African Journal of Ecology

Survival of the African white-backed vulture *Gyps africanus* in north-eastern South Africa

Ara Monadjem[1]*, Andre Botha[2] and Campbell Murn[3]

[1]*Department of Biological Sciences, All Out Africa Research Unit, University of Swaziland, Private Bag 4, Kwaluseni, Swaziland,* [2]*Birds of Prey Programme, Endangered Wildlife Trust, Private Bag X11, Modderfontein, South Africa and* [3]*Hawk Conservancy Trust, Andover, Hampshire, UK*

Abstract

Old World vultures are in decline across their entire range. Although critical for the formulation of effective conservation measures, neither survival nor movement patterns of African vultures are adequately known. This paper presents survival and movement data on the African white-backed vultures (*Gyps africanus*) from South Africa. Survival estimates were modelled on resightings of tagged vultures. Birds were captured *en masse* and resighted between November 2005 and December 2010. A total of 93 adult and subadult birds were fitted with uniquely numbered patagial tags, which were resighted 3707 times (mean of 39.8 resightings per bird). The programme MARK was used to estimate survival. The best model was one where survival and recaptures varied only with time (e.g. year). However, owing to the fading (illegibility) of tags in later years, the relationship with time is probably spurious. The second best model was one where survival and recaptures varied with age and time. Annual survival estimates increased from 85.2% in second-year birds to 99.9% in adults. This corresponds well with the survival of two other *Gyps* vultures that have been studied to date and underscores the point that additional mortality of adults in these long-lived species will result in rapid population declines.

Key words: Gyps africanus, mark and recapture, patagial tag, survival, vultures

Résumé

Les vautours de l'Ancien Monde sont en déclin dans toute leur aire de répartition. Bien que ce soit essentiel pour la formulation de mesures de conservation efficaces, ni leur schéma de survie ni celui de leurs déplacements n'est correctement connu. Cet article présente des données sur la survie et les déplacements du vautour africain (*Gyps africanus*) d'Afrique du Sud. Les estimations de la survie ont été modélisées d'après de nouvelles observations d'oiseaux marqués. Les oiseaux ont été capturés en grand nombre et observés de nouveau entre novembre 2005 et décembre 2010. Au total, 93 oiseaux adultes et subadultes furent pourvus de marques numérotées individuelles à l'aile ; ils ont été revus 3 707 fois (une moyenne de 39,8 observations par oiseau). C'est le programme MARK qui a servi à estimer le taux de survie. Le meilleur modèle était un modèle où la survie et les recaptures ne variaient qu'avec le temps (par exemple par année). Cependant, étant donné que les marques s'effacent et deviennent de moins en moins lisibles avec le temps, la relation avec les années est probablement mal choisie. Le deuxième modèle était un modèle où la survie et les recaptures variaient avec l'âge et le temps. Les estimations de survie annuelle augmentaient de 85,2% pour des oiseaux dans leur deuxième année à 99,9% chez les adultes. Cela correspond avec la survie de deux autres vautours *Gyps* qui ont été étudiés à ce jour, et met en évidence le fait qu'une augmentation de la mortalité des adultes de ces espèces qui vivent longtemps risque d'entraîner un déclin rapide des populations.

Introduction

In the past decade, vulture populations have declined dramatically across the Asian subcontinent (Green *et al.*, 2004; Gilbert *et al.*, 2006; Pain *et al.*, 2008) as well as in the Middle East (Becker *et al.*, 2009) and Africa (Thiollay, 2006; Virani *et al.*, 2011). The causes for some of these declines are well documented, for example, diclofenac poisoning in South Asia (Oaks *et al.*, 2004), but less well understood in Africa, although land use change and poisoning have both been suggested as important factors

*Correspondence: E-mail: ara@uniswa.sz

(Thiollay, 2006; Virani *et al.*, 2011). Declining vulture populations are likely to exhibit reduced survival of adults and/or subadults as survival estimates of these age classes are crucial demographic parameters for the population dynamics of long-lived species (Lebreton & Clobert, 1991). However, survival estimates are typically not available for most vulture species or populations.

Survival has been estimated in the Eurasian griffon (*Gyps fulvus*) and the Cape vulture (*Gyps coprotheres*) using resightings (Sarrazin *et al.*, 1994; Piper, Boshoff & Scott, 1999). Earlier estimates using ring recoveries (e.g. Piper, Mundy & Ledger, 1981) have been shown to be seriously flawed (Anderson, Burnham & White, 1985) and will not be discussed further. Both studies based on resightings showed high survival rates in subadult vultures and even higher survival in the adult Eurasian griffon (Sarrazin *et al.*, 1994; Piper, Boshoff & Scott, 1999); survival of adult Cape vultures could not be estimated and was not reported. A similar pattern was observed for a population of the Egyptian vulture (*Neophronpercnopterus*) breeding in Europe and migrating to Africa (Grande *et al.*, 2009).

The African white-backed vulture (*Gyps africanus*) is widespread across the savannahs of Africa occurring from South Africa north to Ethiopia and west to Senegal (Mundy *et al.*, 1992; Dowsett & Dowsett-Lemaire, 1993). Until recently, it was an abundant species of vulture with an estimated 3300 pairs occurring in South Africa alone (Anderson, 2000), and an estimated total population of 270,000 individuals occurring across the entire continent (Mundy *et al.*, 1992). However, this total is very likely to be an overestimate given the significant declines reported for the species across large parts of its range (Thiollay, 2007; Virani *et al.*, 2011), and its global conservation status has recently been upgraded to Endangered (IUCN, 2012). Its nesting biology is relatively well known (Kemp & Kemp, 1975; Monadjem & Garcelon, 2005; Bamford, Monadjem & Hardy, 2009a; Virani *et al.*, 2010), and some information is available on its movements based on ring recoveries (Oatley *et al.*, 1998). In contrast, virtually nothing is known about its survival.

This study aims to estimate the survival of African white-backed vultures tagged in north-eastern South Africa and resighted across the region. We predict that the survival of this species here is likely to show a fairly natural pattern unaffected by the declines shown elsewhere in its range. Our objectives are as follows: (i) to estimate the survival of African white-backed vultures based on resightings of tagged individuals using the programme MARK; (ii) to estimate the total population size using the vulture restaurant (feeding station) at Moholoholo Wildlife Rehabilitation Centre (the site of capture and release of these birds); and (iii) to document the area over which these tagged birds were resighted.

Methods

Vulture capture

Vultures were captured and tagged at Moholoholo Wildlife Rehabilitation Centre vulture restaurant (24°30′S; 30°54′E, 600 m above sea level), north-eastern South Africa. The site is situated in low-lying savannah within 20 km of the Greater Kruger National Park (i.e. Kruger National Park and adjoining wildlife conservation areas), to the east. The vulture restaurant at Moholoholo is carefully managed and has been in existence since the 1980s. Carcasses or parts thereof are put out for vultures daily. The amount varies according to what is available, but vultures are observed each day.

The birds were captured in a specially designed walk-in trap (Diekmann *et al.*, 2004; Bamford *et al.*, 2009b) that was erected alongside the vulture restaurant. Birds were captured and released, or rehabilitated birds released, on six different sessions between November 2005 and September 2008. Originally, fifteen rehabilitated birds were released on 5 November 2005. Two mass capture sessions resulted in the capture of the majority of the released birds: 29 January 2007 (n = 15 birds) and 13 February 2007 (n = 58 birds).The remaining five vultures were released as rehabilitated birds between May 2006 and September 2008.

Captured birds were aged and had their wing length measured. Ageing was based on plumage characteristics (from Mundy *et al.*, 1992) and birds were assigned to one of four age classes: second-year bird, third-year bird, subadult (4–6 years old) and 7 years old or older. Sexing of African white-backed vultures based on external features has not been reliably described. Thus, birds were not assigned a sex in the field, and sex was dropped as a feature in subsequent analyses. Each bird was fitted with a metal ring issued by AFRING (Animal Demography Unit, University of Cape Town) and a patagial tag. Patagial tags were fitted according to the standard protocol adopted for this practice in southern Africa (Botha, 2007). It involved the use of a double set of standard cattle tags engraved with a unique number which was fitted to the patagial area on each wing of each bird using a tag applicator. This method was extensively assessed prior to this study and found not to be detrimental to the birds' health or inhibiting their ability to forage (Botha, 2007). All tagged vultures were released unharmed and within 120 min of capture.

A dedicated resightings programme was established by publicising the project using television and radio broadcasts, articles to local newspapers and magazines, and posters in Kruger National Park rest camps. Resightings were reported by a wide range of people by phone, e-mail or sms. A significant proportion of resightings was submitted by the staff at Moholoholo who kept a daily watch at the vulture restaurant. Resightings were also reported *inter alia* by managers of other vulture restaurants, game ranchers, farmers and tourists.

We flew aerial censuses using a helicopter over large (±3500 km^2) sample areas in two eco-geographically separate regions of Kruger National Park and counted and georeferenced African white-backed vulture nests visible within predetermined transects. An estimated total number of nests for Kruger National Park were calculated by extrapolating from the surveyed areas. The extrapolation was based on a combination of spatial extent and the expected breeding habitat available within the well-defined landscapes of the park (Gertenbach, 1983).

Data analysis

Survival and recapture were computed, using the standard Cormack-Jolly-Seber model, in the programme MARK (White & Burnham, 1999; White, 2008) using capture-resightings of African white-backed vultures. This model is appropriate as no tagged vultures were recovered dead. A variety of models that included time dependence and age were developed. Models were ranked using Akaike's information criterion (AIC) (Burnham & Anderson, 2002). The model with the lowest AIC_c was deemed the best model, where ΔAIC_c (the difference in AIC_c between models) for any two (or more) models was <2.0, they were both deemed to be equally good. Total population size of the birds was estimated using the POPAN formulation in MARK and was based on the captures during the original release (Nov 2005) and the two mass captures (Jan 2007, Feb 2007).The location of resightings was plotted using ArcGIS 9.3. All mean values are quoted with ±SE.

Results

A total of 93 African white-backed vultures was tagged of which all were resighted at least once. These birds were resighted 3707 times between November 2005 and December 2010 (mean of 39.8 resightings per bird; range: 2–245), covering a period of 61 months.

The best model represented survival and recaptures varying with time, but not with age class (Table 1). The next best model, which differed by an AIC_c of 2.9378, represented both survival and recaptures varying with age and time (Table 1). There were no competing models, and the next best model, which comprised survival varying with age and time recaptures varying with time, was not well supported (AIC_c weight = 0.01672)(Table 1).

Based on the best model of survival varying between years, the annual survival of tagged birds ranged from 1.000 in the first and second years down to 0.742 or 74.2% in the last year (Fig. 1a). Hence, survival changed dramatically over the study period, and this appeared to be related to the loss of tags (see Discussion). The survival

Table 1 The candidate models used to estimate survival in African white-backed vultures captured in north-eastern South Africa. Estimates of survival (phi) and recapture (*p*) were modelled with time (*t*) and/or age class of the vultures (age).The inclusion or exclusion of interactions in the models are symbolized by (+) or (*), respectively. The number of parameters is indicated by 'n'. The models are arranged from best (top of table) to worst (bottom)

Model	Description	AIC	Delta AICc	AICc Weights	n
Phi(*t*) *p* (*t*)	Survival and recaptures vary with time	320.6689	0	0.77067	7
Phi(age + *t*) *p* (age + *t*)	Survival and recaptures vary with age and time	323.6067	2.9378	0.17739	12
Phi(age + *t*) *p* (*t*)	Survival varies with age and time, recaptures vary with time	328.3300	7.6611	0.01672	14
Phi(.) *p* (age + *t*)	Survival constant, recaptures vary with age and time	328.6506	7.9817	0.01424	14
Phi(age) *p* (age + *t*)	Survival varies with age, recaptures vary with age and time	331.8658	11.1969	0.00285	16
Phi(age*t*) *p* (age*t*)	Survival and recaptures vary with age and time	332.3632	11.6943	0.00223	18
Phi(.) *p* (.)	Survival and recaptures constant	343.4893	22.8204	0.00001	2
Phi(age) *p* (age)	Survival and recaptures vary with age	347.7117	27.0428	0	7

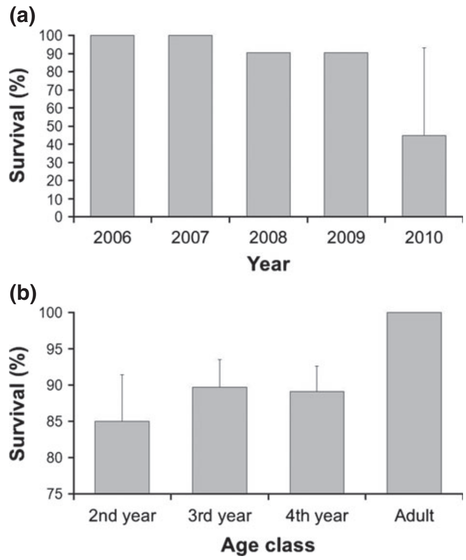

Fig 1 Annual survival of African white-backed vultures based on resightings of tagged birds in South Africa: (a) Annual survival rates in the 5 years of the study based on the best model where survival and recaptures varied with time (i.e. year); (b) Annual survival rates of the four age classes based on the second best model where survival and recaptures varied with both age and time

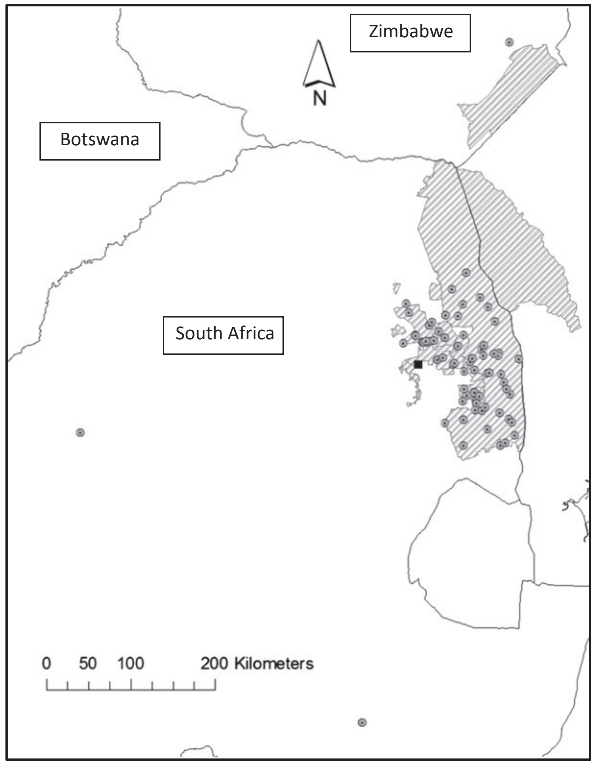

Fig 2 Map showing the resightings (circles) of African white-backed vultures tagged and released at Moholoholo Wildlife Rehabilitation Centre (square). The area hatched in grey is the Greater Kruger National Park (which includes the Kruger National Park, adjoining wildlife reserves and nature reserves and the transfrontier parks)

estimates for the four age classes (based on the second best model where survival and recaptures varied with both age and time) were as follows: second-year birds, 0.8515 (±0.06434); third-year birds, 0.8969 (±0.0784); fourth-year birds, 0.8909(0.03521) and adult birds 0.9999 (±0.00002) (Fig. 1b).

The total population size based on the best model was 921 birds ±619. In this model, survival and total population did not vary with time, whereas recapture and PENT (probability of entrance) varied with time. Correspondingly, we estimated that 624 pairs of African white-backed vulture bred in the Kruger National Park in 2011. Of the 477 nests of this species recorded from aerial surveys, 61 (or 15%) were inactive.

Tagged African white-backed vultures were resighted at 77 different localities, ranging from zero to 430 km away from the site of capture/release (i.e. Moholoholo). The majority of the resightings (n = 3581, or 96% of all sightings) were from the site of capture/release. The remaining 126 sightings were predominantly from the Greater Kruger National Park, with only three sightings beyond this area (Fig. 2). One of these three was from Zimbabwe near the Gona-re-Zhou National Park, which forms part of the Greater Kruger National Park transfrontier reserve. The two remaining resightings were from a protected area (Mankwe Game Reserve, north-west Province, South Africa) and an established vulture restaurant (near Dundee, KwaZulu-Natal Province, South Africa), both further than 400 km from the site of capture/release.

Discussion

Survival estimates of African white-backed vultures in this study were very high in the first 4 years and suddenly declined rapidly in the fifth year, almost certainly as a result of the loss of patagial tags and the fading of the numbers on the tags. Between 2005 and 2009, no loss of tags was reported by the staff at Moholoholo who were reporting sightings at the vulture restaurant. Starting in July 2010, the first tagged birds with faded numbers were being reported. By December 2010, more faded (i.e. illegible) tags were being reported than legible tags. Up to three birds with faded tags were present on any one day at Moholoholo in December 2010. Hence, the best model which did not include age was probably greatly affected by the loss of tags reported here. A similar problem with loss of rings fitted on the Cape vulture was reported by Piper, Boshoff & Scott (1999). This brings into question the efficiency of current tagging methods for estimating adult survival. It is suggested that the use of alternative tags, which will survive and be legible for longer, are investigated.

We present the first survival estimates for the African white-backed vulture. Survival was lowest for second-year birds and highest for adults; however, the best model did not include varying age probably as a result of tag loss. Survival across all age classes was estimated at 90.7%. Obviously, as a result of the fading of the numbers on tags (and probably the loss of the tags themselves), this estimate is a conservative minimum survival rate. The true survival is likely to be somewhat higher. These survival estimates are very similar to those reported for the Eurasian griffon where annual survival in the first 3 years was 85.8% (Sarrazin *et al.*, 1994), compared with 87.4% for second- and third-year birds in our study (we tagged free-flying birds; hence, we do not have estimates for first-year survival). Sarrazin *et al.* (1994) also report an adult annual survival estimate of 98.7% compared with our 99.9%; both these estimates for adult survival are exceptionally high. It should be noted, however, that our estimate of adult survival was based on seven tagged birds. Future studies would do well to estimate adult survival based on a larger sample of birds. Piper, Boshoff & Scott (1999) report slightly lower annual survival estimates for subadult Cape vultures of 42.3% for first-year birds and 79.3% for second- and third-year birds. Their lower values may be related to the fact that Piper, Boshoff & Scott (1999) based their estimates on tagged nestlings; furthermore, they were unable to estimate adult survival owing to tag loss. These three studies of three different *Gyps* vulture species on two different continents confirm that these birds have very high survival rates, further underscoring the point that mortality of adult vultures will lead to rapid population declines. In this regard, the high mortality of adult vultures reported from East Africa (Kendall & Virani, 2012) is particularly alarming.

The estimated population size of birds visiting Moholoholo in this study was 921 individuals, but with a very high standard error. The total number of African white-backed vultures has been estimated for the Kruger National Park as 2048 birds (Kemp *et al.*, 2001), and based on aerial surveys of nests, we estimated 624 pairs of African white-backed vultures to be breeding in 2011. Using the latter figure and the survival estimates for the various age classes presented in this paper (in addition using a fledging success of 0.6 (Kemp & Kemp, 1975; Monadjem 2001), and a survival rate of 0.42 for first-year birds (Piper, Boshoff & Scott, 1999)) we calculate a resident population of 1697 adults, subadults and juveniles. This figure is based on the following assumptions that: immigration equals emigration, birds breed in their 6th year, and that 15% of pairs do not attempt to breed in any one year (see Results). Furthermore, this estimate only relates to the breeding population within Kruger National Park itself. There are further breeding populations in adjacent protected areas within the Greater Kruger National Park, for example, Timbavati and Klaserie reserves (Tarboton & Allan, 1984), Gona-re-Zhou National Park, Zimbabwe (Mundy *et al.*, 1992) and probably the Limpopo National Park in Mozambique (Parker, 1999). Hence, the population of African white-backed vultures in the Greater Kruger National Park is clearly higher than the estimate derived from MARK of 921. Therefore, not all birds within the Greater Kruger National Park are actually visiting Moholoholo. This is supported by the distribution of resightings, which come from only a portion of the Greater Kruger National Park. The map in Fig. 2 shows that resightings of tagged birds predominantly came from the southern half of the Greater Kruger National Park.

A very high proportion of the resightings (96%) were from the Moholoholo vulture restaurant which may have implications for the conservation of this species. The effects of vulture restaurants on this species are currently unknown, and future studies would do well to investigate this relationship. Our high survival estimates suggest that the African white-backed vultures inhabiting the Greater Kruger National Park were not being impacted by unnatural mortality factors (such as poisoning and power line collisions) to any great extent during this study. Hence, our results may be important as baselines for future studies in the area or elsewhere in Africa where these vultures are undergoing rapid declines.

Acknowledgements

We would like to thank Brian Jones, the staff and volunteers at the Moholoholo Rehabilitation Centre for their assistance during the capture and tagging of the vultures at the Centre. Their dedication and diligence in recording and reporting all sightings of tagged vultures is also acknowledged. The support of SANParks and the other associated private nature reserves in the Greater Kruger National Park with regard to the reporting of sightings is also appreciated. The individual members of the public who contributed information and images of resighted birds are also thanked for their support. Leigh Potter, Scott Ronaldson and our pilots, Charles Thompson and Grant Knight, are thanked for assistance with the aerial surveys.

References

Anderson, M.D. (2000) African Whitebacked Vulture. In: The Eskom Red DataBook of Birds of South Africa, Lesotho and Swaziland (Ed. K.N. Barnes). BirdLife South Africa, Johannesburg,South Africa.

Anderson, D.R., Burnham, K.P. & White, G.C. (1985) Problems in estimating age-specific survival rates from recovery data of birds ringed as young. *J. Anim. Ecol.* **54**, 89–98.

Bamford, A.J., Monadjem, A. & Hardy, I.C.W. (2009a) Nesting habitat preference of the African white-backed vulture *Gyps africanus* and the effects of anthropomorphic disturbance. *Ibis* **151**, 51–62.

Bamford, A.J., Diekmann, M., Monadjem, A. & Hardy, I.C.W. (2009b) Development of non-explosive based methods for mass capture of vultures. *S. Afr. J. Wildlife Res.* **39**, 202–208.

Becker, N., Choresh, Y., Bahat, O. & Inbar, M. (2009) Economic analysis of feeding stations to preserve an endangered species: the case of the griffon vulture (*Gyps fulvus*) in Israel. *J. Nature Conserv.* **17**, 199–211.

Botha, A. (2007) A review of colour-marking techniques used on vultures in southern Africa. *Vulture News* **56**, 52–63.

Burnham, K.P. & Anderson, D.R. (2002) Model selection and multimodel inference. A Practical Information-Theoretic Approach, 2nd edn. Springer-Verlag, New York, USA.

Diekmann, M., Scott, A., Scott, M. & Diekmann, J. (2004) Capture and fitting of satellite- and radiotelemetry equipment onto Cape griffon *Gyps coprotheres*, African white-backed *Gyps africanus* and lappet-faced *Torgos tracheliotos* vultures in the Waterberg area, Namibia, in 2004. *Vult News* **51**, 34–45.

Dowsett, R.J. & Dowsett-Lemaire, F. (1993) A contribution to the distribution and taxonomy of Afrotropical and Malagasy birds. Tauraco Research Report 5. 389 pp.

Gertenbach, W.P.D. (1983) Landscapes of the Kruger National Park. *Koedoe* **26**, 9–121.

Gilbert, M., Watson, R.T., Virani, M.Z., Oaks, J.L., Ahmed, S., Chaudry, M.J.I., Arshad, M., Mahmood, S., Ali, A. & Khan, A.A. (2006) Rapid population declines and mortality clusters in three Oriental white-backed vulture *Gyps bengalensis* colonies in Pakistan due to declofenac poisoning. *Oryx* **40**, 388–399.

Grande, J.M., Serrano, D., Tavecchia, G., Carrete, M., Ceballos, O., Díaz-Delgado, R., Tella, J.L. & Donázar, J.A. (2009) Survival in a long-lived territorial migrant: effects of life-history traits and ecological conditions in wintering and breeding areas. *Oikos* **118**, 580–590.

Green, R.E., Newton, I., Shultz, S., Cunningham, A.A., Gilbert, M., Pain, D.J. & Prakash, V. (2004) Diclofenac Poisoning as a Cause of Vulture Population Declines across the Indian Subcontinent. *J. Appl. Ecol.* **41**, 793–800.

IUCN 2012. IUCN Red List of Threatened Species. Version 2012.1. Available from: www.iucnredlist.org. Downloaded on 25 June 2012.

Kemp, A.C. & Kemp, M.I. (1975) Observations on the White-backed Vulture *Gyps africanus* in the Kruger National Park, with notes on other avian scavengers. *Koedoe* **18**, 51–68.

Kemp, A.C., Heroldt, I., Whyte, I. & Harrison, J. (2001) Birds of the two largest parks in South Africa: a method to generate estimates of population size for all species and assess their conservation ecology. *S. Afr. J. Sci.* **97**, 393–403.

Kendall, C.J. & Virani, M.Z. (2012) Assessing mortality of African vultures using wing tags and GSM-GPS transmitters. *J. Raptor Res.* **46**, 135–140.

Lebreton, J.D. & Clobert, J. (1991) Bird population dynamics, management and conservation: The role of mathematical modelling. In: Bird population Studies: Relevance to Conservation and Management (Eds C.M. Perrins, J.D. Lebreton and G.J.M. Hirons). Oxford Univ. Press, Oxford. pp 105–125.

Monadjem, A. (2001) Observations on the African White-backed Vulture nesting at Mlawula Nature Reserve, Swaziland. *Vulture News* **45**, 3–10.

Monadjem, A. & Garcelon, D.K. (2005) Nesting distribution of vultures in relation to land use in Swaziland. *Biodivers. Conserv.* **14**, 2079–2093.

Mundy, P.J., Butchart, D., Ledger, J.A. & Piper, S.E. (1992) The Vultures of Africa. Acorn Books & RusselFriedman Books, Randburg & Halfway House, South Africa.

Oaks, J.L., Gilbert, M., Virani, M.Z., Watson, R.T., Meteyer, C.U., Rideout, B.A., Shivaprasad, H.L., Ahmed, S., Chaudry, M.J.I., Arshad, M., Mahmood, S., Ali, A. & Khan, A.A. (2004) Diclofenac residues as the cause of population decline of vultures in Pakistan. *Nature* **427**, 630–633.

Oatley, T.B., Oschadleus, H.D., Navarro, R.A. & Underhill, L.G. (1998) Review of Ring Recoveries of Birds of Prey in Southern Africa: 1948–1998. Avian Demography Unit, University of Cape Town, South Africa.

Pain, D.J., Bowden, C.G.R., Cunningham, A.A., Cuthbert, R., Das, D., Gilbert, M., Jakati, R.D., Jhala, Y., Khan, A.A., Naidoo, N., Oaks, J.L., Parry-Jones, J., Prakash, V., Rahmani, A., Ranade, S.P., Baral, H.S., Senacha, K.R., Saravanan, S., Shah, N., Swan, G., Swarup, D., Taggart, M.A., Watson, R.T., Virani, M.Z., Wolter, K. & Green, R.E. (2008) The race to prevent the extinction of SouthAsian vultures. *Bird Conserv Int.* **18**, S30–S48.

PARKER, V. (1999) The Atlas of the Birds of Sul Do Save, Southern Mozambique. Avian Demography Unit, University of Cape Town, Cape Town.

PIPER, S.E., BOSHOFF, A.F. & SCOTT, H.A. (1999) Modelling survival rates in the Cape Griffon *Gyps coprotheres*, withemphasis on the effects of supplementary feeding. *Bird Study* **46**, S230–S238.

PIPER, S.E., MUNDY, P.J. & LEDGER, J.A. (1981) Estimates of survival in the Cape Vulture, *Gyps coprotheres*. *J. Anim. Ecol.* **50**, 815–825.

SARRAZIN, F., BAGNOLINI, C., PINNA, J.L., DANCHIN, E. & CLOBERT, J. (1994) High survival estimates of griffon vultures (*Gyps fulvusfulvus*) in a reintroduced population. *Auk* **111**, 853–862.

TARBOTON, W.R. & ALLAN, D. (1984) The Status and Conservation of Birds of Prey in the Transvaal. Transvaal Museum, Pretoria.

THIOLLAY, J.-M. (2006) The decline of raptors in West Africa: long-term assessment and the role of protected areas. *Ibis* **148**, 240–254.

THIOLLAY, J.-M. (2007) Raptor population decline in West Africa. *Ostrich* **78**, 405–413.

VIRANI, M., KIRUI, P., MONADJEM, A., THOMSETT, S. & GITHIRU, M. (2010) Nesting status of African White-backed Vultures *Gyps africanus* in the Masai Mara National Reserve, Kenya. *Ostrich* **81**, 205–209.

VIRANI, M.Z., KENDALL, C., NJOROGE, P. & THOMSETT, S. (2011) Major declines in the abundance of vultures and other scavenging raptorsin and around the Masai Mara ecosystem, Kenya. *Biol. Conserv.* **144**, 746–752.

WHITE, G.C. (2008) Closed population estimation models and their extensions in Program MARK. *Environ. Ecol. Stat.* **15**, 89–99.

WHITE, G.C. & BURNHAM, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**, S120–S138.

(*Manuscript accepted 10 July 2012*)

doi: 10.1111/aje.12009

