the population dynamics of predators and their prey. Moreover, trophic interactions via facultative scavenging may represent "weak links" in food webs among numerous species. Especially in light of recent evidence that such weak links are integral to ecosystem stability and persistence (McCann et al. 1998, McCann 2000), continued research on the fate of animal carcasses in terrestrial ecosystems should contribute substantially to our knowledge of food web patterns. Interestingly, it seems evident that even hypotheses relating to the stability and longevity of species assemblages should incorporate the contributions of carrion resources to community diversity, population growth, and habitat quality.

While the functional role of carrion resources in sculpting ecological processes has been seemingly underappreciated, either as a consequence of the difficulties associated with estimation of carrion consumption or the use of simplifying assumptions, scavenging ecology is clearly a topic which is ripe for further investigation and rich with the potential to advance our understanding of energy flow dynamics in natural systems.

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