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Source: Journal of Raptor Research, 55(3) : 311-327

Published By: Raptor Research Foundation

URL: https://doi.org/10.3356/JRR-20-22

J. Raptor Res. 55(3):311–327

REVIEWING THE ROLE OF VULTURES AT THE HUMAN-WILDLIFE-LIVESTOCK DISEASE INTERFACE: AN AFRICAN PERSPECTIVE

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ABSTRACT.—Vultures are a key component of an effective scavenger guild and have evolved a number of adaptations that allow them to locate and dispose of carcasses quickly and efficiently. The continuing decline of African vultures is threatening the stability of the African scavenger guild, which may result in increased carcass decomposition times and thus, more rapid development of pathogenic bacteria. The absence of competitive regulation by these apex scavengers may also result in changes in the composition of the vertebrate scavenger guild, with an increase in mammalian scavengers giving rise to increased contact rates at carcasses, which may increase the risk of viral disease transmission to humans, livestock, and other wildlife. Although the economic value of vultures in terms of the sanitation services they provide has been evaluated, their contribution to the economics of human health and veterinary care remains to be quantified. Efforts to do so are hampered by lack of data, as well as a number of confounding factors that may mask causality, such as improved disease prevention and surveillance systems. However, the circumstantial nature of the link

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between vultures and disease prevention should not deter efforts to conserve them, as their regulation of mammalian scavengers and the sanitation services they provide place them firmly within the sphere of One Health, thereby warranting their urgent protection. The restoration of vulture populations and the ecosystem services they provide will benefit the welfare of all humans, but particularly those who are most vulnerable to economic instability and the spillover of disease at the human-wildlife-livestock interface.

KEY WORDS: *competitive regulation*; *disease*; *ecosystem service*; *scavenger*; *vulture*.

REVISANDO EL PAPEL DE LOS BUITRES EN LA INTERFAZ DE ENFERMEDADES QUE AFECTAN A HUMANOS, ANIMALES SALVAJES Y GANADO: UNA PERSPECTIVA AFRICANA

RESUMEN.—Los buitres son un componente clave de un gremio efectivo de carroñeros, habiendo desarrollado durante su evolución un número de adaptaciones que les permiten localizar y desechar los cadáveres de modo rápido y eficiente. El continuo declive de los buitres africanos está amenazando la estabilidad del gremio de carroñeros de África, lo que puede ocasionar un incremento en el tiempo de descomposición de los cadáveres y, como resultado, un rápido desarrollo de bacterias patógenas. La ausencia de una regulación por competencia por parte de estos carroñeros tope también puede ocasionar cambios en la composición del gremio de carroñeros vertebrados, con un aumento de carroñeros mamíferos. Consecuentemente, la tasa de contacto de estos carroñeros en estos sitios podría aumentar, incrementando el riesgo de transmisión de enfermedades virales a los humanos, al ganado y a otra fauna silvestre. Aunque el valor económico de los buitres en términos de los servicios de saneamiento que brindan ha sido evaluado, su contribución a la economía de la salud humana y de los cuidados veterinarios debe aun ser cuantificada. Los esfuerzos para hacerlo se ven obstaculizados por la falta de datos como tambien por un número de factores alternativos que pueden enmascarar la causalidad, tales como mejoras en los sistemas de prevención y vigilancia de enfermedades. Sin embargo, la naturaleza circunstancial del vínculo entre los buitres y la prevención de enfermedades no debería desalentar los esfuerzos para conservarlos, ya que su regulación de los mamíferos carroñeros y de los servicios de saneamiento que brindan los ubica fuertemente dentro de la esfera del enfoque Una Salud, garantizando así su protección urgente. La restauración de las poblaciones de buitres y de los servicios ecosistémicos que brindan beneficiará el bienestar de los humanos, particularmente de aquellos que son más vulnerables a la inestabilidad económica y a la propagación de enfermedades en la interfaz humanos, vida silvestre y ganado.

[Traducción del equipo editorial]

INTRODUCTION

Humans, livestock, and wildlife have coexisted for thousands of years, but exponential human population growth along with increased human movement around the globe, the expansion of human encroachment on wildlife habitat, and a substantial increase in organic waste have increased the frequency and intensity of interactions between these three groups and provided ample opportunity for the emergence and adaptation of a variety of pathogens (De Garine-Wichatitsky et al. 2013). Many emerging diseases exist on a continuum between human, wildlife, and domestic animal populations, with a few affecting only one group exclusively (Daszak et al. 2000). Initial recognition and conceptualization of this interrelationship was originally termed One Health (Dos S. Ribeiro et al. 2019), a term which now includes clear recognition of the close interrelationship among wildlife health, human health, and overall ecosystem health. The continued spillover and spillback of infectious diseases raise important concerns, including the risk this may pose to human health, the impact it may have on the economic welfare of farmers depending on wildlife and/or livestock for their livelihoods (De Garine-Wichatitsky et al. 2013), and the substantial veterinary and health-care costs associated with preventative care and treatment (Daszak et al. 2000).

Domestic and wild animal mortalities can be attributed to a number of factors, including predation, senescence, malnutrition, disease, accidents, and natural disasters such as severe storms and wildfires (Houston 1979). Mortality rates may be exacerbated by direct and indirect human impacts, including collisions with motor vehicles, buildings and powerlines, as well as poisoning and pollution (Whelan et al. 2008). Collectively, these causes may give rise to many carcasses that are subject to natural decomposition, a slow process that, if left unchecked, may turn the carcass environment into the ideal reservoir for a range of pathogens that are harmful to animals and humans alike (Houston 1979). Typically, natural carcass decomposition is never allowed to run its course for long because many organisms (known as scavengers) have evolved several adaptations to exploit this niche as a source of food. Vultures are the most efficient terrestrial vertebrate scavenger. They are obligate scavengers that may, in certain circumstances, outcompete their terrestrial counterparts (Houston 1983).

Consumers of refuse and rotting carcasses are of great importance in the spread of disease, and so the role of vultures at the human-wildlife-livestock disease interface deserves urgent attention (IUCN Vulture Specialist Group 2020). The scavenging role could be of special significance in developing countries, where the struggle with infectious diseases is frequently exacerbated by lack of funds, political will, inadequate surveillance, and shortage of experienced personnel (Cosivi et al. 1998, Rupprecht et al. 2001). Unfortunately, the future of Old World vultures is becoming less certain with every passing decade. Facing catastrophic declines in both Asia and Africa, Old World vultures are now regarded as one of the most threatened avian functional guilds in the world (Ogada et al. 2012a, Buechley and Şekercioğlu 2016, Botha et al. 2017, McClure et al. 2018). In accordance with the principles of One Health, which proposes a nexus among veterinary, wildlife, and human medicine for the benefit of human health, animal health, and the global environment (Day 2011), governments and regulating agencies must be convinced to acknowledge the vital role vultures play within this nexus and that their conservation is not a matter of luxury, but of necessity. In turn, this will allow governments that are signatories to the Convention on Biological Diversity (CBD) to adhere to the tenets of Aichi Biodiversity Target 14, which calls for the restoration of ecosystem services that contribute to human health, livelihoods, and well-being, particularly as it relates to local communities, the poor, and the vulnerable (CBD 2018).

Herein, we review the ecosystem services provided by African vultures at the human-wildlife-livestock disease interface, remaining cognizant of the uncertainty related to quantifying those ecosystem services. Specifically, we aim to (1) emphasize the unique position of African vultures within the scavenger guild, (2) describe the ecosystem services that African vultures provide, with particular reference to the disease nexus as well as the efforts that have been made to quantify these ecosystem services, (3) describe the consequences that may result from the continued decline of African vultures, and (4) suggest future research that will inform policy makers of the importance of including vulture conservation in ecosystem management decision frameworks.

THE VERTEBRATE SCAVENGER GUILD

Vultures as Obligate Scavengers. Africa's eleven species of vultures are all obligate scavengers, with the exception of the Palm-nut Vulture (*Gypohierax angolensis*), which is mainly frugivorous (Botha et al. 2017). As obligate scavengers, both Old and New World vultures rely almost exclusively on carrion as a source of food, the only known terrestrial vertebrates that are known to do so (DeVault et al. 2016). African vultures typically target meat, offal, intestines, and bones of domestic cattle or wild ungulates, and can take sufficient food into the crop at one meal to last several days (Botha et al. 2017). They have evolved specialized adaptations that aid in the rapid detection and consumption of carcasses, an ephemeral resource that is unpredictable and sparsely distributed (Mundy et al. 1992). African and Eurasian vultures generally find their food by visually locating a carcass and/or by using the behavior of other vultures as an information network (Cortes-Avizanda et al. 2014). The probability of vultures finding a carcass is increased when a greater number of individuals are present (Jackson et al. 2008, Deygout et al. 2010). Aerial scavengers typically outcompete their terrestrial counterparts, primarily because flight increases the speed at which areas can be searched for carrion (Ruxton and Houston 2004, Whelan et al. 2008). Vultures are adapted for energetically inexpensive soaring-gliding flight that allows them to exploit energy from the environment, and to reduce their own energy expenditure to near-baseline values (Duriez et al. 2014, Harel et al. 2016).

Competition between vultures at carcasses may be fierce, as the uncertainty of the next meal drives individuals to consume as much food as possible in a short period of time (Mundy et al. 1992). This foraging strategy is facilitated by the vulture's crop, which precedes the stomach and allows the storage of the maximum amount of undigested food that will still allow the bird to become airborne (as much as 20% of body weight in the case of *Gyps* vultures; Mundy et al. 1992). Vultures have evolved several adaptations to protect themselves against the pathogens found in carcasses. Their highly acidic stomachs (with a pH that can be as low as 1.0) aid in the digestion of tougher food items such as ligaments and bone, but also ensure that most pathogens passing through the gut are destroyed (Houston and Cooper 1975). Studies on the Black (*Coragyps atratus*) and Turkey (*Cathartes aura*) Vultures suggest that New World vultures' ability to feed on carcasses that may contain harmful pathogens may not merely lie in their genetic adaptations, but also with a range of associated microbes that reside on their facial skin and in their large intestines (Roggenbuck et al. 2014, Zepeda Mendoza et al. 2018). Similar studies are lacking on Old World vultures, but it is possible that convergent evolution may have resulted in similar adaptations. These protective mechanisms resident in the vulture microbiome highlight the important role that vultures may play in cleaning up carcasses that contain microbes that are pathogenic to other vertebrates (Zepeda Mendoza et al. 2018).

Facultative Scavengers. Unlike obligate scavengers, facultative scavengers are opportunistic carrion-feeders, switching between hunting and scavenging according to the season and general availability of food (DeVault et al. 2003, Pereira et al. 2014, Mateo-Tomás et al. 2015, Sebastián-González et al. 2016). Although many species that are generally considered to be mainly predaceous, such as the lion (*Panthera leo*) and the leopard (*P. pardus*), may also scavenge when the opportunity presents itself (DeVault et al. 2011, Pereira et al. 2014, Moleón et al. 2015), the discussion herein will focus on those medium-sized mammalian scavengers, such as jackals (*Canis mesomelas* and *C. adustus*) and hyena (*Crocuta crocuta* and *Hyaena* spp.), that are most likely to be affected by vulture declines.

Mammalian scavengers. Three of the four extant species in the family Hyaenidae are scavengers: the spotted (*Crocuta crocuta*), striped (*Hyaena hyaena*), and brown (*H. brunnea*) hyena (Kingdon and Hoffman 2013). Although hyenas may be efficient hunters themselves, they typically scavenge the kills of other predators, livestock carcasses, and/or human organic waste, and have adapted well to human-transformed landscapes (Mills 1978, Kingdon and Hoffman 2013). Jackals are highly mobile and move freely between farms, protected, and urban areas (Kingdon and Hoffman 2013). They not only feed from the kills of large carnivores, but may also scavenge from rubbish dumps at safari camps, rural homes, farm buildings, and urban areas (Loveridge and Macdonald 2003). The spatial overlap of jackals and hyenas with humans and domestic animals, and their ability for long-distance foraging, have various implications. Certain behaviors, such as killing livestock and even people, and the removal and consumption of human corpses (McShane and Grettenberger 1984, Holmern et al. 2007, Gusset et al. 2009), frequently bring them into conflict with humans, who may then implement harmful practices (such as poisoning) to control their numbers. These behaviors also open up channels for the transmission of disease among wildlife, humans, and livestock.

The domestic dog (*Canis familiaris*), also a member of the Canidae family, is believed to be the most abundant carnivore in the world today (Daniels and Bekoff 1989). Due to their high population densities, physical dominance, nocturnal-diurnal activity, and tolerance of human disturbance, dogs are successful members of the vertebrate scavenger guild (Butler and Toit 2002). By providing companionship and playing roles in herding, hunting, and guarding of property, dogs have become an invaluable part of human society (Khan 2009). However, in many countries, especially those with limited economic growth, increasing numbers of unvaccinated dogs are either abandoned or allowed to roam freely (Food and Agriculture Organization of the United Nations [FAO] 2014), thereby increasing their potential to disrupt ecosystems by harassing or killing wildlife, outcompeting endemic species, and spreading disease (Young et al. 2011).

Dogs frequently breed without restriction, a process facilitated by urbanization and an increase in edible waste (FAO 2014). In countries where resources are limited and the value of livestock is prized above the value of dogs, dog owners are frequently reluctant to pay for vaccinations or proper nutrition for their dogs, which results in dogs that resort to scavenging to supplement their diet (FAO 2014). This, underscored by a lack of veterinary care and general neglect, heightens the risk of dogs contracting and spreading disease (FAO 2014). Unfortunately, governments generally allocate insufficient resources for proactive solutions such as management, vaccination, education, and sterilization, and will only react when dogs negatively impact tourism or increase the need for human health services (FAO 2014). In some developing countries, dog populations (correlated with human population growth) are increasing by 6.5% per annum (Butler and Bingham 2000), so the situation can only worsen. On continents such as Africa, where human population growth is decreasing the distances among wildlife, humans, and their livestock, feral dogs could become dangerous conduits that channel diseases between these three groups.

Other avian scavengers. African facultative scavengers include numerous bird species, including the Bateleur (*Terathopius ecaudatus*), Tawny Eagle (*Aquila rapax*), Black Kite (*Milvus migrans*), African Fish-Eagle (*Haliaeetus vocifer*), Marabou (*Leptoptilos crumenifer*) and various Corvid species. In addition to feeding at carcasses, many of these species, e.g., Marabous and crows, may also feed extensively at landfill sites (Whelan et al. 2008) where an abundance of individuals from different species creates the ideal circumstances for disease transmission. Avian facultative scavengers may harbor and spread many pathogens such as *Salmonella*, or toxins such as botulinum, which in turn may pose major risks to human health and water quality (Carvalho et al. 2003, Whelan et al. 2008). These risks are yet to be evaluated in Africa, an important gap in the literature.

VULTURES AND THE PREVENTION OF DISEASE

Although the exact nature of vultures' role in the prevention of disease has not been quantified, there is anecdotal information that points to two possible avenues that should be considered. First, vultures could directly prevent the development and spread of pathogenic microbes by quickly and efficiently removing carcasses from the environment (Fig. 1A, 1B). Second, by regulating the numbers and composition of the mammalian scavenger guild, vultures could indirectly limit the impact that an increase in mammalian scavengers may have on the spread of disease.

Direct Prevention: Pathogens and the Carcass Environment. A decomposing carcass is a nutrient-rich resource for a variety of organisms (Zepeda Mendoza et al. 2018, Anderson et al. 2019). The first colonizers of a fresh carcass originate foremost from the microbiome carried within the living animal, which may be followed by post-mortem settlement by a range of soil-dwelling bacteria, nematodes, fungi, and insects (Loeffler and Hart 2014, Metcalf et al. 2016, Zepeda Mendoza et al. 2018). Once it dies, an animal's internal microbiome may become pathogenic, with the resultant toxins being a possible adaptation to outcompete other microbes in the carcass environment (Anzen 1970, Vollaard and Clasener 1994, Zepeda Mendoza et al. 2018).

Researchers have identified a large variety of pathogenic microbes that could infect a variety of carrion feeders without having any ill effects on vultures (Zepeda Mendoza et al. 2018). A study conducted in North America, which experimentally excluded Black and Turkey vultures from rabbit carcasses, yielded a ten-fold increase in the number of experimental carcasses that were not fully scavenged (Hill et al. 2018). These experiments were conducted during the warm and humid conditions of summer, when food resources are more abundant, leading researchers to conclude that, under these conditions, facultative scavengers could not functionally compensate for the loss of vultures (Hill et al. 2018). Warmer conditions favor an increase in microbial activity, with some bacteria releasing toxic chemicals to deter mammalian scavengers from consuming a carcass (Hill et al. 2018). However, through various adaptations, vultures have become more tolerant of the toxins produced by decomposers, which allows the vultures more time to consume available carcasses (Hill et al. 2018). In the absence of vultures, remnants of carcasses may persist longer in the environment resulting in a shift from the consumption of carrion by vertebrates to consumption by decomposers, which could have important implications for nutrient cycling and disease transmission (Hill et al. 2018). With climate projections suggesting a mean annual temperature increase of over 2°C across Africa by 2100 (Niang et al. 2014, Van Wilgen et al. 2016), the resultant increase in microbial activity may make the role of vultures in combatting the spread of microbial disease increasingly pertinent.

Vultures may also play a role in consuming the carcasses of animals that have died of serious infectious diseases such as anthrax (*Bacillus anthracis*) and bovine tuberculosis (*Mycobacterium bovis*). In the presence of sufficient nutrients, anthrax will occur in the body in its vegetative form, but it will sporulate if conditions become unfavorable, such as when infected body fluids are exposed to air (Durrheim et al. 2001, Gates et al. 2001). Because vultures are capable of stripping a carcass quickly and efficiently, it may be possible for them to consume a carcass before desiccation stimulates formation of anthrax's hardy spores. The impact should be greatest when a scrum of vultures consists of a range of species, each focusing on its own area of speciality (e.g., *Gyps* vultures consuming muscle and viscera, Lappet-faced Vultures [*Torgos tracheliotos*] eating skin, ligaments, and tendons; and Hooded Vultures [*Necrosyrtes monachus*] picking at any scraps that fall by the wayside [Mundy et al. 1992]). As carcasses infected with *B. anthracis* are regarded as permanently infected (Durrheim et al. 2001), Lappet-faced Vultures could play an important ecological role by removing infected hides.

It has been suggested that, by opening carcasses, vertebrate scavengers (including vultures) facilitate the sporulation of anthrax. However, by experimentally excluding scavengers from anthrax-infected carcasses, Bellan et al. (2013) illustrated that vertebrate scavengers do not play a significant role in the spore production stage of anthrax. Instead, the exclusion of vertebrate scavengers from carcasses resulted in a substantial increase in blowfly maggots which, in conjunction with bloating and skin-rupturing, may be sufficient to open a carcass (Bellan et al. 2013). Blowflies have been implicated in the transmission of anthrax in Kruger National Park (South Africa), as infected material ingested at carcasses are regurgitated on vegetation at heights preferred by browsing herbivores (Basson et al. 2018). A healthy vulture population would curtail extended blowfly activity, and prevent the spread of anthrax spores via this channel.

Other bacterial diseases, such as the economically significant bovine tuberculosis can pass from prey to predator or from dead livestock to mammalian scavengers (Renwick et al. 2007). Low carnivore densities generally preclude the horizontal transmission of bovine tuberculosis (Renwick et al. 2007), but this could change if mammalian scavengers increase in the absence of vultures. Research supporting these hypotheses is lacking at present and should be treated as a priority.

Indirect Prevention: Competitive Regulation of the Vertebrate Scavenger Guild. *Changes in scavenger guild composition.* Vultures, as obligate scavengers, have specialized in the rapid consumption of carcasses. Vultures can strip a 100-kg wildebeest carcass in less than 30 min (Houston and Cooper 1975) and scavenging efficiency is higher in areas where obligate scavengers (i.e., vultures) are present (Morales-Reyes et al. 2017). Facultative scavengers, such as feral dogs and jackals, are not as efficient, which frequently results in the incomplete removal of flesh from bones, leaving ample breeding ground for pathogenic bacteria (Markandya et al. 2008). In some cases facultative scavengers will not consume carcasses unless they have been opened first by by specialized scavengers (Hill et al. 2018). This suggests that obligate scavengers can greatly affect the composition of, and interactions within, a scavenger community (Fig. 1A).

The disruption of a trophic system by the removal, introduction, and/or increase in another key species may have significant impacts that affect all levels in the ecosystem (Brown and Heske 1990, Letnic and Koch 2010). The scavenger guild consists of a wide range of taxa whose complex competitive interactions govern the role of carrion in food webs (DeVault et al. 2011). Thus, the composition of the entire scavenger guild can have significant impacts on ecological communities (DeVault et al. 2011). It has been proposed that, similar to the top-down regulation processes found in most predator-mediated systems, vultures regulate the composition of vertebrate scavenger communities and their decline could remove competition resulting in a type of meso-predator (or meso-scavenger) release (Morales-Reyes et al. 2017, O'Bryan et al. 2019). This could cause an increased abundance in mammalian scavengers that could result not only in increased predation on other species such as small mammals and ground-nesting birds (DeVault et al. 2011, O'Bryan et al. 2019), but also increased opportunities for the spread of disease (Fig. 1B).

An example of a disrupted trophic system was observed in India, where vultures were historically the main scavengers of the carcasses of wild and domestic ungulates (Swan et al. 2006). The vultures' decline (attributed to the use of the veterinary drug diclofenac [Oaks et al. 2004]) resulted in a concomitant increase in rotting carcasses (particularly around human habitation), which in turn likely contributed to a dramatic increase in the abundance of rats and feral dogs (Prakash et al. 2003). This example of the Competitive Exclusion Principle (Hardin 1960) suggests that in the absence of specialized scavengers, facultative scavengers stepped in to fulfil an equivalent ecological role (Şekercioğlu et al. 2004). In an African context, the facultative scavengers most likely to increase in abundance are the hyenas and jackals (Ogada et al. 2012b), although an equivalent increase in rats and feral dogs should not be unexpected. In a study conducted in central Kenya, Ogada et al. (2012b) showed that the absence of vultures resulted in longer carcass decomposition times, an increase in the number of mammals present at carcasses, and an increase in the amount of time these mammals spent

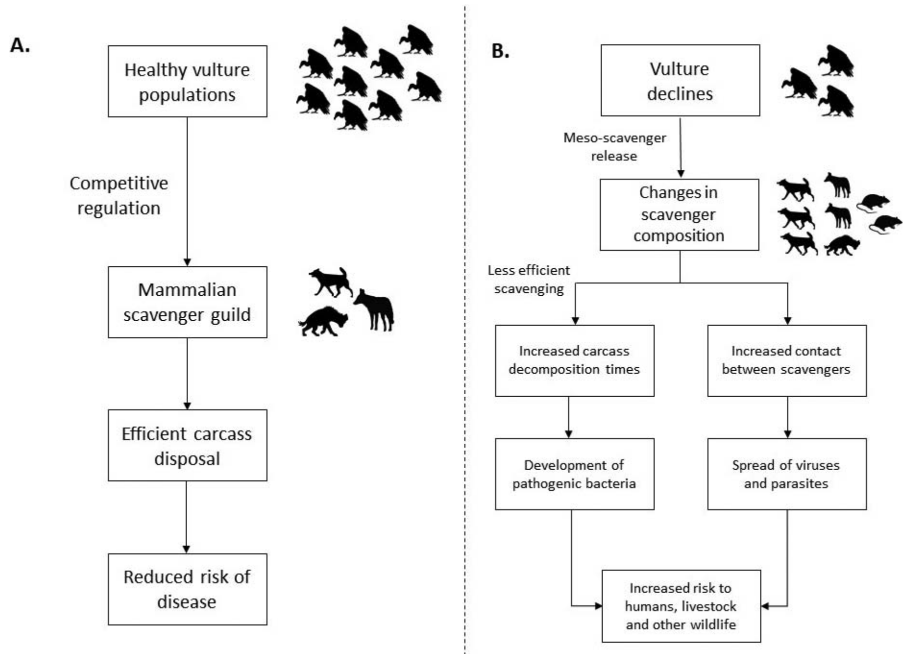

Figure 1. (A) As obligate scavengers, vultures act as competitive regulators, controlling the numbers and composition of the mammalian scavenger guild. (B) A decline in vultures could result in the competitive release of mammalian scavengers, an occurrence that could increase carcass decomposition times and contact rates between mammalian scavengers, facilitating the spread of disease. Adapted from ideas in Şekercioğlu et al. 2004, Markandya et al. 2008, Ogada et al. 2012a, Buechley and Şekercioğlu 2016, Morales-Reyes et al. 2017, O'Bryan et al. 2019.

at carcasses. Their results also suggested a three-fold increase in the frequency of contacts between conspecifics and, because rates of disease transmission depend on the number of susceptible individuals with which an infected individual interacts, this increase in interspecific contact could facilitate pathogen transmission (Ogada et al. 2012b).

This risk is compounded by the significant inter- and intraspecific dominance hierarchies that characterize interactions of mammalian scavengers at carcasses. Scavengers such as spotted hyenas are frequently injured at carcasses by conspecifics and larger predators such as lions (Watts and Holecamp 2009), whereas jackals, often dominated by hyenas, will display significant intra-guild aggression (Loveridge and Macdonald 2002). These interactions create opportunities for bites and the exchange of body fluids such as saliva, which may facilitate the spread of viral diseases such as rabies and canine distemper. Feral dogs can act as an invasive alien species (Clout 1995) and are also capable of having competitive interactions with wild carnivores (Butler et al. 2004). These interactions may take place in wildlife reserves or at reserve boundaries where feral dogs may both compete with other scavengers or fall prey to large carnivores, thereby increasing the potential for disease transmission (Cleaveland et al. 2000, Butler and Toit 2002, Patz et al. 2004). Of special concern are areas where wild predators and dogs occur sympatrically, as they move freely between conservation areas and communal lands (Butler et al. 2004). Spotted hyenas are known to feed on dogs, while lions and leopards are known to scavenge opportunistically on the boundary areas of reserves where they may come into contact with feral dogs (Butler and Toit 2002). The risk of these interactions increases during the dry season, when food scarcity drives dogs further into conservation areas (Butler et al. 2004). In this way, free-ranging dogs may not only become the conduits of disease into reserves, but also out of reserves into commercial farming areas and human habitation. By keeping the numbers of facultative scavengers in check, vultures could fulfil a vital ecological role by limiting not only the spread of viral diseases, but also the associated loads of external and internal parasites which pose equal risks to humans, livestock, and wildlife.

Evidence for the regulatory impact of vultures on the composition and abundance of other avian scavengers is lacking. The propensity of many avian scavengers to frequent landfill sites, and their tendency to harbor and distribute pathogenic bacteria such as *Salmonella* (Carvalho et al. 2003), justifies further research into the possible impact that vulture declines may have on the abundance and distribution of other avian scavengers.

Impacts at the human–wildlife–livestock interface. The spread of viral diseases via bodily fluids may be facilitated by the aggressive interactions between mammalian scavengers at carcass sites. Two viral diseases, i.e., canine distemper and rabies, are of significant conservation and economic importance, with rabies moving freely across the human-wildlife-livestock interface.

Canine distemper is one of the more important infectious diseases affecting free-ranging carnivores, and could decimate predator populations within protected areas (Alexander and Appel 1994). Because canine distemper is spread via body fluids such as saliva, increased contact rates between canids, in the absence of vultures, may facilitate its transmission (Williams 2001). There are concerns about the potential transmission of canine distemper from dogs that are resident in communal lands to wild canids in adjacent nature reserves (Alexander and Appel 1994). For instance, in northwestern Tanzania, canine distemper seroprevalence among pastoralists' dogs reached 90% (Cleaveland et al. 2000) and in South Africa, 25% of diseased dog cases are attributed to canine distemper (Leisewitz et al. 2001). In Zimbabwe, 62% of reserve boundaries adjoin communal land and dogs penetrate protected areas in search of food, which may bring them into contact with predators such as lions, leopards, hyenas, jackals, and wild dogs (*Lycaon pictus*, Butler et al. 2004).

Rabies, transmitted by the bite and/or saliva of infected animals, causes fatal encephalitis in mammals and is found wherever there are large populations of humans, and domestic and feral dogs (Rupprecht et al. 2001). It readily transmits to wild Canidae and Hyaenidae, and both black-backed jackals (*Canis mesomelas*) and side-striped jackals (*C. adustus*) now appear to be the major reservoirs in northern South Africa and Zimbabwe (Rupprecht et al. 2001). Black-backed jackals are highly mobile and share food and water resources, which makes them an ideal vector for rabies (McKenzie 1993). Humans come in contact with spotted hyenas when the hyenas are hunted for human consumption or as trophies, or killed for body parts for belief-based use (Kingdon and Hoffman 2013).

Periodic resurgences of rabies have occurred around the world in recent times, including Paraguay (Amarilla et al. 2018), New York, USA (Chang et al. 2002), and KwaZulu-Natal Province in South Africa (Weyer 2018). According to the World Health Organization (WHO), 95% of rabies cases reported annually are from Africa and South East Asia alone, with disadvantaged communities being particularly vulnerable (WHO 2019). Because 99% of rabies infections in humans are obtained from contact with dogs, dog-bite management and dog vaccinations form the major strategies for management of the disease in these regions. However, some areas have seen an unprecedented increase in feral dog populations. For example, at one carcass dump in India, the feral dog population increased from around 60 in 1992, to over 1200 in 2001, an occurrence likely attributable to the dramatic decline in vulture populations in the region (Prakash et al. 2003). Such an increase could drive a potential surge in the number of dog-bite incidents, and a concomitant increase in the transmission of rabies (Markandya et al. 2008), not only hampering ongoing efforts to manage the disease, but also placing an additional financial burden on existing dog vaccination programs.

Of equal concern are the indirect effects a decline in vultures could have on increased transmission of zoonotic parasites, especially in developing countries. Mammalian scavengers can be hosts to a variety of ecto- and endoparasites, or they may serve as vectors for a range of infectious diseases that could be transferred to humans during hunting, game ranching, and raising of domestic animals (Odeniran and Ademola 2016). Concerns have also been raised about the potential role that companion animals such as domestic cats and dogs could play in disease transmission, especially in areas where these animals are in direct contact with wildlife or feral species and receive minimal veterinary care (Day 2011). In most cases, humans are infected when companion animals transport flies, ticks, fleas, mites, or various internal parasites into the domestic environment.

Those parasites with zoonotic potential include a variety of protozoans (e.g., *Trypanosoma* spp.), trematodes (e.g., *Schistosoma* spp.), cestodes (including *Echinococcus* and *Taenia* spp.) and nematodes (e.g., *Toxocara* spp.), which can cause debilitating symptoms ranging from diarrhea, anemia, abnormalities in the central nervous system, organ dysfunction, abortion, and even death (Odeniran and Ademola 2016). One of the most significant infectious diseases in recent times is visceral leishmaniasis, for which the domestic dog acts as the major reservoir. The disease is endemic to many countries in southern Europe, the Americas, northern Africa and Asia, and it is estimated that up to 12 million people are infected, with a further 350 million people at risk of infection (Day 2011). There are concerns that the disease may extend its traditional range into countries where it is not currently present, especially given the increased mobility of pet animals across borders (Shaw et al. 2009).

VULTURES AS TRANSMITTERS OF DISEASE

By opening carcasses and feeding on infected material, scavengers may not only enable the action of disease vectors but, in some cases, also act as competent hosts and potential vectors of a number of pathogens (Carrasco-Garcia et al. 2018). Although the exact role of scavengers in disease dynamics is still poorly understood, studies have highlighted the horizontal transmission of diseases from scavengers to other wildlife and even livestock (Carrasco-Garcia et al. 2018). For instance, the prions of Chronic Wasting Disease (CWD), have been shown to pass unscathed through the digestive tract of predators such as coyotes (*Canis latrans*; Nichols et al. 2015), and mammalian scavengers have been implicated in the transmission of bovine tuberculosis (Ragg et al. 2000, Barron et al. 2015).

Information on the role of vultures in the spread of disease is scant, and we relied heavily on early work that identified the complex role vultures play in the ecology of disease (Houston and Cooper 1975). Vultures have been suspected of transmitting bacterial diseases such as anthrax, tuberculosis, and brucellosis through regurgitated food items or excreta, or on their feathers and feet (Houston and Cooper 1975, Zepeda Mendoza et al. 2018). More recently, *Salmonella* strains found in free-living vultures have been linked to those found at pig (*Sus scrofa domestica*) farms, which suggests vultures get infected with the bacteria at supplementary feeding sites and then transmit the bacteria to other feeding sites (Marin et al. 2018).

Some bacteria, such as *Streptococcus* spp., may survive the digestive tract of vultures intact (Houston and Cooper 1975). The vegetative form of anthrax is killed when it passes through the digestive tract, although the spores may survive (Urbain and Novel 1946, Houston and Cooper 1975). However, the pathogen must be exposed to air for several hours before sporulation is triggered (Gates et al. 2001). If a vulture is to transfer anthrax spores it would need to be contaminated by a carcass that has had sufficient time to expose its bacterial load to air, an unlikely scenario with functional vulture populations. Hypothetically, spores that have undergone this process could be disseminated by vultures over great distances, as their foraging ranges far exceed those of their mammalian counterparts.

Viruses such as foot-and-mouth-disease are unlikely to be transmitted by vultures as they cannot withstand the extreme acidity of a vulture's stomach (Andrews and Pereira 1967). However, these acidic conditions are unlikely to deter the infectious stages of internal parasites such as nematodes and cestodes (Houston and Cooper 1975). This is supported by research in Croatia that found *Toxocara*-type eggs (most likely ingested from dead stray dogs and cats) in excreta of Griffon Vultures (*Gyps fulvus*, Kocijan et al. 2009). It seems then, that although vultures may play a major role in limiting the risk of infection posed by decomposing carcasses or from animals that have died of disease, they could also introduce pathogens to areas where animals have not been previously exposed. This interaction is complex and warrants further study.

QUANTIFYING THE COST OF VULTURE DECLINES

An urgent need has been identified for the value of ecosystem services provided by birds to be quantified in ways that will justify the protection of these services in land-use recommendations and policy decisions (Daily et al. 2009, Wenny et al. 2011). The ecosystem services provided by vultures are multi-faceted, and include their role in disease regulation, organic waste removal, sanitation, and nutrient recycling. To this must be added other, less tangible, considerations including vultures' roles in cultural provisioning for traditional medicine, the desire to reduce the conflict between humans and wildlife, and the contributions of vultures to environmental aesthetics and ecotourism. The complex interaction between all these factors, both direct and indirect, means that the true financial, environmental, social, and health costs related to the decline of vultures may never be accurately quantified. However, increased attempts should be made to quantify the economic value of ecosystem services provided by vultures.

Human Health and Veterinary Care. The repercussions of vulture declines must be evaluated in terms of the costs associated with health and veterinary care, which are either lacking entirely or beyond the means of the average citizen in many developing countries. There are many diseases that play a significant role at the human-livestock-wildlife interface, but two of the most significant (i.e., rabies and bovine tuberculosis) will be used to illustrate the possible cost of vulture declines. Bovine tuberculosis and rabies pose serious threats to free-ranging wildlife and domestic animals, are heavily concentrated in the developing world, and have significant zoonotic potential (Renwick et al. 2007). As of 2010, the average cost of a human rabies vaccination in Africa and Asia was $45 (all $ figures represent US dollars), while the average salary was often less than $2 per day (Bourhy et al. 2010), placing such preventative care beyond the means of most people in impoverished nations. Unfortunately, it is among these communities that feral dog populations are most likely to increase, resulting in increased risk of exposure to rabies, especially among children. In India, human health costs due to the loss of vultures and subsequent increase in dogs and rabies was estimated at about $1.5 billion per annum (Ogada et al. 2012a). Significantly, diseases such as bovine tuberculosis may also manifest as opportunistic infections in people infected with human immunodeficiency virus (HIV). It is estimated that in sub-Saharan Africa, which is at the center of the current HIV/AIDS pandemic, 70% of people infected with HIV are also infected with bovine tuberculosis (Cosivi et al. 1998). In South Africa it costs approximately $100 per patient per month to provide HIV-infected patients with comprehensive care and treatment, including antiretroviral (ARV) and non-ARV medications, personnel, and clinic overhead costs (Martinson et al. 2009). To this must be added the additional health care costs that are required to combat secondary infections from diseases such as bovine tuberculosis. Long-term resources required to maintain current levels of HIV prevention and treatment in sub-Saharan Africa (i.e., between 2015 and 2050) are estimated to be at least $98 million, a sum that will be heavily dependent on foreign aid (Atun et al. 2016). Because dogs are known to be the source of most rabies infections (Markandya et al. 2008) and mammalian scavengers have been implicated in the spread of bovine tuberculosis (Ragg et al. 2000, Barron et al. 2015), we can conclude that the competitive regulation of vultures on these species may have a significant limiting effect on the spread of these zoonotic diseases which, in turn, may reduce the funds that are needed for their treatment and prevention.

The economic benefits of vultures are not limited to reducing health and veterinary care, but also extend to protecting livelihoods, and minimizing the cost of surveillance and prevention programs. Economic losses are not only incurred when animals die or become less productive as a result of disease (Horan and Wolf 2005). Losses are also incurred when the demand for livestock products decrease, or when strict regulations, trade sanctions, and demands (e.g., mandatory culling) are imposed when herds become infected (Horan and Wolf 2005). Increases in dog numbers may require more intensive surveillance and vaccination programs, both at great financial cost. It is estimated that of the more than $300 million spent per year on the detection, prevention, and control of rabies in the United States, more than $130 million is spent on the vaccination of wildlife such as raccoons (*Procyon lotor*) and skunks (*Mephitis mephitis*) alone (Sterner et al. 2009). Efforts to prevent the transmission of diseases to naive populations of wildlife and livestock can cost millions of dollars. This may include overhead costs such as the construction of electrified fencing, which is expensive to build and electrify, and requires frequent maintenance (Miller et al. 2013).

Quantifying vultures' roles as disease regulators (from both a human health and veterinary perspective) has proven particularly challenging, as efforts are hampered by a lack of reliable data, particularly in developing nations, where surveillance systems are frequently inadequate. Efforts are also hampered by difficulties in ascertaining accurate population-level data for vultures because they (especially juveniles) can be highly mobile and travel vast distances in their search for food (Phipps et al. 2013, Duriez et al. 2019). It can also be difficult to accurately link an increase in disease occurrence to the absence of vultures, when rates of occurrence are reduced by effective preventative care and surveillance programs.

Sanitation Services. Rubbish dumps, organic street waste, and slaughter houses represent a predictable source of abundant food for many scavenger species, including vultures (Plaza and Lambertucci 2017). The densest known population of Egyptian Vultures (*Neophron percnopterus*) is found on Socotra Island (Yemen), where these birds are estimated to consume up to 248 metric tons per year of organic matter from human settlements (Gangoso et al. 2013). In parts of West and East Africa, Hooded Vultures rely on organic waste from slaughterhouses, markets, and rubbish dumps (Gbogbo and Awotwe-Pratt 2008, Ogada and Buij 2011, Odino et al. 2014). Historically, the amount of food consumed by Marabous and vultures in the city of Kampala, Uganda, was estimated at about 100,000 kg annually (Pomeroy 1975). Together with other species scavenging at rubbish dumps (e.g., spotted hyenas, White Storks [*Ciconia ciconia*, Ciach and Kruszyk 2010], Pied Crows [*Corvus albus*], and Black Kites), vultures remove waste that represents a potentially serious health hazard, at no cost to local councils (Pomeroy 1975), although this must be offset against the possible risk of disease transmission at these waste sites.

The advantages related to these sanitation services, both economic and environmental, have not been quantified in Africa, although they may be deduced from studies conducted elsewhere. The global population of Turkey Vultures (estimated at about 13 million birds) render clean-up services valued at $700 million per year across this species' range in North and South America (Grilli et al. 2019). In developed countries such as Spain, the industrial destruction of carcasses averages approximately $85-123 per metric ton but vultures may remove 9.9 million tons of carcasses per year, saving farmers approximately $26 per animal (Margalida and Colomer 2012). Following the bovine spongiform encephalopathy outbreak in Europe, revised sanitation regulations required all livestock carcasses to be collected from farms and transported to authorized processing plants for transformation or destruction, a decision that increased atmospheric CO_2 emissions by 77,334 metric tons per year in Spain alone (Dupont et al. 2012, Morales-Reyes et al. 2015). In the context of global climate change, these increasing emissions can have significant long-term environmental and human health implications. In addition, farmers and regional and national administrations were required to pay approximately $50 million per year to Spanish insurance companies for the removal and processing of livestock carcasses, an avoidable cost if the extensive vulture populations in the region had been allowed to consume these carcasses (Morales-Reyes et al. 2015, DeVault et al. 2016). Although sanitation costs in developing countries may not be as high as those in the developed world (Hoornweg and Bhada-Tata 2012), the economic and environmental benefits related to the removal of carcasses by vultures could still be significant, especially when considered within the context of developing nations such as those in sub-Saharan Africa, where struggling economies and armed conflict frequently prevent governments from providing even the most basic services to their citizens.

Future Research

Although much has been done to illustrate the benefits of vultures at the human-livestock-wildlife disease interface, there remains a stark need for an economic valuation of the ecosystem services they provide. Such an evaluation may help to convince regulators and policy makers to enact stricter penalties for those who threaten or harm vultures. There is also a need for *in situ* and *ex situ* assessment of the role that vultures may play in disease transmission, even though the former is fraught with ethical dilemmas. Risk assessments regarding the loss of vultures should be completed at federal, regional, state, and provincial levels. Researchers and managers need a better understanding of the effects apex scavengers may have on the composition and abundance of mammalian meso-scavenger communities (O'Bryan et al. 2019), as well as on avian facultative scavengers such as crows. We also recommend research to better understand the epidemiological consequences of large numbers of avian facultative scavengers feeding at landfills (Whelan et al. 2008), and whether competitive regulation by vultures could limit the risks of disease transmission at these sites.

Conclusions

The unique adaptations of vultures to clean up carcasses and organic refuse quickly and efficiently make them keystone species of effective scavenger guilds. As such they provide highly effective supporting and regulating ecosystem services that require no monetary investment from local governments (Gangoso et al. 2013, Craig et al. 2018).

It is clear from the discussion, however, that the implications of Old World vulture declines (especially in developing countries) are not yet fully understood, and require urgent investigation. Unfortunately, the ecological services vultures provide have yet to be economically quantified to the point where a monetary value can be placed on the benefits they bring to rural and urban communities. In countries such as India, where vultures have become all but functionally extinct, increased feral dog populations have been linked to the decline in vulture populations. However, the link to a possible rise in rabies incidents remains tenuous, as any correlation may be masked by improved measures for surveillance, treatment, and vaccination. We can conclude from anecdotal information that vultures provide services in preventing the spread of disease from animal to animal and from animal to human. The best evidence to support this comes from case studies in Africa, Europe, and the USA, where the removal of vultures as apex scavengers has resulted in increased carcass decomposition times, increased contact rates between mammalian scavengers, and as a consequence, increased opportunities for the transmission of harmful pathogens. This could pose a significant risk, not only to human health, but also to the livestock and wildlife that form the foundation of many people's livelihoods. This fact alone elevates the value of vultures to levels where concrete steps are warranted to protect them as keystone ecosystem providers in terms of the CBD's Aichi Target 14 (CBD 2018).

It is reasonable to conclude that the investment from governments, NGOs, and private citizens to compensate for the loss of services supplied by vultures would far outweigh the investment required to protect these animals in the wild. Not only is this applicable to the costs of industrial carcass disposal and other sanitation services (as illustrated in Spain), but also to the crippling health care costs associated with zoonotic diseases. Numerous studies in the developed world have also illustrated the massive losses that could potentially be suffered by domestic livestock markets, should outbreaks of diseases require culling of animals, or if trade sanctions on livestock exports are imposed by foreign markets. The previously discussed repercussions resulting from the functional loss of vultures, including the potential loss of endangered wildlife and ecotourism, are not exhaustive, but they should be argument enough for the economics of protection of African vultures, even without hard data in some cases.

In addition, it is important to recognize that citizens of developing countries (such as those of sub-Saharan Africa) frequently have no access to, or funds for, proper health and veterinary care, vaccination, and vector-control programs (Gregor 2007). The fact that the bulk of the global budget for researching and surveillance of zoonotic emerging infectious diseases (EIDs) is focused in developed countries, where the origin of the next important EID is least likely to occur (Jones et al. 2008), serves to reinforce the argument for a broad transnational approach to protect the value vultures bring to societies and their economy. The extent of global travel and the ability of many EIDs to disperse rapidly (as is evident from the recent coronavirus disease of 2019 pandemic), highlight the need for robust early identification systems (Miller et al. 2013), and the global importance of protecting disease-regulating species, especially in countries where early identification systems are lacking. Indeed, the massive and perpetually increasing production of organic waste, driven by unchecked human population growth, will only increase the functional significance of vultures in the developing world (Grilli et al. 2019).

The One Health approach recognises the interconnection between people, animals, plants, and their shared environment (Centers for Disease Control and Prevention 2020). Studies on zoonotic diseases frequently focus on human health, wildlife, or livestock, with findings relegated to their respective compartments. Successful management of zoonotic and episodic diseases at the human-livestock-wildlife interface requires an integrated approach across a multitude of disciplines, sectors, and institutions (Welburn 2011, Moleón et al. 2014). If humanity's welfare is connected to the health of its environment, then the functional extinction of vultures will lead to disruptions in ecosystems and the diminishment of One Health.

Acknowledgments

This review article is a product of an investigation entitled "There is still time to save Africa's vultures," hosted and funded by the National Socio-Environmental Synthesis Center (SESYNC) in Annapolis, MD USA. The authors thank Margaret Palmer and the rest of the SESYNC team for their unstinting support of vulture conservation in Africa. The lead author thanks Neville and Pamela Isdell (Isdell Family Foundation) and Jessica Slack-Jell (Mary Oppenheimer and Daughters Foundation) for their continued support of BirdLife South Africa's Vulture Project.

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Received 14 February 2020; accepted 10 June 2020