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LETTER

Another Continental Vulture Crisis: Africa's Vultures Collapsing toward Extinction

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Keywords

Asian vulture crisis; poisoning; scavenger; vulture population decline; illegal wildlife trade; traditional medicine; bushmeat.

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Abstract

Vultures provide critical ecosystem services, yet populations of many species have collapsed worldwide. We present the first estimates of a 30-year Pan-African vulture decline, confirming that declines have occurred on a scale broadly comparable with those seen in Asia, where the ecological, economic, and human costs are already documented. Populations of eight species we assessed had declined by an average of 62%; seven had declined at a rate of 80% or more over three generations. Of these, at least six appear to qualify for uplisting to Critically Endangered. Africa's vultures are facing a range of specific threats, the most significant of which are poisoning and trade in traditional medicines, which together accounted for 90% of reported deaths. We recommend that national governments urgently enact and enforce legislation to strictly regulate the sale and use of pesticides and poisons, to eliminate the illegal trade in vulture body parts, as food or medicine, and to minimize mortality caused by power lines and wind turbines.

Introduction

Vultures provide essential ecosystem services, yet they are among the most threatened groups of birds worldwide (Ogada, Keesing et al. 2012). Currently, 69% of vultures and condors are listed as threatened or near-threatened by the IUCN, the majority classed as Endangered or Critically Endangered (BirdLife Interna-

tional 2014). The "Asian Vulture Crisis" of the late 1990s saw populations of three species of Gyps vulture collapse throughout South Asia, by >96% in just 10 years, due to incidental Diclofenac poisoning (Prakash 1999; Gilbert et al. 2002; Oaks et al. 2004). Because vultures suppress the number of mammalian scavengers at carcasses, resulting in fewer contacts between potentially infected individuals, levels of disease transmission are likely to

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be greater in the absence of vultures (Ogada, Torchin et al. 2012). Consequently, the Asian Vulture Crisis has resulted in a parallel increase in feral dog populations, which are now the major consumers of carcasses in urban areas in India (Markandya et al. 2008), and also the main reservoir of diseases such as rabies (Sudarshan et al. 2007). The growth in feral dog numbers, following the collapse of vulture populations, will contribute to the risks associated with rabies transmission, both in Africa (Lembo et al. 2008) and in Asia, where it is estimated to have added \$34 billion to healthcare costs in India between 1993 and 2006 (Markandya et al. 2008). Vultures also freely dispose of organic waste in towns. Egyptian Vultures, for example, consumed up to 22% of annual waste in towns on Socotra off the Horn of Africa (Gangoso et al. 2013).

In Africa, significant vulture declines have been reported from widely scattered locations since the turn of the century, by numerous authors using various methods, and working at very different spatial and temporal scales (e.g., Thiollay 2001; Rondeau & Thiollay 2004; Virani et al. 2011; Murn et al. 2013; Krüger et al. 2014). Collectively, these reports suggest that there may be a continental-scale problem, similar in extent—though more protracted—than the Asian situation, and as yet poorly documented.

As representatives of the IUCN Vulture Specialist Group, we present published and unpublished data on Africa's vulture populations, to provide the first comprehensive assessment of their conservation status. We review the major threats to Africa's vultures, identify important knowledge gaps that need to be addressed, and suggest policy-level actions required of governments if they are to ensure the long-term survival of Africa's vultures.

Methods

The impetus for this review came as a result of discussions during the vulture round-table meeting at the 2012 Pan-African Ornithological Congress. Much of the information that forms the basis of this article was discussed and compiled during the Pan-African Vulture Summit 2012 (Botha *et al.* 2012).

We assessed the population status and threats to eight widespread vulture species in Africa: Bearded *Gypaetus barbatus*, Egyptian *Neophron percnopterus*, White-backed *Gyps africanus*, Rüppell's *G. rueppellii*, Cape *G. coprotheres*, Hooded *Necrosyrtes monachus*, Lappet-faced *Torgos tracheliotos*, and White-headed Vulture *Trigonoceps occipitalis*.

This assessment was made using information derived from two main sources: (1) an extensive review of literature already known to the authors, augmented with publications sourced through Google Scholar and (2) unpublished data, mainly from road surveys and counts of dead vultures. Data for specific countries or regions were searched during June-July 2012 using the name of the country/region followed by the term "and vulture." The data collected included: habitat change, timeframe, survey size, methods used, assessment criteria, species surveyed, percent decline, general trends, and threats. These data were collected using a range of methods, including road counts, foot and aerial surveys, and bird atlas records. We eliminated data sets that we judged to be speculative, if they were based on too few survey days, or the majority of species historically present in the country had not been assessed.

Comparisons of declines across countries and regions

Where information was available, each vulture species in each country was assigned to a decline category. We recognised four categories on an ordinal scale, based on the quantitative or qualitative information available on the species' population change in each country, over a period of 19-55 years. The four categories were: (1) extinct or in severe decline (>50%), (2) strong decline (>25%), (3) moderate decline (<25%), and (4) no decline. We included only those countries for which the information was country-wide or included the majority of vulture habitats, and was available for the majority of species present (currently or historically; Table S1). Using a subset of these data, from which change rates could be calculated (i.e., for studies yielding both the degree of change and the time period over which it occurred), we estimated median annualized population change rates for species surveyed in each region (southern, west, east, and north) using bootstrapping analysis (n = 1,000 replicates; Figure 1; Table S2).

Declines within regions and in relation to protected area status

Vulture numbers were estimated from road counts carried out in West Africa (Burkina Faso, Mali, and Niger) and East Africa (Kenya, Uganda) over two time periods: 1969–1973 and 2003–2004 in West Africa, and 1974–1988 and 2008–2013 in East Africa (Figure 2; Table S3). Field methods used in West Africa are described by Rondeau & Thiollay (2004), who surveyed the same routes (transects) during the same months in each time period. In East Africa during 1974–1988, surveys were also carried out by J.M.T., using the same methods as applied in West Africa. The methods used in East Africa

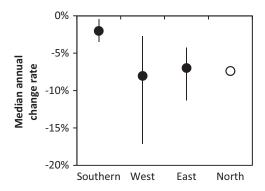


Figure 1 Population change by region. Changes in each species' abundance were converted to annualized rates of change, which were pooled across species and study areas. Bootstrapping analysis (n=1,000 replicates) was used to estimate the median annualized change rate for each region (\bullet); vertical bars indicate 95% percentiles). North Africa (\bigcirc) is represented by a single species and study area; southern Africa by five species, seven areas; West by six species, four areas; East by six species, four areas.

during 2008-2013 (Ogada et al. 2010; Pomeroy et al. 2014) were similar to those applied by J.M.T., but involved different observers. To ensure comparability, we limited the analysis to those transects showing at least partial spatial overlap between the two time periods. To determine the effects of protected area (PA) status on changes in vulture abundance, we distinguished between transects situated within PAs (National Parks, National Reserves, Wildlife Reserves, Forest Reserves, Conservancies, and Game Ranches) and those outside of PAs. In each case, the number of birds detected 100 km⁻¹ was calculated for each transect in each survey year, and the mean (±s.e.) birds detected 100 km⁻¹ was calculated for all transect years, grouped according to PA status, region, and time period. Sufficient data were available to compare detection rates for five of the eight species considered.

Projected population changes over three generations

We estimated the annualized rate of change in abundance for each of the eight vulture species, across a range of study sites surveyed in more than one time period, extracted from 13 published and 3 unpublished accounts (Table S2). The survey methods used often varied between locations, and included road transects (individuals detected 100 km^{-1} of transect) and breeding surveys (occupied nests at cliff sites, tree nest densities). In each case, we converted the overall change (C), observed over a specified time period (t), in years, to an annualized rate of change (r), using the formula $r = -(1 - (1 + C)^{\circ}(1/t))$. For

each species, we calculated the median, Q1 and Q3 annualized change rates from all locations for which estimates were available, using the *quantile* function in R (3.0.1: R Development Core Team 2009; Tables 1 & S4). Details of the algorithm used are given in the Supplementary Information: "Quartile estimation". From the median, Q1 and Q3 annualized change rates, we calculated the rates of change expected over three generations, using the formula $-(1 - (1 + r)^{\hat{}}(3 \times gl))$, where gl = estimated generation length for the species in question. Generation length estimates were provided by BirdLife International (unpublished data; Table S4).

Major threats to vulture populations

We assessed the major threats to African vultures based on quantitative data drawn from peer-reviewed articles, unpublished and newspaper reports documenting vulture deaths during 1961–2014 (Table S5). These were assigned to four categories: (1) Poisoning, including intentional killing (e.g. retaliation by poachers to avoid detection), and unintentional killing (feeding on poison-laced carcasses intended to kill livestock predators), (2) Trade in traditional medicine, (3) Killing for food, and (4) Electrical infrastructure: collision with power lines and wind turbines, and electrocution. The interrelated effects of changes in habitat, food availability, and human disturbance were also considered, and are discussed below.

Results

Population change assessments were available from 22 African countries, covering 58% of Africa's land surface. Of 95 national populations assessed, 85 (89%) were either nationally extinct or had experienced severe declines (>50%) or strong declines (>25%; Table S1). Tanzania is the only country in which only half of the species historically present have shown evidence of a decline. Populations are declining throughout Africa, with West and East Africa showing the greatest declines per annum (Figure 1). Although declines were generally greater in unprotected areas, substantial declines were also evident within protected areas for the five species assessed in both East and West Africa (Figure 2). These trends have been broadly consistent between regions and across species, where this has been measured.

To estimate decline rates across Africa, we determined the median decline rate for each species, drawn from 16 studies conducted in 12 countries (Table 1). While sample sizes varied between species, and were particularly small in the case of Bearded, Egyptian, and Cape Vulture (three sites each), the majority of species were each surveyed in at least six countries. The most rapid

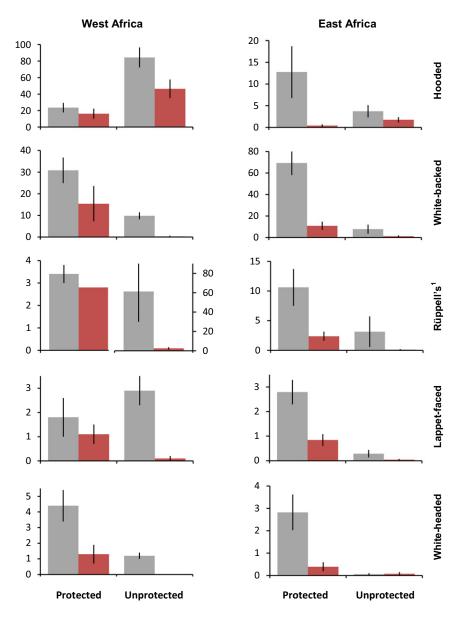


Figure 2 Declines within regions and in relation to protected area status. Patterns of decline in five species for which adequate data were available were broadly similar in West and East Africa. Substantial declines were evident both inside and outside of protected area networks. Mean (±s.e.) birds detected 100 km⁻¹ surveyed are shown in two periods: ■ early (West Africa: 1969–1973; East Africa: 1974–1988); ■ recent (West Africa: 2003–2004; East Africa: 2008–2013). PA: protected areas; Non-PA: land outside the PA network. West Africa: Mali, Burkina Faso, and Niger (Rondeau & Thiollay 2004); East Africa: Kenya and Uganda (J.M. Thiollay, D. Ogada & D. Pomeroy, unpublished).

¹Rüppell's Vulture: in West Africa, during early surveys detection rates were substantially higher in unprotected areas, due to the inclusion of a single large (unprotected) breeding colony, at which numbers had collapsed by 2004. Note the different scale used for unprotected areas.

declines had occurred in White-headed, Rüppell's, Cape, and Egyptian Vulture (Table 1; Figure 3). The median decline rates for these four species varied between 5.1% and 6.1% p.a., and averaged 4.6% p.a. for the eight species assessed. Combined with long generation lengths (mean: 16.6 years) and low annual fecundity, these declines meet or exceed the threshold for species qualify-

ing as Critically Endangered (IUCN 2012; seven species) or Endangered (African populations of the Bearded Vulture; Figure 3). To further evaluate each species' threat status, we examined three measures: the extent to which the species' median and quartile decline rates exceeded the CR threshold (an 80% decline over three generations), the proportion of range states for which trend data

Table 1 Median annualized rates of change in African vulture species, derived from 16 studies conducted in 12 countries

					Annualized change		
	Current status ^a	Studies ^b	Regions ^c	Time span (years) ^d	Median	Lower quartile ^e	Upper quartile ^e
Bearded Vulture Gypaetus barbatus	NT	3 (2)	S,N	30–50	-2.2%	-1.7%	-4.8%
Egyptian Vulture Neophron percnopterus	EN	3 (5)	E,W	29-36	-5.9%	-3.0%	-13.5%
Hooded Vulture Necrosyrtes monachus	EN	7 (6)	E,W	27-39	-3.3%	-1.9%	-4.9%
White-backed Vulture Gyps africanus	EN	8 (7)	S,E,W	27-36	-4.1%	-2.5%	-5.4%
Rüppell's Vulture G. rueppellii	EN	7 (6)	E,W	17–36	-5.8%	-4.8%	-8.4%
Cape Vulture G. coprotheres	VU	3 (5)	S	6-61	-5.1%	-4.1%	-5.8%
Lappet-faced Vulture Torgos tracheliotos	VU	7 (7)	S,E,W	27-36	-3.5%	-2.3%	-4.5%
White-headed Vulture <i>Trigonoceps occipitalis</i>	VU	6 (7)	S,E,W	27–36	-6.7%	-2.8%	-8.8%

^aCurrent global threat status. NT: near-threatened; VU: vulnerable; EN: endangered (BirdLife International 2014).

eQuartile values for Bearded, Egyptian, and Cape Vulture are based on particularly small samples sizes, and should be treated with caution.

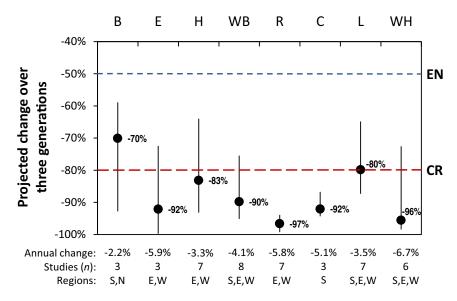


Figure 3 Projected population changes. Median projected rates of change over three generations (●) were estimated from annualized change rates for each species, and from estimates of generation length (BirdLife International, unpublished data). Projected change rates over three generations are expected to meet or exceed the threshold for species qualifying as Critically Endangered (CR: seven species) or Endangered (EN: all species) under IUCN Red List Criterion A4 (IUCN 2012). Vertical bars indicate upper and lower quartiles. The number of studies and regions from which data were collated are shown below the Figure (S = Southern, W = West, E = East, N = North Africa). Species key: B = Bearded, E = Egyptian, H = Hooded, WB = White-backed, R = Rüppell's, C = Cape, L = Lappet-faced, WH = White-headed vulture.

were available (BirdLife International 2014), and the extent to which the species' global range lies within Africa. These measures suggest that the case for uplisting species to CR is more robust for Rüppell's and Cape Vulture, followed by White-backed, Hooded, and White-headed Vulture (scoring equally), and by Lappet-faced Vulture (Table S6). The global threat status of Egyptian and Bearded Vulture is less clear, since their ranges outside of Africa extend from southern Europe to South Asia.

Of 7,819 vulture deaths recorded across 26 countries (Table S5), 61% were attributed to poisoning, 29% to

trade in traditional medicine, 1% to killing for food, and 9% to electrocution or collision with electrical infrastructure (Figure 4). Note, however, that since detection and reporting rates are likely to vary in relation to threat category, these comparisons should be treated with caution.

Discussion

Just as in Asia, African vultures are in crisis, their populations declining at a rate which, in at least six cases, meets or exceeds the threshold for species qualifying as

^bNumber of studies (and countries) from which population change estimates were derived for each species.

^cRegions in which the studies were conducted: S = Southern, W = West, E = East, N = North Africa.

^dMinimum and maximum periods over which population changes were measured by the studies examined.

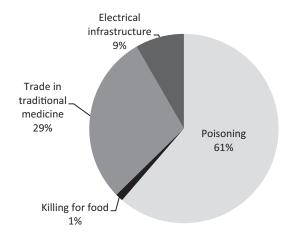


Figure 4 Major threats to vulture populations. Four quantitative factors constituted a serious threat to African vulture populations in 26 countries (n=7,819 recorded deaths; Table S5). "Poisoning" includes dead vultures that were victims of intentional or unintentional poisoning. "Trade in traditional medicine" indicates the number of vultures found dead without their heads, or the number of vultures or their parts counted on sale in markets. "Killing for food" indicates the number of dead vultures or their parts counted either when traders were observed at markets or after they were arrested. "Electrical infrastructure" is the number of vultures found electrocuted below power lines or other electrical infrastructure.

Critically Endangered. There are, however, two important distinctions between the Asian and African vulture crises. First, to date, the rate of decline evident among the four worst-affected African species (equivalent to 41– 50% per decade) has been substantially lower than in Asia (>96% per decade), affording governments the opportunity to enact and enforce legislation to regulate the use of pesticides and other poisons, and hence to reduce the key threat to vultures. There thus remains the potential to avoid the environmental consequences of a collapse in this functionally important group, and the complexities and expense associated with captive breeding and reintroduction. Second, while poisoning and trade in traditional medicine together pose the most serious threat to African vultures, there are a range of other factors involved in their decline that may prove difficult to resolve.

African vultures are often the unintended victims of poisoning incidents, in which carcasses are baited with highly toxic agricultural pesticides to kill carnivores such as lions, hyenas, and jackals (Ogada 2014), or to control feral dog populations (Abebe 2013). Furthermore, the recent rapid increase in elephant and rhino poaching throughout Africa has led to a substantial increase in vulture mortality, as poachers have turned to poisoning carcasses specifically to eliminate vultures, whose overhead circling might otherwise reveal the poachers' illicit

activities (Roxburgh & McDougall 2012; Ogada 2014). Consequently, the decline rates estimated here may have accelerated sharply in recent years; since July 2011, there have been at least 10 poisoning incidents that have, collectively, killed at least 1,500 vultures in six southern African countries (37–600 birds per incident; Ogada 2014).

The illegal trade in vulture body parts for use in traditional medicine is a significant threat that is increasing in intensity (McKean et al. 2013; Saidu & Buij 2013). Vulture body parts have long been valued in many African cultures, especially in South and West Africa, where some believe that they cure a range of physical and mental illnesses, improve success in gambling and business ventures, or increase intelligence in children (Beilis & Esterhuizen 2005; McKean et al. 2013; Saidu & Buij 2013). Similarly, although the consumption of vultures as bushmeat in some West African countries (e.g., Nigeria and Ivory Coast; Rondeau & Thiollay 2004; Thiollay 2006; Saidu & Buij 2013) may be a particular regional concern, smoked vulture meat is known to be trafficked internationally (Rondeau & Thiollay 2004), and our findings suggest that, together, poisoning and the illegal trade in vulture body parts for medicines or as bushmeat, pose a substantial threat, and on a continental

African vultures are also frequent victims of electrocution, particularly in southern and North Africa, where there has been an increase in electrical infrastructure development from power lines and wind farms. "Green energy" initiatives such as wind farms can be detrimental to vultures, if bird-friendly designs and careful placement of turbines and power lines are not observed (Jenkins *et al.* 2010; Rushworth & Krüger 2014).

Other threats that are more difficult to quantify include reduction of habitat, disturbance at nest sites, and food declines. Habitat loss reduces nest site availability for disturbance-sensitive, tree-nesting vultures (Monadjem & Garcelon 2005; Bamford et al. 2009), including Hooded, White-backed, Lappet-faced, and Whiteheaded Vultures. Disturbance around breeding cliffs has resulted in nest failures (Borello & Borello 2002), and the illicit harvesting of eggs and chicks (G. Abert, in litt. in Rondeau & Thiollay 2004; Ogada & Buij 2011), as well as recreational rock climbing (Rondeau & Thiollay 2004), all further threaten Africa's vultures. The impact of wildlife declines on the food supply of vultures is difficult to assess, but has likely affected populations, most substantially inside West Africa's protected areas. Craigie et al. (2010) recorded a composite 59% decline in large mammal populations inside protected areas in 18 countries during 1970-2005, with the greatest regional decline (85%) recorded inside West Africa's protected areas. However, large vulture declines in West Africa during this period were greatest outside of protected areas (–98%), where wild ungulates were already scarce in the 1960s (Thiollay 2006). Also, Hooded Vultures already depended almost entirely on anthropogenic food resources in the 1960s, while the other vulture species fed extensively on livestock (Thiollay 1977; Scholte 1998); populations of which have more than doubled since the 1960s (FAO 2014). This increase will have been offset partly by the modernization of livestock management and improved sanitation at slaughterhouses; impacting mainly on Hooded and Egyptian Vultures (Thiollay 2006; Ogada & Buij 2011; Gangoso *et al.* 2013).

Conservation needs and actions

The situation in Africa requires that a number of environmental and cultural issues are addressed.

These were outlined in a resolution to African governments by the participants of the 2012 Pan-Africa Vulture Summit, where the following specific recommendations were made (Botha *et al.* 2012).

- (1) Effectively regulate the import, manufacture, sale, and use of poisons, including agricultural chemicals and pharmaceutical products known to be lethal to vultures.
- (2) Legislate and enforce stringent measures to prosecute and impose harsh penalties on perpetrators of poisoning and those illegally trading in vultures and/or their body parts.
- (3) Ensure appropriate levels of protection and management for vultures and their breeding sites.
- (4) Ensure that all new energy infrastructure is vulturefriendly and that existing unsafe infrastructure is modified accordingly.
- (5) Support research, capacity building, and outreach programs for the conservation and survival of healthy vulture populations.

We suggest prioritizing the regulation of pesticides and other poisons as an action likely to have the most significant and positive impact, not just for vultures but for all scavengers and predators targeted by pastoralists. The Vulture Specialist Group of the IUCN has made a similar appeal to African governments (IUCN 2013). In November 2014, the Conference of the Parties of the Convention on Migratory Species (CMS) formally adopted a set of guidelines to tackle causes of poisoning (CMS 2014a), which, although not legally binding, will be a significant step toward recognizing and reducing vulture poisoning.

The CMS recommendations include prohibiting the use of poison baits for predator control, creating or improving enforcement legislation, and restricting access to highly toxic substances (CMS 2014b).

National governments must work with conservation NGOs to halt the illegal trade in vultures as bushmeat and for traditional medicine. More effective law enforcement is needed to curb the illegal hunting and sale of vulture meat and body parts. Public awareness campaigns are also needed to highlight the dangers and the potential health implications of extracting traditional medicines from vultures, of which approximately 40% are killed using poisons (McKean *et al.* 2013; Saidu & Buij 2013). Further study is needed to determine the residue levels of toxic pesticides in vultures used for traditional medicine.

National Energy Ministries and energy companies need to work with conservation NGOs to ensure that existing and future energy-related developments are vulturefriendly, and to modify unsafe designs. Many African countries have adopted the resolution on Power Lines and Migratory Birds that applies to migratory vultures (CMS 2011). Best practice guidelines for power lines (Demmer et al. 2006) and for wind energy (Jenkins et al. 2012) need to be integrated into national legislations, and proposed developments that will adversely affect important vulture populations should be modified or relocated (Rushworth & Krüger 2014). Research is urgently needed over vast areas of Africa where energy developments are proposed (see http://www.africa-energy.com), but the potential impacts on vultures and other at-risk species are not known.

The Asian Vulture Crisis has highlighted the important link between vultures and human health, and shown us that when vulture numbers fall to critical thresholds, reestablishing their populations is a slow, difficult, and expensive undertaking (Walters *et al.* 2010). Our findings provide the first continent-wide estimates of decline rates in Africa's vultures. They confirm that African vulture populations are in steep decline and will require governments to act now to avoid the environmental and social consequences of losing what are arguably nature's most important scavengers.

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References

- Abebe, Y.D. (2013). Mass dog poisoning operation in Addis Ababa can have severe repercussions on vulture populations. *Vulture News*, **64**, 74-76.
- Bamford, A.J., Monadjem, A., Anderson, M.D. *et al.* (2009). Trade-offs between specificity and regional generality in habitat association models: a case study of two species of African vulture. *J. Appl. Ecol.*, **46**, 852-860.
- Beilis, N. & Esterhuizen, J. (2005). The potential impact on Cape Griffon *Gyps coprotheres* populations due to the trade in traditional medicine in Maseru, Lesotho. *Vulture News*, **53**, 15-19.
- BirdLife International. (2014). IUCN Red List for birds. http://www.birdlife.org (visited April 20, 2014).
- Borello, W.D. & Borello, R.M. (2002). The breeding status and colony dynamics of Cape Vulture *Gyps coprotheres* in Botswana. *Bird Conserv. Int.*, **12**, 79-97.
- Botha, A.J., Ogada, D.L. & Virani, M.Z., editors. (2012). *Proceedings of the Pan-African Vulture Summit*. Endangered Wildlife Trust, Modderfontein, South Africa & The Peregrine Fund, Boise, ID.
- CMS (2011). Power lines and migratory birds. http://www.cms.int/sites/default/files/document/10_11_powerlines_e_1_0.pdf (visited October 11, 2014).
- CMS (2014a). Governments commit to step up action for migratory animals at UN wildlife conference. http://www.cms.int/sites/default/files/Closing_PR_CMSCOP11_11Nov_0.pdf (visited November 29, 2014).
- CMS (2014b). Review and guidelines to prevent the risk of poisoning of migratory birds. *UNEP/CMS/COP11/Doc.1.2*, pp. 54
- Craigie, I.D., Baillie, J.E.M., Balmford, A., et al. (2010). Large mammal population declines in Africa's protected areas. *Biol. Conserv.*, **143**, 2221-2228.
- Demmer, B., Nohlen, N. & Heimberg, J. (2006). *Suggested practices for bird protection on power lines*. NABU-German Society for Nature Conservation, Berlin. 22 pp.
- FAO 2014. FAOStat: Food and Agriculture Organization of the United Nations - Statistics Division. http://faostat3.fao.org/browse/Q/QA/E (Accessed Nov 27, 2014).
- Gangoso, L., Agudo, R., Anadón, J.D., et al. (2013).

 Reinventing mutualism between humans and wild fauna: insights from vultures as ecosystem services providers.

 Conserv. Lett., 6, 172-179.
- Gilbert, M., Watson, R.T., Ahmed, S., Asim, M. & Johnson, J.A. (2002). Breeding and mortality of Oriental White-backed Vulture *Gyps bengalensis* in Punjab Province, Pakistan. *Bird Conserv. Int.*, 1, 311-326.

- IUCN. (2012). IUCN Red List Categories and Criteria, Version 3.1. IUCN, Gland, Switzerland and Cambridge, UK.
- IUCN. (2013). Vultures the silent victims of Africa's wildlife poaching. http://www.iucn.org/?13529/Vultures-silentvictims-of-Africas-wildlife-poaching (visited October 9, 2014).
- Jenkins, A.R., Smallie, J.J. & Diamond, M. (2010). Avian collisions with power lines: a global review of causes and mitigation with a South African perspective. *Bird Conserv. Int.*, 20, 263-278.
- Jenkins, A.R., vanRooyen, C.S., Smallie, J.J., Harrison, J.A., Diamond, M. & Smit, H.A. (2012). BirdLife South Africa/Endangered Wildlife Trust best practice guidelines for avian monitoring and impact mitigation at proposed wind energy development sites in southern Africa. http://www.cms-family-ors.unep-wcmc.org/answers/1959063/documents/377 (visited October 11, 2014).
- Krüger, S.C., Allan, D.G., Jenkins, A.R. & Amar, A. (2014). Trends in territory occupancy, distribution and density of the Bearded Vulture *Gypaetus barbatus meridionalis* in southern Africa. *Bird Conserv. Int.*, 24, 162-177.
- Lembo, T., Hampson, K., Haydon, D.T., et al. (2008). Exploring reservoir dynamics: a case study of rabies in the Serengeti ecosystem. *J. Appl. Ecol.*, **45**, 1246-1257.
- Markandya, A., Taylor, T., Longo, A., Murty, M.N., Murty, S. & Dhavala, K. (2008). Counting the cost of vulture decline—an appraisal of the human health and other benefits of vultures in India. *Ecol. Econ.*, **67**, 194-204.
- McKean, S., Mander, M., Diederichs, N. *et al.* (2013). The impact of traditional use on vultures in South Africa. *Vulture News*, **65**, 15-36.
- Monadjem, A. & Garcelon, D.K. (2005). Nesting distribution of vultures in relation to land use in Swaziland. *Biodivers. Conserv.*, **14**, 2079-2093.
- Murn, C., Combrink, L., Ronaldson, G.S., Thompson, C. & Botha, A. (2013). Population estimates of three vulture species in Kruger National Park, South Africa. *Ostrich*, **84**, 1-9
- Oaks, J.L., Gilbert, M., Virani, M.Z. *et al.* (2004). Diclofenac residues as the cause of vulture population decline in Pakistan. *Nature*, **427**, 630-633.
- Ogada, D.L. (2014). Power of poison: pesticide poisoning of Africa's wildlife. *Ann. NY Acad. Sci.*, **1322**, 1-20.
- Ogada, D.L. & Buij, R. (2011). Decline of the Hooded Vulture Necrosyrtes monachus across its African range. Ostrich, 82, 101-113.
- Ogada, D.L., Thomsett, S., Virani, M.Z., Kendall, C. & Odino, M. (2010). *Raptor road counts in Kenya: with emphasis on vultures*. Report to the Royal Society for the Protection of Birds, 17 pp.
- Ogada, D.L., Keesing, F. & Virani, M.Z. (2012). Dropping dead: causes and consequences of vulture population declines worldwide. *Ann. NY Acad. Sci.*, **1249**, 57-71.
- Ogada, D.L., Torchin, M.E., Kinnaird, M.F. & Ezenwa, V.O. (2012). Effects of vulture declines on facultative scavengers

- and potential implications for mammalian disease transmission. *Conserv. Biol.*, **26**, 453-460.
- Pomeroy, D., Shaw, P., Opige, M., Kaphu, G., Ogada, D.L. & Virani, M.Z. (2014). Vulture populations in Uganda: using road survey data to measure both densities and encounter rates within protected and unprotected areas. *Bird Conserv. Int.* DOI: 10.1017/S095927091400029X.
- Prakash, V. (1999). Status of vultures in Keoladeo National Park, Bharatpur, Rajasthan, with special reference to population crash in *Gyps* species. *J. Bombay Nat. Hist. Soc.*, **96**, 365-378.
- R Development Core Team (2009). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Rondeau, G. & Thiollay, J.M. (2004). West African vulture decline. *Vulture News*, **51**, 13-33.
- Roxburgh, L. & McDougall, R. (2012). Vulture poisoning incidents and the status of vultures in Zambia and Malawi. *Vulture News*, **62**, 33-39.
- Rushworth, I. & Krüger, S.C. (2014). Wind farms threaten southern Africa's cliff-nesting vultures. *Ostrich*, **85**, 13-23.
- Saidu, Y. & Buij, R. (2013). Traditional medicine trade in vulture parts in northern Nigeria. *Vulture News*, **65**, 4-14.

- Scholte, P. (1998). Status of vultures in the Lake Chad Basin, with special reference to Northern Cameroon and Western Chad. *Vulture News*, **39**, 3-19.
- Sudarshan, M.K., Madhusudana, S.N., Mahendra, B.J. *et al.* (2007). Assessing the burden of human rabies in India: results of a national multi-center epidemiological survey. *Int. J. Infect. Dis.*, **11**, 29-35.
- Thiollay, J.M. (1977). Distribution saisonnière des rapaces diurnes en Afrique Occidentale. *L'Oiseau et la Revue Française d'Ornithologie*, **47**, 253-294.
- Thiollay, J.M. (2001). Long-term changes of raptor populations in northern Cameroon. *J. Raptor Res.*, **35**, 173-186.
- Thiollay, J.M. (2006). The decline of raptors in West Africa: long-term assessment and the role of protected areas. *Ibis*, **148**, 240-254.
- Virani, M.Z., Kendall, C., Njoroge, P. & Thomsett, S. (2011). Major declines in the abundance of vultures and other scavenging raptors in and around the Masai Mara ecosystem, Kenya. *Biol. Conserv.*, **144**, 746-752.
- Walters, J.R., Derrickson, S.R., Fry, D.M., Haig, S.M. & Marzluff, J.M. (2010). Status of the California Condor (*Gymnogyps californianus*) and efforts to achieve its recovery. *Auk*, **127**, 969-1001.