# Causes and Effects of Temporospatial Declines of *Gyps* Vultures in Asia

## A Global Perspective of *Gyps* Vultures

There are eight species in the genus *Gyps*: *Gyps africanus*, *G. coprotheres,* and *G. rueppellii* in Africa; *G. bengalensis*, *G. indicus*, *G. tenuirostris*, *G. himalayensis* in Asia; *G. fulvus* in Europe, Africa, and Asia. The ranges of many of these species overlap, and wintering *G. fulvus* overlap with several resident species in Asia and Africa (Fig. 1). *Gyps* species share a similar feeding ecology, scavenging the soft tissues of large mammals, usually ungulates. They tend to be colonial nesters and communal feeders, feeding alongside conspecifics and other vulture species. Densities of *Gyps* vultures can be high in areas with suitable breeding habitat and abundant carrion. An extreme example is *G. bengalensis*, which often lives in close association with humans. During the 1970s and early to mid-1980s, densities of 12 nests/$km^2$ were recorded at Keoladeo National Park, Rajasthan, India (Prakash 1989), and there were nearly 3 nests/$km^2$ in the city of Delhi (Galushin 1971), where flocks of several thousand birds were present at carcass dumps. As recently as 1985, *G. bengalensis* was regarded as "possibly the most abundant large bird of prey in the world" (Houston 1985).

Despite *Gyps* population declines across Southeast Asia, until recently only one species of Africa, *G. coprotheres,* was considered globally threatened (vulnerable; BirdLife International 2000), largely because of the indiscriminate use of poisons in southern Africa (Mundy et al. 1992). Following the recent population crash in *Gyps* species across the Indian subcontinent, three other species, *G. bengalensis, G. indicus,* and *G. tenuirostris*, are now listed as critical (BirdLife International 2000), placing them among the most threatened birds in the world.

## Historical Declines and Likely Causes in Southeast Asia

During the first half of the twentieth century, two species of *Gyps* vulture (*G. bengalensis* and *G. tenuirostris*) were well distributed and often specifically noted as abundant in Southeast Asia (including adjacent Yunnan Province, China). By the end of that century, both species were extinct across almost the entire area. A small area of northeastern and northern Cambodia holds relict populations of both species, with some extension into adjacent parts of Laos and Vietnam. Elsewhere in these countries, and in Malaysia, Thailand, and Yunnan, the few recent records probably indicate wandering birds. The situation in Myanmar remains unclear, but a major decline has also occurred there, at least locally. Table 1 illustrates changes in populations of *G. bengalensis* over this period.

The breeding success of remaining birds in Southeast Asia appears to be low (Timmins & Ou Ratanak 2001). Uncontrolled hunting has led to wholesale population collapses of wild ungulates in this region (Srikosamatara & Suteethorn 1995; Duckworth et al. 1999; Hilton-Taylor 2000) that, together with changes in husbandry of domestic stock (Cambodian Wetland Team 2001), have resulted in a huge reduction in the carrion available for vultures. It seems likely that food supplies are no longer predictable enough to allow regular breeding. Persecution of vultures when they are gorged on carcasses and at nests may also have played a role (Thewlis et al. 1998). Persecution may be at a level that makes birds shy enough to be affected by incidental disturbance (authors' unpublished data), and, given the high human density across much of the region, this factor should not be underestimated. Habitat loss, except insofar as it has contributed to ungulate declines, can be discounted as anything other than a local threat (Thewlis et al. 1998). The role of agrochemicals remains unclear; there is no persuasive indication that they can explain region-wide losses in Southeast Asia, although they may have caused local declines (Cheke 1972).

Circumstantial evidence suggests that infectious disease was not a cause of this decline or today's extremely low population density. The decline affected not only *Gyps* vultures but also all other scavenging birds, such as the Red-headed Vulture (*SarcoGyps calvus*), Greater Adjutant (*Leptoptilos dubius*), Black Kite (*Milvus migrans*), Brahminy Kite (*Haliastur indus*), and Large-billed Crow (*Corvus macrorhynchos*). The status of these species varies across the region, with perhaps the steepest declines in Laos, where even the Large-billed Crow is absent from large areas (Lekagul & Round 1991; Thewlis et



Conservation Biology, Pages 661–671
Volume 17, No. 3, June 2003

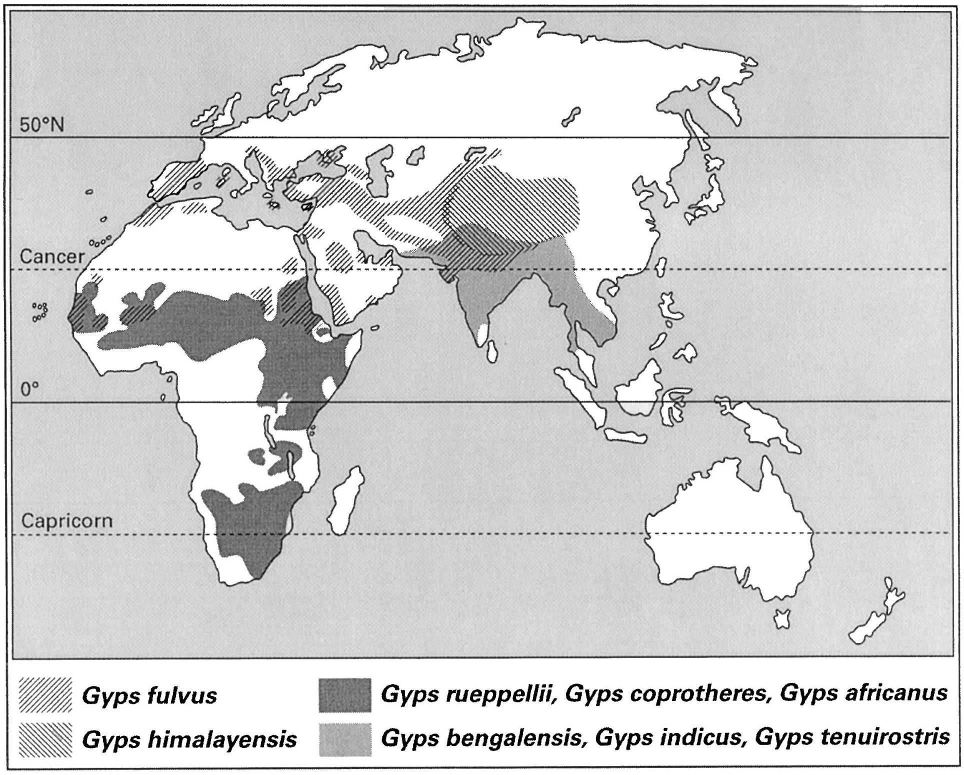


*Figure 1. Breeding and wintering distribution of* Gyps *vultures in the old world (after Mundy et al. [1992] and based on updated distribution information from Robson [2000]). The Southeast Asian range shown is historical.*

al. 1998; Wells 1999; Duckworth et al. 1999, 2002; Round 2000).

Although vulture declines have been marked throughout Southeast Asia, there is some patchiness to the severity of the losses, again with Laos having suffered some of the steepest declines. This comparison is instructive because the country retains large tracts of habitat suitable for these species, has a relatively low human population density, and is unlikely to have used environment-contaminating chemicals at high levels across the ancestral vulture range. Laos did, however, lose most of its open-country wild ungulates during the second half of the twentieth century (through hunting), and it probably experienced significant changes in livestock husbandry (Duckworth et al. 1999). Cambodia, the core area for the relict *Gyps* populations of Southeast Asia, differs from the rest of Indochina. A relatively large open-country landscape has until recently remained sparsely settled (because of the Khmer Rouge and other security concerns), wild ungulate populations persist locally, and the villages in and abutting this area still practice extensive free-ranging of domestic bovids during the dry season (Timmins & Ou Ratanak 2001). The remnant *Gyps* populations in adjacent Laos and Vietnam are unlikely to be viable under current conditions without this Cambodian vulture population.

Although data are too scant to be certain of the reasons for the *Gyps* declines in Southeast Asia, food shortage appears to be the most credible general explanation, although other factors including persecution and contaminants may have played a part locally.

## Recent Declines across the Indian Subcontinent

During the 1970s and 1980s, when *Gyps* vultures were absent or scarce across most of Southeast Asia (Table 1), *G. bengalensis*, and to a lesser degree *G. indicus,* remained extremely abundant in India, especially around towns and cities. This abundance resulted from the large number of cow carcasses available for vultures in northern and central states of India, where religious beliefs prohibit their slaughter (Grubh et al. 1990). Cattle carcasses are left in the open in rural areas and, along with slaughterhouse offal, are taken to carcass dumps outside the towns and villages, where vultures consume them. Numbers of vultures around settlements were so high in the 1980s that they were considered a serious hazard to aircraft (Grubh et al. 1990). During the 1980s and 1990s, numbers of *G. bengalensis* and *G. indicus* were monitored at Keoladeo National Park (KNP), a World Heritage Site in eastern Rajasthan. Prakash (1999) recorded >95% declines in numbers of these two species in the park between the mid-1980s and late 1990s. *G. bengalen-*

**Table 1. Population status and distribution of *Gyps bengalensis* in Asia in throughout the twentieth century.**

| *Country* | *Pre-1950 population and distribution* | *Post-1950 population and distribution* | *Last record and location* | *Reference** |
|---|---|---|---|---|
| Southeast Asia | | | | |
| China | no records, but survey of Yunnan patchy | southwest only (Yunnan province); scarce or rare | southern Yunnan, 1959 & 1960; now considered extinct | Tso-hsin 1987; Guangmei & Qishan 1998 |
| Myanmar | widespread and common, including large numbers in towns and suburbs | scarce in many areas by 1950s; subsequent history poorly known | still localized small numbers (Chin Hills & Kachin State); status poorly known | Smythies 1953; Robson et al. 1998 |
| Thailand | widespread resident throughout country; fairly common to locally abundant | still fairly common in 1960s but rare by 1970s and almost extinct by 1980s | probably extinct as a breeding bird; occasional reports of individuals until winter 2000 | Deignan 1945, 1963; Round 1988; Wells 1999; P.D.R., unpublished data |
| Malaysia | fairly widespread resident, still common in 1930s | by mid-twentieth century, almost extinct, except adjacent to Thailand | few records, rare nonbreeding visitor (Kampung Penyirang, June 1979) | Wells 1984, 1999 and references therein |
| Laos | widespread and common to abundant | 1950s–1980s poorly known; by 1990s restricted to far south | very small numbers in southern provinces of Champasak & Attapu; could become extinct (2000) | Thewlis et al. 1998; Duckworth et al. 1999 and references therein |
| Cambodia | once relatively abundant in suitable habitat | data patchy, but by late 1990s, when survey work resumed, only a few populations remained | centered on the northeast provinces of Preah Vihear, Stung Treng, Mondulkiri, and Ratanakiri | Timmins & Men Soriyun 1998; Goes 1999; BirdLife International 2001; Timmins & Ou Ratanak 2001; J.W.D., C.M.P., R.J.T., unpublished data |
| Vietnam | widespread, locally abundant resident in central and southern regions | widespread and commonest vulture in south Vietnam until at least late 1960s | one adult in Dak Lak province, 1997–1998; other nationwide surveys found none | Delacour & Jabouille 1931; Wildash 1968; Le Xuan Canh et al. 1997 |
| Indian subcontinent | | | | |
| India | widely distributed resident throughout all but southernmost tip; common to abundant | widespread and abundant to very abundant until the mid-late 1990s, when population crashes were reported throughout the country | still widespread but at comparatively low densities; local extinctions have wiped out many colonies | Rahmani 1998; Prakash 1999; Prakash et al. 2003 |
| Nepal | widespread and common throughout lowlands | widespread and common throughout lowlands; local population declines reported over last few decades (e.g., Chitwan) | still recorded throughout lowlands but high mortality and population declines have occurred since late 1990s | Scully 1879; Rand & Fleming 1957; Inskipp & Inskipp 1991 |
| Bhutan | no records | records from Bhutan date from 1991–1999; uncommon to approximately 100 birds near Teesta valley in mid-1990s | birds seen in several places in early to mid 1990s, but few birds reported since 1998 | Inskipp & Inskipp 1993; BirdLife International 2001 and references therein |
| Bangladesh | widely distributed and common | widespread; still relatively common but numbers lower than in 1980s and early 1990s | locally common throughout the country and a common resident breeder in village areas | Husein & Sarkar 1971; BirdLife International 2001 and references therein |
| Pakistan | widespread and common resident in suitable habitat (e.g., Indus plain) | widely distributed in many areas and may have expanded into new areas in Sindh post 1960s; abundant in Indus plain (Punjab, Sindh, Northwest Frontier) by 1991 | still widely distributed; large-scale mortality in many areas over last 5+ years (see text) | Roberts 1991–1992; BirdLife International 2001 and references therein |

**Reference is given to a recent national status overview where available; these are indicated by "and references therein." For countries lacking a recent status overview, key historical and recent references are listed, with BirdLife International (2001) as a general regional source.*

*sis* used to nest at KNP, and numbers of nests declined from 250–350 in the mid-1980s to none by 2000 (Prakash 1999; Prakash et al. 2003). Nesting success (total number of active nests producing young) declined from 82% in 1985–1986 ($n$ = 244 nests) to zero in 1997–1998 ($n$ = 25) and subsequently. The declines were associated with high adult and juvenile mortality, and small numbers of birds were observed in a weakened state perched in trees in the park. In general, these birds retained a characteristic slumped posture with drooping necks for several weeks before dying. In 1985 and 1986, >1700 *G. bengalensis* were recorded in KNP, and 14 birds (7 adult, 7 juvenile) were found dead. In 1997–1998, when the population numbered just a few hundred birds, 73 adults and 10 juveniles were found dead. The population decline and high mortality was unexplained. The food supply had not altered over the period of decline, and no other avian genera were similarly affected.

The dramatic and unexplained declines at KNP, along with unsubstantiated reports of vulture declines from across the country, prompted the Bombay Natural History Society to conduct wide-scale vulture surveys in 2000. These were repeats of surveys conducted in 1991–1993, which covered states in north, west, and east India. Minimum declines in numbers of *G. bengalensis* and *G. indicus* of 96% and 92%, respectively, were recorded (Prakash et al. 2003). (*G. indicus* is now considered to include two distinct species, the Indian Vulture [*G. indicus*] and the Slender-billed Vulture [*G. tenuirostris*] [Rasmussen & Parry 2000]. We treated *G. indicus* as one species because the two forms were not differentiated during fieldwork. However, most of the birds recorded in west Bengal within the "east region" were *G. tenuirostris*. Because declines were similarly elevated in all areas, *G. tenuirostris* and *G. indicus* have probably declined to a similar extent.)

The extent of declines did not differ between protected and unprotected areas, and although there was some evidence for larger declines in the north than in the west, declines of *G. bengalensis* were >90% in all regions. Also, apparently sick birds with drooping necks were reported in all regions. Preliminary results from repeated surveys in 2002 indicate that, at least for *G. bengalensis*, declines have continued, resulting in many local extinctions (V.P., unpublished data).

High mortality and declines in *Gyps* vultures have recently occurred in neighboring Nepal and Pakistan. In Nepal, high adult mortality was recorded in *G. bengalensis* during the 2000–2001 breeding season at Koshi Tappu Wildlife Reserve (eastern Nepal). Although the breeding colony is relatively small (67 nests found, of which 27 were active), 45 *G. bengalensis* were found dead, 34 (75.5%) of which were adults (Virani et al. 2001). In Pakistan, during the 2000–2001 breeding season, Gilbert et al. (2002) estimated minimum annual mortality rates in the adult breeding populations of *G. bengalensis* from two colonies to be 11.4% and 18.6%. The authors acknowledge that these are likely considerable underestimates because they assume that (1) all dead birds were found (in fact, only carcasses in the immediate vicinity of nests not removed by scavengers were found) and (2) only dead adults were used to estimate annual mortality in the breeding population (whereas an unknown proportion of the breeding population had subadult plumage).

High mortality, especially of adults, and low breeding success caused the population declines in India, Pakistan, and Nepal. *Gyps* vultures are generally long-lived; one captive *Gyps fulvus* lived for 37 years (Newton 1979). They reproduce slowly, reaching maturity in 4–6 years, and produce one egg during breeding years (Mendelssohn & Leshem 1983; Simmons 1986; del Hoyo et al. 1994). Adult survival is high. Wild-born *G. fulvus* from a reintroduced, increasing population in France had mean adult survival rates of 0.987 ± SE of 0.006 and juvenile (<3 years old) rates of 0.857 ± 0.039 (Sarrazin et al. 1994).

## Causes of Declines across the Indian Subcontinent

In contrast to the relatively slow declines of *Gyps* vultures in Southeast Asia, Indian populations have declined by >95% within the past decade, a rate of decline unprecedented among common raptors in its rapidity and one that appears to be continuing. There are several possible explanations for the high mortality and reduced breeding success of *Gyps* vultures in southern Asia, including food shortage, persecution, contaminants, and infectious disease.

### Food Shortage

Although there is convincing circumstantial evidence to implicate food shortage in *Gyps* declines in Southeast Asia, food availability has remained high throughout the Indian subcontinent during the period of decline. During vulture surveys in India in 2000, Prakash et al. (2003) recorded numbers of livestock carcasses seen and their attendant scavengers. Of 262 carcasses seen, only 12 (<5%) had vultures present; most were attended by crows *Corvus* spp. and feral dogs. Counts of *Gyps* vultures at three carcass dumps that remained active between 1990 and 2000 showed declines of 87–100% in numbers of visiting vultures. In 1999, of 1920 completed questionnaire returns, approximately 80% of respondents indicated that dumping of carcasses in the open remained the predominant form of disposal in their region (Prakash et al. 2003). Although carcasses remained common and available to vultures, there was some indication that they were less abundant than 10 years ago (76% of respondents reported carcasses as fairly or very common in 1990; 63% in 2000).

Although few data exist, there is some evidence that the Red-headed Vultures, underwent a significant ($p = 0.03$) but less severe (48%) population decline between 1991–1993 and 2000 (Prakash et al. 2003). It is conceivable that, in the absence of the mortality factor that has caused the *Gyps* population crash, numbers of avian scavengers could be declining slowly in India due to a gradual reduction in available food. Although monitoring data are scarce, populations of other scavenging birds show no obvious signs of decline, and some scavengers, such as feral dogs, are reported to be increasing across India (Cunningham et al. 2001). Finally, there has been no evidence of starvation being a contributing factor to the death of vultures necropsied from across India and Pakistan (Gilbert et al. 2002; Prakash et al. 2003). Consequently, food shortage is an unlikely explanation for the recent vulture population crash across the Indian subcontinent.

### Persecution

Persecution, particularly through deliberate or accidental poisoning, can have a significant impact on raptor populations, especially on communal feeders such as vultures. Poisoning campaigns eliminated scavenging birds and large eagles from the huge stock farming area of Namibia in the 1980s. In the neighboring national parks of Kalahari Gemsbok and Etosha, however, these same species remained abundant (Mundy et al. 1992). While a significant threat in Africa, persecution is unlikely to have played a large part in vulture declines across the Indian subcontinent. Vultures are generally valued within Indian society for their role in environmental health. They also have an important cultural and religious significance. The Parsee religion depends upon vultures to remove their dead, and the vulture saint, Jatayu, is an important figure in Hindu religion. Some poisoning almost certainly occurs, but it is unlikely to have more than a local impact and cannot explain rapid nationwide declines of the type experienced by *Gyps* spp. This is because, as in Africa, such poisoning would likely affect other avian scavengers, such as the Steppe Eagle (*Aquila nipalensis*), and would result in regional differences in rates of decline. However, there is no evidence that this is happening.

### Contaminants

Chemical poisoning by contaminants in widespread use, such as agricultural chemicals, could result in massive mortality and reduced breeding success in raptors at a national scale, as DDT did in many countries (Ratcliffe 1967*a*, 1967*b*; Newton et al. 1982, 1986). Large amounts of pesticides are used in India, and use increased considerably in India in the 1980s. Official statistics indicate overall declines in pesticide use through the 1990s (Directorate of Economics and Statistics website http://agricoop.nic.in/statistics/consum1.htm), but this masks trends in individual chemicals and chemical groups. For a chemical to cause the widespread vulture declines recorded, it would need to have been either introduced de novo and applied across a huge geographical area or used previously and applied in a novel way that increased its availability to vultures within the last 10–20 years. No pesticides have been identified that obviously meet these criteria. Toxicological analyses have been conducted on many dead vultures from Pakistan, and tissues have been tested for organochlorines, organophosphates, carbamates, and heavy metals. None of these substances have been detected at levels consistent with toxicity (Oaks et al. 2001). This and the lack of regional patterns in the declines and obvious effects in any other genera of scavenging bird or mammal suggest that contaminant poisoning alone is unlikely responsible for the declines. Little wildlife monitoring exists, however, and the role of contaminants cannot be discounted.

### Infectious Disease

The rapidity and ubiquity of the vulture declines in India suggest either a simultaneous subcontinent-wide exposure to a toxic contaminant or a rapid spread of disease through the *Gyps* vulture population. The occurrence of declines across international borders, the patterns of mortality, and the declines in breeding and roosting colonies are more indicative of the latter than the former. Once birds exhibit the neck-drooping condition, the illness, which appears to be invariably fatal, gradually spreads throughout the colony over a period of several years (Cunningham et al. in press; Prakash et al. 2003). No affected colonies have recovered from this mortality factor, although further data are required to verify this. It is unknown whether colony extinction is due entirely to vulture mortality or whether, once the population number or density falls below a certain level, surviving (and possibly infected and infectious) vultures desert the site to join other colonies.

Postmortem analyses of *G. bengalensis*, *G. indicus*, and one *G. himalayensis* from India (Cunningham et al. 2001, in press; Pain et al. 2002) and *G. bengalensis* from Pakistan (Oaks et al. 2001; Gilbert et al. 2002) identified renal and visceral gout (crystallization of uric acid in the tissues) in the majority of birds found dead, and enteritis in a high proportion of the birds from India (Cunningham et al., 2001, in press). Few other gross findings are consistently observed. The presence of visceral gout in tissues of dead birds from both countries supports the hypothesis that the same mortality factor is responsible for all these deaths. Although renal gout is often attributed to kidney disease, in these cases the gout was acute (i.e., occurring only a few hours before death), suggesting that this condition is a consequence of the primary disease and not the disease itself (Cunningham et al. 2001, in press). Visceral gout and enteritis are nonspecific lesions and could result from, for example, a contaminant insult or an infectious disease process. Histological analyses of tissues from Indian birds, however, found higher than expected proportions of vultures with inflammation of blood vessel walls and proliferation in the brain of glial cells (inflammatory cells specific to the central nervous system) (Cunningham et al. in press). In the absence of findings other than vasculitis, gliosis is generally associated with viral infection.

The epidemiology of vulture mortality, which includes pandemic declines, apparent rapid spread to other countries, and specificity to the genus *Gyps*, is consistent with a hypothesis of infectious disease. Postmortem findings and the lack of positive toxicological results similarly support this hypothesis. Although we cannot be certain that an infectious disease is responsible until a causal agent has been identified, this is currently the most tenable hypothesis, so it is important to consider the implications of this explanation.

### Potential Spread outside Asia

There are eight species in the genus *Gyps* distributed across Asia, the Middle East, Europe, and Africa (Fig. 1). The risk of disease spread from the Indian subcontinent depends on many factors: whether the disease will cross species barriers, the rate and method of transmission, the time course between infection and death, the period of infectiousness, the degree of isolation of individual species, and others. Three *Gyps* species (*G. bengalensis, G. indicus, G. tenuirostris*) have been affected by the same mortality factor in India, Pakistan, and Nepal, although a fourth (*G. himalayensis*) may also be affected (Cunningham et al. in press). All eight *Gyps* species may therefore be susceptible. The rate of the declines across India and apparent spread into Pakistan and Nepal suggest a highly infectious disease. Transmission is probably facilitated by the species' behavior: they breed, roost, and feed communally and travel great distances (Houston 1974, 1983). To evaluate potential spread and its effects, let us assume in a worse-case yet realistic scenario that infectious disease is the sole cause of the declines and that it can affect all members of the *Gyps* genus with fatal consequences.

No *Gyps* species is completely geographically isolated from its congenerics (Fig. 1). All *Gyps* species forage widely (Houston 1974, 1983), and juveniles may disperse more widely or be more nomadic than adults. *G. fulvus* breeding in Turkey are migratory, and in many regions immature individuals undertake distinct north-south migrations (del Hoyo et al. 1994; Ferguson Lees & Christie 2000). Birds from Western Europe cross the straights of Gibraltar to North Africa (e.g., 2160 birds recorded in autumn 1993; Griesinger 1996). Eastern populations from Asia and the Middle East migrate to North and East Africa, although migration routes are unknown. In recent years, unusually large numbers of juvenile *G. fulvus* of unknown origin have been overwintering in western India (e.g., approximately 850 were seen at a single carcass dump in western Rajasthan in January 2002; Prakash et al. 2003), presumably because of the increased availability of food. It is not yet clear, however, whether they are susceptible to the mortality factor affecting other *Gyps* vultures. It is possible that birds infected in India will not show evidence of disease while in India because the incubation period is unknown. Also, any population declines of "front-line," at-risk *G. fulvus* may currently be masked by the increased influx of winter migrants.

If disease spreads outside the Indian subcontinent, it will likely be via *G. fulvus* and *G. himalayensis* (Fig 1). As a conceptual tool, it is useful to divide potential spread into two phases: first, radiation from the subcontinent through the centers of distribution of Himalayan and Eurasian Griffons and, second, continued spread into European and African *Gyps*. The distributions of Eurasian and Himalayan Griffon vultures (Ferguson-Lees & Christie 2000) and regional geography suggest four routes of primary spread from the subcontinent: (A) west through southern Iran to the Zagros Mountains (*G. fulvus*); (B) northwest through Afghanistan and northern Iran into the Caucasus (*G. fulvus*); (C) north through the Pamir knot and into the Tien-Shan of the former Soviet Union (*G. fulvus* and *G. himalayensis*); and (D) northeast from the Himalayas onto the Tibetan Plateau (*G. himalayensis*) (letters match those on Fig. 2). A possible fifth route (E) could be across the Straight of Hormuz from southern Iran to the tip of the United Arab Emirates (*G. fulvus*).

The second stage of disease spread, via *G. fulvus,* would likely extend (F) into the more fragmented populations of the southern Alps and Pyrenees in Europe and (G) along the mountains of the Middle East and into Ethiopia and sub-Saharan Africa. Passage into Africa could be from Jordan and Israel down into Egypt and then south into sub-Saharan Africa, and/or across Saudi Arabia to Yemen and across to Djibouti. Even where there are obvious discrete gaps in distribution between *Gyps* species, we know some mixing between species occurs because of the large distances individual birds travel. This can be 1000 km or more (*G. africanus, G. coprotheres*), and even resident breeding birds will forage >100 km from breeding sites (Houston 1974, 1976; Ferguson Lees & Christie 2000). For example, a satellite-tagged Eurasian griffon moved >1500 km from Israel to Yemen in 2002 (O. Bahat, personal communication, http://www.birds.org.il).

## Current and Predicted Effects of Vulture Declines

*Gyps* vultures are extremely effective and efficient scavengers. In the

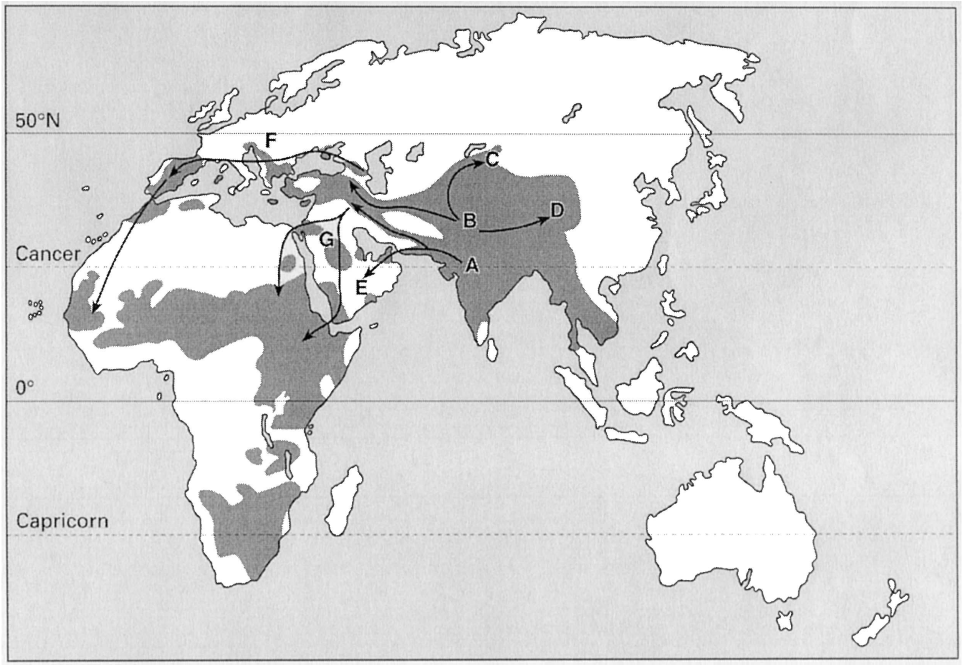


*Figure 2. Likely routes of spread from India of a* Gyps*-specific infectious disease. Shaded areas represent* Gyps *distributions. Likely routes of spread A–G are detailed in text.*

Serengeti ecosystem in Tanzania, for example, vultures are the major consumers of dead ungulates, accounting for greater meat consumption than all mammalian carnivores combined (Houston 1979). A similar situation likely occurred in India prior to the declines, particularly in the many regions where *Gyps* vultures were the primary scavengers.

The effective loss of *Gyps* vultures from the Indian subcontinent will undoubtedly have important repercussions, both for the environment and for human health and well-being. For example, an abundance of uneaten carcasses (Prakash et al. 2003; V.P. et al., unpublished observation) poses a direct threat to public health because the rotting flesh provides a breeding ground for potentially pathogenic bacteria, posing the possibility of direct or indirect infection. Uneaten carcasses are also likely to provide sources of disease, such as anthrax, for humans, livestock, and wildlife. In removing carcasses of large ungulates rapidly and efficiently, vultures cleanse the environment. The acidic conditions in the stomach of *Gyps* vultures kills many pathogenic bacteria, such as anthrax, reducing the risk of disease spread (Houston & Cooper 1975).

The ecological extinction of *Gyps* vultures in India is also leading to further changes in the species complement of scavengers. The surfeit of available food, for example, appears to be driving a rapid and marked increase in the number of small, predatory mammals, such as feral dogs, and probably rats (*Rattus* spp.). Such species have relatively short lives and high reproductive potential. At one carcass dump in western Rajasthan, the numbers of dogs increased from approximately 60 in 1992 to >1200 in 2000 (Prakash et al. 2003; V.J. et al., unpublished observation).

Because carcass dumps are often close to human habitation, they create a growing problem of dog attacks on people, which can be fatal. In addition, increasing populations of feral rats and dogs pose a significant risk of infectious disease to human beings, livestock, and wildlife. As the populations of feral rats and dogs increase, so too will the rates of infectious disease transmission within these populations and from these species to others. Important zoonotic diseases, such as rabies and bubonic plague, which are endemic within India and for which dogs and rats, respectively, are the primary reservoirs, are likely to increase as a consequence of the vulture declines. More humans die from rabies in Asia than other regions, and the majority of these deaths occur in India (World Health Organization 1998).

Wildlife and domestic livestock may also be at increased risk from dog- and rat-borne pathogens, including canine distemper virus, canine parvovirus, and *Leptospira* spp. bacteria. The increase in mammalian scavengers at carcasses may have unknown ecological consequences. Most scavengers are also predatory, and increases in their populations as a result of the abundance of carrion is likely to lead to higher predation pressure on wildlife such as mammals, ground-nesting birds, reptiles, and amphibians.

Vultures are important not only for environmental health but also for their considerable cultural and religious significance in India and elsewhere. For thousands of years and in different parts of the world, humans have laid out their dead for consumption by scavengers (Schüz & König 1983). Of these, the best known and documented are the Parsees, 70% of whom live in Mumbai. The Parsees believe that fire, earth, and water are sacred and, as such, must not be contaminated with human corpses. The Parsees therefore ritualize the practice of putting out the dead for scavengers by building "towers of silence" to limit access to corpses exclusively to airborne scavengers. In Mumbai the towers were built 400 years ago and have become an intrinsic part of the Parsees' lives. Until the population crash, vultures visited the towers on a daily basis, gathering on them at funeral time, consuming almost the entire body within half an hour. On average, three bodies a day are placed in the towers, but in the absence of vultures only kites and crows visit, and they are too small to have a significant impact. The hygienic way of disposing of their dead that the Parsee practiced for generations has gone, and they are faced with a dilemma. Some Parsees advocate a more modern disposal method, such as electrical cremation, whereas others disagree and wish to adhere strictly to their faith.

The economic impacts of the vulture declines are manifold and include the costs to villagers of disposing of carcasses that would otherwise rot and increase the risk of disease, the costs associated with increased dog bites and associated human disease, and many others that are difficult to quantify without detailed socioeconomic analyses. Collecting cattle bones for the fertilizer industry is an old trade among India's poor, and vultures effectively and rapidly "cleaned" skeletons of all soft material and facilitated the bone collector's job. Today, carcasses are rotting in areas with few scavengers, and even where feral dog populations have increased massively, carcasses are not cleaned thoroughly because dogs only scavenge choice tissues. This, and the attempted burning of carcasses in some localities, removes a source of income for the bone collectors.

## Conclusions

Four of the eight species in the genus *Gyps* are now listed as globally threatened; three of these are critical (BirdLife International 2000) because of the population crash across the Indian subcontinent over the last 10–15 years. Massive declines in avian scavengers and other large birds have also occurred across Southeast Asia, primarily during the middle of the last century. Although conclusive evidence is lacking, these declines probably resulted from the loss of wild ungulates and free-ranging domestic cattle and water buffalo. Other factors such as persecution and pesticides may have played a part in local demographic changes.

Today, relict populations of *Gyps* vultures in Southeast Asia remain only in and adjacent to Cambodia. *Gyps* vultures were common or abundant across much of the Indian subcontinent until the late 1980s to early 1990s, after which populations of at least three species, *G. bengalensis, G. indicus,* and *G. tenuirostris,* started to decline at an alarming and unprecedented rate. These declines have resulted in local extinctions across much of India. The causal factor(s) have not been identified, but it is extremely unlikely that either food shortage or persecution have played an important part. Although the role of widespread contaminants has not been discounted, current information suggests infectious disease, possibly a genus-specific virus, as the most likely cause of the declines. Should this prove to be the case, there is real potential for disease spread across the Middle East and Central Asia, into Europe and through Africa. Vulture declines are already having a measurable ecological impact in India and present many risks to wildlife and human health, social systems, and local economies. Should *Gyps* vultures be similarly affected in Africa, savanna ecosystems and local people would suffer similar effects.

That disease may be responsible for such a dramatic and widespread population crash is unusual because it does not appear to be a major cause of mortality in populations of *Gyps* vultures elsewhere in the world (Benson 2000). Diagnosis of disease in wild bird populations is seldom attempted, however, and the importance of disease as a population regulator remains poorly understood and probably greatly underestimated (Daszak et al. 2000; Friend et al. 2001). If, as seems likely, infectious disease is responsible for the declines, it probably resulted from the introduction of an alien disease, or perhaps the introduction of a vector for a disease from which the vultures were previously ecologically isolated. It is also possible that some environmental contaminant may have increased their susceptibility to a disease to which they were previously resistant.

Species that have evolved in the absence of exposure to a particular disease tend to be more susceptible to its effects. A good example is the endemic Hawaiian avifauna that, in the absence of the mosquito vector, had never been exposed to malarial parasites, *Plasmodium* spp. although they were probably present sporadically in Hawaii in the tissues of migratory birds. When the mosquito vector, *Culex quinquefasciatus,* was accidentally introduced in 1826, malaria had a devastating effect on low-elevation native forest birds, which are particularly susceptible to this disease (Warner 1968; Atkinson et al. 1995). It is too early to speculate about the possible origins of an infectious disease affecting *Gyps* vultures, but for a disease to have such a rapid and devastating effect on a population, it is likely to be something to which the population was previously immunologically naive.

## Research and Monitoring Needs

Identifying the mortality factor(s) responsible for the vulture declines is an obvious priority. Until this has been done, it will be extremely difficult to identify action needed to improve the situation where declines have occurred or arrest the spread of the problem. Although current information suggests that investigations should focus on an infectious disease as the most likely cause, it is important that other potential causes, particularly the role of contaminants, are not ignored. Even if infectious disease has played a part in the declines, there may be other underlying factors.

On the basis of current evidence, it is realistic to assume that the mortality factor will continue to spread and could rapidly move beyond the Indian subcontinent. *G. fulvus* is the species most likely to facilitate the spread of disease from India and Pakistan across the Middle East and Central Asia and into Europe and Africa. Monitoring of the number and health status of *Gyps* species at colonies across their range states should be initiated rapidly to identify the routes and rate of spread of the problem. Satellite tracking of *G. fulvus* in India and across the Middle East is underway to help elucidate the most likely routes of spread. Although monitoring of *Gyps* species is essential, other avian scavengers should not be ignored. Other species do not appear to have suffered the fate of *Gyps* vultures, but monitoring is poor or nonexistent, and there is not yet conclusive evidence that *Gyps* species alone are affected.

There is an urgent need to conserve the relict *Gyps* populations in Cambodia and adjacent parts of Laos and Vietnam. Should the cause of declines prove to be infectious disease, these populations will assume increasing importance because they are now relatively isolated, with a low risk of exposure to the agent killing birds in India. It is therefore important to reverse the population decline there through effective conservation management in northeastern Cambodia. Efforts should also be made to use the small numbers of *G. bengalensis* in captivity in Western Europe and elsewhere to initiate a captive breeding program to guard against the extinction of this species. We know of no *G. indicus* or *G. tenuirostris* in captivity.

Declines of the scale and rapidity seen in *Gyps* vultures are unprecedented for a large bird of prey. Conservation of *Gyps* species requires a concerted international effort, involving a wide range of disciplines, including biologists, wildlife pathologists, epidemiologists, and captive breeding specialists. These declines do not simply represent the potential extinction of a species or, eventually, a genus, serious though extinction would be. Vultures are keystone species, and their disappearance is having and will have major impacts on both the ecosystems they inhabit and the humans associated with them.

It is rare that nothing can be done to stem or manage a decline when the causal agent has been identified. Although unlikely, it is possible that no action can be taken to stem the *Gyps* declines. Should this be the case, at a minimum, actions should be identified that will minimize the consequences for wildlife and human health of loss of *Gyps* vultures in African ecosystems and elsewhere.

## Acknowledgments

We thank M. Virani of the Peregrine Fund for useful discussions, D. Gibbons for comments on the manuscript, and J. Ginsberg for suggesting this piece and for his helpful comments. Much of the research on vultures in India was funded by the Darwin Initiative for the Survival of Species (United Kingdom) and the U.S. Fish and Wildlife Service.

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