Humans and Scavengers: The Evolution of Interactions and Ecosystem Services

MARCOS MOLEÓN, JOSÉ A. SÁNCHEZ-ZAPATA, ANTONI MARGALIDA, MARTINA CARRETE, NORMAN OWEN-SMITH, AND JOSÉ A. DONÁZAR

Since the origin of early Homo *species during the Late Pliocene, interactions of humans with scavenging birds and mammals have changed in form through shifting ecological scenarios. How humans procured meat during the Quaternary Period changed from confrontational scavenging to hunting; shepherding of wild animals; and, eventually, intensive husbandry of domesticated animals. As humans evolved from carcass consumers to carcass providers, the overall relationship between humans and scavengers shifted from competition to facilitation. These changing interactions have translated into shifting provisioning (by signaling carcass location), regulating (e.g., by removing animal debris and controlling infectious diseases), and cultural ecosystem services (e.g., by favoring human language and social cooperation skills or, more recently, by enhancing ecotourism) provided by scavenging vertebrates. The continued survival of vultures and large mammalian scavengers alongside humans is now severely in jeopardy, threatening the loss of the numerous ecosystem services from which contemporary and future humans could benefit.*

Keywords: ecosystem services, global environmental change, human evolution, interspecific interactions, scavenger

Ecological interactions, such as predation, parasitism, competition, and mutualism, are strong selective forces driving the evolution of populations, communities, and ecosystems. However, these processes do not act in isolation, and environmental changes can induce variations in conditions, resource availability, and biodiversity that may shift interspecific interactions over time (Tylianakis et al. 2008). Hominins have substantially contributed to environmental change, especially since *Homo sapiens* expanded worldwide, which has precipitated the extinction of large mammalian herbivores, apex predators, and scavenging birds (Koch and Barnosky 2006). Other anthropogenic impacts have also been linked to major changes in the prevailing ecological conditions during the Quaternary Period (e.g., Lupo 1995).

Humans and scavenging vertebrates, such as vultures and hyenas, have been interdependent since the Late Pliocene, when early hominins turned to meat as a food source (Lewis 1997, Brantingham 1998, de Heinzelin et al. 1999, Domínguez-Rodrigo and Pickering 2003). Indeed, this long relationship has both helped shape human evolution (Owen-Smith 1999, Stanford and Bunn 2001, Larsen 2003, Bickerton and Szathmáry 2011) and induced phenotypic and genetic differentiation among scavengers (Agudo et al. 2010). The close relationship with scavenging birds and mammals has benefited humans since the origin of early *Homo* species in multiple ways. For instance, the removal of animal debris before putrefaction has played an important hygienic role for millennia (Markandya et al. 2008, Ogada et al. 2012a).

Such benefits can be understood within an ecosystem services framework. As the term was defined by the Millennium Ecosystem Assessment, *ecosystem services* are benefits people obtain from ecosystems and their constituent organisms (box 1; MA 2005). This concept, which is increasingly appreciated by society worldwide (Daily and Matson 2008), recognizes human needs that have developed in changing environments since the origin of the first humans. Unfortunately, appreciation of the ecosystem services provided by scavengers to humanity is emerging only as vertebrate scavenger populations are more at risk than ever. Currently, vultures and opportunistic scavengers among large mammalian carnivores are widely missing or threatened around the globe (Hoffmann et al. 2010, Ogada et al. 2012a), which could dramatically affect the supply of ecosystem services from which humans have traditionally benefited.

Given the ancient links between humans and scavengers and the current scavenger conservation crisis, the following major questions arise: What have been the prevailing interactions between humans and scavengers during the course of human evolution? How have humans benefited from

BioScience 64: 394–403.
doi:10.1093/biosci/biu034 Advance Access publication 26 March 2014

Box 1. Glossary.

Amensalism: any interaction between two individuals or groups of the same or different species in which one organism or group is harmed but the other is unaffected.

Carrion: any type of dead animal tissue.

Coevolution: reciprocal selective pressure that makes the evolution of one taxon partially dependent on the evolution of another (Brantingham 1998).

Commensalism: any interaction between two individuals or groups of the same or different species in which one organism or group benefits without affecting the other.

Competition: any interaction between two individuals or groups of the same or different species that reduces access to a shared resource or set of resources. Competition is *direct* (interference) if one organism or group affects the ability of another to consume a given limiting resource or *indirect* (exploitation) if the consumption of a given limiting resource by one organism or group makes the resource unavailable for another.

Ecosystem services: benefits people obtain from ecosystems (MA 2005) or the set of ecosystem functions that are useful to humans (Kremen 2005). These include *provisioning* (products obtained from ecosystems), *regulating* (related to the regulation of ecosystem processes), and *cultural* (nonmaterial benefits) services that directly affect people, as well as the supporting services needed to maintain other services. Provisioning, regulating, and cultural services typically have relatively direct and short-term impacts on people, whereas the impact of supporting services is often indirect or occurs over a very long time period (MA 2005).

Facilitative processes: those processes whose effects on a given organism are beneficial and increase its development or fitness.

Facultative scavenger: an animal that scavenges at variable rates but that can subsist on other food resources in the absence of carrion. All mammalian predators (e.g., jackals, hyenas, and lions in Africa and southern Asia; foxes, raccoons, wolves, and bears in temperate ecosystems), numerous birds of prey (e.g., kites, most large eagles), and corvids (e.g., ravens, crows), as well as other vertebrates (e.g., crocodiles), can be considered, to a greater or lesser extent, facultative scavengers (DeVault et al. 2003, Pereira et al. 2014).

Mutualism: any beneficial and reciprocal interaction between two individuals or groups of different species. This relationship of mutual dependence can be obligate (when a given organism or group cannot survive or reproduce without its mutualistic partner).

Obligate scavenger: a scavenger that relies entirely or near entirely on carrion as food resource. Among Quaternary terrestrial vertebrates, only vultures (both Old and New World species—families Accipitridae and Cathartidae, respectively) are considered obligate scavengers.

Predation: an interaction in which one animal kills and eats all or part of another. Predation can affect prey through the two fundamental mechanisms of direct consumption and capture risk.

Scavenging: an interaction in which one animal eats all or part of a dead animal. Scavenging is *active* (also called *confrontational, aggressive,* or *power* scavenging) when the predator that was responsible for the kill is chased away and most of the meat on the carcass is procured, or it is *passive* when the bones, which may contain fragments of meat, marrow, and skull contents, are collected.

them? What is the likely outcome of human domination of the Earth for the services that scavengers had formerly provided? Our aim in this review, which is focused on nonforest environments where both humans and scavenging vertebrates are most abundant, is threefold: first, to describe how humans (genus *Homo*) and scavenging vertebrates have been subjected to different scenarios of ecological interactions during the Quaternary Period; second, to synthesize the past and present operation of the ecosystem services provided by vertebrate scavengers; and, third, to show how the ecosystem services provided by these scavengers are currently threatened by the global changes associated with human domination. Defined by the major means of meat procurement, we can differentiate four consecutive periods along human evolution, characterized by (1) confrontational scavenging, (2) hunting, (3) shepherding of wild animals, and (4) intensive husbandry of domesticated animals. For each period, we emphasize how ecosystem services emerged from the prevailing interactions between humans and scavengers.

Diet of early humans: Food provisioning and the onset of cultural services

Around the time of the Pliocene–Pleistocene transition, increasing seasonality in precipitation occurred in African savannas (Cerling et al. 2011a). This forced the australopithecine ancestors of humans to diversify their diet in order to cope with the developing seasonal bottleneck in fruits and other soft plant foods. While hominins of the genus *Paranthropus* became adapted to exploit durable seeds, roots, and sedges (Cerling et al. 2011b, Klein 2013, Sponheimer et al. 2013), the lineage leading to *Homo* turned to the meat provided by large vertebrate carcasses to overcome the effects of the increasingly seasonal production of fruits and new plant growth (Foley and Lee 1989, Bunn and Ezzo

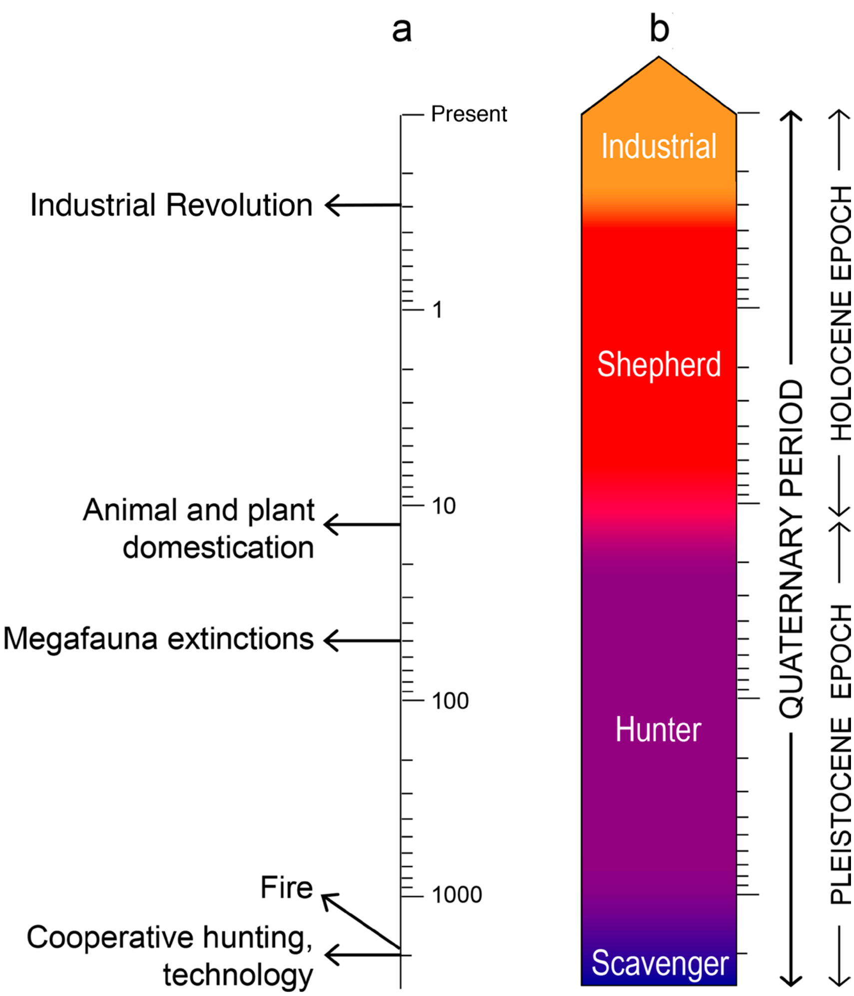

Figure 1. Major meat acquisition strategies of humans (*Homo *spp.) in relation to key events during the Quaternary Period. (a) A logarithmic time scale (in thousands of years ago) showing the main human-related events that occurred during the Quaternary Period that shaped the interactions between humans and scavenging vertebrates. (b) The major means of meat acquisition by humans during the Quaternary Period. See the text for further details.

1993, Ungar et al. 2006, Klein 2013). Although the relative role of hunting and scavenging by early humans remains controversial (Domínguez-Rodrigo 2002, Ungar et al. 2006, Pickering 2013), many anthropologists contend that the earliest humans obtained animal food largely through confrontational scavenging (also called *power scavenging* and *aggressive scavenging*) by driving large carnivores from their kills (figure 1; O'Connell et al. 1988, Bunn and Ezzo 1993, Brantingham 1998, Ragir 2000, Domínguez-Rodrigo and Pickering 2003, Klein 2009, Bickerton and Szathmáry 2011). Indeed, it has been proposed that the emergence of endurance running could have helped early humans to secure sufficient access to the scattered and ephemeral resource that is carrion, although this might have been a later feature facilitating the hunting of live ungulate prey (Bramble and Lieberman 2011).

Interference and resource competition probably accounted for most of the interactions among the earliest humans, vultures, bone-cracking hyenids, and other vertebrate scavengers (Bunn and Ezzo 1993, Owen-Smith 1999, Bickerton and Szathmáry 2011, Bramble and Lieberman 2011). In addition, confrontational scavenging would have exposed early humans to increased risks of injury or death while they were driving away the large carnivores that had killed the carcasses or driving away other fearsome scavengers present at them (Bunn and Ezzo 1993, Bickerton and Szathmáry 2011). But facilitatory interactions could also have been a feature, as it happens in current vertebrate scavenger guilds (Cortés-Avizanda et al. 2012, Pereira et al. 2014). For instance, observations of contemporary hunter–gatherers who actively exploit scavenging opportunities suggest that watching the behavior of vultures and large mammalian carnivores could have helped early humans locate carcasses (O'Connell et al. 1988). Such food provisioning probably represents the first ecosystem service that humans gained from scavenging vertebrates.

Moreover, a major function of the earliest stone tools crafted by early hominins was the processing of large carcasses to yield meat and marrow, a pattern of butchery that extended well into the Pleistocene (de Heinzelin et al. 1999). Competition with other scavengers probably contributed to the refinement of these tools and their use and, therefore, to cultural diversity. In addition, selective pressures associated with confrontational scavenging—specifically, the spatiotemporal unpredictability of carcasses and exposure to predation—probably contributed to the most distinctive features of humans: collaborative cooperation and language development (both of which were used to express where the resource was imagined to be awaiting; Bickerton and Szathmáry 2011). In turn, the improved diet quality due to increasing meat consumption has been related, along with other factors, to the extraordinary brain enlargement within the human lineage (Bramble and Lieberman 2011, Navarrete et al. 2011). Therefore, (confrontational) scavenging helped shape our modern cognitive identity.

Human hunters and the diversification of cultural services

Several key events during the Pleistocene might have provided both a challenge and an opportunity for humans to widen their niche with respect to dietary behavior (Lewis 1997, Ragir 2000). The emergence of cooperative hunting and the systematic use of stone technology approximately 2 million years ago improved human hunting abilities dramatically (figure 1; Brantingham 1998, Richards et al. 2000, Larsen 2003). In addition, cooking—possibly initiated by early *Homo erectus* around 1.9 million years ago—raised the nutritional value and reduced the parasite load of provisioned food (Wrangham and Carmody 2010). This could have contributed further to larger body and brain sizes (Wrangham and Carmody 2010, Aiello and Antón 2012, Antón and Snodgrass 2012), which perhaps facilitated hunting success. Indeed, stable isotope analyses, along with other indirect evidence, have indicated that late Pleistocene humans (*Homo neanderthalensis*) were probably largely predators, with scavenging pushed into a secondary role (see Richards et al. 2000, Klein 2009).

As early humans developed their hunting skills, the remains of the carcasses that they provided probably became an important source of food for vultures and other scavenging vertebrates. However, this positive facilitation was probably affected to some extent when humans began to cook meat, because the exposure of bones to heat and flames results in very little nutritional residue for bone eaters such as spotted hyenas (*Crocuta crocuta*; Lupo 1995). Evidence from paleontology, climatology, archaeology, and ecology supports the idea that humans were sufficiently effective hunters of large mammals to precipitate megafaunal extinctions through most continents outside of Africa during the late Pleistocene (from approximately 50,000 to approximately 10,000 years ago; Koch and Barnosky 2006). Associated with the large mammal extinctions was a loss of vulture species diversity (e.g., Hertel 1994).

The close association between human hunters and vertebrate scavengers probably played a role in the diversification of cultural services. Hominins had, at some stage, developed unprecedented cognitive abilities related to symbolism and abstraction, approaching those of modern humans. Recent studies suggest that Neanderthal people regularly exploited scavenging birds for the use of their feathers or claws as personal ornaments in symbolic behavior (Finlayson et al. 2012).

Human shepherds and the golden age of cultural and regulating services

Food production arose independently in (at most) nine areas of the world, with the *H. sapiens* that inhabited the Fertile Crescent of the Middle East becoming the world's first farmers and herders around 12,000 years ago (figure 1; Diamond 2002, Zeder 2008, Klein 2009). Thereafter, domestic ungulates became a major food source for vultures and other carrion eaters in many regions (Donázar 1993, Donázar et al. 2009a). In turn, scavengers provided an important hygienic benefit to humans by consuming the leftover parts of domestic animals around villages (Donázar et al. 2009a). Therefore, commensalism and mutualism became established as the main interactions between scavengers and humans (Gangoso et al. 2013). This relationship included the consumption of human corpses (Donázar 1993, Ogada et al. 2012a).

By shortening the persistence of rotting carcasses (Ogada et al. 2012b, Olson et al. 2012), vultures and various facultative scavengers contributed greatly to the control of disease and pests (Ogada et al. 2012b). Although vultures may occasionally spread pathogens, such as anthrax, to wild and perhaps to domestic ungulates (Bengis et al. 2003), the existing evidence mostly supports the idea that the rates of transmission of infectious diseases to humans and their livestock would be substantially higher in the absence of vultures (e.g., Houston and Cooper 1975, Koenig 2006, Markandya et al. 2008, Ogada et al. 2012a, 2012b).

Late during this period, spiritual, religious, and aesthetic values inspired by scavengers flourished worldwide. For example, the Egyptians represented the goddess Nekhbet as a vulture, Native Americans included condors (*Vultur gryphus*) in many ceremonies (Gordillo 2002), and several human cultures around the world offered the corpses of their dead relatives to the vultures (Donázar 1993, Ogada et al. 2012a).

Industrial humans: The cost of supplanting ecosystem services

In contemporary times, human–scavenger relationships have changed once again, at least in the more developed countries. Intensive livestock husbandry became the principal means for humans to secure animal food after the Industrial Revolution and especially after World War II (figure 1; Larsen 2003). An exponentially growing human population (Ehrlich et al. 2012) coupled with extensive environmental transformation have directly (e.g., through hunting and poisoning; Margalida 2012) and indirectly (e.g., through the contamination of carrion with veterinary drugs and through the constriction of the supply of carrion; Pain et al. 2003, Ogada et al. 2012a) depleted vulture and other scavenger populations worldwide (Şekercioğlu et al. 2004, Ogada et al. 2012a). Sharp declines of carrion availability can also lead to occasional predation by vultures, an extreme example of human-induced modification of animal behavior that leads to further human–wildlife conflicts (Margalida et al. 2011). Therefore, in recent decades, humans have had strong negative impacts on scavenging vertebrates.

The economic benefits related to the regulating services provided by scavengers have not been recognized until quite recently. In Europe, the detection of the variant (vCJD) and new variant (nvCJD) prions causing Creutzfeldt–Jakob disease in humans, acquired from cattle infected by bovine spongiform encephalopathy, led to the application of restrictive sanitary legislation. This greatly limited the use of animal byproducts not intended for human consumption and led to livestock carcasses being systematically removed from large regions (Donázar et al. 2009b, Margalida et al. 2010). Both governmental agencies and farmers have been paying the costs of these sanitary measures (including the transport and incineration of the corpses) for more than a decade, a service that vultures and other scavengers had been providing freely to humans for many eons. It is estimated that the Spanish vulture population removes, on average, 134–201 metric tons of bones and 5551–8326 tons of meat each year, with a minimum economic savings of approximately $1.19 million to $1.94 million (Margalida and Colomer 2012). Also, the drastic vulture declines that took place on the Indian subcontinent a decade ago because of the toxicity of the veterinary drug diclofenac was followed by an increase in the populations of feral dogs and possibly rats, which are primary reservoirs of rabies and bubonic plague, respectively (Pain et al. 2003, Markandya et al. 2008). This entails a risk to human health, especially in the rural and poorest areas. For instance, the costs in terms of medicines, doctor remuneration, and so on associated with human rabies transmitted by feral dog bites following the loss of vultures in India have been estimated to be about $2.43 billion annually (Markandya et al. 2008). These are the first large-scale economic estimates of ecosystem services provided by scavengers.

Recreation and ecotourism activities associated with scavengers are currently flourishing worldwide and providing important economic benefits. There is an increasing interest of people in viewing and photographing vultures and other carrion-feeding vertebrates (Becker et al. 2005, Markandya et al. 2008, Donázar et al. 2009a). Becker and colleagues (2005) estimated that the potential annual tourist value of threatened griffon vultures (*Gyps fulvus*) at a nature reserve in Israel was $1.1 million to $1.2 million and that 85% of the visitors came to the park to view the vultures. Viewing large carnivores, such as lions (*Panthera leo*) or hyenas, which scavenge facultatively, is a major goal of ecotourists from around the globe (Lindsey et al. 2007).

We can identify a number of additional ecosystem services that are important, at least locally, to contemporary industry and cultural diversity. In India, scavengers—particularly vultures—facilitate the traditional collection of cattle bones to supply the fertilizer industry because they efficiently clean cattle carcasses. In the absence of scavengers, bones are less readily available, of poorer quality, and more difficult to collect, with resultant economic losses (Markandya et al. 2008). In addition, Zoroastrianism-practicing Parsis in Asia retain the tradition of leaving dead human corpses to vultures for purification in what they call *towers of silence* (Ogada et al. 2012a). Moreover, vultures and other scavengers, such as corvids or large mammalian carnivores, play a significant role in artistic, literary, and musical expression on all of the continents (Donázar 1993, Gordillo 2002).

Furthermore, carrion constitutes a vast reservoir of nutrients and energy (Wilson and Wolkovich 2011). By consuming much of the biomass remaining in vertebrate carcasses, vertebrate scavengers contribute importantly to nutrient cycling, a key global supporting service. The absence of vultures and large mammalian carnivores can critically slow the rate at which nutrients are redistributed (DeVault et al. 2003, Ogada et al. 2012b), thus indirectly affecting other services.

Conclusions

We have reviewed the ecological interactions linking humans and vertebrate scavengers and the ecosystem services provided by the latter since the origin of the first hominins until modern times. Although our review was organized within the framework of four major stages of human evolution, we recognize that the transitions between these periods were prolonged and that there was interspecific and regional variation among humans within such periods (Antón and Snodgrass 2012). Nevertheless, our main finding is that both interactions and services have evolved through time. Humans and scavengers have been subjected to changing interspecific relationships under shifting ecological scenarios (table 1). Once humans became hunters, their close relationship with scavengers, especially vultures, could be considered a model of coexistence and mutualism. However, contemporary human activities have disrupted the mutually beneficial relationship between humans and scavengers (box 2, figure 2). One of the most important effects of

*Table 1a. The main interspecific interactions associated with the meat acquisition strategies (MAS) of humans (*Homo *spp.) during the Quaternary Period.*

	Scavenging		Hunting		Shepherding		Industrialization	
Type of interaction	H	A	H	A	H	A	H	A
Amensalism							0	–
Commensalism			0	+	0	+	0[a]	+[a]
Competition	–	–						
Predation[b]	–	+	±[a]	±[a]	+[a]	–[a]	+[a]	–[a]
Mutualism	+[a]	+[a]	+	+	+	+		

Note: The signs in the figures indicate positive (+), negative (–), and neutral (0) effects on the short-term population growth rate, the long-term population size, or the short-term relative fitness of the interactants. *Abbreviations:* A, effect on animals; H, effect on humans. [a]These interactions are considered to be relatively marginal (according to the literature reviewed here). [b]The direction of predation determines the effect value (i.e., the effect on the predator is positive).

*Table 1b. The main scavenger-provided ecosystem services associated with the meat acquisition strategies of humans (*Homo *spp.) during the Quaternary Period.*

	Meat acquisition strategy			
Ecosystem service	**Scavenging**	**Hunting**	**Shepherding**	**Industrialization**
Provisioning	Food			
Regulating	Disease and pest control	Disease and pest control	Disease and pest control	Disease and pest control; economic benefits related to sanitary measures; industry services
Cultural	Cultural diversity and knowledge systems	Cultural diversity and knowledge systems; spiritual, religious, inspiration, and aesthetic values	Spiritual, religious, inspiration, and aesthetic values	Spiritual, religious, inspiration, and aesthetic values; recreation and ecotourism
Supporting	Nutrient cycling	Nutrient cycling	Nutrient cycling	Nutrient cycling

Box 2. Human impacts on scavenger life style: The cases of the California condor and the spotted hyena.

California condors (*Gymnogyps californianus*) used to feed on both terrestrial megafauna and marine mammals during the Pleistocene. Following megafaunal massive extinctions (around 50,000 years ago; Koch and Barnosky 2006), which were most probably precipitated by humans, condors were relegated to coastal areas and had to focus on the corpses of marine mammals. More recently (by the 1700s), after the depletion of marine mammals through uncontrolled harvesting and the development of commercial hunting and cattle ranching, condors became highly dependent on anthropogenic subsidies. At the present, the diet of wild-living condors is mostly based on domestic cattle debris from dairy farms or feedlots (Chamberlain et al. 2005).

Yirga and colleagues (2012) also clearly illustrated how dependent scavengers are nowadays on humans. Humans have depleted most of the natural prey base of spotted hyenas (*Crocuta crocuta*) in northern Ethiopia. There, the vast majority of people follow the Ethiopian Orthodox Tewahedo Church calendar, which includes several fasting periods in a year. In such periods, people do not consume animal products, which leads to a sharp decline in waste availability for scavengers. As a result, hyenas alternate scavenging on waste and predating on donkeys during nonfasting and fasting periods, respectively.

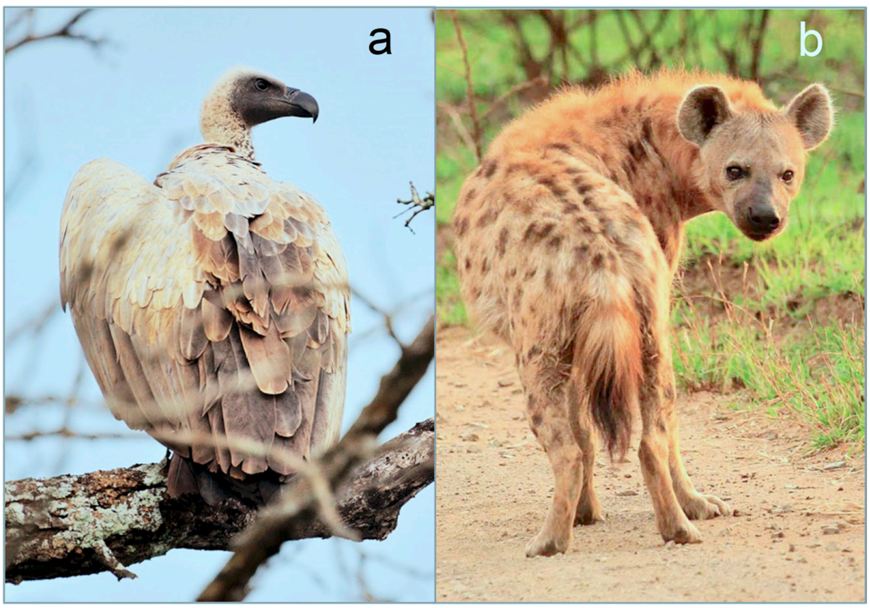

*Figure 2. Both (a) obligate (e.g., white-backed vultures [*Gyps africanus*]) and (b) facultative (e.g., spotted hyenas [*Crocuta crocuta*]) scavengers have shared a long-standing relationship with humans. Abundant populations of vultures, hyenas, and many other vertebrate scavengers are, however, compromised by contemporary anthropogenic impacts on natural environments. Photographs: (a) David Carmona-López and (b) Sebastián Justicia-Carmona, taken in Hluhluwe-iMfolozi Park, South Africa.*

human-mediated global change is the widespread extirpation of vultures and large mammalian carnivores (Hoffmann et al. 2010, Ogada et al. 2012a), with consequent losses of the regulating, cultural, and supporting services that these species once provided (table 1).

Human actions have also altered the supply of carrion, thereby affecting scavenging-related ecosystem services. On one hand, sanitary regulations directed to the reduction of livestock carcasses available in the field might lead to catastrophic effects on the populations of vultures and other scavengers, such as kites (Donázar et al. 2009b, Margalida et al. 2010). On the other hand, the carrion supply becomes more seasonally pulsed in the absence of large predators (Wilmers and Getz 2005, Pereira et al. 2014), which could be detrimental to not only obligate but also facultative scavengers during critical periods in which alternative food resources are scarce. Overcoming the food shortage imposed by such sanitary measures and the seasonal nadir in carcasses generated from causes besides predation through providing feeding stations or “vulture restaurants” can have counterintuitive and undesirable consequences for populations of both targeted and nontargeted scavengers (Donázar et al. 2009a, Cortés-Avizanda et al. 2012). In turn, the reduction, aggregation, and incineration of domestic animal carcasses change nutrient cycles and increase emissions of carbon dioxide to the atmosphere (Donázar et al. 2009a).

Some relevant advances have been made to reestablish the ecological services that scavengers provide. For instance, recommendations made by scientists, conservationists, and managers have adjusted regulations to allow European farmers to abandon the remains of livestock in certain areas (Margalida et al. 2012). In Asia, the governments of India, Pakistan, and Nepal have moved to ban the veterinary use of diclofenac and to replace it with low-toxicity substances such as meloxican (Cuthbert et al. 2011). These are outstanding examples of how scientific arguments lead to positive political action that helps reconcile biodiversity conservation and human activities.

Further research, framed within an interdisciplinary and social–ecological context (Kremen 2005, Carpenter et al. 2009), is strongly needed. Here, we outline several research priorities. First, the assessment and quantification of the ecosystem services provided by scavenging birds and mammals began only after the catastrophic die-off of vultures in South Asia and parts of Africa (Koenig 2006), coupled with the risks of extirpation of European vultures (Donázar et al. 2009b). Therefore, we need more studies that quantify the ecosystem services currently provided by scavengers—in particular, those related to disease and pest control; cultural services, such as ecotourism; and nutrient cycling. Understanding the economic costs of the elimination of vultures and large mammalian carnivores could contribute to the conservation of these globally threatened organisms. Second, studies in which the relative importance of different ecosystem services and the trade-offs between those services and potential disservices (e.g., the case of disease control versus disease spread) are compared should be encouraged. Third, studies aimed at quantifying how vultures and large mammalian carnivores might be replaced by less threatened facultative scavengers would be helpful (Şekercioğlu et al. 2004). Moreover, most of the interactions and services described above persist in a world displaying wide contrasts in economic development, and the relationship between humans and scavengers is more complex than ever. For example, carcasses resulting from game hunting are an important resource for scavengers in developed countries (e.g., Donázar et al. 2009a, Sánchez-Zapata et al. 2010), especially in areas where large carnivore populations have been depleted. Modern hunting activities could, therefore, be comparable to those of Pleistocene hominins. Consequently, ecosystem services research must take into account this social, temporal, and spatial heterogeneity of human cultures. Because there is a decreasing probability of finding evidence as temporal distance increases (Wrangham and Carmody 2010, Antón and Snodgrass 2012), we also encourage research focused on establishing human–scavenger relationships during the earliest (and longest) periods of human evolution. In this sense, stable carbon isotope analyses are increasingly illuminating the dietary patterns of the first hominins and related taxa (Klein 2013). A more comprehensive understanding of the diet of the first hominins, their predecessors, and contemporary scavengers and large predators may provide promising insight into early human ecology and evolution.

Finally, we emphasize that innovative political, financial, scientific, and management efforts are still required to promote a broader rehabilitation of the ecosystem services provided by scavengers (e.g., see Cuthbert et al. 2011). Given that such ecosystem services change over time, we stress the need to preserve these organisms in the long term. Promoting a better balance between the negative and the positive influences of humans on scavengers (box 3, figure 3) might not only retain scavenger diversity but also promote a valuable component of our own well-being and ecological and evolutionary identity.

Box 3. Effects of contemporary humans on scavengers and associated ecosystem services.

Vultures and large mammalian scavengers worldwide are threatened by (a) human persecution, mainly through poisoning but also through shooting; (b) other nonnatural mortality causes (e.g., power lines, wind farms, lead intoxication, road kills); (c) factors such as sanitary regulations that ban the carcasses of domestic animals from being left in the field; (d) the contamination of livestock carcasses with veterinary drugs; and (e) habitat loss and degradation (e.g., Hoffmann et al. 2010, Ogada et al. 2012a). Low population numbers of these major scavengers mean a decrease in their potential to provide ecosystem services (figure 3a; Luck et al. 2003). However, conservation schemes (including reintroduction programs) and new sanitary and veterinary regulations that are more in line with conservation goals (Cuthbert et al. 2011, Margalida et al. 2012) can help reestablish healthy populations of vultures and large mammalian carnivores (e.g., Meretsky et al. 2000) and can thereby restore the ecosystem services provided by these scavengers (figure 3b). There is an interesting feedback between actions devoted to globally improve scavengers’ conservation status and the ecosystem services that scavengers can provide to humanity (Carpenter et al. 2009). For instance, ecotourism dependent on opportunities to view scavengers feeding on carcasses is an emerging activity with great conservation potential (Becker et al. 2005, Donázar et al. 2009b), provided that care is taken to minimize human disturbance (Carrete and Tella 2010).

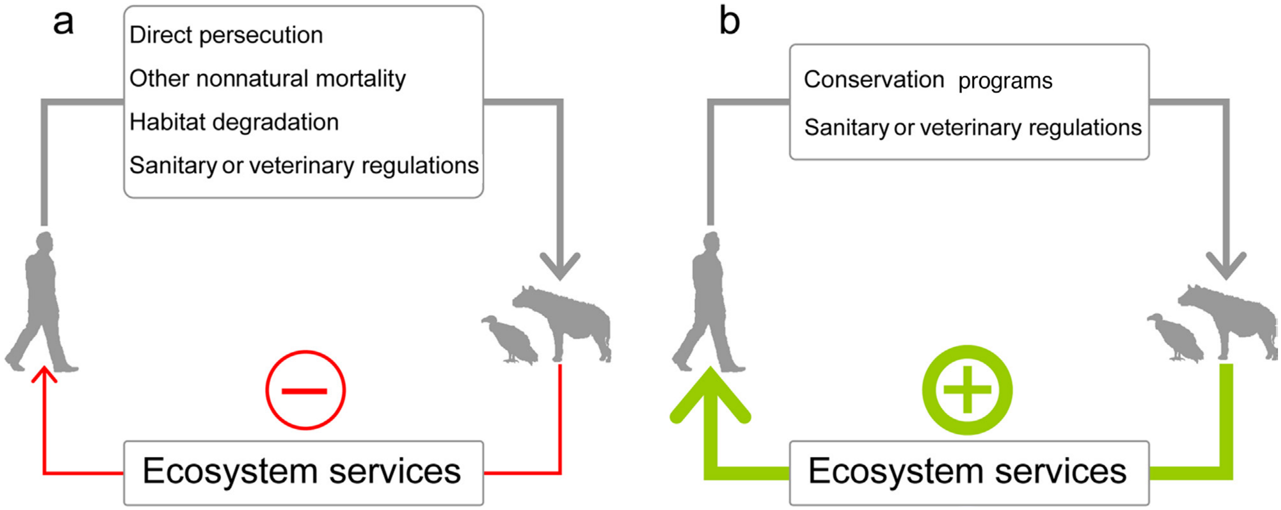

Figure 3. The main (a) negative and (b) positive effects that contemporary humans have on scavengers. The factors that jeopardize and favor scavenger populations translate to decreased and increased ecosystem services, respectively. See box 3 for further details.

Acknowledgments

This study was partly supported by the Spanish Ministry of Economy and Competitiveness through project no. CGL2012-40013-C02-02 and by the European Regional Development Fund. MM was supported by a postdoctoral grant from the Spanish Ministry of Education through the Plan Nacional de Investigación Científica, Desarrollo, e Innovación Tecnológica 2008–2011, and MC and AM were supported by Ramón y Cajal research contract no. RYC-2009-04860 from the Spanish Ministry of Science and Innovation and no. RYC-2012-11867 from the Spanish Ministry of Economy and Competitiveness, respectively. The comments of four anonymous referees substantially improved earlier versions of the manuscript.

References cited

Agudo R, Rico C, Vilà C, Hiraldo F, Donázar JA. 2010. The role of humans in the diversification of a threatened island raptor. BMC Evolutionary Biology 10 (art. 384).

Aiello LC, Antón SC. 2012. Human biology and the origins of *Homo*: An introduction to supplement 6. Current Anthropology 53 (suppl. 6): S269–S277.

Antón SC, Snodgrass JJ. 2012. Origins and evolution of genus *Homo*: New perspectives. Current Anthropology 53 (suppl. 6): S479–S496.

Becker N, Inbar M, Bahat O, Choresh Y, Ben-Noon G, Yaffe O. 2005. Estimating the economic value of viewing griffon vultures *Gyps fulvus*: A travel cost model study at Gamla Nature Reserve, Israel. Oryx 39: 429–434.

Bengis RG, Grant R, de Vos V. 2003. Wildlife diseases and veterinary controls: A savanna ecosystem perspective. Pages 349–369 in du Toit J, Rogers KH, Biggs HC, eds. The Kruger Experience: Ecology and Management of Savanna Heterogeneity. Island Press.

Bickerton D, Szathmáry E. 2011. Confrontational scavenging as a possible source for language and cooperation. BMC Evolutionary Biology 11 (art. 261).

Bramble DM, Lieberman DE. 2011. Endurance running and the evolution of *Homo*. Nature 432: 345–352.

Brantingham PJ. 1998. Hominid–carnivore coevolution and invasion of the predatory guild. Journal of Anthropological Archaeology 17: 327–353.

Bunn HT, Ezzo JA. 1993. Hunting and scavenging by Plio-Pleistocene hominids: Nutritional constraints, archaeological patterns, and behavioural implications. Journal of Archaeological Science 20: 365–398.

Carpenter SR, et al. 2009. Science for managing ecosystem services: Beyond the Millennium Ecosystem Assessment. Proceedings of the National Academy of Sciences 106: 1305–1312.

Carrete M, Tella JL. 2010. Individual consistency in flight initiation distances in burrowing owls: A new hypothesis on disturbance-induced habitat selection. Biology Letters 6: 167–170.

Cerling TE, Wynn JG, Andanje SA, Bird MI, Kimutai Korir D, Levin NE, Mace W, Macharia AN, Quade J, Remien CH. 2011a. Woody cover and hominin environments in the past 6 million years. Nature 476: 51–56.

Cerling TE, Mbua E, Kirera FM, Kyalo Manthi F, Grine FE, Leakey MG, Sponheimer M, Uno KT. 2011b. Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. Proceedings of the National Academy of Sciences 108: 9337–9341.

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

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

Cuthbert R, Taggart MA, Prakash V, Saini M, Swarup D, Upreti S, Mateo R, Chakraborty SS, Deori P, Green RE. 2011. Effectiveness of action in India to reduce exposure of *Gyps* vultures to the toxic veterinary drug diclofenac. PLOS ONE 6 (art. e19069).

Daily GC, Matson PA. 2008. Ecosystem services: From theory to implementation. Proceedings of the National Academy of Sciences 105: 9455–9456.

De Heinzelin J, Clark JD, White T, Hart W, Renne P, WoldeGabriel G, Beyene Y, Vrba E. 1999. Environment and behavior of 2.5-million-year-old Bouri hominids. Science 284: 625–629.

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

Diamond J. 2002. Evolution, consequences and future of plant and animal domestication. Nature 418: 700–707.

Domínguez-Rodrigo M. 2002. Hunting and scavenging by early humans: The state of the debate. Journal of World Prehistory 16: 1–54.

Domínguez-Rodrigo M, Pickering TR. 2003. Early hominid hunting and scavenging: A zooarcheological review. Evolutionary Anthropology 12: 275–282.

Donázar JA. 1993. Los Buitres Ibéricos: Biología y Conservación. Reyero.

Donázar JA, Margalida A, Campión D, eds. 2009a. Vultures, feeding stations and sanitary legislation: A conflict and its consequences from the perspective of conservation biology. Sociedad de Ciencias Aranzadi.

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

Ehrlich PR, Kareiva PM, Daily GC. 2012. Securing natural capital and expanding equity to rescale civilization. Nature 486: 68–73.

Finlayson C, et al. 2012. Birds of a feather: Neanderthal exploitation of raptors and corvids. PLOS ONE 7 (art. e45927).

Foley RA, Lee PC. 1989. Finite social space, evolutionary pathways, and reconstructing hominid behavior. Science 243: 901–906.

Gangoso L, Agudo R, Anadón JD, de la Riva M, Suleyman AS, Porter R, Donázar JA. 2013. Reinventing mutualism between humans and wild fauna: Insights from vultures as ecosystem services providers. Conservation Letters 6: 172–179.

Gordillo S. 2002. El cóndor andino como patrimonio natural y cultural de Sudamérica. Pages 327–342 in Primer Congreso Internacional de Patrimonio Cultural. Universidad Nacional de Córdoba.

Hertel F. 1994. Diversity in body size and feeding morphology within past and present vulture assemblages. Ecology 75: 1074–1084.

Hoffmann M, et al. 2010. The impact of conservation on the status of the world's vertebrates. Science 330: 1503–1509.

Houston DC, Cooper JE. 1975. The digestive tract of the white-back griffon vulture and its role in disease transmission among wild ungulates. Journal of Wildlife Diseases 11: 306–313.

Klein RG. 2009. The Human Career: Human Biological and Cultural Origins, 3rd ed. University of Chicago Press.

———. 2013. Stable carbon isotopes and human evolution. Proceedings of the National Academy of Sciences 110: 10470–10472.

Koch PL, Barnosky AD. 2006. Late Quaternary extinctions: State of the debate. Annual Review of Ecology, Evolution, and Systematics 37: 215–250.

Koenig R. 2006. Vulture research soars as the scavenger's numbers decline. Science 312: 1591–1592.

Kremen C. 2005. Managing ecosystem services: What do we need to know about their ecology? Ecology Letters 8: 468–479.

Larsen CS. 2003. Animal source foods and human health during evolution. Journal of Nutrition 133: 3893S–3897S.

Lewis ME. 1997. Carnivoran paleoguilds of Africa: Implications for hominid food procurement. Journal of Human Evolution 32: 257–288.

Lindsey PA, Alexander R, Mills MGL, Romañach S, Woodroffe R. 2007. Wildlife viewing preferences of visitors to protected areas in South Africa: Implications for the role of ecotourism in conservation. Journal of Ecotourism 6: 19–33.

Luck GW, Daily GC, Ehrlich PR. 2003. Population diversity and ecosystem services. Trends in Ecology and Evolution 18: 331–336.

Lupo KD. 1995. Hadza bone assemblages and hyena attrition: An ethnographic example of the influence of cooking and mode of discard on the intensity of scavenger ravaging. Journal of Anthropological Archaeology 14: 288–314.

[MA] Millennium Ecosystem Assessment. 2005. Ecosystems and Human Well-being: Synthesis. Island Press.

Margalida A. 2012. Baits, budget cuts: A deadly mix. Science 338: 192.

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

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

Margalida A, Campión D, Donázar JA. 2011. Scavenger turned predator: European vultures' altered behaviour. Nature 480: 457.

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

Markandya A, Taylor T, Longo A, Murty MN, Murty S, Dhavala K. 2008. Counting the cost of vulture decline: An appraisal of the human health and other benefits of vultures in India. Ecological Economics 67: 194–204.

Meretsky VJ, Snyder NFR, Beissinger SR, Clendenen DA, Wiley JW. 2000. Demography of the California condor: Implications for reestablishment. Conservation Biology 14: 957–967.

Navarrete A, van Schaik CP, Isler K. 2011. Energetics and the evolution of human brain size. Nature 480: 91–93.

O'Connell JF, Hawkes K, Blurton Jones N. 1988. Hadza scavenging: Implications for Plio/Pleistocene hominid subsistence. Current Anthropology 29: 356–363.

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

Ogada DL, Torchin ME, Kinnaird MF, Ezenwa VO. 2012b. Effects of vulture declines on facultative scavengers and potential implications for mammalian disease transmission. Conservation Biology 26: 453–460.

Olson ZH, Beasley JC, DeVault TL, Rhodes OE Jr. 2012. Scavenger community response to the removal of a dominant scavenger. Oikos 121: 77–84.

Owen-Smith N. 1999. Ecological links between African savanna environments, climate change, and early hominid evolution. Pages 138–149 in Bromage TG, Schrenk F, eds. African Biogeography, Climate Change, and Human Evolution. Oxford University Press.

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

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

Pickering TR. 2013. Rough and Tumble: Aggression, Hunting, and Human Evolution. University of California Press.

Ragir S. 2000. Diet and food preparation: Rethinking early hominid behavior. Evolutionary Anthropology 9: 153–155.

Richards MP, Pettitt PB, Trinkaus E, Smith FH, Paunović M, Karavanić I. 2000. Neanderthal diet at Vindija and Neanderthal predation: The evidence from stable isotopes. Proceedings of the National Academy of Sciences 97: 7663–7666.

Sánchez-Zapata JA, Eguía S, Blázquez M, Moleón M, Botella F. 2010. Unexpected role of ungulate carcasses in the diet of golden eagles *Aquila chrysaetos* in Mediterranean mountains. Bird Study 57: 352–360.

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

Sponheimer M, et al. 2013. Isotopic evidence of early hominin diets. Proceedings of the National Academy of Sciences 110: 10513–10518.

Stanford CB, Bunn HT, eds. 2001. Meat-Eating and Human Evolution. Oxford University Press.

Tylianakis JM, Didham RK, Bascompte J, Wardle DA. 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters 11: 1351–1363.

Ungar PS, Grine FE, Teaford MF. 2006. Diet in early *Homo*: A review of the evidence and a new model of adaptive versatility. Annual Review of Anthropology 35: 209–228.

Yirga G, De Iongh HH, Leirs H, Gebrihiwot K, Deckers J, Bauer H. 2012. Adaptability of large carnivores to changing anthropogenic food sources: Diet change of spotted hyena (*Crocuta crocuta*) during Christian fasting period in northern Ethiopia. Journal of Animal Ecology 81: 1052–1055.

Wilmers CC, Getz WM. 2005. Gray wolves as climate change buffers in Yellowstone. PLOS Biology 3 (art. e92).

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

Wrangham R, Carmody R. 2010. Human adaptation to the control of fire. Evolutionary Anthropology 19: 187–199.

Zeder MA. 2008. Domestication and early agriculture in the Mediterranean Basin: Origins, diffusion, and impact. Proceedings of the National Academy of Sciences 105: 11597–11604.

Marcos Moleón (mmoleonpaiz@hotmail.com) was a postdoctoral researcher, and Norman Owen-Smith is an emeritus professor, in the School of Animal, Plant, and Environmental Sciences, at the University of the Witwatersrand, South Africa. MM is now an associate researcher, and José A. Sánchez-Zapata is a professor, in the Department of Applied Biology, at the University Miguel Hernández, in Spain. Antoni Margalida is an associate researcher at the Division of Conservation Biology at the Institute of Ecology and Evolution, at the University of Bern, Switzerland, and in the Department of Animal Production, Division of Wildlife, at the University of Lleida, Spain. Martina Carrete is an associate researcher in the Department of Physical, Chemical, and Natural Systems at the University Pablo de Olavide, in Spain. José A. Donázar is a research professor in the Department of Conservation Biology at Doñana Biological Station, a center of the Consejo Superior de Investigaciones Científicas, in Spain.