Carrion ecology modelling for vulture conservation: are vulture restaurants needed to sustain the densest breeding population of the African white-backed vulture?

A. Kane[1,2], A. L. Jackson[1,2], A. Monadjem[3,4], M. A. Colomer[5] & A. Margalida[6,7]

1 Department of Zoology, School of Natural Sciences, Trinity College Dublin, Dublin, Ireland
2 Centre for Biodiversity Research, Trinity College Dublin, Dublin, Ireland
3 All Out Africa Research Unit, Department of Biological Sciences, University of Swaziland, Kwaluseni, Swaziland
4 Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, Pretoria, South Africa
5 Department of Mathematics, University of Lleida, Lleida, Spain
6 Department of Animal Production (Division of Wildlife), University of Lleida, Lleida, Spain
7 Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Bern, Switzerland

Abstract

As obligate scavengers, vultures are entirely dependent on carrion resources. In this study, we model the carrion ecology of an ecosystem in Swaziland which is home to the densest breeding population of the African white-backed vulture *Gyps africanus*. We collected data on life-history parameters of the avian scavenging guild of the area as well as the potential food available from the ungulate fauna. Using novel Population Dynamics P-Systems, we show that carrion provided by wild ungulates biomass is currently enough to sustain this vulture species. However, in light of the forecasted population increases, food will become a limiting factor. We discuss the significance of mass closure of supplementary feeding stations in Swaziland which now forces these birds to forage farther afield endangering them to poisoning events. We put these results in the context of biomass management and suggest conservation actions to secure the viability of vulture populations and the important ecosystem services they provide.

Introduction

Carrion ecology examines the link between the organic material provided by animal carcasses and ecosystem functioning (Barton *et al.*, 2013). Carcasses are an ephemeral resource and among members of the scavenger community, avian scavengers are probably the group with the most evident adaptive traits to utilize it (DeVault, Rhodes & Shivik, 2003; Wilson & Wolkovich, 2011). Indeed, the *Gyps* vultures are entirely dependent on dead animal biomass (Mundy *et al.*, 1992). Given the patchiness of carrion, vultures are under selection pressures to be as energetically conservative as possible in order to exploit such an unpredictable food (Ruxton & Houston, 2002, 2004).

In sub-Saharan Africa, alongside poisoning, food reduction and habitat loss are the key threats to the avian scavenging guild (Monadjem *et al.*, 2003). Thus, the practice of providing supplementary resources is a common conserva-

tion tool (Piper, Boshoff & Scott, 1999; Piper, 2005). As these 'vulture restaurants' or 'feeding stations' can make carrion more predictable in space and time (Oro *et al.*, 2008), there are implications for the ecosystem services and foraging behaviour of the species affected (Deygout *et al.*, 2010; Margalida *et al.*, 2013; Monsarrat *et al.*, 2013). Although these issues have important management and conservation implications, studies focused on the effects of food shortage on vulture species have not been documented until recent times (Piper, 2005; Camiña & Montelío, 2006; Zuberogoitia *et al.*, 2010).

The African white-backed vulture (AWBV) population of Swaziland is an interesting case study for examining the effect of potential fluctuating food availability given that, at an estimated 300 pairs, it represents the densest nesting population of the birds in the world (Monadjem & Garcelon, 2005). Historical data show that this AWBV population has increased during the latter part of the 20th

century (Monadjem *et al.*, 2003). In one conservation area (Mkhaya), the species founded a nesting population in the 1980s which grew to 15 pairs in the late 1990s (Monadjem *et al.*, 2003). Supplementary feeding sites have also been established in the country, but of seven vulture restaurants that were operational in Swaziland at the turn of the century only one is currently operational. These sites would have provided the vultures with a significant proportion (40%) of their annual food requirements (Monadjem, 2003). This represents an apparent paradox because the population of vultures has not declined in the face of this reduction in available food (Monadjem & Garcelon, 2005). Thus, we hypothesized that there are enough carcasses from wild fauna to sustain the AWBV population of Swaziland. Our aim was to determine the energy balance for these birds and use this information to inform conservation measures.

In order to address this question, we needed to determine where the birds forage, how much carrion they require and how much naturally occurring food is available to them. To achieve this, we assessed the potential foraging movements of the AWBV population, estimated food availability for the population in Swaziland and modelled whether current trophic resources are theoretically sufficient to maintain their population.

Materials and methods

Study area and species

The Hlane-Mlawula-Mbuluzi reserve network in Swaziland contains the majority (at least 202 nests) of the country's AWBV breeding population (Monadjem & Garcelon, 2005) (Fig. 1). Located in the east of Swaziland, the area is characterized as lowveld savanna (Acocks, 1988) with *Acacia* providing suitable nesting trees for the vultures present (Monadjem & Garcelon, 2005). The rest of the nesting birds are known from other non-contiguous conservation areas (*c*. 12 nests at Mkhaya) and protected cattle ranches (19 nests at the Big Bend Conservancy and six at Inyoni nyoni Yami Swaziland Irrigation Scheme) (Monadjem & Garcelon, 2005). AWBVs appear to actively avoid unprotected government ranches in the country, but their reason for doing so is unclear (Monadjem & Garcelon, 2005). In total, Swaziland is home to six avian scavenger species (obligate and facultative) which take a considerable portion of their diet as carrion. The majority of the large ungulates in Swaziland also live in this Hlane-Mlawula-Mbuluzi reserve (Monadjem *et al.*, 2003) (Table 1).

Model parameters for avian scavengers and ungulate carrion

We first determined the potential foraging range of the vultures to see which habitats harbouring natural fauna are available to the birds. We used an extension of the central place forager theory known as the foraging radius concept

which was developed by Pennycuick (Sinclair & Norton-Griffiths, 1995). The concept states that every animal is energetically constrained in terms of the spatial range they can cover while foraging (Sinclair & Norton-Griffiths, 1995). Factors such as cost of movement, basal metabolic rate, presence of dependent young, etc., contribute to the overall cost of foraging (Ruxton & Houston, 2002). Many animals must return to a site after they forage every day (as central place foragers). The idea is especially applicable to birds during the breeding season where the origin from which they range is the nest. After foraging, the adults must return to incubate the egg, relieve their mate or feed their young. The following is a model describing the energy budget of the closely related Ruppell's vulture *Gyps rueppellii* which was used to estimate the foraging radius of that species (Ruxton & Houston, 2002):

$$r = \frac{Qc + Qdt - T\left(E_{ma} + \dfrac{E_{mc}}{2}\right)}{2k + \dfrac{2Qd}{V}}.$$

We employed the same model and applied values from our focal species, the AWBV, where available. Q is the energy density of the carrion (5.2×10^{-6} J) (Ruxton & Houston, 2002), c is the bird's crop capacity (1.2 kg) (Houston & Cooper, 1975), d is the digestion rate (0.055 kg h^{-1}) (Ruxton & Houston, 2002), T is the foraging cycle (48 h) and refers to the fact that the parents take turns to forage with one remaining on the nest each day (Mundy *et al.*, 1992), k is the flight cost (2.0 J m^{-1}) (Pennycuick, 1972), V is the flight speed (45 km h^{-1}) (Pennycuick, 1972; Tucker, 1988) and r is the foraging radius. If values for the AWBV were not available, we used other *Gyps* species as a close approximation, in this case for t, the foraging time (8 h) (Xirouchakis, 2007); E_{ma} and E_{mc} are the adult and chick's metabolic rate respectively (24 and 42 W) (Houston, 1976; Sinclair & Norton-Griffiths, 1995). The energy requirements were calculated using hand-reared individuals but Houston (1976) argues the costs between wild and captive birds are similar owing to the low energies that are required for flight.

The food requirements of individual AWBV have been described before (Houston, 1976; Mundy *et al.*, 1992). We compiled data on both the adult and nestling energetic requirements for Swaziland using these studies and followed the same approach for the other species in the Swaziland avian scavenging guild. We also collected data on relevant life-history traits such as age at sexual maturity and longevity (see Supporting Information Table S1A–F) (Pennycuick, 1976; Mundy, 1982; Brown, 1991; Mundy *et al.*, 1992; Monadjem *et al.*, 2003, 2012).

To determine carrion availability, we collected the most recent ungulate population data covering all of Swaziland (Monadjem *et al.*, 2003), life-history values from the PanTHERIA database (Jones *et al.*, 2009) and estimates of adult and infant mortality (Sinclair & Norton-Griffiths, 1995). (More details can be found in the Supporting Information – 'Details of Model Assumptions'.)
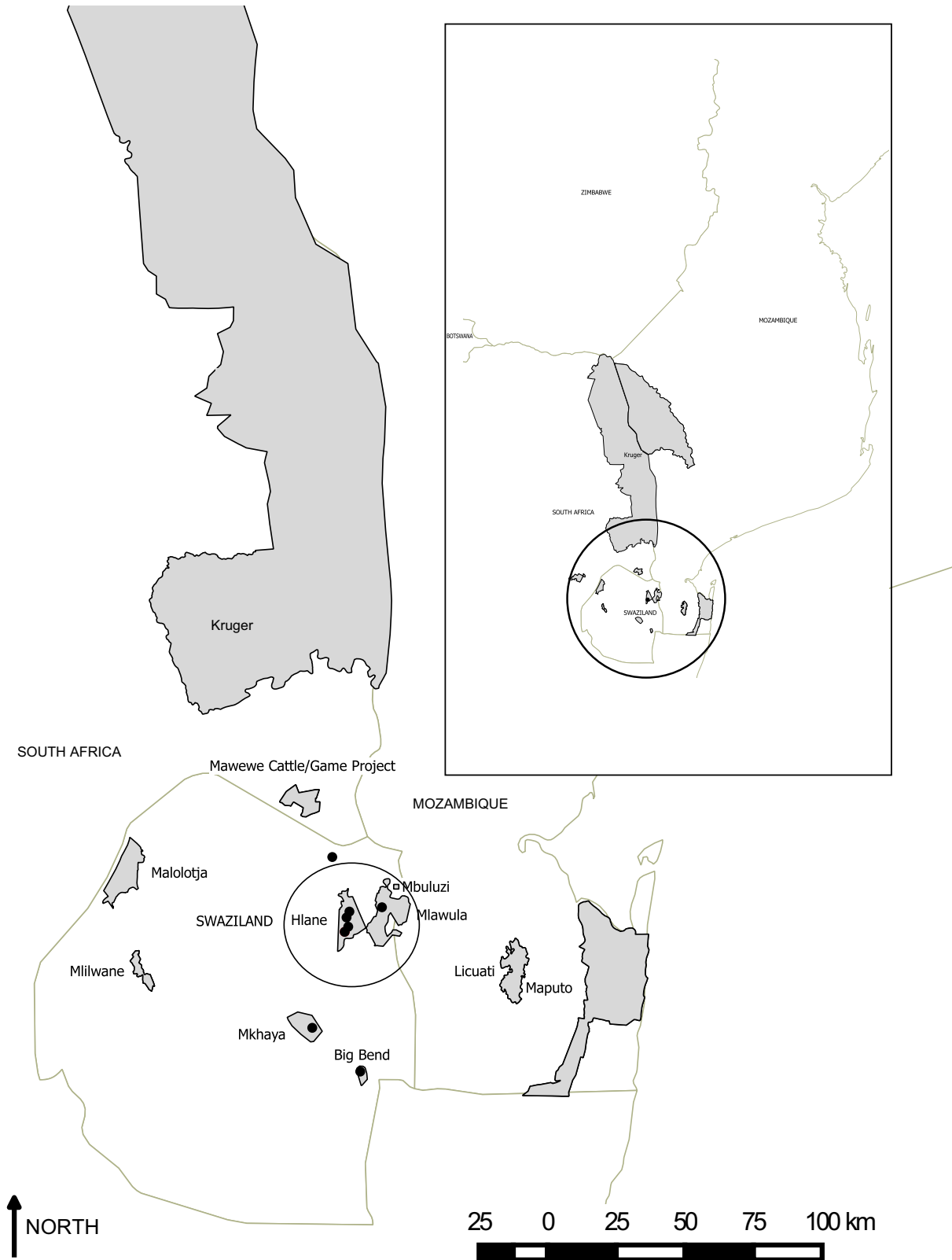
Figure 1 Foraging radius (45 km) of African white-backed vultures when they have dependants on the nest. The points represent recorded nesting sites with Hlane as the origin of the circles. Some major national parks are highlighted. The inset shows the possible feeding range (260 km) when there are no young but the bird is still nesting in Swaziland.

Table 1 Identity, number of species and average carrion provided per year of the ungulate population of Swaziland

Species	Initial population size (individuals)	Average carrion per year (kg)	Percentage of total carrion
Aepyceros melampus	16 500	48 233.35	32.92
Connochaetes taurinus	1700	18 666.35	12.74
Equus burchelli	1500	13 276.95	9.06
Phacochoerus aethiopicus	2300	12 791.8	8.73
Loxodonta africana	40	11 439.45	7.81
Tragelaphus strepsiceros	1300	10 039.95	6.85
Ceratotherium simum	50	8570.25	5.85
Giraffa camelopardalis	80	4909.35	3.35
Tragelaphus angasii	1000	4231.5	2.89
Kobus ellipsiprymnus	260	4174.25	2.85
Hippopotamus amphibius	25	3976.75	2.71
Syncerus caffer	40	1478.4	1.01
Taurotragus oryx	40	1284.95	0.88
Tragelaphus scriptus	250	700.9	0.48
Sylvicapra grimmia	550	563.65	0.38
Redunca arundinum	120	480.3	0.33
Hippotragus niger	20	419.4	0.29
Redunca fulvorufula	200	364.65	0.25
Hippotragus equinus	7	364.5	0.25
Damaliscus lunatus	16	208.55	0.14
Oreotragus oreotragus	200	122.85	0.08
Raphicerus campestris	140	95.15	0.06
Cephalophus natalensis	80	55.05	0.04
Ourebia ourebi	50	51.9	0.04

Population dynamics P system model

Using this information, we developed a population dynamics P system (PDP) model (Colomer, Margalida & Pérez-Jiménez, 2013). This integrated data on food availability, food requirements and population dynamics of the avian scavenging guild and the ungulate populations of Swaziland (Fig. 1 and Supporting Information) to determine if carcass availability could meet the demands of the AWBV population over a 20-year period [AWBVs have been recorded as living for 20 years (Flower, 1938)]. PDP models are computational methods that are analogous to the machinery of cells (Colomer *et al.*, 2013). The analogy of a PDP system to a real ecosystem has been drawn before (Colomer *et al.*, 2011, 2013; Margalida, Colomer & Sanuy, 2011) and serves well to illustrate the intuition behind this relatively new method. The cells of the model correspond to the physical space of the environment. Animals (which along with things such as resources, are represented by model 'objects') will feed, reproduce, develop, etc., within an environment which is accounted for by a set of mathematical rules describing these behaviours in the model. Just as animals can move between different areas when circumstances become unfavourable (e.g. food shortages), their simulated counterparts can migrate between the different spatial environments of the model (e.g. between South Africa and Swaziland). The membranes within the cells of an environment separate out specific processes that are applied to the objects in the model (e.g. the different rules associated with different seasons) (see Supporting Information 'PDP Model Components').

The advantage of this approach is that PDP models can integrate a large volume of information and compute the output of a large number of species in parallel and in a relatively short time. In addition, PDP models have been developed and applied to similar ecosystems before (Margalida & Colomer, 2012).

There are two environments in our model delimited by the foraging radius of the birds when they are on the nest as defined in our foraging radius calculations. So when the reduced foraging radius of the birds is no longer applicable, the birds are able to forage in the new environment where food is not limiting (Fig. 1). This restricts the birds to game reserves in Swaziland when they have a reduced foraging potential. A bird outside of the breeding season could range hundreds of kilometres on a single foraging trip. A year in the model was divided into four temporal periods: Period 1 = July–August, Period 2 = September–October, Period 3 = November–April and Period 4 = May–June. These periods reflected differences in food availability, foraging ranges and food requirements (this is described in Table S3 in the Supporting Information).

Results

Foraging radius

During the period of nestling dependency, the foraging radius of the breeding vultures is estimated at 45 km (Fig. 2). If we remove the cost of provisioning the chick, it gives a value of approximately 260 km. Thus, the foraging
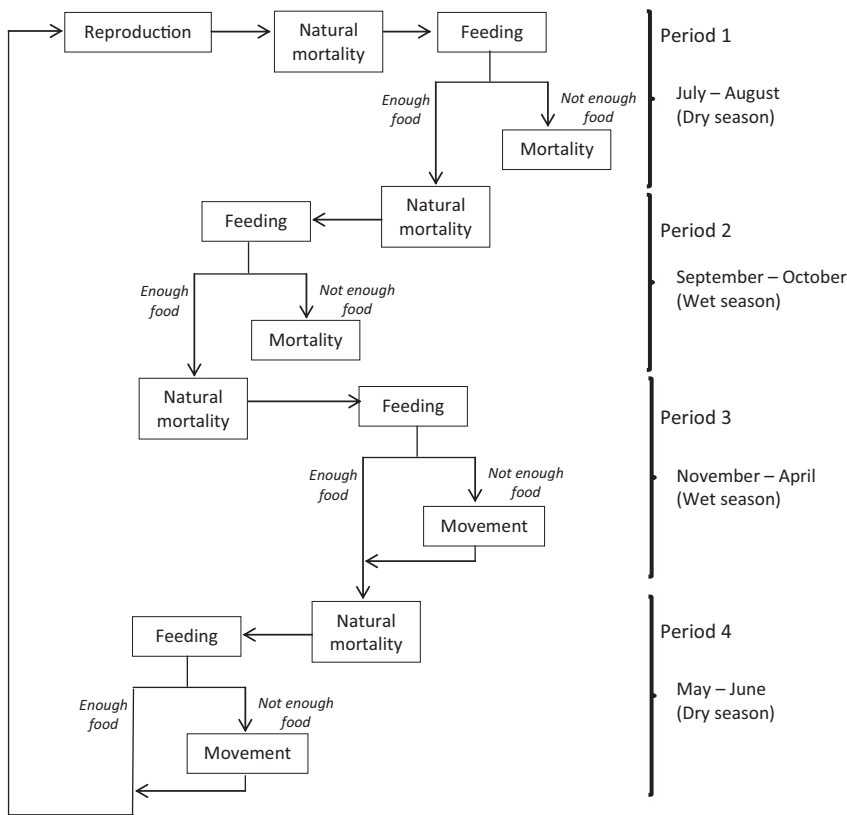
Figure 2 Flow diagram representing the changes in the status of the avian scavengers through time (Periods 1–4). The italicized text show conditionals for food availability which determine the path the birds can take. If we start at the 'Reproduction' stage, at the upper left hand side, this represents the point at which the birds have their young on the nest. They will undergo 'Natural mortality' during this period and 'Feeding'. If there is enough food during this time, they can progress to period 2; otherwise they perish and so on through the year until they reproduce again. The 'Movement' stages indicate points whereby the birds can leave Swaziland because they are not constrained by the presence of young.

radius the vultures have during the time of nestling dependence restricts them to foraging in the national parks of Swaziland.

PDP model

According to our model, most of the biomass available to the scavengers is provided by impala *Aepyceros melampus* (33%), blue wildebeest *Connochaetes taurinus* (13%) and zebra *Equus burchelli* (9%) with the remaining 21 species contributing the remaining carrion (Table 1). Initially, only period 3 (from November–April) has insufficient food for the scavenging guild but eventually as the scavenger populations grow periods 1 (July–August) and 2 (September–October) see a net food deficit at year 5 and 13 respectively. Period 4 (May–June) also develops a decline, although at a shallower rate (see Fig. 3). Period 3, which never sees enough carrion to sustain the scavengers, is a time when the birds can forage outside of Swaziland. In general, the avian scavengers see an increase in their number over the 20-year run of the model (although note that stochastic effects see the single pair of Lappet-faced vultures go extinct in the system) (Fig. 4).

Discussion

The key prediction from our model is that the carrion of Swaziland is sufficient to cover the energetic requirements of the current AWBV population and most of the other scavenging avifauna (Fig. 4), but only for the time being (Fig. 3). The trend of the energy balance makes it clear that, as vulture numbers rise, food will soon become a limiting factor. There is already a predicted net deficit in energy balance for six months of the year, from November to April (Fig. 4). Fortunately, this is a period during which the birds can forage outside of Swaziland. However, this reduction in available food could force the birds to spend more time foraging outside of protected areas, increasing the risk of non-natural mortality factors, such as poisoning, with important consequences on population dynamics if adult survival is affected (Monadjem *et al.*, 2013).

The radius we obtained for the vulture foraging movements is consistent with values reported from the literature. For instance, the average movement recorded in the Serengeti was 51 km and in Kruger 34 km (Mundy *et al.*, 1992). A more recent study of immature AWBV showed a mean distance travelled per day of 33.39 km (Phipps *et al.*, 2013). It has been noted that, while nesting without a chick, the birds can fly over 240 km between the nest and a carcass and this is consistent with our value of 260 km (Houston & Cooper, 1975). Kruger National Park is almost 100 km from Hlane, the main site of the nesting birds, and smaller reserves such as Mawewe Cattle/Game Project are all in excess of the radius.

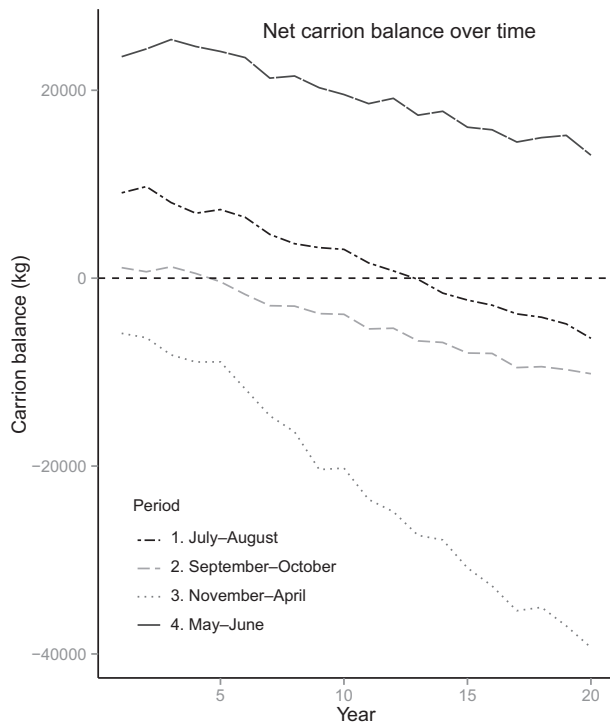These findings suggest further intervention and modification of existing strategies will be required. Vulture

Figure 3 Carrion balance across time in the different periods of the year. The horizontal bar represents the point at which the demands of the avian scavenging guild are no longer met by the carrion provided by wildlife in Swaziland. Periods 1 and 2 are the life stages when young are present and food requirements are higher as a result.

Figure 4 Number of pairs of avian scavengers living in Swaziland across time. All species, except the Lappet-faced vulture, see a population increase because of the amount of wild carrion available. The one extinction occurs owing to its tiny initial population size. The bottom panel shows the African white-backed vulture trend separately for reasons of clarity because of its much larger population size.

restaurants could be established and stocked more frequently during times of food deficiency. Although there are a number of problems associated with supplying supplementary food to wild populations, such as a conditioned dependence on supplemental food (Robb *et al.*, 2008), a well-managed vulture restaurant could minimize these issues while maximizing the benefits. For instance, Monsarrat *et al.* (2013), in their study of *Gyps fulvus*, showed that 'feeding stations were particularly used when resources were scarce (summer) or when flight conditions were poor (winter), limiting long-ranging movements'. Supplementary feeding can minimize the risk of poisoning (increasing survival) that follows from species foraging outside of protected areas which has been documented in other vulture species (Oro *et al.*, 2008). Although our model suggests that AWBVs in Swaziland will see an increase in their population for a while, the temporal food shortages identified could reduce their breeding output during this period of growth. In Europe, for example, after the outbreak of bovine spongiform encephalopathy in 2001, carcasses were destroyed in authorized plants which reduced the amount of food available to the vultures (Margalida *et al.*, 2010). A long-term study on bearded vultures *Gypaetus barbatus* showed this reduction provoked a delay in laying dates, a regressive trend in clutch size, breeding success and survival following this policy change (Margalida, Colomer & Oro, 2014).
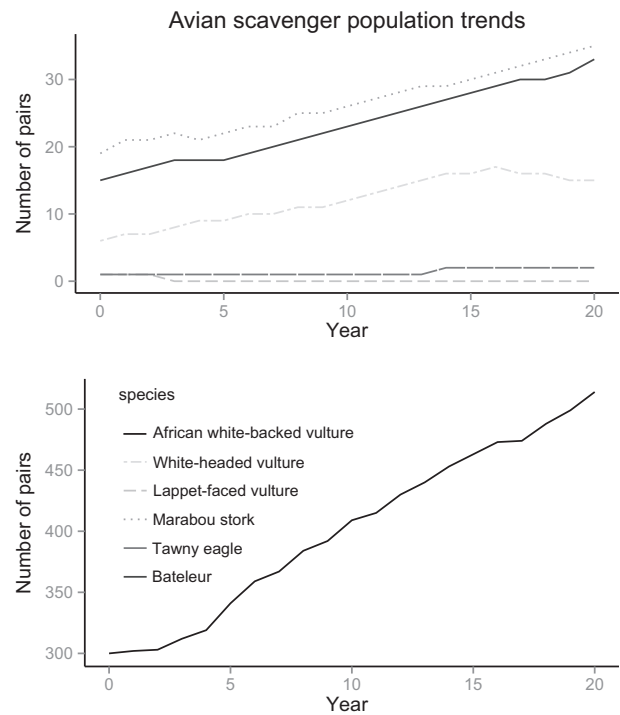
Swaziland seems well placed to act as a habitat for a greater number of AWBVs than that of the current population. With the species on the decline globally, it is incumbent on us to secure this valuable population. By ensuring that there is no deficit of carrion at any stage of the year (Fig. 3), we would give the birds the best chance to flourish in this area. Indeed, it could act as a source population for other suitable areas in the region as its population increases.

There is another advantage to creating a long-term vulture restaurant in that it would create the opportunity to capture and tag these birds. High resolution data on the foraging behaviour of this population specifically and AWBVs in general are lacking. We know little of their age-class structure and whether other vagrant populations visit Swaziland without nesting in the county (Monadjem *et al.*, 2003). Tracking data would improve our knowledge about these issues allowing managers and policymakers to adopt more objective decisions based on the evidence.

The value of theoretical modelling, such as the PDP P systems, is also underscored by the results generated in this study and others like it (Margalida *et al.*, 2011; Margalida & Colomer, 2012). We should note that any model is only as good as the data used to parameterize it. Consequently, basic and up to date biological data are of utmost importance if we are to derive accurate predictions. These

methods are another tool for stakeholders to use in identifying threats and solutions to conserving the target species.

The conservation implications obtained with this theoretical approach is that the carrying capacity of AWBV in Swaziland is reaching maximum values according to natural food provided by the ecosystem. The dependence of the birds on food resources provided by neighbouring areas shows the importance of international agreements for conservation and the coordination of management actions (Lambertucci *et al.*, 2014). The establishment of well-managed vulture restaurants in Swaziland should be seriously considered.

Acknowledgements

References

Acocks, J.P.H. (1988). *Veld types of South Africa*. Pretoria: Botanical Research Institute.

Barton, P.S., Cunningham, S.A., Lindenmayer, D.B. & Manning, A.D. (2013). The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. *Oecologia* **171**, 761–772.

Brown, C. (1991). Declining martial *Polemaetus bellicosus* and tawny *Aquila rapax* eagle populations and causes of mortality on farmlands in central Namibia. *Biol. Conserv.* **56**, 49–62.

Camiña, A. & Montelío, E. (2006). Griffon vulture *Gyps fulvus* food shortages in the Ebro Valley (NE Spain) caused by regulations against bovine spongiform encephalopathy (BSE). *Acta Ornithol.* **41**, 7–13.

Colomer, M., Margalida, A., Sanuy, D. & Pérez-Jiménez, M.J. (2011). A bio-inspired computing model as a new tool for modeling ecosystems: the avian scavengers as a case study. *Ecol. Model.* **222**, 33–47.

Colomer, M.À., Margalida, A. & Pérez-Jiménez, M.J. (2013). Population Dynamics P System (PDP) Models: a standardized protocol for describing and applying novel bio-inspired computing tools. *PLoS ONE* **8**, e60698.

DeVault, T.L., Rhodes, O.E. Jr. & Shivik, J.A. (2003). Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* **102**, 225–234.

Deygout, C., Gault, A., Duriez, O., Sarrazin, F. & Bessa-Gomes, C. (2010). Impact of food predictability on social facilitation by foraging scavengers. *Behav. Ecol.* **21**, 1131–1139.

Flower, S. (1938). Further notes on the duration of life in animals.-IV. Birds. By Major STANLEY SMYTH FLOWER, O.B.E., F.L.S., F.Z.S. *Proc. Zool. Soc. Lond.* **A108**, 195–235.

Houston, D. (1976). Breeding of the White-backed and Ruppell's griffon vultures, *Gyps africanus* and *G. rueppellii. Ibis* **118**, 14–40.

Houston, D.C. & Cooper, J. (1975). The digestive tract of the whiteback griffon vulture and its role in disease transmission among wild ungulates. *J. Wildl. Dis.* **11**, 306–313.

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L., Safi, K., Sechrest, W., Boakes, E.H., Carbone, C., Connolly, C., Cutts, M.J., Foster, J.K., Grenyer, R., Habib, M., Plaster, C.A., Price, S.A., Rigby, E.A., Rist, J., Teacher, A., Bininda-Emonds, O.R.P., Gittleman, J.L., Mace, G.M. & Purvis, A. (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* **90**, 2648.

Lambertucci, S.A., Alarcón, P., Hiraldo, F., Sanchez-Zapata, J.A., Blanco, G. & Donázar, J.A. (2014). Apex scavenger movements call for transboundary conservation policies. *Biol. Conserv.* **170**, 145–150.

Margalida, A. & Colomer, M.À. (2012). Modelling the effects of sanitary policies on European vulture conservation. *Sci. Rep.* **2**, 753.

Margalida, A., Donazar, J.A., Carrete, M. & Sánchez-Zapata, J.A. (2010). Sanitary versus environmental policies: fitting together two pieces of the puzzle of European vulture conservation. *J. Appl. Ecol.* **47**, 931–935.

Margalida, A., Colomer, M.À. & Sanuy, D. (2011). Can wild ungulate carcasses provide enough biomass to maintain avian scavenger populations? An empirical assessment using a bio-inspired computational model. *PLoS ONE* **6**, e20248.

Margalida, A., Carrete, M., Hegglin, D., Serrano, D., Arenas, R. & Donázar, J.A. (2013). Uneven large-scale movement patterns in wild and reintroduced pre-adult bearded vultures: conservation implications. *PLoS ONE* **8**, e65857.

Margalida, A., Colomer, M.À. & Oro, D. (2014). Man-induced activities modify demographic parameters in a long-lived species: effects of poisoning and health policies. *Ecol. Appl.* **24**, 436–444.

Monadjem, A. (2003). Nesting distribution and status of vultures in Swaziland. *Vulture News* **48**, 12–19.

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

Monadjem, A., Boycott, R.C., Parker, V. & Culverwell, J. (2003). *Threatened vertebrates of Swaziland: Swaziland red data book: fishes, amphibians, reptiles, birds*

and mammals, Ministry of Tourism, Environment and Communications.

Monadjem, A., Kane, A., Botha, A., Dalton, D. & Kotze, A. (2012). Survival and population dynamics of the Marabou Stork in an isolated population, Swaziland. *PLoS ONE* **7**, e46434.

Monadjem, A., Wolter, K., Neser, W. & Kane, A. (2013). Effect of rehabilitation on survival rates of endangered Cape vultures. *Anim. Conserv.* **17**, 52–60.

Monsarrat, S., Benhamou, S., Sarrazin, F., Bessa-Gomes, C., Bouten, W. & Duriez, O. (2013). How predictability of feeding patches affects home range and foraging habitat selection in avian social scavengers? *PLoS ONE* **8**, e53077.

Mundy, P.J. (1982). *The Comparative Biology of Southern African Vultures*. Johannesburg: Vulture Study Group.

Mundy, P.J., Butchart, D., Ledger, J. & Piper, S. (1992). *The Vultures of Africa*. London: Academic Press.

Oro, D., Margalida, A., Carrete, M., Heredia, R. & Donázar, J.A. (2008). Testing the goodness of supplementary feeding to enhance population viability in an endangered vulture. *PLoS ONE* **3**, e4084.

Pennycuick, C. (1972). Soaring behaviour and performance of some East African birds, observed from a motor-glider. *Ibis* **114**, 178–218.

Pennycuick, C. (1976). Breeding of the lappet-faced and white-headed vultures (*Torgos tracheliotus* Forster and *Trigonoceps occipitalis* Burchell) on the Serengeti Plains, Tanzania. *Afr. J. Ecol.* **14**, 67–84.

Phipps, W.L., Willis, S.G., Wolter, K. & Naidoo, V. (2013). Foraging ranges of immature African white-backed vultures (*Gyps africanus*) and their use of protected areas in Southern Africa. *PLoS ONE* **8**, e52813.

Piper, S.E. (2005). Supplementary feeding programmes: how necessary are they for the maintenance of numerous and healthy vulture populations. Conservation and Management of Vulture Populations. Thessaloniki, Greece, 41–50.

Piper, S.E., Boshoff, A.F. & Scott, H.A. (1999). Modelling survival rates in the Cape Griffon *Gyps coprotheres*, with emphasis on the effects of supplementary feeding. *Bird Stud.* **46**, 230–238.

Robb, G.N., McDonald, R.A., Chamberlain, D.E. & Bearhop, S. (2008). Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Front. Ecol. Environ.* **6**, 476–484.

Ruxton, G. & Houston, D. (2002). Modelling the energy budget of a colonial bird of prey, the Ruppell's griffon vulture, and consequences for its breeding ecology. *Afr. J. Ecol.* **40**, 260–266.

Ruxton, G.D. & Houston, D.C. (2004). Obligate vertebrate scavengers must be large soaring fliers. *J. Theor. Biol.* **228**, 431–436.

Sinclair, A.R.E. & Norton-Griffiths, M. (1995). *Serengeti: dynamics of an ecosystem*. Chicago: University of Chicago Press.

Tucker, V.A. (1988). Gliding birds: descending flight of the white-backed vulture, *Gyps africanus*. *J. Exp. Biol.* **140**, 325–344.

Wilson, E.E. & Wolkovich, E.M. (2011). Scavenging: how carnivores and carrion structure communities. *Trends Ecol. Evol.* **26**, 129–135.

Xirouchakis, S.M. (2007). Seasonal and daily activity pattern in Griffon Vulture (*Gyps fulvus*) colonies on the island of Crete (Greece). *Ornis Fenn.* **84**, 39–46.

Zuberogoitia, I., Martínez, J.E., Margalida, A., Gómez, I., Azkona, A. & Martínez, J.A. (2010). Reduced food availability induces behavioural changes in Griffon vulture *Gyps fulvus*. *Ornis Fenn.* **87**, 52–60.

Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. A, B, C, D, E and F. Parameter values used in the model
Table S2. Parameters and definitions used in the model.
Table S3. A summary of the changes in ungulate mortality, vulture food requirements and foraging radius throughout the year and according to the periods considered.