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Dropping dead: causes and consequences of vulture population declines worldwide

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Vultures are nature's most successful scavengers, and they provide an array of ecological, economic, and cultural services. As the only known obligate scavengers, vultures are uniquely adapted to a scavenging lifestyle. Vultures' unique adaptations include soaring flight, keen eyesight, and extremely low pH levels in their stomachs. Presently, 14 of 23 (61%) vulture species worldwide are threatened with extinction, and the most rapid declines have occurred in the vulture-rich regions of Asia and Africa. The reasons for the population declines are varied, but poisoning or human persecution, or both, feature in the list of nearly every declining species. Deliberate poisoning of carnivores is likely the most widespread cause of vulture poisoning. In Asia, *Gyps* vultures have declined by >95% due to poisoning by the veterinary drug diclofenac, which was banned by regional governments in 2006. Human persecution of vultures has occurred for centuries, and shooting and deliberate poisoning are the most widely practiced activities. Ecological consequences of vulture declines include changes in community composition of scavengers at carcasses and an increased potential for disease transmission between mammalian scavengers at carcasses. There have been cultural and economic costs of vulture declines as well, particularly in Asia. In the wake of catastrophic vulture declines in Asia, regional governments, the international scientific and donor communities, and the media have given the crisis substantial attention. Even though the Asian vulture crisis focused attention on the plight of vultures worldwide, the situation for African vultures has received relatively little attention especially given the similar levels of population decline. While the Asian crisis has been largely linked to poisoning by diclofenac, vulture population declines in Africa have numerous causes, which have made conserving existing populations more difficult. And in Africa there has been little government support to conserve vultures despite mounting evidence of the major threats. In other regions with successful vulture conservation programs, a common theme is a huge investment of financial resources and highly skilled personnel, as well as political will and community support.

Keywords: scavenger; condor; ecosystem services; carcass decomposition; disease transmission; vulture decline; poisoning; persecution; Africa; Asian vulture crisis; vulture conservation; diclofenac; furadan

Introduction

Charles Darwin thought vultures were "disgusting."[1] From a human perspective, perhaps they are, but vultures are nature's most successful scavengers, and they provide us with an extensive array of ecological, economic, and cultural services. Most notably, vultures dispose of carrion and other organic refuse, providing a free and highly effective sanitation service. The vulture-governed cleaning service protects the health of humans, domesticated animals, and wildlife because the abundance of other scavengers, some of which are well-known disease reservoirs, increases substantially at carcasses without vultures.[2,3,4] Scavenging of carcasses by vultures promotes the flow of energy through food webs,[5,6] and vultures have been shown to facilitate African predators, such as lions and hyenas, in locating food resources.[7,8]

In this review, we highlight the unique adaptations of vultures to scavenging. We then describe the dramatic recent and historic declines in many

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vulture species worldwide. We explore the apparent causes and consequences of these declines in different regions, and we conclude by characterizing the elements that appear to be necessary for successful vulture conservation programs.

Taxonomy, distribution, and unique adaptations to scavenging

Globally, there are 23 species of vultures (including condors), of which the majority ($n = 16$) occur in the Old World and within the family Accipitridae. The remaining seven species comprise the New World Cathartidae family. Most species ($n = 15$) occupy a range within one continent comprised of two or more countries. Four species, the Griffon vulture (*Gyps fulvus*), Bearded vulture (*Gypaetus barbatus*), Egyptian vulture (*Neophron percnopterus*), and Cinereous vulture (*Aegypius monachus*), have or historically had large ranges that span three continents. Two species, Turkey (*Cathartes aura*) and Black vultures (*Coragyps atratus*), range widely within both North and South America. Cape vultures (*G. coprotheres*) in southern Africa and California condors (*Gymnogyps californianus*) in North America have historically small ranges,[9,10] though fossil evidence suggests that California condors were once found throughout the United States, southern Canada, and northern Mexico.[10] Vulture-rich regions include Central and South America ($n = 6$ spp.), South Asia ($n = 10$ spp.), and Africa ($n = 11$ spp.).

Outside of the oceans, vultures are the only known obligate scavengers.[11] They are uniquely adapted to exploit a transient food source that occurs intermittently over large areas.[11,12] Using gliding flight, vultures take advantage of upward air movements that enable them to travel rapidly over long distances with relatively little energy expenditure.[13] This allows them to search for food efficiently. They can also search communally by observing other birds from the air. Aerial searching also gives them a considerable advantage over terrestrial scavengers because the latter have limited feeding ranges, higher energy expenditures to locate carcasses, and comparatively poor visibility from the ground.[14,15] The superior foraging efficiency of avian scavengers is nowhere more apparent than in the Serengeti, where only vultures have the ability to follow migratory ungulates over vast distances and benefit from heavy mortality that occurs along the way.[14] It has been estimated that vultures in the Serengeti consume more meat than all the other mammalian carnivores combined.[12]

All vultures locate carcasses using keen eyesight. New World *Cathartes* vultures also have a well-developed sense of smell that is used for locating food in forested areas.[16,17,18] Once they have located food, they can travel quickly to reach it, avoiding displacement by larger terrestrial scavengers.[12] For example, vultures in the Serengeti entirely consumed 84% of experimentally placed carcasses before any mammalian scavengers appeared.[8] Facultative scavengers, such as hyenas and especially lions, use the activity of vultures to detect carrion,[7] but vultures more than compensate for this competition by arriving rapidly and in large numbers.[12]

Vultures are among the largest of flying birds. Their size allows them to consume more food at each carcass discovery and to carry greater body reserves, which is important given their erratic food supply. A large body also helps them to outcompete smaller scavengers at carcasses and because flight speed is largely determined by body mass;[11] it increases the area that they can search each day. A recent study using satellite tracking devices determined that the mean foraging range for two immature Cape vultures (one was likely a Cape x White-backed (*G. africanus*) hybrid vulture) was an astounding 480,000 km^2 over an eight-month period.[19] Physiologically, vultures have low pH levels in their digestive tracts (pH 1–2); this destroys most microscopic organisms and greatly reduces the probability that vultures act as sources of infection at carcasses.[20] Finally, vulture life history is characterized by delayed maturity, low productivity, and relatively high adult survivorship. Vultures and especially condors have some of the lowest reproductive rates among birds, and their populations are particularly vulnerable to high mortality, whether by natural or human causes.[21]

Historical and recent vulture population trends

Vulture population declines in Europe and North American likely began as early as the mid-19th century.[22,23] One hundred years later, some populations of Bearded vultures in Europe and the California condor in North America were already nearing extinction.[22,23] Further reports of population

Table 1. Overview of historical vulture declines

Species	Range	Area declining	Peak of declines	Causes of decline	References
Egyptian vulture	Africa, Asia, Europe	Europe (first), Asia, Africa	20th century	Persecution through poisoning and hunting	26
Bearded vulture	Africa, Asia, Europe	Europe (first), Africa	Began 1860 through 1900 when nearly extirpated	Persecution, poisoning, also electrocution	22, 27
California condor	North America	North America	19th century through 1937	Lead poisoning, persecution, collision with overhead wires, secondary poisoning	28, 29
Cape vulture	Southern Africa	Southern Africa	1900	Poisoning, decline in food supply, electrocution, persecution, disturbance at breeding sites	9
White-rumped, Slender-billed, Red-headed vultures	Asia	South Asia (Malaysia, Laos, Cambodia, Thailand rare if not extinct) and Burma, Bangladesh and Pakistan seriously declined, with exception of India	1950–1970s	Decline in food supply due to overhunting and changes in livestock husbandry practices (primarily) also persecution and poisoning	3, 24, 25

declines of Cape vultures and of vultures in South Asia testify to the global nature of declines that had already begun prior to the mid-20th century (Table 1 and Refs. 9, 24, and 25).

In few areas, if any, have vulture populations maintained historical levels of abundance, but there are substantial differences in the numbers of species declining and in population trends among regions (Table 2). In the Middle East, populations of three species are reported to be in decline in the United Arab Emirates,[51] and five species present in Israel are similarly declining.[52] In Europe and North America, which have historically recorded large population declines,[22,23,27] the majority of vulture populations are now increasing or stable (Table 2). In vulture-rich regions, large population declines have occurred in recent decades, particularly in Asia and Africa.

Within the Central and South American region, half of the vulture species are estimated to be in decline, though the region has comparatively little published research on vulture populations apart from that on the Andean condor (*Vultur gryphus*).[31,53,54,55]

Table 2. **Conservation status of the world's vultures. References are listed in respect to recent status overviews where available; these are indicated by "and references therein." For species lacking a recent status overview, important historical and recent references are listed, with BirdLife International (2011) as a general source.**

Species	Scientific name	Region(s)	IUCN Red List category[a]	Current status	References
California condor	*Gymnogyps californianus*	North America	CR	Small population increasing, though lead shot in carcasses remains a threat	30 and references therein
Turkey vulture	*Cathartes aura*	Americas	LC	Population increasing	31–33 and references therein
Black vulture	*Coragyps atratus*	Americas	LC	Population increasing	31–33 and references therein
Andean condor	*Vultur gryphus*	South America	NR	Moderately rapid decline	31, 34 and references therein
Lesser Yellow-headed vulture	*Cathartes burrovianus*	Central and South America	LC	Apparently stable	31
Greater Yellow-headed vulture	*Cathartes melambrotus*	South America	LC	Slow decline	31
King vulture	*Sarcoramphus papa*	Central and South America	LC	Slow decline	31
Egyptian vulture	*Neophron percnopterus*	Europe, Africa, Middle East, Asia	EN	Declining significantly throughout most of its range. Rapid declines in India	26, 31, 35, 36
Bearded vulture	*Gypaetus barbatus*	Europe, Africa, Middle East, Asia	LC	Slow decline throughout much of range	27, 31 and references therein
Griffon vulture	*Gyps fulvus*	Europe, Africa, Middle East, Asia	LC	Increasing in Europe, stable in central Asia and decreasing in North Africa and Turkey	31
Cinereous vulture	*Aegypius monachus*	Europe, Africa,[b] Middle East, Asia	NT	Slow to moderate decline	31, 37 and references therein

Continued

Table 2. *Continued*

Species	Scientific name	Region(s)	IUCN Red List category[a]	Current status	References
Hooded vulture	*Necrosyrtes monachus*	Africa	EN	Rapid decline of at least 50% over three generations	38 and references therein
White-backed vulture	*Gyps africanus*	Africa	NT	Large declines in West Africa, but apparently stable in other parts of Africa	16, 31, 39–42
Rüppell's vulture	*Gyps rueppellii*	Africa	NT	Extremely rapid declines in West Africa and moderate declines elsewhere	16, 31, 39–42
Lappet-faced vulture	*Torgos tracheliotos*	Africa, Middle East	VU	Moderately rapid decline	16, 31, 39–42
White-headed vulture	*Trigonoceps occipitalis*	Africa	VU	Declining at slow to moderate rate	16, 31, 39–42
Cape vulture	*Gyps coprotheres*	Africa	VU	Declining at ∼20% over three generations	9, 31, 43–45
Palm-nut vulture	*Gypohierax angolensis*	Africa	LC	Apparently stable	31
Indian vulture	*Gyps indicus*	Asia	CR	Extremely rapid declines of >97% over 10–15 years	4, 31, 46–49
Himalayan vulture	*Gyps himalayensis*	Asia	LC	Apparently stable	31
White-rumped vulture	*Gyps bengalensis*	Asia	CR	Extremely rapid decline of >99% over 10–15 years	4, 31, 46–50
Red-headed vulture	*Sarcogyps calvus*	Asia	CR	Rapid decline in excess of 90% over 10 years in India	31, 35
Slender-billed vulture	*Gyps tenuirostris*	Asia	CR	Extremely rapid declines	4, 31

[a] IUCN Red List category abbreviations are as follows: LC, least concern; NT, near threatened; V, vulnerable; EN, endangered; CR, critically endangered.
[b]Considered extinct in the region.[16]

Vulture populations in South Asia have incurred the most precipitous and rapid declines ever recorded. Prakash[48] first reported population declines of >95% for *Gyps* vultures in Keoladeo National Park, India, which occurred within a 10-year period. Subsequent surveys over the next decade confirmed massive declines (>96%) of three species of *Gyps* vultures in India.[4,49] Rapid declines have been similarly noted in Pakistan[46,47,50] and Nepal.[56,57] More recent declines in Egyptian and Red-headed vultures (*Sarcogyps calvus*) have been documented throughout India.[35]

In Africa, recent population collapses have been recorded, particularly in West and East Africa. In West Africa, populations of all vultures except the Hooded vulture (*Necrosyrtes monachus*) have declined by an average of 95% in rural areas over the last 30 years.[40,41,58] In protected areas of the Sudanese zone, their collective populations fell by an average of 42% over the same period.[40,41,58] In East Africa, vulture declines of 70% were recently recorded over a three-year period in north-central Kenya.[59] Even the wildlife-rich Masai Mara region has lost an average of 62% of its vultures over the past 30 years, and annual vulture mortality as high as 25% has recently been recorded.[42,60] The situation for vultures in North Africa is dire, particularly in Morocco, where two species, Cinereous and Lappet-faced vultures (*Torgos tracheliotos*), have been extirpated.[61] Others are predicted to follow, and the rest of the region offers little hope for long-term vulture conservation.[61] Vulture research and conservation have a relatively long history in southern Africa, beginning with the formation of the Vulture Study Group in 1977. That group produced the seminal book *The Vultures of Africa* and ingrained vulture research within the ornithological community. Vulture populations in the region continue to be the best studied in Africa and rival the level of study of those in Europe and North America. However, there are a few species whose populations continue to decline, and one, the Egyptian vulture, is believed to be extinct as a breeding species in southern Africa.[62] Throughout Africa, the Hooded vulture, a widespread human commensal, has declined by an average of 62% over the past 40–50 years, and in some areas the decline has been much more rapid.[38]

Causes of declines

There are numerous reasons behind the global vulture decline. However, either poisoning or human persecution, or both, feature in the list of nearly every declining vulture population. We define poisoning as the *unintentional* killing or harming of vultures through consumption of contaminated carcasses or remains. Human persecution refers to the *intentional* killing or disturbance of vultures through actions such as shooting, harassment, and deliberate poisoning.

Vultures are particularly vulnerable to toxic substances due to a combination of foraging behaviors and life history traits found collectively only in vultures.[63] First, most vultures are obligate scavengers that rely on eating dead animals or waste products; this may increase their likelihood of exposure to contaminants. Second, because vultures feed communally, large numbers can be poisoned at a single carcass. Finally, vultures are very long lived and at a high trophic level, which increases their vulnerability to bioaccumulation. Bioaccumulation may have sublethal effects on reproductive success, behavior, immune response, and physiology.[64]

The deliberate poisoning by humans of carnivores, which kills scavengers as well as the intended victims, is likely the most widespread cause of vulture poisoning. Carnivore poisoning continues to be common, especially in Europe and Africa.[65–75] In Europe, poisoning is used to kill predators of game animals (e.g., rabbits, pheasants, and partridges) because hunters believe carnivores such as foxes and mongooses reduce their hunting success.[76] In both Europe and Africa, poisoning is used to “protect” livestock from predators. In Europe, it is regarded as the first option to deter carnivores from attacking livestock, while in Africa poisoning is largely used to avenge the killing of livestock (D. Ogada, pers. obs.[76]).

Some European countries (e.g., Spain and UK) have reduced poisoning incidents through more stringent penalties; tougher restrictions on the use of toxic chemicals; increased public awareness; and cooperation between government ministries, landowner associations, and nongovernmental organizations.[76,77] Spain has taken an innovative approach to tackling this problem by training dogs to detect specific poisons (baits and carcasses of poisoned animals) that are most commonly used against wildlife. Dogs detected 70% more poisoned baits than did specialized (human) detection teams. Funded by the regional government, the canine unit assists in the discovery of offenders as well as in dissuading poisoning through routine inspections in known hotspots.[78] In Africa, interventions are largely spearheaded by nongovernmental organizations, such as the Endangered Wildlife Trust in South Africa and WildlifeDirect in Kenya. While some success has been achieved, there is a need for greater financial support and more training and enforcement if prevention programs are to be sustainable and effective (D. Ogada, pers. obs.[72]).

Poisoning of vultures by ingestion of nonsteroidal anti-inflammatory drugs, particularly diclofenac-sodium, has caused rapid and severe population declines in Asian *Gyps* vultures. During the 1990s, researchers first noted high mortality rates in three *Gyps* species. Subsequent postmortem analyses indicated the vultures died of renal failure triggered by diclofenac residues found in livestock carcasses.[46,47,79] In South Asia, diclofenac was a widely used veterinary analgesic in livestock that typically is consumed by scavengers if they die of disease or injury. Studies showed that diclofenac concentrations in treated livestock were sufficient to cause the high levels of vulture mortality that had been recorded.[79] Contaminated carcasses were subsequently linked to vulture population declines across the subcontinent, and models further confirmed the correlation between vulture declines and diclofenac residues in carcasses.[80,81] In response to the vulture crisis, the governments of three of the most affected countries—India, Pakistan, and Nepal—withdrew manufacturing licenses for veterinary diclofenac in 2006. Recent surveys in India indicate that the ban on veterinary use of diclofenac has markedly reduced its presence in livestock carcasses to levels almost half of what they were prior to and immediately after the ban.[82,83] Despite the reduction of diclofenac in carcasses, prevalence levels still remain sufficiently high to continue to cause a rapid rate of vulture decline that has been estimated at 18% year for Oriental White-backed vultures (*G. bengalensis*).[83]

Lead poisoning through the ingestion of pellets or fragments of lead-based bullets in hunter-killed carcasses is a serious threat to some vulture populations, most notably the California condor. Lead poisoning has been implicated as the leading cause of death in the Arizona population of the condor (~40% of the worldwide population), and it had been estimated that without the intensive intervention of veterinarians, this population would not be self-sustaining in the wild.[29,84–86] However, in 2005 the Arizona Game and Fish Department implemented a hunter-education campaign and provided free, nonlead ammunition for hunters in condor habitats. With >80% participation by hunters, the severity of lead exposure during 2007 was low and there were no lead-related condor deaths.[87] However, there were three lead-related condor deaths after the 2009 hunting season.[30]

In contrast to unintentional poisoning, deliberate persecution of vultures has occurred for centuries. Most vultures have been victimized due to people's ignorance, superstition, wantonness, and retaliation.[9] Vultures have been believed to spread diseases such as anthrax, to be responsible for blowfly plagues, to foul drinking water provided for livestock, and to represent evil spirits, among other beliefs.[9,88]

Shooting and intentional poisoning are the two main forms of persecution. Shooting vultures has long been documented in the United States, Europe, and North Africa, where the activity appears to be largely for sport.[22,28,29,61] Documented cases of intentional poisoning of vultures have been noted as being in retaliation for the suspected killing of newborn lambs, to disguise the locations of poachers' activities, and to obtain vulture parts for traditional medicine.[65,72,87,89,90] The acquisition of vulture parts for traditional medicine has been documented in West and southern Africa[72,91–93] and is suspected in parts of East Africa (N. Baker, pers. comm.). Though it is likely to be a substantial threat to vultures in those areas, there have been no documented efforts to tackle the problem. Interventions by local governments appear unlikely due to cultural beliefs and practices that remain deeply entrenched in African societies.[91,94] In addition to use in traditional medicines, vultures, and in particular the Hooded vulture, are hunted for food in West Africa.[40,41] Though it is difficult to ascertain population-level effects of persecution on individual species, it is thought to be a significant cause of mortality for some species and populations, including European Bearded vultures, Cape griffons in South Africa, Hooded vultures in West Africa, and large vultures in Nigeria.[22,27,40,41,91,92]

Poisoning and persecution are not the only threats to vulture survival. Electrocution and collision with power lines have also caused significant levels of vulture mortality,[95–99] and the recent proliferation of wind farms as a source of green energy production also has had adverse effects. In recent studies, Griffon vultures suffered among the highest levels of mortality after collision with wind turbine blades.[100,101] Given the rapid increase in the development of "green" technology and electricity infrastructure worldwide, these threats are likely to increase in coming decades. Mass drowning of vultures (of up to 38 birds at a time) has also been reported, particularly in semiarid areas of South Africa where the birds enter artificial reservoirs presumably to bathe or cool off, only to be unable to extricate themselves due to vertical reservoir walls.[67,102]

Other threats to vultures mentioned in the literature include habitat changes and food shortage. Habitat loss and degradation are suspected to have played roles in the dramatic declines (>98%) of large vultures outside of protected areas in West Africa where human population growth has been very rapid.[41,58] Declines in large game birds and mammals have also been noted.[41,58] Lack of food—due to overhunting or changes in livestock husbandry—could have major impacts on vultures[18] and is thought to have contributed to large-scale vulture declines in West Africa,[40,58] Southeast Asia,[24] and Europe.[36] More recently, an outbreak of bovine spongiform encephalopathy in Europe led to the passing of sanitary legislation that restricted the use of carcasses and animal by-products.[103] Vultures and other avian scavengers have been hard hit by the ensuing food shortage, which has been linked to lower breeding success and higher mortality in juvenile vultures.[104]

Consequences of declines

Given the rate at which vultures are declining, there have been surprisingly few studies about the ecological consequences of the widespread disappearance of these scavenging birds.[105–107] Communities of facultative scavengers are highly structured (not random) and complex, and birds contribute most to this structure because they are the most specialized scavengers.[108] For example, in a Polish forest, well-adapted scavengers such as ravens and foxes were nearly ubiquitous at carcasses, whereas rare or sporadic scavengers associated with the main scavenger species and did not scavenge randomly, but rather on those carcasses where carrion specialists were present.[108] As carrion specialists, the absence of vultures from carcasses may affect the community composition of scavengers at carcasses, which could alter scavenging rates for individual species.

In localized regions where vultures are functionally extinct, such as in India, the absence of vultures at carcasses appears to have driven a rapid increase in the abundance of opportunistic species such as feral dogs and rats (*Rattus rattus*).[3,4] Feral dogs have been shown to compete directly with vultures for food and are capable of displacing vultures from carcasses. In areas adjacent to communal lands in Zimbabwe, feral dogs dominated carcasses, but inside protected reserves, vultures were the major scavengers at carcasses.[109] Both feral dogs and rats are well-known disease reservoirs, and their increase at carcasses in the absence of vultures may increase rates of infectious disease transmission to other species. Diseases such as rabies and bubonic plague, for which dogs and rats respectively are the primary reservoirs, may increase as a consequence of vulture declines. Wildlife and livestock could also be at increased risk from dog- and rat-borne pathogens, including canine distemper virus, canine parvovirus, and *Leptospira* spp. bacteria.[3] In India, rising cases of human anthrax due to handling infected carcasses or consuming poorly cooked meat of infected livestock are believed to be linked to the precipitous decline of vultures.[110]

A recent confirmed the important role of vultures in decomposing carcasses, maintaining community structure, and moderating contact between mammalian scavengers at carcasses.[2] In Kenya, in the absence of vultures, carcass decomposition time nearly tripled, and both the number of scavenging mammals and the time they spent at carcasses increased threefold. Further, there was a nearly threefold increase in the number of contacts between mammalian scavengers at carcasses without vultures, suggesting that the demise of vultures could facilitate disease transmission at carcasses.[2]

In addition to ecological impacts, vulture declines have already had socioeconomic and cultural impacts in South Asia, where they hold important social significance. Amongst the Zoroastrian-practicing Parsi community in India, who believe that fire, water, air, and earth are pure elements that need to be preserved, the dead are laid in "Towers of Silence." Built on hilltops or low mountains, these circular pillars of stone enclose corpses that are left in the open to be disposed of by scavengers, principally vultures.[111,112] This ancient custom, also known as sky burial and similarly practiced by Tibetan Buddhists, has come to an abrupt end in the last decade due to the collapse of vulture populations in the region. The Parsi community has unsuccessfully turned to solar reflectors in the hopes of hastening decomposition.[112,113]

Economic consequences of vulture declines include increased costs to human health. Estimates of the human health costs of the loss of vultures and subsequent increases in dogs and rabies are about \$1.5 billion annually in India.[111] In Nepal, the economic benefits of conserving vultures were estimated at \$6.9 million, and interviews in communities within Important Bird Areas showed they were considered significantly beneficial to humans.[114] In Uganda, Hooded vultures consume primarily internal organs from diseased animals thrown from abbatoirs, thereby saving local councils the expense of a more sophisticated system of collection and disposal of refuse.[115]

Comparison of the situation in Asia versus Africa

The catastrophic declines in vulture populations in South Asia have generated considerable attention from the media and the scientific community, which has catalyzed vulture research, particularly in Africa.[116,117] There are many similarities between Africa and South Asia. In particular, both regions harbor human populations that are mostly rural and poor, growing rapidly, and divided into many ethnic groups. Although the causes may differ, there have also been similar levels of decline in vulture populations in both regions.[4,40–42,46,47,59]

The prospects for vultures and their continued survival, however, differ between the two regions. In particular, the regions could not be more disparate in the level of attention given to the issue from local governments, the international scientific and donor communities, and the media. There are undoubtedly many reasons for this, but the fact that the Asian vulture crisis has been largely pinpointed to a single source—diclofenac poisoning—may be crucial. The discovery of diclofenac has focused conservation efforts (and hence funding) and media attention on a single target, and it has provided a mechanism whereby success of conservation interventions can be directly measured.

Although the situation for Asian vultures is critical and it will likely remain so over coming decades, the governments within the region have played a crucial role in halting the declines and protecting and bolstering remaining populations.[82] Indeed, evidence from four years since the ban on veterinary diclofenac has shown that productivity of Indian vultures (*G. indicus*) in southeast Pakistan and in the Indian states of Rajasthan and Madhya Pradesh has already begun to increase.[118,119] The identification of veterinary diclofenac as the primary cause of vulture population declines in South Asia took at least four years of intensive field and diagnostic research.[82,120,121] The results of this work were published in a prominent journal[79] and presented to South Asian government authorities at a Kathmandu Summit Meeting organized by The Peregrine Fund in February 2004. The dissemination of scientific research to government authorities plus advocacy work can play a crucial role in achieving conservation results. The key was getting governments to listen and to understand the gravity of the vulture situation and its consequences should conservation interventions fail. The role of conservation organizations in India, Nepal, and Pakistan was critical in advocating for a ban on the manufacture, sale, and import of veterinary diclofenac. In addition, conservation organizations in South Asia, along with their overseas partners embarked on large-scale education and outreach programs to ensure that rural people understood the lethal impacts of administering veterinary diclofenac to livestock. The Indian government in particular was extremely supportive in providing the necessary framework for legislation, financial support, and assistance with developing vulture captive breeding and restoration efforts (MZV, pers. obs.). Also significant to the conservation of vultures on the subcontinent is the role of vultures in Hindu mythology where they are highly esteemed, as evidenced by the existence of a vulture god, Jatayu, which is regarded as a holy bird.[111,113]

The situation in Africa is vastly different because there are many significant threats to vultures, not just one. In addition, the threats vary by region. For example, the cause(s) of vulture disappearances in West Africa remain unclear, though many suggestions have been made, including food shortage, poisoning, and persecution for traditional medicine and food.[40,41] Whereas in South Asia recent population surveys have indicated that declines have slowed or ceased in some areas and the threat from diclofenac poisoning has reduced substantially,[83,118,119] in Africa there is little similar evidence.[122,123]

In addition, the vast majority of African governments, with the exception of South Africa, have provided little, if any, support for vulture conservation or have attempted to resolve known vulture threats. In West Africa, studies of vultures over the past 40 years are virtually nonexistent[122] though seven years have passed since the first reports of massive vulture population declines there were first published.[40] Kenya and Uganda are the only two East African countries where some populations of vultures have been studied and monitored for many decades (S. Thomsett unpub. data,[42,115,124]). In Kenya, two recent studies have shown large declines in most species, and there exist both scientific and anecdotal reports linking the declines to poisoning, primarily to the agricultural pesticide Furadan.[42,59,75,125] In addition to over 350 vultures known to have been poisoned in the past seven years, Kenya's lion population has similarly plummeted, largely due to illegal poisoning.[126] Indeed, wildlife poisoning is so rife in Kenya that a national taskforce, first spearheaded by conservationists and later incorporated under the Ministry of Agriculture, was initiated in 2008 to tackle the problem. The primary aim of conservationists engaged in the Stop Wildlife Poisoning Taskforce was to implore the Kenyan government to ban the registration of carbamate pesticides, of which Furadan is the most notorious, for sale in Kenya.[127] In lieu of a ban on carbamate pesticides, the taskforce also lobbied for tighter restrictions on the sale of Furadan in Kenya, as it is used to poison both wildlife and feral dogs. These pesticides are affordable, highly effective, and easily accessible.[128,129] Apart from reports of wildlife poisoning, Furadan is known to be used to kill birds and fish that are later sold for human consumption.[130–132] Despite the raft of evidence provided to Kenyan government officials and a report on the situation as requested by the Prime Minister's office,[131] the Kenyan government has yet to take any action restricting its use or sale in the country despite the existence of pesticides that are purported to be less toxic to wildlife.[128]

Overview of successful conservation programs and species

While the Asian vulture crisis is still unfolding and the full results of vulture conservation efforts will not be known for some years to come, in Europe and the United States a number of conservation programs have already succeeded in bolstering dwindling vulture populations. Three of the most successful programs involved the reintroduction and supplementary feeding of California Condors in the United States, Griffon vultures in the Massif Central region of France, and Bearded vultures in the European Alps.[133] In addition to releasing and feeding vultures, intensive public education programs were launched that targeted hunters, farmers, and livestock keepers, and all released individuals have been marked and in some cases are intensively monitored.[134–136] Common themes among these successful conservation efforts are a huge investment, at both national and international levels, of financial resources and highly skilled personnel, as well as political will and community support.

While reintroductions have boosted populations of some species, populations of Turkey and Black vultures have experienced major increases throughout much of their ranges in North America since the mid-1970s without any human intervention.[32,137] Although the reasons for their population increases have not been well studied, a number of suggestions have been made, including substantial decreases in persecution, increases in food availability due to the large resurgence of White-tailed deer populations (*Odocoileus virginianus*), and decreases in secondary poisoning, especially exposure to DDE (through DDT spraying), which induced eggshell thinning in many raptor species.[32] While both species are susceptible to the effects of DDT spraying, their susceptibility to other toxins is mixed. Turkey vultures have been shown to be relatively insensitive to some rodenticides but quite sensitive to strychnine and cyanide. It has also been suggested that both species may be particularly sensitive to lead poisoning.[32] A review of poisoning cases in the United States[138] suggests that both Turkey and Black vultures may be less susceptible to poisoning than some other raptor species. In general, raptors are more susceptible to poisoning compared to birds of a similar size; their stomachs have low pH levels that increase their susceptibility to lead poisoning.[138,139] A review of data presented by Mineau *et al.*[138] shows that 181 raptor deaths were attributed to the labeled use of pesticides, implying that the raptor deaths were accidental and were not as a result of persecution. No mortality of Turkey or Black vultures was recorded, despite mortality of scavenging Red-tailed hawks, Bald eagles, and Swainson's hawks, representing 31%, 17%, and 11% of cases, respectively.[138] While the results are only suggestive that both species may exhibit a reduced susceptibility to poisons, they do not suggest whether physiological and/or behavioral traits may play a greater role. In a recent study, Turkey vultures showed no signs of toxicity after being dosed with diclofenac at >100 times the lethal dose for *Gyps* vultures.[140] Turkey vultures have also been shown to have exceptional immune function.[141] Behaviorally, vultures may limit their susceptibility to toxins by foraging in smaller group sizes. The mean number of vultures poisoned per carcass appears to be proportional to their foraging group size (data from Ref. 16). In addition to physiological or behavioral adaptations that may benefit populations of Turkey and Black vultures, we posit that the governments of some countries in the Americas have stronger conservation policies, more political will, and more resources to conserve vultures as compared to countries in Asia and Africa.

Other ongoing and potentially important conservation initiatives consist of public involvement in vulture research or citizen science programs and increasingly through public education and outreach programs. Citizen science programs have largely focused on creating awareness of wing-tagged vultures and requesting the public to report sightings of marked individuals. The use of vulture restaurants could also be particularly useful to obtain reports of wing-tagged vultures from citizen scientists. Results from South Africa indicate that 4,443 resightings from a sample of 120 vultures have been reported, largely by citizen scientists at vulture restaurants over a five-year period (A. Botha, pers. comm.). Public education focused on the plight and importance of vultures has recently come to the forefront with the recognition of International Vulture Awareness Day (www.vultureday.org). International Vulture Awareness Day aims to have conservation organizations worldwide, including zoos and local government agencies, organize a one-day celebration of vultures that publicizes the conservation of vultures to a wider audience and highlights important work being carried out by vulture conservationists throughout the world.

Conclusions

A summary of the available evidence has shown that scavenging birds, and vultures in particular, are the most threatened group of birds in the world, and presently 61% are listed on the IUCN Red List of Threatened Species.[31,106] As a consequence of being highly specialized, vultures are particularly prone to poisoning, which has led to widespread and serious population declines in many species. Though the long-term impacts of these declines are not fully understood, ecosystem services provided by vultures have already plummeted, and novel research has shown that disease transmission at carcasses may increase. The two most important regions for Old World vultures—Asia and Africa—have witnessed recent catastrophic population declines in most species. While the declines in Asia have been linked to poisoning by the veterinary drug diclofenac, the reasons for the declines across Africa remain little understood. The Asian vulture crisis has highlighted the importance of collaboration between scientists, regional governments, donors, and the media to effectively conserve vultures over the vast areas where they range. In many African countries, vulture populations remain little known and even less is being done on the ground to ensure their survival. In countries such as South Africa and Kenya, where vulture conservation programs are ongoing, efforts are largely driven by or with the support of local conservation organizations. As the Asian vulture crisis has shown, without support and backing from national governments and local communities, any conservation efforts are likely to be met with limited success over the long term.

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Conflicts of interest

The authors declare no conflicts of interest.

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