Carrion Availability in Space and Time

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P. P. Olea et al. (eds.), *Carrion Ecology and Management*, Wildlife Research Monographs 2, https://doi.org/10.1007/978-3-030-16501-7_2

Introduction

Availability of carrion to scavengers is a central issue in carrion ecology and management, and is crucial for understanding the evolution of scavenging behaviour. Compared to live animals, their carcasses are relatively unpredictable in space and time in natural conditions, with a few exceptions (see below, especially Sect. "Carrion Exchange at the Terrestrial-Aquatic Interface"). Carrion is also an ephemeral food resource due to the action of a plethora of consumers, from microorganisms to large vertebrates, as well as to desiccation (i.e., loss of water content; DeVault et al. 2003; Beasley et al. 2012; Barton et al. 2013; Moleón et al. 2014). With a focus on vertebrate carcasses, here we give an overview of (a) the causes that produce carrion, (b) the rate of carrion production, (c) the factors affecting carrion quality, and (d) the distribution of carrion in space and time, both in terrestrial and aquatic environments (including their interface). In this chapter, we will focus on naturally produced carrion, whereas non-natural causes of animal mortality are described in chapter "Human-Mediated Carrion: Effects on Ecological Processes". However, throughout this chapter we also refer to extensive livestock carrion, because in the absence of strong restrictions such as those imposed in the European Community after the bovine spongiform encephalopathy crisis (Donázar et al. 2009; Margalida et al. 2010), the spatiotemporal availability of carrion of extensive livestock and wild ungulates is similar.

Causes of Carrion Production

Animals commonly die from natural causes such as predation, starvation, parasites, disease, adverse climatic conditions and accidents. Many animals die naturally during the most susceptible stages of life: early when vulnerability reduces their survival, late because of senescence. Also, animals may die from casualties related to humans (see chapter "Human-Mediated Carrion: Effects on Ecological Processes"), which include intentional mortality sources such as game hunting, fisheries, deliberate poisoning and poaching, as well as unintentional mortality causes such as collisions with infrastructures, road kills, ship strikes, emerging infectious diseases and environmental toxins (Burkholder et al. 1992; Harvell et al. 1999; Laist et al. 2001; Fisher et al. 2006; Lambertucci et al. 2010; Collins and Kays 2011; Koch et al. 2013; Jepson et al. 2013; Wright et al. 2013; Kühn et al. 2015; Benbow et al. 2016). Further, these causes of death often work in concert (Newton 1998). For instance, cold weather conditions may increase the requirement of energy intake and thus increase the risk of starvation (Begon et al. 2006; Conover et al. 2013). Moreover, animals weakened by disease are more prone to predation (Schaller 1972) and, in some cases, collisions with automobiles (Møller et al. 2011).

In terrestrial biomes, most vertebrates usually die due to predation and diseases. Food and water shortage are major drivers of herbivore mortality, either directly or indirectly via enhancing vulnerability to predation, pathogens and others (Pereira et al. 2014). Moreover, exhaustion suffered during long-distance migrations may increase ungulate, bat, and bird mortality rates through different mechanisms (e.g., Geluso et al. 1976; Mduma et al. 1999). Apex carnivores, in contrast, mostly die as a consequence of competition (including intraguild—both inter- and intraspecific—killing; Palomares and Caro 1999; Thompson et al. 2015), parasites, and senescence.

In aquatic ecosystems, for some anadromous fish species (e.g. Pacific salmonids *Onchorhynchus* spp.), reproduction coincides with death. Necropsies of stranded marine mammals and turtles revealed these animals are susceptible to a wide range of parasites and viruses (Harvell et al. 1999; Arbelo et al. 2013; Work et al. 2015). Toxic diatom blooms can produce massive mortalities among sea lions (Scholin et al. 2000). Furthermore, mortality events can be also associated with large-scale climatic perturbations (Evans et al. 2005). In the South Pacific, for instance, mass mortality of Pygmy killer whales (*Feresa attenuata*) was linked with extreme meteorological conditions, such as the hurricanes Marylyn and Jim (Clua et al. 2014). Furthermore, fish kills can be attributed to natural conditions of oxygen deficiency (Stachowitsch 1984), extreme cold waters (Marsh et al. 1999; Hoag 2003) or river water acidification (Fjellheim and Raddum 1990). Similar to large animals in terrestrial ecosystems, whales and large sharks are probably subject to reduced predation risk and thus senescence and disease must be the most important natural causes of mortality, at least for adults.

Estimates of Carrion Production

Quantifying how much carrion is produced in ecosystems is one of the most important, although probably the most overlooked, aspect of carrion ecology (Oro et al. 2013). This is mostly due to methodological difficulties in obtaining empirical data in both terrestrial and aquatic systems. Estimating how much carrion is produced temporally and spatially is a complex issue that requires intensive fieldwork (e.g., Selva 2004), sometimes in combination with sophisticated modelling approaches (e.g., Wilmers and Getz 2004, 2005; Margalida et al. 2011).

Overall

In terrestrial ecosystems, as we show in Table 1, only a few studies have provided estimates of carrion biomass production per units of time and space in natural conditions (provision to dumps and vulture feeding stations, intensive livestock debris and game hunting remains are considered in chapter “Human-Mediated Carrion: Effects on Ecological Processes” because of their human origin). All these studies have focused on ungulates (wild, domestic or both). When all mortality causes are considered together, carrion is produced at an annual rate of up to ca. 700 kg/km^2. In all cases, carrion supply ranged between tens to hundreds of kg/km^2, although estimation methodologies, as well as the species evaluated, were highly heterogeneous among the reviewed studies (Table 1).

In well-preserved coastal systems, carcass supply can be substantially higher than inland. On the Isle of May (Scotland), an average of ca. 7000 kg of grey seal (*Halichoerus grypus*) placenta and dead pups and adults are produced annually, which means localised concentrations of as much as ca. 15,000 kg/km^2 (Quaggiotto et al. 2018). Up to 530 kg/km of stranded carrion accumulates annually along the shoreline of the Gulf of California (Polis and Hurd 1996b), whereas seabird colonies within the same gulf provided carrion with densities ranging between 5 and 100 kg/km^2, depending on the nesting island (Sánchez-Piñero and Polis 2000).

Table 1 Carrion biomass (kg/km^2) produced in different terrestrial systems by natural causes such as predation or disease

Continent	Country	Location	Carrion biomass	Species	Period	Reference
Africa	Zimbabwe	Rural Zimbabwe	696	Domestic and wild ungulates	Annual	Butler and Du Toit (2002)
Europe	Poland	Białowieża Primeval Forest	89	All wild ungulates	Annual	Selva (2004)
	Spain	Continental Spain	195	Extensive livestock	Annual	Morales-Reyes et al. (2017a)
		Cantabrian Mountains	2.1–40.3	Extensive livestock (transhumant)	Annual	Olea and Mateo-Tomás (2009)
			1.5–8.7	Extensive livestock (resident)	Annual	Olea and Mateo-Tomás (2009)
	Sweden	Sarek National Park	0.6–9.6	Reindeer (wolverine and Eurasian lynx kills)	Annual	Mattisson et al. (2011)
	UK	Scottish Highlands	264	Sheep and red deer	Annual	Brown and Watson (1964)
		Pastoral land (Wales)	190	Sheep	Annual	Newton et al. (1982)
North America	USA	Yellowstone	69–104	Red deer	Cold season	Houston (1979)
			13–63	All ungulates	Cold season	Gese et al. (1996)
			9	Red deer (wolf kills)	Cold season	Wilmers et al. (2003a, b)
South America	Chile	Central Patagonia	0.2	All ungulates (puma kills)	Annual	Elbroch and Wittmer (2012)

Studies evaluating human-mediated carrion (e.g. dumps, vulture feeding stations, intensive livestock debris or game hunting) are considered separately in Chap. 8

Covering over 70% of the planet's surface with a volume of 1332 billion km^3, the marine system is both the largest environment on earth and also one of the least accessible and least understood (Glover et al. 2010; Ramirez-Llodra et al. 2010). Natural food falls and fish carcasses are, in fact, relatively unusual observations (Soltwedel et al. 2003). This is probably because most of the seafloor is deep (>200 m); an environment which is hard to observe and where carrion is rapidly consumed (Isaacs and Schwartzlose 1975; Bailey and Priede 2002). Considering the nine largest whale species, it has been calculated that at any given time there is a fresh (i.e., with soft tissue) whale carcass on the sea floor every 16–36 km (Smith and Baco 2003).

In some rivers of the North Atlantic and North Pacific regions, salmon runs may signify a massive input of nutrients. For example, rivers of the Bristol Bay in Alaska (400 km long and 290 km wide) receive annually around 5.4×10^7 kg of adult salmon from the ocean. These salmon, whose biomass was gained mostly in the sea, will die shortly after spawning, thus subsidizing a complex array of both terrestrial and fresh water scavengers and decomposers (Gende et al. 2002). Terrestrial animals can also subsidized aquatic ecosystems through the provision of carrion (Pringle 2017). For instance, the mass drowning of wildebeests (*Connochaetes taurinus*) crossing the Mara River in the Serengeti (Africa) during the annual migration provides an annual input of 1,100 tonnes of biomass entering the river system (Subalusky et al. 2017).

Per Mortality Cause

Both in terrestrial and aquatic systems, carrion biomass provision depends chiefly on the mortality cause. Among natural sources of mortality, the main distinction is made between carrion supplied in the form of predator kills and other sources of carrion (see Sect. "Causes of Carrion Production"). While the latter result in complete carcasses being available to scavengers, only a portion of predator kills (i.e., the part not consumed by the predator) can be accessed by scavengers. In Białowieża Forest (Poland), Selva (2004) found that 35% of ungulate carrion was provided by disease and/or starvation, whereas predation by wolves (*Canis lupus*) and Eurasian lynxes (*Lynx lynx*) was responsible of 30% and 1% of carrion supply respectively (the remaining 34% of total ungulate carrion biomass was carrion of harvested animals left in the forest). In the Serengeti (Tanzania), 55–92% (depending on the month) of ungulate carcass supply to vultures comes from causes other than predation (Houston 1974). The abundance and nature of the predator is also important in determining how much of the predator kill is available to scavengers (Moleón et al. 2014; Table 1). For instance, solitary carnivores and those that do not return to their kills once satiated (e.g., cheetah *Acinonyx jubatus*) may leave more carrion per individual carcass in general than social ones (e.g., lions *Panthera leo*; Hunter et al. 2006; Elbroch and Wittmer 2012) and those that guard their kills for future consumption (e.g., leopards *P. pardus*; Kruuk 1967; Hunter et al. 2006).

Carrion Production in Relation to Species and Individuals

Carrion supply can also be strongly influenced by species identity, as it will determine carcass size and the rate at which carcasses are produced. Thus, large species would provide more carrion than smaller ones, and highly productive species would produce more carcasses than less productive ones (Fig. 1). 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 the former. In addition, obviously, population abundance must be considered when determining how much carrion biomass can be produced by a given species. In Białowieża Forest, red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) supply more carrion per year (3522 and 2417 kg, respectively) than larger (moose *Alces alces*, 404 kg; European bison *Bison bonasus*, 1600 kg) and smaller ungulates (roe deer *Capreolus capreolus*, 100 kg; Selva 2004).

Megaherbivores, i.e., herbivores weighing above 1000 kg (Owen-Smith 1988), are normally free from predation, especially as adults. Thus, megaherbivore carrion supply, mostly in the form of whole carcasses from sick, malnourished and senescent individuals, is an important contribution to the total carrion biomass in some African ecosystems, especially once depression of populations of elephants (*Loxodonta africana*) and other large herbivores by humans ceases and a stationary age distribution is reached (Pereira et al. 2014). The same basic pattern is expected to occur in the oceans, where whales, large sharks, marine mammals and large turtles are scarcely subject to predation (e.g., Heithaus et al. 2008).

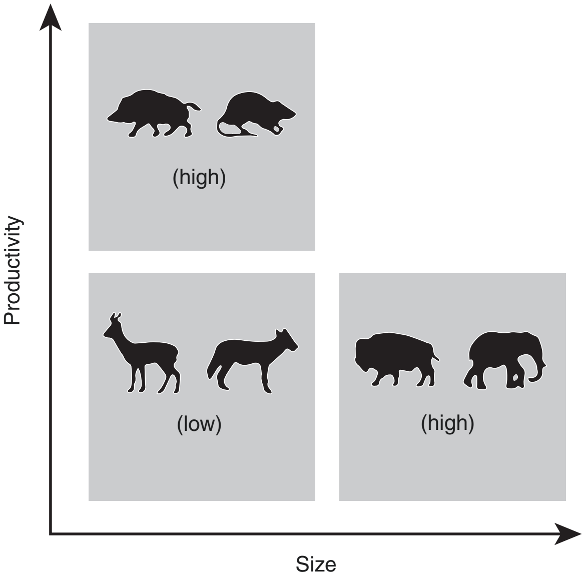

Fig. 1 Carrion supply magnitude (high *vs*. low) in relation to the size and productivity of animals under natural conditions. Note that there are no very large *and* very productive animals. Credits: the chapter authors

Another major factor influencing how much carrion is produced is individual identity. Sex, age and body condition strongly determines individuals' vulnerability to mortality (Pereira et al. 2014). For instance, newborns, calves and old animals (Husseman et al. 2003; Barber-Meyer et al. 2008), as well as pregnant females (Molinari-Jobin et al. 2004) and male ungulates competing for mating rights (FitzGibbon 1990), are especially vulnerable to predation.

Because of their high biomass, marine mammals are almost certainly one of the main contributors of vertebrate carrion to the marine system. However, the evidence of carcasses is rare. Marine mammal mortality is in fact estimated by monitoring their population through regular censuses, and losses from the population can be identified by simultaneous analysis of live resighting and dead recovery mark-recapture data. This method has been used to estimate an average first year survival in grey seals in Britain of ca. 20% for males and ca. 60% for females (Hall et al. 2001).

Factors Modulating Carrion Availability and Quality

The number of animals dying within and across ecosystems, the cause of death and the species and individual identity of carcasses are not the only factors influencing the amount of carrion biomass available to vertebrate scavengers. Carcass location, weather conditions and biotic interactions can greatly modulate carrion accessibility to scavengers in space and time. For scavengers that rely mainly on visual cues to detect food, vegetation cover and structure may crucially influence the rate and speed at which carrion is encountered (Ogada et al. 2012; Fig. 2). Some debilitated

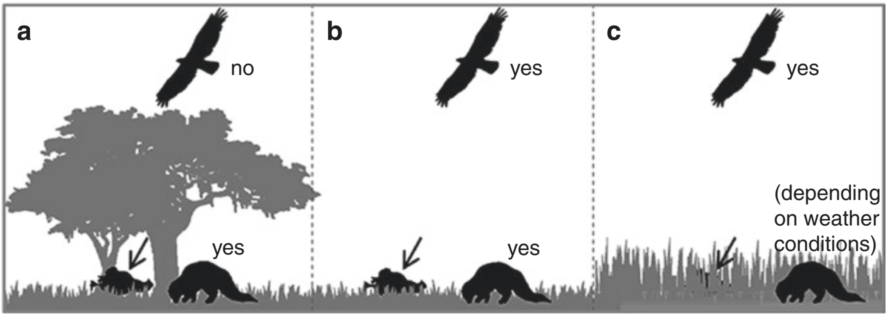

Fig. 2 Vegetation cover and structure may influence the ability of scavengers to locate carcasses (indicated by arrows). Soaring scavengers will rarely see a carcass located below dense tree canopy (**a**), whereas carcasses located in open habitat (**b**, **c**) may be easily found. Non-flying scavengers may readily see a carcass located within short grass, irrespective of the presence (**a**) or absence (**b**) of trees; however, they will find more difficulties in seeing a carcass located within tall grass (**c**). Difficulties in locating carcasses by sight can be overcome by acute sense of smell, provided that weather conditions do not dissipate odorants produced by carrion. Similar scenarios can be expected in aquatic environments. Credits: the chapter authors

animals such as malnourished megaherbivores often die near surface water (Conybeare and Haynes 1984). Due to vegetation encroachment along river and lake margins, such carcasses may be hardly accessible to certain scavengers such as large birds. Windy and rainy conditions will limit the capacity of soaring birds such as vultures and other large raptors to forage (Houston 1979; Selva et al. 2005). Rainfall can also reduce the olfactory capacity of mammalian carnivores (Savage 1977; Ruzicka and Conover 2012). In addition, carcass location by olfactory scavengers may be constrained by high temperatures and low humidity (Ruzicka and Conover 2012). In general, large carcasses are more accessible compared to carcasses of small animals that may appear in hollows inaccessible to most scavengers (Cox and Smith 1992, but see DeVault and Krochmal 2002).

Both inter- and intra-specific interactions, mediated by differences in behavioural, ecological, morphological and physiological traits among vertebrate obligate and facultative scavengers may influence the ability to find and consume carrion (Kendall 2013; Moleón et al. 2014; Sebastián-González et al. 2016; Moreno-Opo et al. 2016. First, mentioned above, predator kills may provide important quantities of food to scavengers (e.g., Kruuk 1967). Indeed, carrion provided by predators such as wolves is increasingly important in northern areas where milder winter weather conditions are reducing the number of carcasses produced by other causes during this critical period (Wilmers et al. 2003a, b; Selva et al. 2005; Wilmers and Getz 2005; Wilmers and Post 2006; Wikenros et al. 2013). Second, predators themselves and scavengers that rapidly arrive to the carcass may signal carcass location to other scavenger species and individuals (Attwell 1963; Kruuk 1967, 1972; Prior and Weatherhead 1991; Cortés-Avizanda et al. 2012; Kendall 2013; Cortés-Avizanda et al. 2014; Kane et al. 2014). Third, large mammalian carnivores and certain vultures may facilitate access to the interior of thick-skinned carcasses to less powerful scavengers by tearing open the tough hide (Attwell 1963; Stahler et al. 2002; Selva et al. 2003). Fourth, competition, both exploitative and interference (Birch 1957; Begon et al. 2006), may limit access to carrion by competitively inferior scavengers such as small mammalian carnivores (Kruuk 1967, 1972; Schaller 1972; Houston 1974, 1979; Kendall et al. 2012; Kendall 2013; Moleón et al. 2015). In this sense, the lack of specialist carrion consumers—such as *Gyps* vultures that quickly locate and deplete carrion resources (Houston 1979; Sebastián-González et al. 2013; Cortés-Avizanda et al. 2014; Sebastián-González et al. 2016; Morales-Reyes et al. 2017b)—in cold environments increases the duration of carcasses and thus could favour other carrion consumers. In British Columbia (Canada), in absence of obligate scavengers, biomass of salmon carrion—which is highly predictable and easy to handle—in estuarine environment was positively related not only with the abundance of scavengers but also with the diversity of the scavenging community (Field and Reynolds 2013).

The composition of invertebrate communities also can affect the temporal availability of carcass resources and, by extension, the composition of vertebrate scavenger communities. Houston (1985) showed how fly larvae completely consume carcasses of 2–10 kg within 3 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, 1988). Houston (1985) speculated that this temporal regulation of the food supply by invertebrates contributed to the presence of vultures in forested regions in South America, as opposed to Africa, where vultures are confined to open savannahs and grasslands.

Microbial decomposers can quickly render carcasses inedible to most would-be scavengers by producing toxic compounds on carcasses (Janzen 1977; Burkepile et al. 2006; Shivik 2006). Microbes are more active as temperatures increase (Putman 1983; Carter et al. 2007), and several studies have demonstrated that vertebrates consume fewer available carcasses in warm weather compared to cold weather (DeVault et al. 2004; Selva et al. 2005; Parmenter and MacMahon 2009), likely due to increased activity of decomposers at higher temperatures. A factor closely related to microbial activity is carcass size: the larger the carcass, the longer the time needed to be consumed and, consequently, the greater the putrefaction (Pereira et al. 2014; Moleón et al. 2015). However, competition for food among vertebrate scavengers is reduced at very large carcasses (Moleón et al. 2015).

Similar to the terrestrial environment, the temporal availability of carrion to marine scavengers may be influenced by bacteria which affect carrion consumption. Unlike in terrestrial systems, internal decomposition may make the carcass buoyant so that it leaves the seafloor, removing carrion from the reach of some scavengers and giving access to others. Another difference in marine systems is that in large carrion items such as whale falls in deep water, the actions of bacteria result in overlapping stages of ecological succession (Bennett et al. 1994; Smith et al. 1998; Beasley et al. 2012). In these circumstances anaerobic bacterial decomposition of bone lipids (sulphophilic stage) occur after the removal of the soft tissue by necrophages (mobile-scavenger stage) and the colonisation of the bones and the nutrients-enriched sediments by assemblages of macro-benthic organisms (enrichment-opportunist stage). During decomposition, a chemosynthetic assemblage may develop where carbon is fixed from the water column using the energy released by the oxidation of sulphides in whale bones. In shallow waters, microbes were found to cover the skin of marine mammal carrion creating a bacterial mat that possibly prevents consumption by larger carrion consumers (Glover et al. 2010; Quaggiotto et al. 2016). Microbe-laden fish carrion, in fact, was colonised at lower extent than fresh carrion by scavengers such as crabs, demonstrating that bacteria can act as deterrent to scavenging activity (Burkepile et al. 2006).

Spatial Variation in Carrion Availability

The most likely place to find carrion is, of course, where live animals can be found, and more specifically, where they die (Olea and Mateo-Tomás 2009; Mateo-Tomás and Olea 2010). Thus, to determine spatial variation in carrion availability, one must consider where animals spend time during various activities. Also, because some individuals are consumed completely by predators immediately after their death and thus do not contribute to the pool of carrion available to scavengers (Houston 1974, 1979), spatial variation in carrion availability is also influenced by differences in cause-specific mortality across species and locations (see above). In this section, we briefly consider factors that affect carrion availability across space by examining where animals tend to die, and how the cause of death influences carrion availability across locations. First, we focus on terrestrial ecosystems, which differ from aquatic ecosystems in that animals that die on land typically do not move after death before consumption, whereas animal carcasses in water often sink, float or are moved by currents (Beasley et al. 2012; see Sect. "Aquatic Ecosystems").

Terrestrial Ecosystems

Some areas of the home range are more dangerous than others, and thus certain causes of death are associated with predictable locations. In an example highlighting particularly risky locations, male birds reduced nest visits to feed incubating females when perceived predation risk increased, suggesting that mortality is higher at the nest than elsewhere in the home range (Ghalambor and Martin 2002). Carrion also can be found predictably along migration routes and at grazing areas for wild and domestic ungulates (Houston 1974; Olea and Mateo-Tomás 2009; Kendall et al. 2014). Scavengers are known to take advantage of predictable carcass locations; for example, some scavenging birds preferentially forage for carrion along roads (Lambertucci et al. 2009).

Unfortunately, few data are available on locations of animal carcasses that die from exposure to toxins, parasites, disease, extreme elements, or starvation, as studies of cause-specific mortality rarely report this information (see Collins and Kays 2011). Even so, it seems likely that individuals dying from these causes might come to rest in less predictable locations than those that are killed by predators or human-related causes (e.g., collisions with vehicles and structures). For example, rodents exposed to anticoagulant poisons were found dead both in the open and in underground burrows (Cox and Smith 1992; Howald et al. 1999; Tuyttens and Stuyck 2002). We note that although underground carcasses might be unavailable to many scavengers, some species such as snakes could be well suited to detect, find, and consume such carcasses (Cowles and Phelan 1958; DeVault and Krochmal 2002). Sometimes, places of death are predictable at the microhabitat scale. For instance, weakened African elephants tend to die near water holes (Conybeare and Haynes 1984).

At a biogeographical scale, some patterns in carrion availability can be identified. Neotropical forests seem to provide a greater food supply to vertebrate scavengers than Afrotropical forests due to the higher biomass and average turnover of herbivorous mammals in the former (Houston 1985). In addition, as mentioned in Sect. "Factors Modulating Carrion Availability and Quality", carcasses remain available to vertebrates in Neotropical forests for longer periods than in Afrotropical forests likely due to interactions among the invertebrate community.

Aquatic Ecosystems

Fresh marine mammal carrion may not often be detectable because it is rapidly scavenged or decomposed at sea (Gulland 2006), making it challenging to determine its distribution in space. The fact that their skeleton or bones last longer could reveal some spatial patterns. However, the discrepancy occurring between where a marine mammal dies and where its body is transported, regardless it ends up with either a fall onto the seabed or a stranding on the shore, suggests that movements of carrion in the aquatic ecosystem involve a larger spatial and three-dimensional scale than carrion originated on land (Beasley et al. 2012). In water, mobility of carrion can be facilitated not only by currents and waves, but also by body density of the carcass and decomposition processes undergoing inside it. Body composition (blubber and lean) of the carcass determines its buoyancy (Peltier et al. 2012); putrefaction gases can cause its flotation (Reisdorf et al. 2012). Pressure and temperature also concur in facilitating movements of carrion: in particular, conditions of 15 atmosphere (atm) of hydrostatic pressure prevent the re-floating of large whales (>40 tons) in cold water (Smith and Baco 2003); whereas a carcass of a harbour porpoise (*Phoceona phocoena*, ca. 60–70 kg) at temperature above 4 °C is likely to surface in shallow waters (Moreno et al. 1992). Over the process of decomposition and consumption individual carrion items may be available to more than one type of scavenging assemblage depending on where the carcass is transported, with different consequences for the eventual fate of the energy and nutrients within it. Floating bodies may be exposed to scavenging birds when floating at the water surface or when stranded on the shore (Hewson 1995). Damage by scavenging birds may compromise the integrity of floating carcasses (Hewson 1995) and cause its sinking back to the seabed making it available again to the marine community. Overall, whale carcasses are expected to be most frequently found along migration routes and around feeding grounds, which use to be located near ocean margins (Smith and Baco 2003).

An environment where carrion is naturally available in high abundance is iceberg-scoured shallow coastal waters. Here benthic communities are periodically crushed and scraped from rocks, or ploughed into/from the sediment by the action of moving ice. Scavenger assemblages and activity are highly spatially variable. This variation can be between areas of different aspect (Smale et al. 2007) and depth (Dunlop et al. 2014). These differences presumably reflect the supply of carrion and the risk of death to the scavengers themselves. There is presumably an intermediate level of carrion impact, which is optimal for scavenging. At extremely high level of scouring there will never be much biomass to turn into carrion, with only biofilms having time to grow between impacts and the scavengers themselves could not survive. At very low levels of impact there will be little mortality to provide the carrion and so an intermediate level of iceberg impact is necessary (Dunlop et al. 2014).

In North Atlantic and North Pacific rivers, salmon carrion is expected to concentrate around spawning sites, where most adult mortality occurs (Gende et al.

2002). Naturally, currents, physical barriers and consumption rates by scavengers will largely determine to which extent this pulse of salmon carrion is expanded down the river.

Temporal Variation in Carrion Availability

Much like spatial variation in carrion availability, temporal variation in carrion availability is dependent on the cause of death. Starvation, predation, disease, exposure to extreme elements, and several human-related causes of death can fluctuate substantially in magnitude and thus provide carcasses to scavengers at differing rates across the year and between years (DeVault et al. 2003; Wilson and Wolkovich 2011; Pereira et al. 2014).

Terrestrial Ecosystems

Seasonality in carrion supply is a common feature of seasonal ecosystems, where ungulate mortality resulting from causes other than predation is related to the period of the year when food availability is limited and thermal stress is maximum. In northern latitudes, this takes place during the winter, while in African savannahs, it occurs toward the end of the dry season (see Pereira et al. 2014 and references therein). These limiting conditions can be especially harsh in some years, thus producing inter-annual oscillations in carcass production. For example, herbivore carcasses in Kruger National Park are very abundant during disease outbreaks and severe droughts, to the point that a number of them may remain uneaten (Owen-Smith and Mills 2008).

Although carrion resources are often produced in pulses, in some areas carrion is present consistently across the year and between years at the landscape scale. This consistency in available carrion is evident by the occurrence of resident vulture communities (e.g., across much of the Americas and parts of Africa, Asia and Europe), which subsist almost exclusively on carrion (Houston 1979; DeVault et al. 2003; Moleón et al. 2014).

Carrion availability through time can be strongly influenced by vertebrate predators. In one well documented example, Wilmers and colleagues (Wilmers et al. 2003a; Wilmers and Getz 2004, 2005; Wilmers and Post 2006) studied how carrion resources in Yellowstone National Park, USA, changed after the reintroduction of wolves. They found that predation on elk by wolves changed the nature of carrion available to scavengers from a predominantly pulsed resource resulting from a late-winter influx of whole carcasses (caused by starvation of elk and other herbivores in harsh environmental conditions) to a more temporally-stable resource resulting from partial consumption of elk killed by wolves. Wolves thus provided a temporal subsidy to their smaller congeners, coyotes (*Canis latrans*), and other vertebrate scavengers by reducing the variation in carrion availability within and across years.

Aquatic Ecosystems

Without human interference, carrion in the ocean is infrequent in time and space (Britton and Morton 1994). Carrion availability derived from marine mammals such as whales has changed over historical time (Smith and Baco 2003). Before whaling there would have been natural mortality, leading to the majority of cetacean carcasses being made available to scavengers. Nowadays, after implementation of conservative measures, whale falls may follow a seasonal pattern according to annual migrations (Smith and Baco 2003; Roman et al. 2014) and environmental conditions occurring at that time. For instance, the unusually high mortality of grey whales (*Eschrichtius robustus*) along the migratory route in 1999 was linked to the undernourished body conditions displayed by the stranded animals due to low amphipod biomass, their main food source. Higher sea temperatures, together with an increase in whale population density, were hypothesised to be the principal reason explaining the fatally low prey availability (e.g. Le Boeuf et al. 2000). Little is known about temporal availability of carrion in the ocean as most of the information available on this topic is the result of analysis on seasonal patterns of strandings (Peltier et al. 2013), whereas direct observations of carcasses at sea are rare (Smith et al. 2015).

Fish populations also change in predictable ways, probably providing temporal, but also spatial, variation in the carrion they supply. Deep sea fish populations appear to respond to changes in carrion availability due to migration. Inter-annual variation in abyssal fish numbers can be linked to variation of the Pacific hake (*Merluccius productus*) spawning aggregation in the waters overlying them (Drazen et al. 2012). Temporal trends in fish mass mortality can be predicted by determined environmental conditions more likely to occur seasonally (Stachowitsch 1984; Schoenebeck et al. 2012) or globally driven (Marsh et al. 1999). Salmon carcasses in rivers of the northern Hemisphere are available only in a short period of time after spawning (Gende et al. 2002).

Iceberg action leading to carcass production is also highly seasonal, dropping dramatically in winter when sheets of “fast ice” lock icebergs into position and occurring again in the spring. Cold winters with longer periods of fast ice presence result in lower levels of iceberg scouring (Smale et al. 2008).

Carrion Exchange at the Terrestrial-Aquatic Interface

Coastal regions are often massively affected by marine-derived inputs transferred from the ocean to the terrestrial ecosystem (Polis and Hurd 1996a, b; Polis et al. 1997; Rose and Polis 1998) by biotic factors such as marine currents, air circulation and weather conditions. Strandings of carrion, which are the evident results of mortality events happening at sea, occur when positively buoyant carcasses disperse from the original location of death and drift towards the coastline. Natural mortality of cetaceans, for instance, generates single unpredictable carcasses in the ocean, which can be possibly washed on the coast. Mass stranding can be classified as unusual mortality events (UMEs; Marine Mammal Protection Act) when for initially unknown reasons a large part of the population dies. These events, whose causes can be related to biotoxins, bacteria, parasites, human interactions and oceanographic conditions, are also spatially unpredictable phenomena, in which marine mammals strand in a delimited space and during a limited time (Wilkinson 1991). Stranding data can reveal supplementary information on the spatial distribution of fatalities and their post-mortem movements: from the position of the stranding it is possible, in fact, to estimate the original location where the animal died by reconstructing the animal's drift by modelling local sea currents and tides (Peltier et al. 2012; Santos et al. 2018).

Mass mortality caused by El Niño, instead, might be predicted as it periodically affects the east-central tropical Pacific Ocean. During the El Niño, California sea lion (*Zalophus californianus*) fatalities were dominated by malnourished juveniles (Greig et al. 2005), as the mothers spent more time at sea searching for food, which was drastically reduced by the environmental perturbation, instead of lactating the pups (Ono et al. 1987). The lack of food and the anomalous sea conditions created during El Niño can affect the survival of seabirds, which also die at sea and are washed ashore (Piatt and van Pelt 1997).

In addition to the abiotic transfer of resources, transport of marine nutrients can also occur when animals move from one system to another. Salmon, for instance, has already been shown to play a fundamental role in this process affecting different components of the ecosystem (Cederholm et al. 1999). Every year, in defined spawning areas up stream, salmon carcasses represent a source of carrion that enriches soils and plants, locally releasing nutrients (e.g. Quinn et al. 2009; Hocking and Reimchen 2009). This impact is long term as its signal is still detectable in historically salmon-bearing stream (Koyama et al. 2005). Moreover, predictability of salmon runs in riparian systems is responsible for the synchronisation between feeding strategy and food input in black bears (*Ursus americanus*) and more recently in wolves (Reimchen 2000; Darimont et al. 2003). Carcasses of moose, which widely forage on aquatic plants, mean an important nutrient transfer pathway from freshwater to terrestrial systems in the circumpolar region (Bump et al. 2009).

Likewise, marine mammals affect coastal systems and their impact is substantial when they assemble in colonies for breeding. Here, they provide sources of nutrients in terms of carrion which are used either directly by above ground secondary consumers, or indirectly by increasing the input of nutrients from excreta (Anderson and Polis 1998). In Scotland, for instance, placentae and dead seals produced at a grey seal (*H. grypus*) colony represent a valuable food resource for scavenging gulls during the cold season (Quaggiotto et al. 2018). Due to the proximity to the sea and the inherent tidal and wave action, carcasses may be dislodged and potentially affect also the intertidal and sublittoral marine scavengers.

Conclusions and Future Perspectives

Death is a fundamental component of ecosystems. Every year, many kilograms of carrion biomass (tens to hundreds according to the reviewed studies) are produced in terrestrial systems per km^2 (see chapter "Human-Mediated Carrion: Effects on Ecological Processes" for human-mediated carrion and the possible impact of global environmental change on the spatiotemporal availability of carrion resources). This figure can be substantially higher in well-preserved coastal environments with large colonies of marine mammals. Also, salmon and other fish spawning provide massive carrion pulses. The magnitude of carcass supply, as well as its quality and availability to scavengers, is the result of many interacting factors such as animal density and turnover rates, the cause of death, carcass location, weather conditions and biotic interactions (both among and within vertebrates, invertebrates and microorganisms). In addition, carrion biomass available to scavengers may vary among species and individuals. However, despite its paramount importance for understanding carrion ecology, carrion supply remains largely understudied compared to carrion consumption. For instance, the relationship between interspecific interactions and carrion provision and nutritive value deserves further scientific attention.

The spatial predictability of carrion varies greatly, depending on carcass type, cause of death, and ecosystem. Future research on cause-specific mortality (Collins and Kays 2011) should consider reporting the exact location of death (i.e., for radiomarked animals) so that spatial variation in carrion availability can be more accurately defined. The availability of carrion to scavengers can also vary according to the temporal scale considered. In some situations, temporal variation of carrion supply is linked to spatial variation. For example, shortly after spawning (once per year), semelparous salmon die in large numbers in rivers, and many scavengers take advantage of this resource in the limited area where it occurs (Bennetts and McClelland 1991; Hewson 1995). In contrast, animals in temperate and arctic regions commonly die from starvation during extended periods of cold weather (Wilmers et al. 2003a); these carcasses are produced in a temporal pulse, but can be found scattered across extensive areas.

The spatiotemporal availability and quality of carrion can substantially influence the density and diversity of scavengers occupying an area (DeVault et al. 2003; Wilson and Wolkovich 2011; Barton et al. 2013). The growing field of scavenging ecology would benefit from further investigations quantifying the spatiotemporal availability of carrion for vertebrate scavengers across regions. More studies are needed in some continents and on islands. Quantitative studies in aquatic systems are especially encouraged, as well as those evaluating carrion exchange between terrestrial and aquatic environments. Multi-species approaches would be especially welcome. For instance, quantifying carrion biomass produced by small and highly productive animals versus large and less productive animals may be particularly interesting. The influence of microhabitat characteristics on carcass availability and accessibility to scavengers that rely on vision versus those with high olfactory skills should be further investigated. In summary, the fields of carrion ecology and management would largely benefit from the study of the many mysteries related to the spatial and temporal availability of carrion that remain unresolved.

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