Wildlife Research Monographs 2

Pedro P. Olea
Patricia Mateo-Tomás
José Antonio Sánchez-Zapata *Editors*

Carrion Ecology and Management

Springer

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Pedro P. Olea • Patricia Mateo-Tomás
José Antonio Sánchez-Zapata
Editors

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Editors
Pedro P. Olea
Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM)
Universidad Autónoma de Madrid
Madrid, Spain

Departamento de Ecología
Universidad Autónoma de Madrid
Madrid, Spain

Patricia Mateo-Tomás
Centre for Functional Ecology (CFE)
Department of Life Sciences
University of Coimbra
Coimbra, Portugal

Research Unit of Biodiversity
(UMIB, UO/CSIC/PA)
Mieres, Spain

José Antonio Sánchez-Zapata
Departamento de Biología Aplicada
Universidad Miguel Hernández
Elche, Spain

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Foreword

The dog said to the bone: "If you are hard, I have time." Not in vain, one of my surnames is *Sancho*, as the manchego squire from Don Quixote, so I beg you to allow me to start with one anonymous sentence which I think is appropriate. Here, the "bone" is the ecology of scavenging, the central theme of the book you hold in your hands. The "dogs" (no offense intended) are all the researchers who have devoted much or all of their professional activity to the study of these processes. Seen from the current perspective of ecology, the topic is undoubtedly attractive and deserves to be at the forefront of cutting-edge science. This was not the case, however, just a few decades ago. Then, the "bone" was hard, and attempts to gnaw it sometimes involved risking the splintering of teeth. After all, scientists are not anomalies, but they are like anyone else, subject to the imponderables of the world in which they live. Among them, there are those that seek quick results and professional victories (lamentably more and more), which does not mesh well with the patience, observations, and setbacks that typically accompany investigation in the field. For this reason, working with carrion has not traditionally been on the radar of research teams in ecology. This is evident just reading the textbooks of three or four decades ago, when those of us who were already combing through gray hair were on the faculties of our venerable research institutions. Take that test and you will see.

But researchers arrived with a hard tooth, and after several decades of effort and tenacity, they are chipping away at the bone. The number of works on scavenging ecology has grown exponentially and continues to grow, thanks to the courage of researchers such as those that have edited and contributed to this book. I believe that I am not mistaken in affirming that a fundamental driver of the qualitative leap that has taken place has been the conservation of the great birds and mammals for whom scavenging is a way of life. The global crisis of biodiversity that we are facing has been ahead of the, until recently, flourishing populations of large vultures of the Old World as well as large carnivorous mammals. In parallel, the human obsession for achieving an "aseptic" world has nearly led to the end of traditional abandonment of carrion of domestic animals in the countryside. The impact of this change could affect the entire panoply of organisms that take advantage of discarded remains, including arthropods, bacteria, and many vertebrate facultative scavengers. This trend was born in the south of Europe, specifically in Spain, the refuge of the last healthy populations of carrion birds. Thus, it is not coincidental that the editors and many of the authors of these chapters carried out their work in the Mediterranean biome. I also think that, and this is a personal opinion of course, the appeal of "scavenging ecology" for many ecologists is anchored in something that is very much at our roots as human beings. There is no doubt that the use of carrion had a mark on our beginnings as a species: imagine the first humans, and our "cousins" the Neanderthals, harvesting the huge carcasses of mammoths and mastodons. What would it have meant for those groups of humans, always between life and death, to have access to a resource of this caliber? What challenges would they have been willing to face, such as carnivores and other beasts, to take this valuable booty? This, without a doubt, left its mark.

Prologues usually discuss the contents of subsequent chapters. I will not bore you more with descriptions and summaries of the corresponding texts. I also think that such a summary is unnecessary because the structure of the book is clear, and in a few pages, you will find a very detailed explanation of the contents. This is such a monumental work (it is difficult to find another word) that I am sure it will be a must for ecologists for many years to come. I invite you to immerse yourself in the texts and, for those who are less familiar with the topic, to enjoy learning. Let me finish with another reference, this time to a Cordovan philosopher born thousands of years ago in the empire that gave birth to the civilization in which we live. Seneca said that the effort calls the best. In the pages that follow, the best are represented, invigorating, with their hard work, a field of ecology for which they are passionate and which, beyond texts, chapters, and papers, transports us back, for a moment, to our beginnings: bipedal, erect, and trembling, making our way in a world of beasts guarding their precious treasures.

José Antonio Donázar Sancho
Department of Conservation Biology
Estación Biológica de Doñana (CSIC)
Sevilla, Spain

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Contents

About the Editors

Pedro P. Olea is professor and researcher at the Department of Ecology and at the Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad Autónoma de Madrid, Spain. His research focuses on understanding how worldwide human activities, such as hunting, livestock, and crop farming, affect patterns and processes in species, communities, and ecosystems at different spatial scales and how to apply this knowledge for their management and conservation. At present, one of his main research lines is focused on the emerging field of carrion ecology. The results from his research have been published in the most important scientific journals of ecology and conservation.

Patricia Mateo-Tomás is a postdoctoral researcher at the Centre of Functional Ecology at Coimbra University, Portugal, and Oviedo University, Spain. Her work focusses on the ecology and conservation of scavengers, especially vultures but also other facultative vertebrate scavengers, and their relationships with human activities such as hunting and livestock rearing (including transhumance) developed in natural ecosystems. She is also interested in exploring new ways for effective science communication.

José A. Sánchez Zapata is professor of ecology at the Department of Applied Biology, Universidad Miguel Hernández de Orihuela. His research initially focused in the ecology and conservation of raptors. During the last decade, he has broadened the topics including the role of scavenger guilds in ecosystem functioning and services under a socio-ecological framework. He has conducted research in Africa, America, Asia, Australia, and Europe reflected in scientific publications, most of them in ecology, biology, and biodiversity and conservation journals.

Introduction to the Topic of Carrion Ecology and Management

Pedro P. Olea, Patricia Mateo-Tomás, and José A. Sánchez-Zapata

Contents

Carrion Ecology: Key Concepts and State of the Art

Besides the "green world" composed of living organisms, another outstanding "brown world" exists which consists of dead organic matter, i.e. organic detritus (Swift et al. 1979; Moore et al. 2004). Detritus is ubiquitous in ecosystems as most of terrestrial plant biomass is not consumed by herbivores (up to 90%; Gessner et al. 2010) and a large number of animals die by causes other than predation (i.e. injuries, malnutrition, extreme weather conditions, parasites and disease; Young 1994, DeVault et al. 2003). For instance, >95% of reindeer in Svalbard (DeVault et al. 2003) and about 70% of all large ungulates in the African savannah die from causes other than predation (Houston 1979). In the Serengeti ungulate migrations,

P. P. Olea (✉)
Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad Autónoma de Madrid, Madrid, Spain

Departamento de Ecología, Universidad Autónoma de Madrid, Madrid, Spain
e-mail: pedrop.olea@uam.es

P. Mateo-Tomás
Centre for Functional Ecology (CFE), Department of Life Sciences, University of Coimbra, Coimbra, Portugal

Research Unit of Biodiversity, (UMIB, UO/CSIC/PA), Mieres, Spain

J. A. Sánchez-Zapata
Departamento de Biología Aplicada, Universidad Miguel Hernández, Elche, Spain
e-mail: toni@umh.es

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6250 carcasses (~1100 tons of biomass) of drowned wildebeest (*Connochaetes taurinus*) enter the river each year when the mass herds cross the Mara River (Subalusky et al. 2017). In marine ecosystems, about 69,000 large whales die by natural causes each year (Smith and Baco 2003), providing between 6×10^5 and 2×10^6 tons of dead biomass (see chapter "Carrion Availability in Space and Time" for more details on how much carrion is produced in different terrestrial and marine ecosystems). Moreover, preys left uneaten by predators frequently enter the detritus pool too. Depending on the pack size, wolves (*Canis lupus*) can supply between 100 and 1200 kg of elk (*Cervus elaphus*) carrion from their captures during one winter in Yellowstone National Park (Wilmers et al. 2003a). This sizeable nonliving organic component is subject to consumption, degradation or decomposition, i.e. a series of processes that ultimately recycle the energy and nutrients embodied into dead matter (see chapter "Carrion Decomposition"), thereby being critical to ecosystem functioning (Swift et al. 1979; Moore et al. 2004; Parmenter and MacMahon 2009; Barton et al. 2013; see chapter "Ecological Functions of Vertebrate Scavenging"). Despite the large amount of dead animal biomass present in the ecosystems, the study of decomposition of dead animals and its role in the functioning of ecosystems has received very little attention (but see Putman 1977, 1978a, b; Putman 1983; Carter et al. 2007; Parmenter and MacMahon 2009; Benbow et al. 2013; Subalusky et al. 2017) especially compared with that of dead plant matter (e.g. Swift et al. 1979; Putman 1983; Gessner et al. 2010; García-Palacios et al. 2013).

Detritus, *sensu lato*, is highly variable in origin and quality, from low-quality dead plant matter to high-quality dead animal tissue, i.e. carrion (Moore et al. 2004; Wilson and Wolkovich 2011). Carrion is yet a distinct component from the others that form the detritus pool in ecosystems (e.g. dead wood, dead plant biomass, animal dung), as its rate of decay is much faster, it is spatially patchy (Barton et al. 2013; chapter "Carrion Decomposition") and generally unpredictable and ephemeral (DeVault et al. 2003). Therefore, carrion is considered as a high-quality food pulsed resource (Yang et al. 2008) that usually appears in the form of carcasses in all aquatic and terrestrial ecosystems (Fig. 1). These carcasses are exploited by a plethora of invertebrate and vertebrate scavengers (see chapters "Invertebrate Scavenging Communities" and "Vertebrate Scavenging Communities") along with microorganisms (bacteria and fungi). It is therefore not surprising that competition for carrion occur among microorganisms, arthropods and vertebrates (Putman 1983; DeVault et al. 2003).

The unpredictable and ephemeral nature of carrion has constrained the evolution of true specialists on this resource (DeVault et al. 2003; Ruxton and Houston 2004; Kane et al. 2017). Species that rely entirely upon carrion must exhibit a high displacement speed at a low locomotion cost to search over large areas in order to attain a rate of encounter with the resource enough to meet their energetic demands (Carbone et al. 2011; Kane et al. 2017). Other adaptations required would be a high ability of sensory detection of carcasses and low metabolism in order to extend the inter-feeding time (Kane et al. 2017). Once localized the carcass, an efficient scavenger must possess a large body size in order to outcompete other competitors and

Fig. 1 Carrion, dead animal matter, appears as a pulsed food resource in the form of carcasses in all aquatic and terrestrial ecosystems. In human-modified ecosystems, fallen stock from livestock grazing is left in the open in many countries; in the pictures, carcasses of domestic ungulates in mountain ecosystems in northern Spain. Photo credits: José Vicente López-Bao

process the carrion rapidly to avoid its decay and the toxins from microorganisms decomposing the carrion (Kane et al. 2017). Consequently, a limited number of species have strictly specialized in the sole consumption of carrion, i.e. as obligate scavengers. Among vertebrates, no mammals or reptiles have evolved into obligate scavengers, and among extant birds only large soaring vultures are obligate carrion consumers (22 species, Houston 1979; DeVault et al. 2003; Ruxton and Houston 2004; Fig. 2). However, many other species use this resource optionally (facultative scavengers; Figs. 2 and 3) including early humans.

A wide diversity of species ranging from small primary consumers to top predators (e.g. lions, eagles and sharks) use carrion (Fallows et al. 2013; Mateo-Tomás et al. 2015). Terrestrial insects found in carcasses range from 30 to 522 species (Tabor et al. 2005), although it can include predators and parasites of scavengers and other species that use the carrion as habitat. In marine ecosystems, as many as 407 species of vertebrates and invertebrates can be found on whale falls (Smith and Baco 2003). Reptiles are less studied but at least twenty six species of snakes have been documented scavenging (DeVault and Krochmal 2002). Mammals and birds are most frequently registered consuming carrion. In Bialowieza Forest (Poland) and in Spanish ecosystems as many as 33 and 31 vertebrate species scavenged upon ungulate carcasses respectively (Mateo-Tomás et al. 2015). At a global scale, a review of the literature reported that at least 69 vertebrate species consumed carrion of wild ungulates with variable frequency (Mateo-Tomás et al. 2015). However, it is still unknown how many species show scavenger behavior globally. Depending on the biome considered, between 2 and 11% of the total terrestrial vertebrates present in an ecosystem consume carrion (Mateo-Tomás et al. 2015), suggesting that hundreds of vertebrate species may be facultative scavengers worldwide (i.e. 675–3700

Fig. 2 Vultures, with 22 species present in the world, are the only obligate scavengers among vertebrates as they are spezialized in the rapid location of carrion, e.g. the top picture shows griffon (*Gyps fulvus*) and cinereous (*Aegypius monachus*) vultures gathering at the guts left by hunters in the center of Spain. Besides vultures, carrion attracts many other facultative species (e.g. red fox *Vulpes vulpes* in the bottom image). Photo credits: Patricia Mateo-Tomás/Pedro P. Olea

Fig. 3 Carrion creates a local hotspot of biodiversity as many species from large vertebrates to invertebrates gather around the carcasses. Chimangos *Milvago chimango*, caracaras *Caracara plancus*, black *Coragyps atratus* and turkey *Cathartes aura* vultures feeding on a cow carcass in Argentina (above); tiny invertebrates such as the European bone-skipper fly *Thyreophora cynophila* on a horse carcass in Spain (bottom left image). Photo credits: María Eugenia Cabrera-García (above) and Jesús Fernández Carro (bottom left)

species from the 33,770 species of terrestrial vertebrates described worldwide; IUCN 2014). Altogether, these figures underscore the relevant role of carrion as a fundamental food resource for biodiversity worldwide.

The presence of carrion in the ecosystems attracts a wide diversity of species of invertebrates and vertebrates to specific locations creating a hotspot of biodiversity (Figs. 2 and 3). Not only there are species that visit the carrion to feed on the carcass, other ones come to search for prey, hosts or habitat (Tabor et al. 2005; Carter et al. 2007). Also, species visiting the carrion leave remains in the carcass (e.g. feathers, hair, urine, excrements, exuviae), attracting in turn more species and creating altogether a biological activity center in and around the carcass (Carter et al. 2007; Moleón and Sánchez-Zapata 2016). This intense animal activity along with the chemical and microbial processes contributes to decomposition of the carcass creating what is called a "cadaver decomposition island" (CDI; Carter et al. 2007). This CDI is usually visible as dead plant and bare soil appear due to trampling and the release of carcass fluids and maggot activity (Putman 1983; Carter et al. 2007). Carrion decomposition is a fundamental ecological process through which occurs the breakdown of the dead animal, and the recycling of the nutrients and energy embodied in the carcass. Therefore, "life concentrates biologically limiting resources", and death disperses them (chapter "Carrion Decomposition"). Dispersal of nutrients such as carbon, nitrogen or phosphorus away from carrion is conducted by arthropod and vertebrate scavengers (Barton et al. 2013; Subalusky et al. 2017). The movement of carrion nutrients can also occur across ecosystem or habitat boundaries (Payne and Moore 2006). In the Serengeti, for example, transfer of nutrients from terrestrial into aquatic ecosystem occurs via mass drowned wildebeests in the Mara River (see above; Subalusky et al. 2017). On the contrary, carcasses of Pacific salmon (*Oncorhynchus spp*) in Alaska are transported by biotic vectors such as wolves, bears and gulls from marine and fluvial ecosystem to terrestrial ecosystems (Payne and Moore 2006). Despite this dispersal of nutrients away from the carrion, other important part of the carcass nutrients are locally retained and led belowground by leakage of fluids and transport of carrion tissues by invertebrates. Thus, soil properties (pH and nutrient content) change. Fungi and bacteria from belowground participate in the degradation of complex organic molecules and conversion from organic to inorganic elements (mineralization), making it available to plants. Therefore, the CDI or pulse of fertility that form the carcass create a natural disturbance, which along with the remains of the invertebrate and vertebrate activity and the "passive" response of plant communities increase heterogeneity in the landscape (Carter et al. 2007).

The high diversity of species that gather around carrion point out to scavenging (i.e. carrion consumption) as a widespread feeding strategy in natural ecosystems (DeVault et al. 2003; see chapters "Invertebrate Scavenging Communities" and "Vertebrate Scavenging Communities") and underscores the importance of carrion for biodiversity conservation worldwide (see chapter "Ecological Functions of Vertebrate Scavenging"). Despite it, the role of scavengers in food webs has been traditionally underestimated by 16% (estimated by the number of trophic links involving scavenging; Wilson and Wolkovich 2011). Also, the energy transferred per scavenger link is 124-fold higher than per predation link; therefore, considering scavenging in food webs would lead to more accurate estimates of energy flows (Wilson and Wolkovich 2011). Provided that facultative scavengers consume multiple prey species, the inclusion of scavenging makes more complex reticulate webs, thereby stabilizing the food webs (Wilson and Wolkovich 2011).

Rapid carrion consumption by scavenger communities limits disease spreading and prevents soil and water contamination (Buechley and Şekercioğlu 2016; see chapter "Ecological Functions of Vertebrate Scavenging"). All these important ecological functions of carrion eaters provide additional benefits to humans, i.e. ecosystem services, such as waste disposal and disease regulation (O'Bryan et al. 2018), thus reducing the economic costs of maintaining public health or of carcass transport and disposal (Markandya et al. 2008; Morales-Reyes et al. 2015).

Increasing consumption by a growing human population is altering ecosystems worldwide at an unprecedented pace and extent (Corlett 2015). Besides directly threatening the conservation of scavenging species and their habitats (e.g. hunting, poaching, pollution, land degradation; Dirzo et al. 2014), the increasing consumption of natural resources by humans gives rise to an increasing production of waste (Hoornweg et al. 2013), including human-mediated carrion from, for example, livestock farming, hunting or fisheries (Figs. 1 and 3; Oro et al. 2013; Mateo-Tomás et al. 2015; see chapter "Human-Mediated Carrion: Effects on Ecological Processes"). Human-mediated carrion emerges therefore as a resource subsidizing scavengers across the world ecosystems (Wilmers et al. 2003b; Mateo-Tomás et al. 2015; Mateo-Tomás et al. 2016). Hunting activity produces ~1.0×10^8 tons of carrion per year in European ecosystems, and ~6.9×10^5 tons per year in USA (Vicente et al. 2011; Oro et al. 2013). Fisheries discards (i.e. fish catch which is thrown back, often dead, into the sea) account for ~7.3×10^6 tons per year across the world (Bicknell et al. 2013). Anthropogenic carrion does not only support scavengers but also is frequently related with conservation threats for biodiversity. Livestock carcasses treated with veterinary drugs (e.g. diclofenac) or hunting remains containing fragments of lead ammunition are known sources of toxicity for many scavenging species (Oaks et al. 2004; Finkelstein et al. 2012; Mateo-Tomá et al. 2016; see chapter "What Makes Carrion Unsafe for Scavengers? Considerations for Appropriate Regulatory Policies and Sound Management Practices"). Additionally, human-mediated carrion depends on sectorial policies such as sanitary or economic regulations that constrain its flow into ecosystems and thus impact also on scavenging dynamics and scavenger conservation. Sound examples of this are the sanitary regulations affecting the disposal of livestock carcasses after the outbreak of the Bovine Spongiform Encephalopathy (BSE) or "mad cow disease" in Europe in the 1990s (Tella 2001; Donázar et al. 2009) or the recent reform of the Common Fisheries Policy (CFP) regulating fisheries discards (Bicknell et al. 2013). To effectively deal with the increasing human impacts on the environment under the current scenario of global environmental change, it is necessary to know how the decomposer system works, as this is a crucial piece of ecosystem functioning (Swift et al. 1979).

What Is in This Book

This book focuses on carrion (i.e. dead animal matter; see Glossary in Box 1.1) and its role in ecosystems. The scope of the book is mainly ecological, but it provides also some insights into the conservation and management of scavengers and scavenging. The role of carrion in the environment is examined at different ecological levels, from individuals to populations and communities, as well as on the functioning of the ecosystem. Provided that ecosystems are increasingly altered by human activities and subsidized by anthropogenic carrion (e.g. from livestock, big game or fisheries), this book also deals with human-mediated carrion, examining its potential effects on the conservation of species and ecosystems and how to manage them. This book deals with carrion and their ecological processes involved in both terrestrial and aquatic (freshwater and marine) ecosystems, although a greater attention have been paid to terrestrial ecosystems according to the larger amount of evidence available.

In this book, carrion refers to dead (vertebrate) animal tissues ranging in size from small (e.g. mouse, shrew) to large vertebrates (e.g. elephant, whale; see Box 1.1). Although an abundant dead biomass of invertebrates exists in ecosystems (Nowlin et al. 2008), we have not considered it in this book, due in part to the scarce information still available on the topic (Barton et al. 2013). Yet, an important part of the book is devoted to invertebrates as key consumers of carrion along with vertebrates. Microorganisms that participate in the process of carrion decomposition are mentioned across the chapters, but a more detailed analysis is outside the scope of this book.

This introduction maintains a holistic conceptual view, considering carrion within the detritus pool as in, for example, Swift et al. (1979), Moore et al. (2004), Wilson and Wolkovich (2011) and Barton et al. (2013); thereby the carrion concept is rooted in the general ecological theory. Nonetheless, we consider carrion as a clearly distinct component from other ones (e.g. dead plant matter) within the detritus pool in ecosystems (see above; Wilson and Wolkovich 2011; Barton et al. 2013). The breakdown of dead organic matter into smaller fragments through biological processes that lead to its transformation and mass loss is usually referred to as "decomposition". Here we consider decomposition of carrion in a broad sense, which includes the consumption of carrion by invertebrate and vertebrate scavengers (i.e. scavenging) within the decomposition processes (Wilson and Wolkovich 2011), yet, recognizing the distinct role of scavengers and microorganisms in this process (Putman 1983; Barton et al. 2013). Following Putman (1983) there are two groups of organisms considered as decomposers: scavengers and true decomposers. Scavengers are those organisms (i.e. invertebrates and vertebrates) with holozoic nutrition, i.e. they feed by ingesting and digesting pieces of other organisms (e.g. removing fragments of the carrion); while saprophytes and saprozoic organisms (true decomposers, microorganisms) show saprozoic nutrition through which organisms release externally digestive enzymes, then absorbing from the environment the products resulting from the enzymatic action (reducing it *in situ*). Provided that both kinds of organisms and feeding strategies take part in carrion decay and the recycling of nutrients, it may be considered that both groups of scavengers form part altogether of the decomposition ecological processes of dead animal matter (Putman 1983). It should also be noted that both invertebrates and vertebrates share a similar feeding strategy (i.e. digestion after ingestion; see above), provided that only the *per-capita* removed material size of the carcass would make the difference (Putman 1983). However, as the reader can observe throughout this book, different authors use different terms to refer to carrion decomposition and the organisms that take part in it. Some authors consider scavenging by vertebrates within the decomposition process (e.g. chapter "Carrion Decomposition"), while other authors clearly separate scavenging, as driven by vertebrate scavengers, from decomposition undertaken by invertebrates and microorganisms (e.g. chapter "Ecological Functions of Vertebrate Scavenging").

In the current context of scientific knowledge on carrion decomposition above described, this book details on carrion ecology, paying special attention to the increasing dead animal biomass produced worldwide as a result of human activities. The effects that human-mediated food subsidies such as fisheries and hunting discards or dead livestock on ecosystems are widely recognized from individual to ecosystem level (e.g. Oro et al. 2013), but still poorly understood. For instance, it is largely unknown how ecosystems are assimilating these subsides or how to manage them to avoid conservation problems. This book tries to fill this gap, putting together the last scientific knowledge on carrion ecology with that on carrion management for biodiversity conservation. In this regard, the second part of the book includes three chapters devoted to human-mediated carrion and its management. This is not yet a comprehensive review on this topic since much knowledge is still lacking to accomplish a deep understanding of how human-mediated carrion is impacting subsidized ecosystems.

This book offers an up-to-date scientific review on carrion ecology and management for researchers of these and related disciplines. This volume gathers also information of interests for teachers and graduate students who can benefit from the materials here presented dealing with a fundamental process in ecology and their management applications. Finally, this work emerges as an useful guide for wildlife and conservation managers. The chapters have underwent a double peer review process by the editors and external reviewers (see Acknowledgements).

Literature Review

Although carrion and scavenging have been traditionally understudied in the scientific literature as compared with other topics in ecology, the number of investigations on the field seems to have increased during the last years (Moleón and Sánchez-Zapata 2015). In this section we review and analyze this temporal evolution of the scientific literature about carrion ecology. We examine whether carrion research has recently received a greater relative attention within the ecology discipline and relative to other traditionally more studied topics such as predation.

A Scopus search for "(carrion OR carcass) AND (scaveng*)" in "Title, Abstract and Keywords" of scientific works published until 31 December 2017, and then filtered by the presence of the terms "ecology OR conservation" throughout the manuscript, retrieved a total of 944 publications. There has been a sharp increase in the number of scientific works yearly dealing with carrion and scavenging since the first publication in 1965 until the 84 works published in 2017 (mean ± SD: 18 ± 23 works/year; Fig. 4a). However, when standardized by the total number of papers published in the Scopus categories of "Environment Sciences" and "Agricultural and Biological Sciences", the number of articles dealing with carrion and scavenging

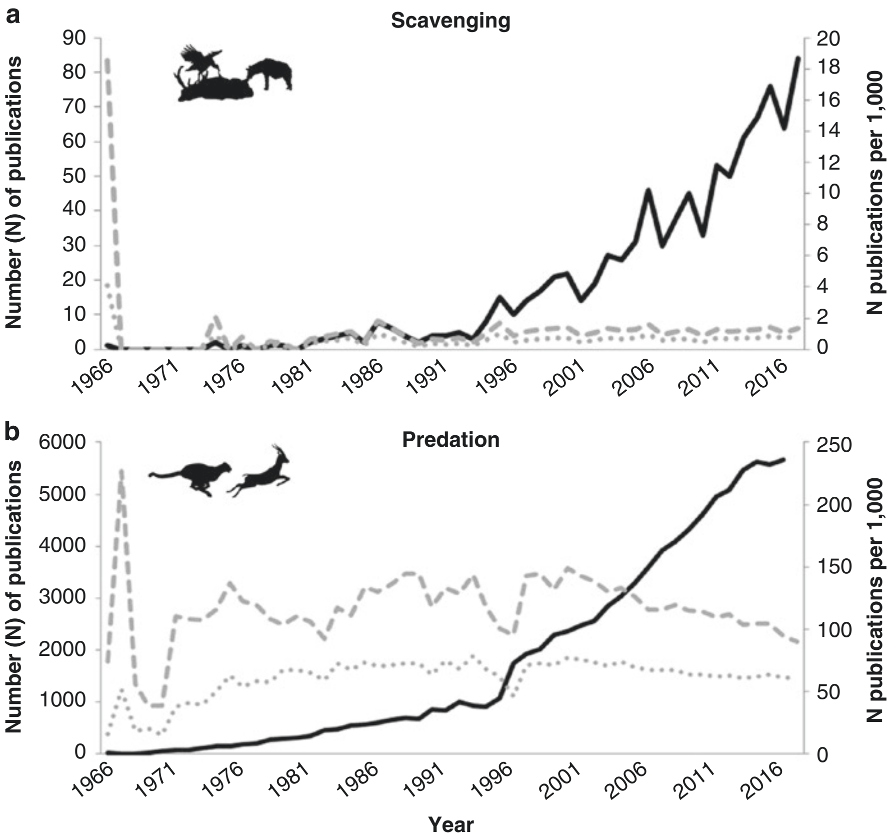

Fig. 4 Number of scientific publications (N) per year retrieved from a Scopus search for (**a**) "(carrion OR carcass) AND (scaveng*)" and (**b**) "predat*" in "Title, Abstract and Keywords" and filtered by the presence of the terms "ecology OR conservation" (solid black lines). The absolute number of publications per topic and year are standardized, i.e. dividing by each 1000 articles yearly published in the categories of "Environmental Sciences" (dashed grey line) and "Agricultural and Biological Sciences" (dotted grey line). Credits: the chapter authors

have been steady since the 1980s (i.e. 1–1.5 works per 1000 per year; Fig. 4a), indicating that the number of articles on this theme has grown at the same pace that the categories where they were included. Therefore despite its increase, there does not seem to be a higher relative intensity of research in the field of carrion and scavenging in the last years. Moreover, the same pattern of increase in the absolute number of publications is also observed in traditional research hot topics such as predation (i.e. as retrieved from a Scopus search for "predat*" in "Title, Abstract and Keywords" using the same parameters described above; Fig. 4b). Contrasting with the steady trend recorded for research in scavenging, the relative number of scientific publications on predation seems to have slightly decreased in the last years (i.e. from almost 150 works per 1000 per year in the 1990s to <100 in 2017; Fig. 4). However, the number of works yearly published on predation is 60–70 times higher than that of publications on carrion/scavenging, indicating the limited scientific attention still received by carrion ecology.

Book Organization

This section summarizes the book content to provide a synthetic picture of how it approaches the state of the art on carrion ecology and management. Additionally, through this summary, the reader can identify topics of interests within the two major sections of the book. The first section focusses on the main characteristics of carrion and the ecological processes triggered by its presence in ecosystems. The second part of the book deals with the role of humans as carrion providers through both the direct generation of carrion and the management of carrion in ecosystems. Finally, the book includes a methodological section intended to provide detailed descriptions and examples of some techniques frequently used in research in carrion ecology and management.

In chapter "Carrion Availability in Space and Time", Moleón et al. analyze the spatiotemporal availability of carrion in both terrestrial and marine ecosystems, including the terrestrial-aquatic interface. To disentangle how animal carcasses appear in ecosystems is of paramount importance for understanding the ecological processes and patterns observed at carrion. Here, the authors discuss the main natural causes for carrion appearance in ecosystems, and how different biotic and abiotic interactions may influence carrion availability for scavengers in space and time. From weather conditions, including extreme events such as El Niño–Southern Oscillation (ENSO; Greig et al. 2005) or hurricanes (Clua et al. 2014), to the key role of predation, accident or disease (see chapter "The Role of Scavenging in Disease Dynamics" for details on the role of disease in carrion ecology), several natural sources of mortality influence the generation of carrion in ecosystems. Similarly, habitat characteristics, weather conditions and inter- and intra-specific interactions (including competition among vertebrates, invertebrates and microorganisms; e.g. Houston 1979, DeVault et al. 2003) determine also carrion accessibility by different scavenging species. The authors highlight the role of species- and individual-specific characteristics such as life stage, body size and condition, sex or gregariousness that greatly determine how much carrion is available, where and when. Additionally, this chapter provides further insights in the different processes that determine carrion availability in terrestrial and marine ecosystems; highlighting, for example, the higher mobility of carrion in marine versus aquatic environments. The chapter focuses on naturally produced carrion (see chapter "Human-Mediated Carrion: Effects on Ecological Processes" for human-mediated carrion), including also extensive livestock because of their similar spatiotemporal availability to that of wild ungulates in many ecosystems around the world.

In chapters "Invertebrate Scavenging Communities" and "Vertebrate Scavenging Communities", Anderson et al. and Selva et al. describe the invertebrate and vertebrate communities, respectively, that consume carrion once it appears in ecosystems. According to the wide range of species that are known to scavenge (e.g. at least 2–11% of the vertebrate species in an ecosystem; Mateo-Tomás et al. 2015), to identify the species that consume carrion is key for biodiversity conservation, and thus for maintaining ecosystem functions and services (Wilson and Wolkovich 2011; see chapter "Carrion Decomposition").

In chapter "Invertebrate Scavenging Communities", Anderson et al. focus on the use of carrion by invertebrates in both terrestrial and aquatic (both freshwater and marine) ecosystems. The authors highlight the role of different groups of invertebrates (i.e. arthropods, nematodes, and molluscs), and the biotic and abiotic factors that influence their occurrence and succession at decaying carcasses. Insects, and especially flies, are the most important scavenging group among terrestrial invertebrates (Fig. 5), while, in marine ecosystems Crustacea have taken over the role of insects. Chapter "Invertebrate Scavenging Communities" shows that, contrasting with terrestrial ecosystems—where obligate and facultative invertebrate scavengers occur—no truly necrophagous aquatic insects exist that feed exclusively on carrion. Anderson et al. highlight the prominent role that temperature has in shaping invertebrate scavenging communities in terrestrial and aquatic ecosystems. A close two-way relationship exists among decomposition, as the process of chemical and material breakdown of carrion, and scavenging by invertebrates.

Fig. 5 The European bone-skipper fly *Thyreophora cynophila* (Panzer) is associated with animal carcasses. Once thought to be the first case of a dipteran species driven to extinction by humans, was rediscovered in 2007, after 160 years from its last observation in the 1840s (Martín-Vega et al. 2010 Syst. Entomol. 35(4): 607–613). Credit: Eva López García

Fig. 6 Among vertebrates, no mammals have evolved into obligate scavengers, yet the hyena is likely the most specialized mammal in the consumption of animal carcasses. Credit: Eva López García

In chapter "Vertebrate Scavenging Communities", Selva et al. describe the composition and structure of vertebrate scavenger communities from the main terrestrial biomes, from polar ecosystems to deserts and abyssal seabed. The authors show that birds and mammals dominate vertebrate scavengers worldwide, but reptiles, fishes and other taxa are also present within the large proportion of scavenging vertebrates that consume carrion as a high-quality food resource. The subchapter provides insights into the traits that characterize obligate (i.e. species exclusively feeding on carrion) versus facultative (i.e. species scavenging as part of a wider diet) vertebrate scavengers (Fig. 6); showing how obligate scavengers dominate carrion consumption in Africa, Asia and Mediterranean Europe while facultative scavengers replace them in higher latitudes. The authors highlight that, although scavenging has traditionally been considered a random and opportunistic process, vertebrate scavenger communities can show non-random complex patterns such as nestedness (i.e. the species feeding on carcasses visited by few consumers are subsets of those species feeding on carcasses visited by more consumers; Selva and Fortuna 2007).

In chapter "Carrion Decomposition", Barton and Bump focus on the decomposition of carrion, i.e. all biotic and abiotic processes that affect the breakdown of an animal carcass. Carrion decomposition is a central ecological process that releases energy and nutrients key to sustain biodiversity and ecosystem functioning (see chapter "Ecological Functions of Vertebrate Scavenging"). The authors detail how the previously described major groups of organisms (i.e. microorganisms, invertebrates and vertebrates; see chapters "Invertebrate Scavenging Communities" and "Vertebrate Scavenging Communities") gear together in carrion decomposition, which also implies intrinsic chemical and physical processes. The chapter provides a description of the temporal decay stages of carrion (i.e. fresh, bloat, active, advance, and dry decay; Michaud et al. 2015), which are pervasively used in entomological and forensic grounds. The contribution of different biotic and abiotic factors such as temperature, moisture or vegetation and habitat characteristics to carrion decomposition is also discussed. The authors further assess the role of scavengers in carrion decomposition in light of ecological theories such as, for example, succession, competition or coexistence and aggregation, as well as other processes operating at larger scales (e.g. movement of carrion across ecosystems, spatiotemporal patchiness of animal carcasses; see chapter "Carrion Availability in Space and Time"). The chapter finally discuss why and how new technologies (e.g. molecular analysis) and interdisciplinary collaboration should be incorporated in research in carrion decomposition.

In chapter "Ecological Functions of Vertebrate Scavenging", Beasley et al. discuss the main ecological functions and services (i.e. ecosystem functions that directly benefit humans) supported by scavengers in both terrestrial and aquatic ecosystems. The chapter highlights the important role of scavengers in food webs, summarizing how different advances in these conceptual frameworks have allowed new insights to better understand scavenging in ecosystems. Concretely, the authors provide detailed descriptions of key ecosystem functions supported by scavengers such as nutrient cycling, biodiversity maintenance, and disease control. These descriptions are illustrated with examples from well-studied systems, from the pristine habitats of the Białowieża Primeval Forest in Poland (Selva 2004) and the Yellowstone National Park in United States (Wilmers et al. 2003a) to farmlands in midwestern USA (DeVault et al. 2003). Although the chapter focuses on the biodiversity-ecosystem function (BEF) and -ecosystem services (BES) relationships of vertebrate scavengers, similar processes are described for invertebrates and microorganisms. Beasley et al. also discuss the impact that different anthropogenic activities influencing carrion availability exert on the ecosystem functions supported by scavengers, a topic of growing importance for scavenging dynamics under the current scenario of global change (see chapter "Human-Mediated Carrion: Effects on Ecological Processes"). The authors highlight the need for more integrative and manipulative research on scavenging ecology across many world ecosystems, especially island, arctic, tropical, and freshwater aquatic habitats.

In chapter "The Role of Scavenging in Disease Dynamics", Vicente and VerCauteren address the complex relationships that exist between wildlife disease dynamics and the epidemiological role of carrion and scavengers. Increasing the scarce knowledge on this topic is crucial to preserve biodiversity and ecosystem integrity but also to safeguard public health. The authors identify important aspects that are central to properly understand this interaction, i.e. the species that consume carrion and their exposure to disease, the role of scavenging for the spread and maintenance of pathogens in ecosystems, and the importance of human-related factors, e.g., for increasing the risks of disease transmission (Daszak et al. 2000). Vicente and VerCauteren highlight also the double dimension of the disease-scavenging interaction. A positive impact of disease on scavengers and scavenging exists; since diseases are important regulators of animal populations, death from disease can produce important pulses of carrion in ecosystems (see chapter "Carrion Availability in Space and Time"). On the other hand, Vicente and VerCauteren discuss also the potential role of carrion and scavengers for transmission and spread of infectious diseases or contaminants (Naranjo et al. 2008), noticing the key role of scavengers in limiting disease spreading (Ogada et al. 2012; see chapter

“Ecological Functions of Vertebrate Scavenging”). The authors review the state of the art in this challenging and often controversial topic, and update the current knowledge to identify major knowledge gaps that should guide future research. Furthermore, as stated in the *Human-mediated carrion* section of this book, this chapter points out the paramount role that humans play in the disease-scavenging dynamics through both directly managing carrion availability in ecosystems (Mateo-Tomás et al. 2015) and indirectly through managing populations of wild and domestic species (Gortázar et al. 2006). The authors call for collaboration between wildlife ecologists, veterinarians and public health professionals to properly tackling this topic.

In chapter “Human-Mediated Carrion: Effects on Ecological Processes” Moreno-Opo and Margalida provide a detailed description of how humans are becoming major providers of carrion worldwide (e.g. Mateo-Tomás et al. 2015) and how this may affect carrion ecology (Fig. 7). To assess how human-mediated carrion is subsidized into natural ecosystems provides further guidance for the effective management of scavengers and the ecosystem functions and services they support (see chapter “Ecological Functions of Vertebrate Scavenging”). The authors make a detailed review of how changes in carrion management influence from individuals to populations of scavenging species as well as the associated ecological processes at community and ecosystem levels (Oro et al. 2013). The chapter also discusses the consequences of these ecological alterations for human well-being (e.g. increasing human health issues and the associated economic costs, vultures’ attacks to livestock; Markandya et al. 2008; Margalida et al. 2014).

Fig. 7 Griffon vultures *Gyps fulvus* are known to track the spatiotemporal distribution of potential food sources, such as transhumant livestock (Olea and Mateo-Tomás 2009). Credit: Eva López García

In chapter "What Makes Carrion Unsafe for Scavengers? Considerations for Appropriate Regulatory Policies and Sound Management Practices" Ogada et al. discuss how the quality of carrion have decreased worldwide due to human intervention, thus threatening scavenger conservation and the ecosystem functions and services associated (see chapter "Ecological Functions of Vertebrate Scavenging"). The authors outline a series factors that make carrion unsafe to scavengers, especially to obligate feeders such as vultures. These threats include accidental toxicity due to the consumption of carrions with residues of non-steroidal anti-inflammatory drugs (NSAIDs) and other veterinary drugs used to treat livestock (Oaks et al. 2004), lead ammunition used to hunt wild ungulates (Finkelstein et al. 2012), or insecticides and rodenticides used in pest control (Olea et al. 2009). Additionally, the chapter also delves into the role of human-wildlife conflicts for scavenger conservation, highlighting the deliberate poisoning of carcasses to kill predators of livestock or game species such as lions, wolves, eagles and hyenas (Fig. 8). The authors analyze the relevance of all these threats for scavenger's conservation across the globe, alerting also of the increase in deliberate poisoning of vultures by ivory poachers in Africa (Ogada et al. 2016). Based on the conservation and management experience of the authors, the chapter offers some recommendations and guidelines for developing appropriate regulatory policies, and vigilant management practices to properly safeguard scavengers from contaminated carrion.

At the end of this book the reader can find some *Methodological approaches* detailing some of the most common and/or novel methods used to research on carrion ecology. In chapter "Methods for Monitoring Carrion Decomposition in Aquatic Environments", Anderson and Wallace describe the techniques and facilities used to study scavenging underwater in freshwater and marine ecosystems. The authors provide further details on the Victoria Experimental Network under Sea (VENUS) observatory (Ocean Networks Canada), an elaborate cabled underwater laboratory in the west coast of Canada and the US. In chapter "Studying Movement of Avian Scavengers to Understand Carrion Ecology", Duriez et al. review the state of the art regarding the use remote technologies for tracking scavengers, focusing on the use of GPS telemetry for vulture monitoring. The authors provide also detailed descriptions of some techniques used to trap and tag these birds and of the usefulness of the information retrieved from these telemetry studies.

Fig. 8 The red kite *Milvus milvus* is a facultative scanvenger highly affected by poison due to this species feeding on small carcasses that are frequently used as poisoned baits. Credit: Eva López García

Book editors provide in chapter "Synthesis and Future Perspectives on Carrion Ecology and Management" a synthesis of the book content; a general picture of carrion ecology and how the existing knowledge on the topic may support carrion management for conservation. The editors highlight the main concepts and topics outlined by the authors of each chapter, including the existing knowledge as well as future research pathways and needs. A visual summary of the book content across the globe is also provided here.

Box 1.1 Glossary

Cadaver: Dead mammal, frequently used to refer to dead human bodies.

Cadaver decomposition island (CDI): As described by Carter et al. 2007, this term refers to the biological, chemical and microbial activity center created in and around a carcass during its decomposition process.

Carcass: Dead corpse of an animal. A usual form for carrion to naturally appear in ecosystems.

Carrion: Dead animal tissues characterized for its high-quality in terms of nutrient richness and assimilation efficiency by consumers. Generally unpredictable and ephemeral, due to a much faster rate of decay than other detritus such as, for example, plant litter.

Consumption: The direct consumption (i.e. feeding) of dead animal tissues by living organisms is part of the process of carrion decomposition.

Decomposer: Living organism contributing to the process of carrion decomposition. Putman (1983) classifies decomposers into two groups of organisms: scavengers (see below) and true decomposers. True decomposers are saprophytes and saprozoic organisms (i.e. microorganisms) with saprozoic nutrition, i.e. they release externally digestive enzymes, then absorbing from the environment the products resulting from the enzymatic action.

Decomposition: the breakdown of dead organic matter into smaller fragments through biological processes that lead to its transformation and mass loss. This is a fundamental ecological process through which occurs the recycling of the nutrients and energy embodied in the dead organic matter.

Degradation: Physical and chemical breakdown of detritus resulting from the action of abiotic factors such as temperature, oxygen concentration, mechanical action of water, wind…

Detritus: Dead organic matter of different origin (e.g. dead plants and animals but also animal dung and other teguments) and quality, i.e. in terms of chemical composition and assimilation efficiency by consumers. Carrion is considered as a high-quality detritus.

Scavenger: Organism (invertebrates and vertebrates) that consumes carrion uniquely (obligate scavenger) or optionally (facultative scavenger).

Scavenging: The process of feeding on carrion by invertebrates and vertebrates.

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