The Living Dead: Time to Integrate Scavenging into Ecological Teaching

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In recent years, exciting scientific evidence has emerged highlighting the ecological importance of dead animals (i.e., carrion) and their consumption (i.e., scavenging), to the point that we could consider this the golden age of scavenging research. We now have a considerable body of theoretical and empirical work that indicates that scavenging is fundamental to properly understanding not only food web, community, and population ecology but also evolution, biodiversity conservation, and human well-being. However, universities fail to integrate scavenging into ecological teaching, as can be judged from the lack of importance of this process in ecology textbooks. We consider this a paramount gap in ecological education, and we advocate that students should be aware of the important role that carrion and scavengers play in ecosystems. Integrating scavenging principles and applications into ecology textbooks will broaden the ecological foundation of the next generation of ecologists.

Keywords: carrion, ecology textbook, food web, higher education, scavenger

Scavenging—carcasivory, or the consumption of carrion by gatherer animals (Getz 2011)—is not new among ecologists (Tenney 1877). However, classical food webs have been regarded as modules of interacting producers, consumers (e.g., primary, secondary), and top predators, with no mention of scavengers (figure 1a). The later addition of nutrient recycling and decomposition into multitrophic models brought to light the key contribution of detritus to the dynamics and stability of food webs (figure 1b; Moore et al. 2004, McCann 2012). In general, *detritus* refers to small fragments of decaying organic matter consumed mainly by invertebrates and microorganisms, but whole animal carcasses, especially vertebrate carcasses, have been largely ignored in both theoretical and empirical food web research for several reasons that range from the human aversion to decomposing matter to the difficulties of quantifying scavenged materials in diet studies and the perception of scavenging as an anecdotal and random process (DeVault et al. 2003). Moreover, ecologists have tended to accept that scavenging involves only bottom-up effects, with no influence on the population dynamics of consumed organisms (Wilson and Wolkovich 2011).

This is the traditional view that is generally conveyed in classical ecology textbooks. A review of 20 textbooks commonly used by ecology students and found in university libraries (we reviewed the most recent editions; see supplemental appendix S1) clearly shows that scavenging has been largely ignored. Among trophic interactions, detritivory and, mostly, herbivory and predation are pervasive and often considered in individual chapters. In contrast, scavenging receives weak or no attention. To illustrate the point, scavenging is never mentioned in the tables of contents. Moreover, key terms such as *scavenging*, *scavenger*, and *carrion* are almost completely missing from indices (except in five books in which *scavenger* or *scavenging vertebrates* appear and one book in which *carrion consumption* is also mentioned; see appendix S1). In these books, the content devoted to scavenging ranges from one paragraph to barely two pages and is always included—in a very descriptive way—as a part of *saprobism*, *other interactions*, or *ecological succession* (in particular, degradative or heterotrophic succession—i.e., the sequence of local appearances and extinctions of consumer species on dead organic matter; Schoenly and Reid 1987).

The scavenging revolution

Several review papers have recently highlighted the growing body of evidence supporting the essential role of carrion and scavenging in ecology (DeVault et al. 2003, Wilson and Wolkovich 2011, Beasley et al. 2012, Barton et al. 2013, Moleón et al. 2014a, Pereira et al. 2014, Mateo-Tomás et al. 2015). The number of papers dealing with scavenging in journals within the category *Ecology* has increased abruptly during the last decade. A search of the *Web of Science* using the term *scaveng** resulted in 64 papers (publication period: 1900–2013) with the term in the title (many more included it in other parts of the manuscripts), with 73% published from 2004 to 2013. The number of papers that included

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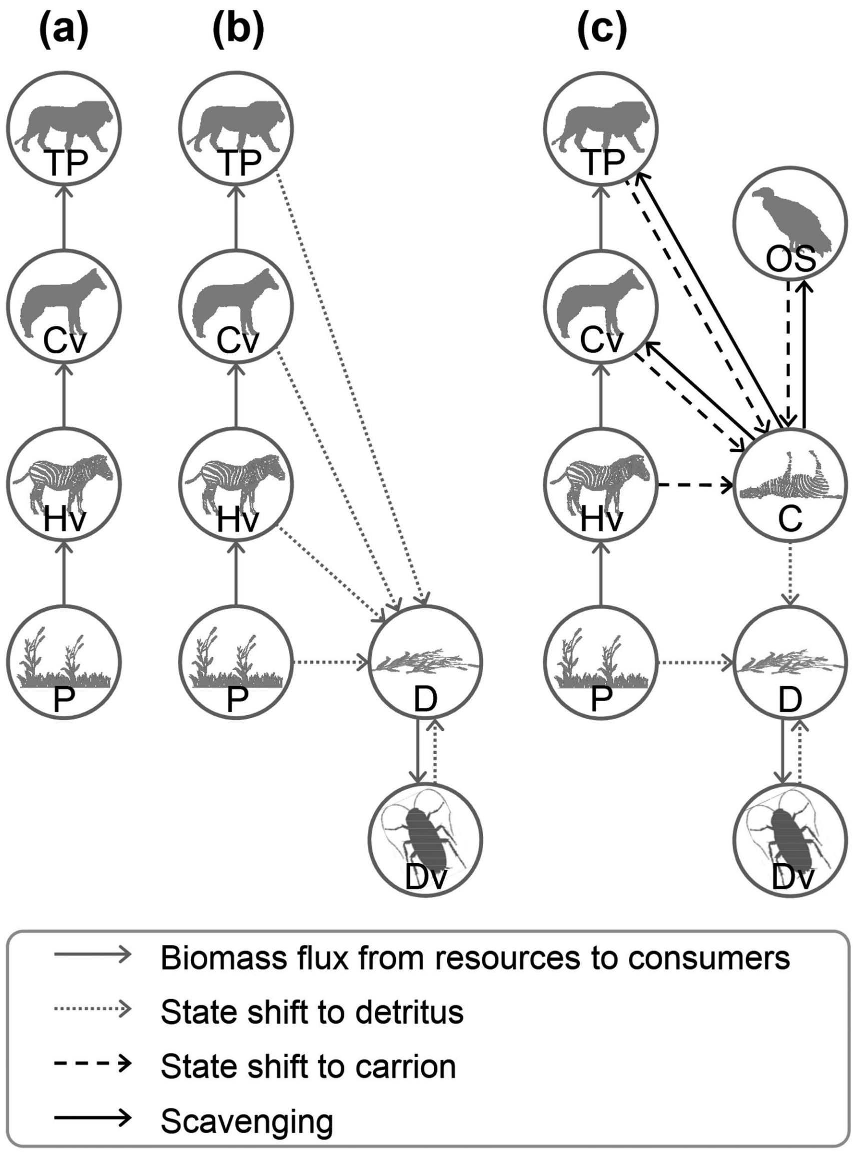

Figure 1. Food web models. (a) Classical models typically include producers (P), primary consumers (herbivores; Hv), secondary consumers (carnivores; Cv), and top predators (TP). (b) Classical models can be improved by including detritivory (D) by detritivore species (Dv). (c) Modern, more realistic models should also recognize scavenging or the consumption of carrion (C) by both obligate (OS) and facultative scavengers (Cv and TP).

carrion and *vulture* (two terms closely related to the scavenging process) in the title was 149 and 188, respectively, of which 52% and 65% were published in the last decade (figure 2). For comparison, the percentage of papers with the terms *detritivor**, *decompos**, *predat**, and *herbivor** in the title published in the last 10 years (2004–2013) were 50% (total N for the period 1990–2013 = 129), 39% (total n = 2267), 52% (total n = 13,265) and 35% (total n = 6562), respectively.

Previously, scavenging had been mainly associated with obligate or specialist scavengers, such as vultures, which depend entirely on carrion, and some facultative or opportunistic scavengers, such as hyenas that are known to scavenge frequently (Moleón et al. 2014a). A key milestone for the growing interest in scavenging was the recent recognition that most, if not all, carnivore species (i.e., animals that eat other animals) scavenge when opportunities present themselves (e.g., DeVault et al. 2003), including many species commonly believed to never eat carrion, such as snakes (table 1, figure 3; DeVault and Krochmal 2002). In fact, scavenging is a pervasive process in both terrestrial and aquatic ecosystems (boxes 1 and 2, figure 4; Britton and Morton 1994, DeVault et al. 2003, Smith and Baco 2003, Beasley et al. 2012) and is an important energy-transfer pathway at the terrestrial–aquatic interface (table 1; Gende et al. 2002, Schlacher et al. 2013). It has been pointed out that food webs clearly underestimate scavenging links and that the energy transferred per scavenging link substantially exceeds that transferred per predation link, which has frequently led to the inflation of predation impacts and the underappreciation of indirect effects (Wilson and Wolkovich 2011). Importantly, thanks to the direct and indirect effects that emerge when considering the facultative consumption of carrion by predators, scavenging also involves top-down effects on the populations of consumed species (Moleón et al. 2014a). Facultative scavenging by predators also leads to a close connection between predation and scavenging (Nolting et al. 2008, Moleón et al. 2014a, Pereira et al. 2014, Moleón et al. 2015), two processes that had traditionally been regarded as independent. Also, carrion is significantly involved in disease dynamics (Gulland 1995, Getz 2011, Turner et al. 2014). Growing evidence supports the idea that scavenging networks can be highly structured (Selva and Fortuna 2007, Cortés-Avizanda et al. 2012, Killengreen et al. 2012, Sebastián-González et al. 2013, Allen et al. 2014, Mateo-Tomás et al. 2015, Moleón et al. 2015). Overall, scavenging has the potential to stabilize ecosystems, such as through increasing the number of feeding links and enhancing multichannel feeding (DeVault et al. 2003, Wilson and Wolkovich 2011, Moleón et al. 2014a). These findings may be fundamental to comprehensively understanding not only food web, community, and population ecology but also evolution, biodiversity conservation, and human well-being.

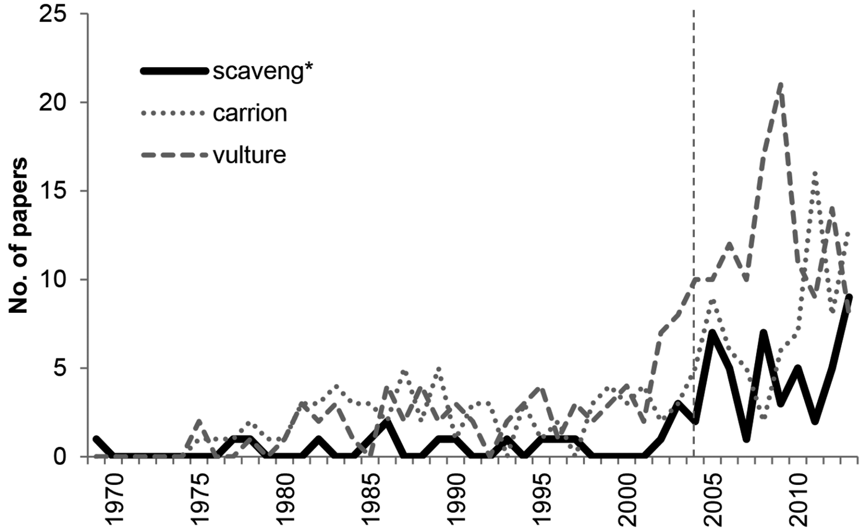

Figure 2. The number of papers published in SCI journals within the category* Ecology *that include the terms* scaveng*, carrion, *and* vulture *in the title (source:* Web of Science*). Results are shown since 1969, when the first* scaveng* *paper was published. The vertical dashed line indicates the beginning of the last decade (2004–2013).

For instance, scavenging by early hominins was decisive in triggering our lineage, and interactions with scavengers have provided a multitude of ecosystem services throughout the course of human evolution (e.g., improving human culture, disease control, and ecotourism; Moleón et al. 2014b).

Unfortunately, the scavenging process is threatened by the increasing human pressure that the planet Earth is currently facing (DeVault et al. 2003, Wilson and Wolkovich 2011, Beasley et al. 2012, Barton et al. 2013, Moleón et al. 2014a, 2014b, Pereira et al. 2014, Mateo-Tomás et al. 2015). For instance, drastic changes in the spatiotemporal availability of carrion (e.g., through predictable anthropogenic food subsidies, emerging infectious diseases, and the application of controversial sanitary regulations) are leading to important alterations of the behavior and survival of particularly sensitive species, from insects to vultures, and the functioning of whole scavenging assemblages (e.g., Butman et al. 1995, Pain et al. 2003, Chamberlain et al. 2005, Donázar et al. 2009, Margalida et al. 2010, Martín-Vega and Baz 2011, Cortés-Avizanda et al. 2012, Margalida and Colomer 2012, Ogada et al. 2012, Oro et al. 2013, Mateo-Tomás et al. 2015). Consequently, much research has been devoted in the last years to

Table 1. Main groups of scavengers consuming vertebrate carcasses, according to different ecosystems and biomes.

Ecosystem	Biome	Main scavenger group	References
Terrestrial	Tundra	Birds (e.g., birds of prey[a], corvids), mammals (e.g., large carnivores, mesocarnivores)	DeVault et al. 2003, Killengreen et al. 2011, Wilson and Wolkovich 2011, Mateo-Tomás et al. 2015
	Boreal forest	Birds (e.g., birds of prey[a], corvids), mammals (e.g., large carnivores, mesocarnivores)	DeVault et al. 2003, Wilson and Wolkovich 2011, Mateo-Tomás et al. 2015
	Temperate	Birds (e.g., vultures, birds of prey[a], corvids), mammals (e.g., large carnivores, mesocarnivores, suids, didelphids)	DeVault et al. 2003, Selva and Fortuna 2007, Wilson and Wolkovich 2011, Mateo-Tomás et al. 2015
	Mediterranean	Birds (e.g., vultures, birds of prey[a], corvids), mammals (e.g., large carnivores, mesocarnivores, suids), invertebrates (e.g., flies, beetles)	DeVault et al. 2003, Martín-Vega and Baz 2011, Wilson and Wolkovich 2011, Mateo-Tomás et al. 2015
	Savanna	Birds (e.g., vultures, birds of prey[a], corvids), mammals (e.g., large carnivores, mesocarnivores, suids)	Wilson and Wolkovich 2011, Mateo-Tomás et al. 2015, Moleón et al. 2015
	Tropical forest	Birds (e.g., vultures, birds of prey[a]), mammals (e.g., large carnivores, mesocarnivores), invertebrates (e.g., ants, flies)	DeVault et al. 2003
Freshwater		Reptiles (e.g., crocodiles, turtles, snakes), fish, invertebrates (e.g., leeches, flies)	Wilson and Wolkovich 2011, authors pers. observ.
Marine		Birds (e.g., sea birds), mammals (e.g., killer whales, dolphins), fish (e.g., sharks, hagfishes), invertebrates (e.g., amphipods, isopods, crabs, cephalopods, sea snails, sea stars, brittle stars)	Britton and Morton 1994, Smith and Baco 2003, Whitehead and Reeves 2005, Furness et al. 2007, Wilson and Wolkovich 2011, Beasley et al. 2012
Land-water interface	Land–freshwater	Birds (e.g., vultures, birds of prey[a], corvids), mammals (e.g., large carnivores, mesocarnivores, suids), reptiles (e.g., crocodiles, turtles, snakes), invertebrates (e.g., flies, stone flies)	Gende et al. 2002, Wilson and Wolkovich 2011, authors pers. observ.
	Land–marine	Birds (e.g., vultures, birds of prey[a], corvids, sea birds), mammals (e.g., large carnivores, mesocarnivores), reptiles (e.g., monitors), invertebrates (e.g., crabs, beetles, flies)	Wilson and Wolkovich 2011, Schlacher et al. 2013

Note: [a]Other than vultures.

Figure 3. Vertebrate scavengers are represented by many charismatic species throughout all the continents and marine environments. These scavengers include birds such as vultures and other avian raptors, mammals such as large predators and smaller species, and species pertaining to other taxonomic groups (see supplemental appendix S2 for scientific names and photo credits). We indicate the conservation status of each species according to the International Union for Conservation of Nature Red List of Threatened Species (LC: least concern; NT: near threatened; VU: vulnerable; CR: critically endangered; DD: data deficient). Many charismatic scavengers, especially vultures and large predators, are globally threatened.

reconcile human activities and needs with scavenger conservation and function. Therefore, the good news is that now we have science-based arguments to guide management actions in a wide array of ecological situations. For instance, concise and practical guidelines have been provided to optimize supplementary feeding stations for vultures and other threatened scavengers (e.g., Cortés-Avizanda et al. 2010, Fielding et al. 2014, Moreno-Opo et al. 2015), to improve the sanitary regulations and practices that compromised scavenger populations (e.g., Swan et al. 2006, Donázar et al. 2009, Margalida et al. 2010, 2012), to minimize avian scavenger mortality in power lines and wind farms (Lehman et al. 2007, Guil et al. 2011, Carrete et al. 2012), and to enhance the ecosystem services provided by scavengers (e.g., Deygout et al. 2009, Dupont et al. 2012, Morales-Reyes et al. 2015).

Perspectives and benefits

Our aim is to call attention to the important mismatch that exists between scientific evidence of the ecological significance of scavenging and its teaching as reflected by its lack of relevance in ecology textbooks. Food webs should no longer be regarded as only producer–consumer interactions; we need an integrative perspective that includes scavenging—that is, carrion and its consumption by scavengers (figure 1c, figure 5). Considering the direct and indirect trophic interactions associated with scavenging could improve energy flux models (Getz 2011, Wilson and Wolkovich 2011, Moleón et al. 2014a). Benefits may be especially fruitful when addressing the challenges imposed by global environmental change (DeVault et al. 2003, Wilmers and Getz 2005, Wilson and Wolkovich 2011, Beasley et al. 2012, Barton et al. 2013, Moleón et al. 2014a, 2014b, Pereira et al. 2014). For instance, apex predators are able to dampen

Box 1. Whale falls.

Sunken whale carcasses yield massive, long-lasting pulses of organic matter to the deep-sea floor that are exploited by a diverse and characteristic faunal community, as was revealed by accidental and experimental observations using manned submersibles and remotely operated vehicles. In the bathyal zone, the consumption of whale carrion (up to 160 metric tons in the case of blue whale, *Balaenoptera musculus*, carcasses) passes typically through three main stages. The first stage, which lasts months to approximately 5 years, is dominated my mobile consumers (around 38 macrofaunal species have been described). During this stage, hagfishes, sleeper sharks (*Somniosus pacificus*), and invertebrate scavengers such as amphipods and crabs remove around 90% of whale soft tissue (the soft tissue constitutes around 90% of the total whale weight) at rates of approximately 1.7–2.5 kilograms (kg) per hour. This could be considered the main “scavenging” stage, which gives way to an increasing representation of detritivores (with sessile species being more and more frequent) and microorganisms. A numerous community of invertebrates dominated by polychaetes (20,000–45,000 individuals per meter [m] within 1 m of the skeleton) exploit the organically enriched sediments in the vicinities of the carcass and exposed bones during the months to years before skeleton decomposition, which may last for decades (at least 50 years for the largest whale carcasses; Smith and Baco 2003).

Calculations taking into account the nine largest whale species indicate that there is a fresh (i.e., retaining soft tissue) whale carcass at the sea floor every 16–36 kilometers (km; the figure diminishes up to 5 km for older carcasses), although carcass densities may be higher along whale migration routes and feeding grounds. This suggests that whale falls are regular food resources for marine scavengers. However, it is worth noting that before industrial whaling (i.e., prior to 1800), whale population sizes are thought to have been 50%–90% higher than current estimates. The drastic drop of whale populations and, consequently, sunken whales during the last two centuries has led to an impoverishment of the deep-sea biodiversity because of the extinction of some of the most specialized whale carrion feeders (Butman et al. 1995).

Box 2. Scavenging in the African savannah.

A recent study conducted in the African savannah has pointed out that the structure and functioning of vertebrate scavenging assemblages is largely dependent on carcass size (Moleón et al. 2015). The relationship between the particle size of the food resource and community structure and dynamics is pervasive in many food webs and other ecological networks, although it had not been explicitly explored in a scavenging context to date. Moleón and colleagues (2015) used motion-sensing cameras (as is illustrated by this example and that in box 1, technological improvement has favored recent scavenging research) to monitor carcasses ranging in size from *small* (2 kilograms [kg] domestic chickens) to *medium* (impalas, *Aepyceros melamphus*, and nyalas, *Tragelaphus angasi*) and *large* carcasses (from wildebeest, *Connochaetes taurinus*, to elephants, *Loxodonta Africana*, weighing 4 metric tons). Carcass consumption time and rate increased with carcass size, whereas carcass detection time and the percentage of carrion biomass consumed negatively related to carcass size. Mean scavenging rate ranged from 0.14 kg per hour for small carcasses to 4.45 kg per hour for large carcasses. Compared with whale falls consumption, the latter rate is much higher (see box 1). Vultures and large predators, mainly lions *Panthera leo* and spotted hyenas *Crocuta crocuta*, consumed most of the carrion available: near 50% for small carcasses and near 100% for medium and large carcasses. Only horns and a few hard bones (other bones were frequently consumed by hyenas and lions) and skin shreds remained after 1.6–419.1 hours of carcass placement (see figure 4). The role of invertebrates and microorganisms in consuming the soft tissue of the studied carcasses was negligible. Scavenging networks tended to be more structured (i.e., nested) at larger carcasses, at which there were more scavenger species (mean = 4.75 species per carcass) and interspecific interactions. The most diverse scavenger community was that consuming small carcasses (14 species in total), likely because these carcasses were relatively difficult to find by dominant scavengers (i.e., vultures, lions, and hyenas). In addition, the lower presence of apex predators at small carcasses and the subsequent diminished predation risk allowed the presence of mesocarnivores such as genets and mongooses, which were lacking at medium and large carcases.

fluctuations in carrion production, which are increasing because of climate change (Wilmers and Getz 2005, Wilmers and Post 2006, Wilmers et al. 2007). Also, encouraging the conservation of key scavenger species such as vultures and large predators, which are in serious jeopardy worldwide (because of, e.g., poisoning, both intentional and unintentional; shooting; power-line and wind-farm casualties; road kills; lead intoxication; habitat loss and degradation; Şekercioğlu et al. 2004, Ogada et al. 2012, Ripple et al. 2014; also see figure 3), is an urgent need that will be extremely difficult unless there is broad recognition of their crucial ecological role, including their provision of ecosystem services (Moleón et al. 2014b).

In conclusion, we are witnessing the golden age of scavenging research. We already have a considerable body of theoretical and empirical evidence supporting scavenging as a ubiquitous, nonrandom, high-magnitude energy-transfer pathway with wide implications from the individual to

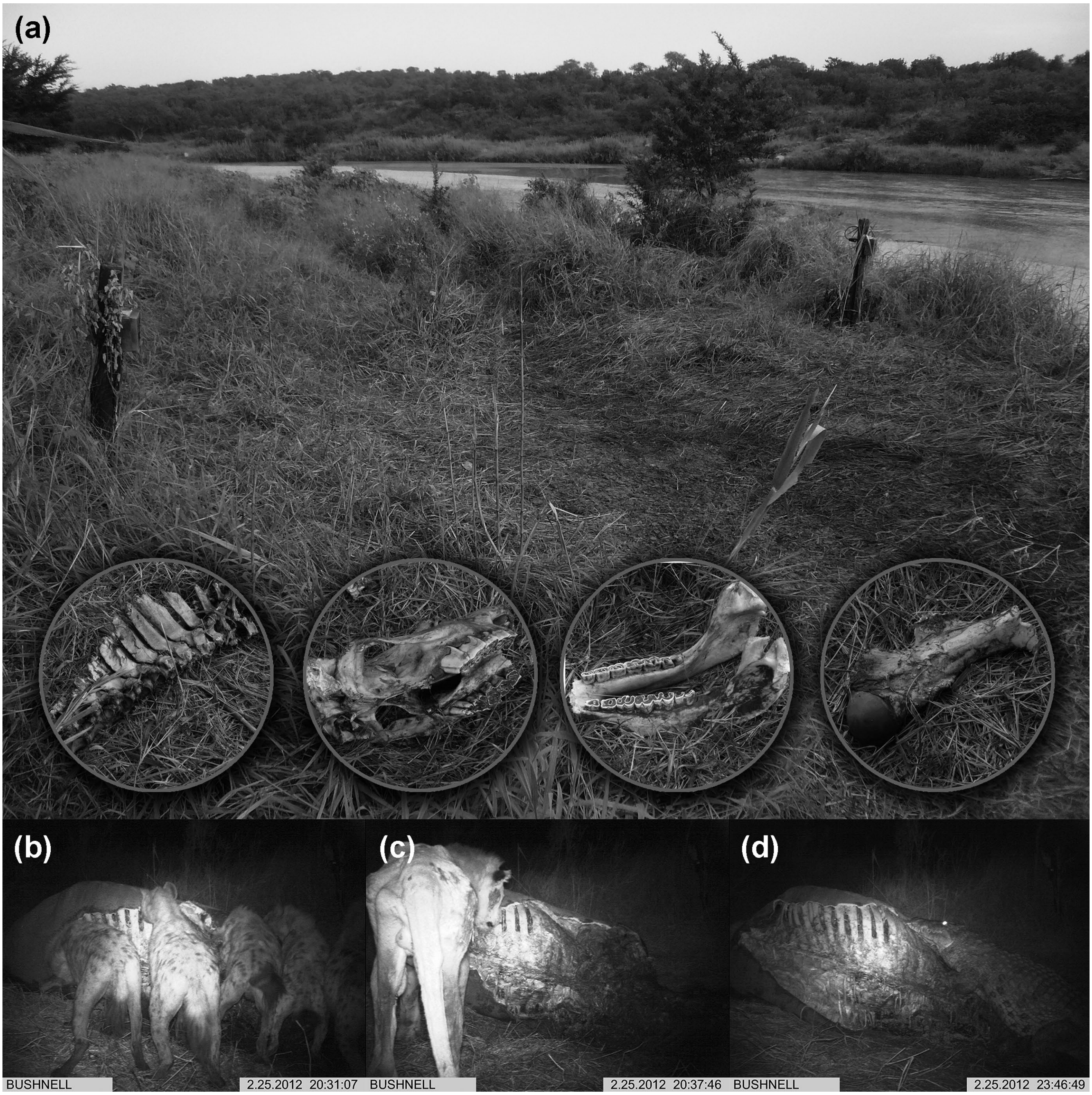

*Figure 4. Scavengers in complex ecosystems such as the African savannah are highly efficient. The large image (a) shows a 2000-kilogram male white rhino (*Ceratotherium simum*) carcass site, following its complete consumption by spotted hyenas (*Crocuta crocuta*) (b), lions (*Panthera leo*) (c), and Nile crocodiles (*Crocodylus niloticus*) (d). Three and a half days after the rhino death, only a few hard bones remained (small images). The rhino was killed by another male rhino during a fight. Photographs: Marcos Moleón (scavenger photographs were taking by means of motion-sensing cameras, which can be seen in the large image).*

the population, community, and ecosystem levels; with close connections to other ecological processes; and with ramifications for other scientific disciplines. This modern conception of scavenging should be considered when planning ecological curriculum in our universities (see box 3). Although we acknowledge the logical delay between knowledge generation and its incorporation into general books, we encourage efforts to make students aware of the important role that carrion and scavengers play in ecosystems. Integrating scavenging principles and applications into ecology textbooks will broaden the ecological foundation of the next generation of ecologists.

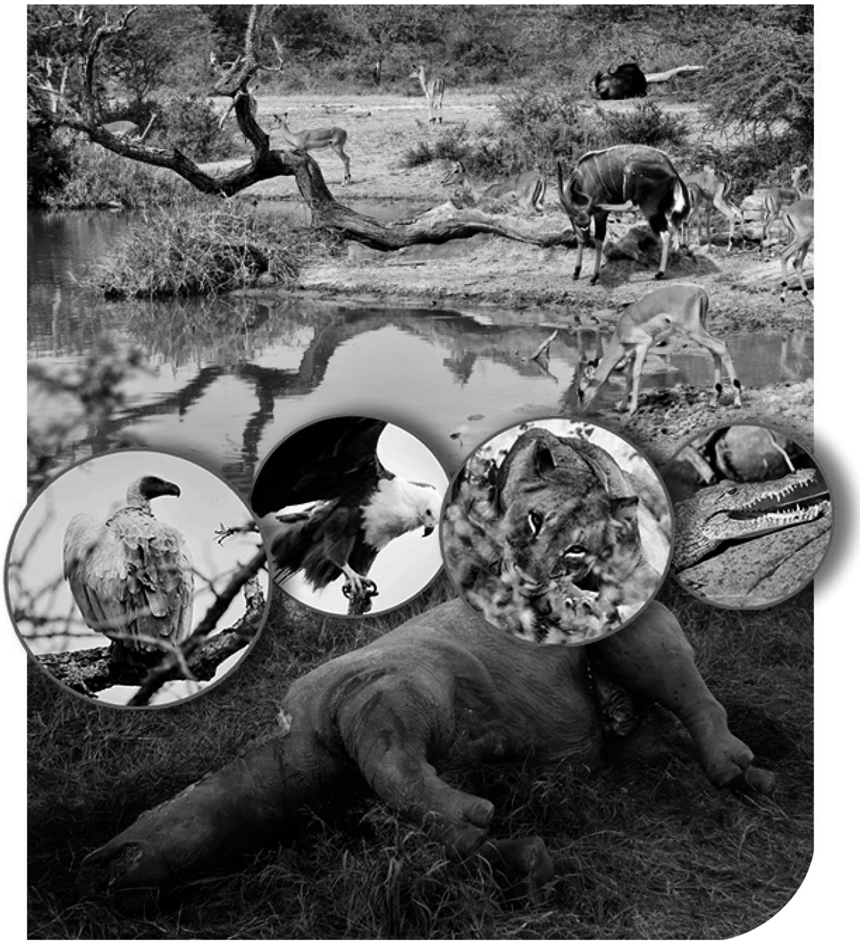

Figure 5. Considering scavenging is fundamental to comprehensively understand the structure and functioning of natural communities, in which carrion is a ubiquitous and high-quality food resource widely exploited not only by obligate scavengers (e.g., vultures) but also by a plethora of facultative or opportunistic scavengers pertaining to very diverse animal groups (see table 1 and figure 3). All animals die eventually, and a huge quantity of biomass in the form of carrion (including leftovers of animals killed by predators) is readily available to scavengers. Photographs: Marcos Moleón (white rhino carcass) and David Carmona-López (the rest).

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Supplemental material

The supplemental material is available online at *http://bioscience.oxfordjournals.org/lookup/suppl/doi:10.1093/biosci/biv101/-/DC1.*

References cited

Barton PS, Cunningham SA, Lindenmayer DB, Manning AD. 2013. The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. Oecologia 171: 761–772.

Beasley JC Olson ZH, DeVault TL. 2012. Carrion cycling in food webs: Comparisons among terrestrial and marine ecosystems. Oikos 121: 1021–1026.

Britton JC, Morton B. 1994. Marine carrion and scavengers. Oceanography and Marine Biology: An Annual Review 32: 369–434.

Butman CA, Carlton JT, Palumbi SR. 1995. Whaling effects on deep-sea biodiversity. Conservation Biology 9: 462–464.

Chamberlain CP, Waldbauer JR, Fox-Dobbs K, Newsome SD, Koch PL, Smith DR, Church ME, Chamberlain SD, Sorenson KJ, Risebrough R. 2005. Pleistocene to recent dietary shifts in California condors. Proceedings of the National Academy of Sciences 102: 16707–16711.

Carrete M, Sánchez-Zapata JA, Benítez JR, Lobón M, Montoya F, Donázar JA. 2012. Mortality at wind-farms is positively correlated to large-scale distribution and aggregation in griffon vultures. Biological Conservation 145: 102–108.

Box 3. A proposal for integrating scavenging into ecology textbooks.

The large body of theoretical and empirical scientific knowledge already existing on scavenging—both in terrestrial and aquatic systems—allows its comprehensive treatment in ecology textbooks, which could include the following basic contents:

- Fundamental concepts: carrion, scavengers, and scavenging.
- The spatiotemporal availability of carrion.
- The evolution of scavenger traits and scavenging assemblages, including human evolution.
- The structure of scavenging assemblages.
- The functioning of scavenging assemblages: scavenging rate, top-down versus bottom-up regulation of scavengers and consumed organisms, and so on.
- The function of scavenging (e.g., ecosystem services provided by scavengers, including nutrient cycling).
- The connections among scavenging, predation, and other ecological processes.
- The consequences of scavenging for species coexistence and ecosystem stability.
- The global-change impacts on scavenging assemblages: human-mediated carrion production, vulture and apex predator declines, and so on.
- The management of the scavenging process and scavenger conservation.

Cortés-Avizanda A, Carrete M, Donázar JA. 2010. Managing supplementary feeding for avian scavengers: Guidelines for optimal design using ecological criteria. Biological Conservation 143: 1707–1715.

Cortés-Avizanda A, Jovani R, Carrete M, Donázar JA. 2012. Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: A field experiment. Ecology 93: 2570–2579.

DeVault TL, Krochmal AR. 2002. Scavenging by snakes: An examination of the literature. Herpetologica 58: 429–436.

DeVault TL, Rhodes OE, Shivik JA. 2003. Scavening by vertebrates: Behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos 102: 225–234.

Deygout C, Gault A, Sarrazin F, Bessa-Gomes C. 2009. Modeling the impact of feeding stations on vulture scavenging service efficiency. Ecological Modelling 220: 1826–1835.

Donázar JA, Margalida A, Carrete M, Sánchez-Zapata JA. 2009. Too sanitary for vultures. Science 326: 664.

Dupont H, Mihoub JB, Bobbé S, Sarrazin F. 2012. Modelling carcass disposal practices: Implications for the management of an ecological service provided by vultures. Journal of Applied Ecology 49: 404–411.

Fielding G, Newey S, van der Wal R, Irvine RJ. 2014. Carcass provisioning to support scavengers: Evaluating a controversial nature conservation practice. AMBIO 43: 810–819.

Furness R, Edwards AE, Oro D. 2007. Influence of management practices and of scavenging seabirds on availability of fisheries discards to benthic scavengers. Marine Ecology Progress Series 350: 235–244.

Gende SM, Edwards RT, Willson MF, Wipfli MS. 2002. Pacific salmon in aquatic and terrestrial ecosystems. BioScience 52: 917–928.

Getz WM. 2011. Biomass transformation webs provide a unified approach to consumer–resource modelling. Ecology Letters 14: 113–124.

Guil F, et al. 2011. Minimising mortality in endangered raptors due to power lines: The importance of spatial aggregation to optimize the application of mitigation measures. PLOS ONE 6 (art. e28212).

Gulland FMD. 1995. The impact of infectious diseases on wild animal populations: A review. Pages 20–51 in Grenfell BT, Dobson AP, eds. Ecology of Infectious Diseases in Natural Populations. Cambridge University Press.

Killengreen ST, Stromseng E, Yoccoz NG, Ims RA. 2012. How ecological neighbourhoods influence the structure of the scavenger guild in low Arctic tundra. Diversity and Distributions 18: 563–574.

Lehman RN, Kennedy PL, Savidge JA. 2007. The state of the art in raptor electrocution research: A global review. Biological Conservation 136: 159–174.

Margalida A, Colomer MA. 2012. Modelling the effects of sanitary policies on European vulture conservation. Scientific Reports 2 (art. 753).

Margalida A, Donázar JA, Carrete M, Sánchez-Zapata JA. 2010. Sanitary versus environmental policies: Fitting together two pieces of the puzzle of European vulture conservation. Journal of Applied Ecology 47: 931–935.

Margalida A, Carrete M, Sánchez-Zapata JA, Donázar JA. 2012. Good news for European vultures. Science 335: 284.

Martín-Vega, D, Baz, A. 2011. Could "vulture restaurants" be a lifeboat for the recently rediscovered bone-skippers (Diptera: Piophildae)? Journal of Insect Conservation 15: 747–753.

Mateo-Tomás P, Olea P, Moleón M, Vicente J, Botella F, Selva N, Viñuela J, Sánchez-Zapata JA. 2015. From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. Diversity and Distributions. doi:10.1111/ddi.12330

McCann KS. 2012. Food Webs. Princeton University Press.

Moleón M, Sánchez-Zapata JA, Selva N, Donázar JA, Owen-Smith N. 2014a. Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. Biological Reviews 89: 1042–1054.

Moleón M, Sánchez-Zapata JA, Margalida A, Carrete M, Owen-Smith N, Donázar JA. 2014b. Humans and scavengers: The evolution of interactions and ecosystem services. BioScience 64: 394–403.

Moleón M, Sánchez-Zapata JA, Sebastián-González E, Owen-Smith N. 2015. Carcass size shapes the structure and functioning of an African scavenging assemblage. Oikos. doi:10.1111/oik.02222

Morales-Reyes Z, Pérez-García JM, Moleón M., Botella F, Carrete M, Lazcano C, Moreno-Opo R, Margalida A, Donázar JA, Sánchez-Zapata JA. 2015. Supplanting ecosystem services provided by scavengers raises greenhouse gas emissions. Scientific Reports 5 (art. 7811).

Moreno-Opo R, Trujillano A, Arredondo Á, González LM, Margalida A. 2015. Manipulating size, amount and appearance of food inputs to optimize supplementary feeding programs for European vultures. Biological Conservation 181: 27–35.

Moore JC, et al. 2004. Detritus, trophic dynamics and biodiversity. Ecology Letters 7: 584–600.

Nolting B, Paullet JE, Previte JP. 2008. Introducing a scavenger onto a predator prey model. Applied Mathematics E 8: 214–222.

Ogada DL, Keesing F, Virani MZ. 2012. Dropping dead: Causes and consequences of vulture population declines worldwide. Annals of the New York Academy of Sciences 1249: 57–71.

Oro D, Genovart M, Tavecchia G, Fowler MS, Martínez-Abraín A. 2013. Ecological and evolutionary implications of food subsidies from humans. Ecology Letters 16: 1501–1514.

Pain DJ, et al. 2003. Causes and effects of temporospatial declines of *Gyps* vultures in Asia. Conservation Biology 17: 661–671.

Pereira LM, Owen-Smith N, Moleón M. 2014. Facultative predation and scavenging by mammalian carnivores: Seasonal, regional and intraguild comparisons. Mammal Review 44: 44–55.

Ripple WJ, et al. 2014. Status and ecological effects of the world's largest carnivores. Science 343 (art. 1241484).

Schlacher TA, Strydom S, Connolly RM, Schoeman D. 2013. Donor-control of scavenging food webs at the land–ocean interface. PLOS ONE 8 (art. e68221).

Schoenly K, Reid W. 1987. Dynamics of heterotrophic succession in carrion arthropod assemblages: Discrete seres or a continuum of change? Oecologia 73: 192–202.

Sebastián-González E, Sánchez-Zapata JA, Donázar JA, Selva N, Cortés-Avizanda A, Hiraldo F, Blázquez M, Botella F, Moleón M. 2013. Interactive effects of obligate scavenger and community richness on lagomorph carcass consumption patterns. Ibis 155: 881–885.

Şekercioğlu CH, Daily GC, EhrlichPR. 2004. Ecosystem consequences of bird declines. Proceedings of the National Academy of Sciences 101: 18042–18047.

Selva N, Fortuna MA. 2007. The nested structure of a scavenger community. Proceedings of the Royal Society B 274: 1101–1108.

Smith CR, Baco AR. 2003. Ecology of the whale falls at the deep-sea floor. Oceanography and Marine Biology: An Annual Review 41: 311–354.

Swan G, et al. 2006. Removing the threat of diclofenac to critically endangered Asian vultures. PLOS Biology 4 (art. e66).

Tenney S. 1877. A few words about scavengers. American Naturalist 11: 129–135.

Turner WC, et al. 2014. Fatal attraction: Vegetation responses to nutrient inputs attract herbivores to infectious anthrax carcass sites. Proceedings of the Royal Society B 281 (art. 20141785).

Whitehead H, Reeves R. 2005. Killer whales and whaling: The scavenging hypothesis. Biology Letters 1: 415–418.

Wilmers CC, Getz WM. 2005. Gray wolves as climate change buffers in Yellowstone. PLOS Biology 3: 571–576.

Wilmers CC, Post E. 2006. Predicting the influence of wolf-provided carrion on scavenger community dynamics under climate change scenarios. Global Change Biology 12: 403–409.

Wilmers CC, Post E, Hastings A. 2007. The anatomy of predator–prey dynamics in a changing climate. Journal of Animal Ecology 76: 1037–1044.

Wilson EE, Wolkovich EM. 2011. Scavenging: How carnivores and carrion structure communities. Trends in Ecology and Evolution 26: 129–135.

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