



Terms and Conditions of Use of Digitised Theses from Trinity College Library Dublin

Copyright statement

All material supplied by Trinity College Library is protected by copyright (under the Copyright and Related Rights Act, 2000 as amended) and other relevant Intellectual Property Rights. By accessing and using a Digitised Thesis from Trinity College Library you acknowledge that all Intellectual Property Rights in any Works supplied are the sole and exclusive property of the copyright and/or other IPR holder. Specific copyright holders may not be explicitly identified. Use of materials from other sources within a thesis should not be construed as a claim over them.

A non-exclusive, non-transferable licence is hereby granted to those using or reproducing, in whole or in part, the material for valid purposes, providing the copyright owners are acknowledged using the normal conventions. Where specific permission to use material is required, this is identified and such permission must be sought from the copyright holder or agency cited.

Liability statement

By using a Digitised Thesis, I accept that Trinity College Dublin bears no legal responsibility for the accuracy, legality or comprehensiveness of materials contained within the thesis, and that Trinity College Dublin accepts no liability for indirect, consequential, or incidental, damages or losses arising from use of the thesis for whatever reason. Information located in a thesis may be subject to specific use constraints, details of which may not be explicitly described. It is the responsibility of potential and actual users to be aware of such constraints and to abide by them. By making use of material from a digitised thesis, you accept these copyright and disclaimer provisions. Where it is brought to the attention of Trinity College Library that there may be a breach of copyright or other restraint, it is the policy to withdraw or take down access to a thesis while the issue is being resolved.

Access Agreement

By using a Digitised Thesis from Trinity College Library you are bound by the following Terms & Conditions. Please read them carefully.

I have read and I understand the following statement: All material supplied via a Digitised Thesis from Trinity College Library is protected by copyright and other intellectual property rights, and duplication or sale of all or part of any of a thesis is not permitted, except that material may be duplicated by you for your research use or for educational purposes in electronic or print form providing the copyright owners are acknowledged using the normal conventions. You must obtain permission for any other use. Electronic or print copies may not be offered, whether for sale or otherwise to anyone. This copy has been supplied on the understanding that it is copyright material and that no quotation from the thesis may be published without proper acknowledgement.

The Ecology of Obligate Scavengers from Individual Behaviour to Population Dynamics

by

Adam Kane

B.Sc.(Hons), University College Dublin, 2007

M.Sc., Dublin City University, 2010

A thesis submitted in partial fulfillment of
the requirements for the degree of

Doctor of Philosophy

School of Natural Sciences
(Zoology)

Trinity College Dublin

January 2015

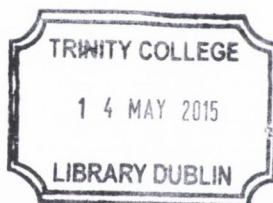
© Adam Kane, 2015

Declaration

I declare that this thesis has not been submitted as an exercise for a degree at this or any other university and it is, unless otherwise referenced, entirely my own work. I agree to deposit this thesis in the University's open access institutional repository or allow the library to do so on my behalf, subject to Irish Copyright Legislation and Trinity College Library conditions of use and acknowledgement.

Adam Kane

Adam Kane



Thesis 10490

Summary

Studies on vultures are on the rise, and just as well given the sharp declines in many of the 23 species. Indeed it seems these population crashes are responsible for this research boost. However, there remain obvious gaps in our knowledge when it comes to the world's only terrestrial example of vertebrate obligate scavengers. It has been suggested that a human aversion to carrion is one of the reasons scavengers are reviled by the public and understudied by science. Broadly, the following body of work is an attempt to fill in some of these gaps. To achieve this I use a variety of methods and look at a range of species. I start by giving a description of the impressive ranging abilities of one species, the Cape Vulture, in Southern Africa, and identify causes of variation in these home ranges. I then move to Kenya where I identify a producer-scrounger game occurring between the *Gyps* vultures and scavenging eagles of the area. I use a suite of empirical data and modelling approaches to show vultures use eagles in identifying the location of carcasses. The results of which underscore the importance of ecosystem-level management. Then in chapter 3, I collect data on the food required by the avian scavenging guild of Swaziland and use a novel method, namely population dynamics P systems, to ascertain if the wild fauna of the country can meet this need. Although sufficient for the time being carrion will soon become limiting and I advocate the creation of supplementary feeding sites in the country to counter this. Finally, I visit the Cretaceous Period where I use my understanding of modern day carrion ecology to explore a putative scavenger in *Tyrannosaurus rex*, the infamous carnivorous dinosaur. A proposed hypothesis that *T.rex* took on more carrion in its diet across ontogeny is shown to be false owing to the huge cost of movement as the animal grew.

Acknowledgements

The infamous 'they' warn that, with a bad supervisor, a PhD is a hellish experience. Thank God then for Andrew Jackson who made the previous three years of 'work' one of the most enjoyable periods of my life. The wonderful atmosphere of the zoology department certainly helped too. Luke McNally and Mafalda Viana guided me from my first year as the senior PhDs in the office. Deirdre McClean and Seán Kelly were my early morning catalysts whose mania ensured no Monday morning was ever a drudge. While Kevin Healy's cynicism and creativity complemented this well. The academic odd couple of Thomas Guillerme and Sive Finaly along with their supervisor Natalie Cooper were always there to help me get unstuck. Joe Colgan deserves mention for advertising the department in such an appealing light; I was encouraged to start a PhD given his experience (Alain Finn take note). All the other members of NERD club, I thank you for stimulating discussions.

In the field Ara Monadjem is owed a debt for preventing mine on more than one occasion which made our collaborations a lot more successful. Mduduzi Ngwenya and the members of All Out Africa all helped to navigate me through my time in Swaziland.

Thanks too to my co-authors outside of Trinity College, Kerri, Walter, Graeme, Antoni, M.Angels, and Darcy. You provided the data and helped me with the analysis, all of which made this piece of work possible.

My mam and dad were responsible for getting me interested in science in the first place and for it they, along with my brothers Alex and Tom, have suffered/listened to someone who has no problem telling them how interesting it is.

Dank je wel to Gwendoline, we began at the same time as the PhD, and she has made my time outside of zoology just as enjoyable as my time spent within.

Table of Contents

Table of Contents	v
List of Tables	vii
List of Figures	viii
1 General introduction	1
1.1 The biology of scavengers	1
1.2 Conservation status	4
1.3 Research outline	5
1.4 Additional work	7
2 Movement ecology of the Cape Vulture	8
2.1 Abstract	9
2.2 Introduction	10
2.3 Methods	11
2.4 Results	12
2.5 Discussion	16
3 Vultures acquire information on carcass location from scavenging eagles	18
3.1 Abstract	19
3.2 Introduction	20
3.3 Test for producer scrounger dynamics	21
3.4 Producer scrounger model	24
3.5 Test of competitive ability	29
3.6 Effect of raptor density on vulture foraging efficiency	30
3.7 Discussion	32
4 Are vulture restaurants needed to sustain the densest breeding population of the African White-backed Vulture?	34
4.1 Abstract	35
4.2 Introduction	36
4.3 Model building	37
4.4 Results	45
4.5 Discussion	46
5 Did Tyrannosaurus rex tend towards scavenging with age?	49
5.1 Abstract	50
5.2 Introduction	51
5.3 Methods	53
5.4 Results	56
5.5 Discussion	57
6 Discussion	59
6.1 How the environment selects for scavengers	59
6.2 All models are wrong	60
6.3 The value of data	61

6.4	Conservation prospects	62
6.5	Future directions	62
	Bibliography	65
	Appendices	76
a	Vultures acquire information on carcass location from scavenging eagles - Supplementary information.	76
b	Are vulture restaurants needed to sustain the densest breeding population of the African White-backed Vulture? - Supplementary information	84
c	Other Publications.	110

List of Tables

Table 2.1	Home range data	14
Table 2.2	Daily distance travelled by immature birds	15
Table 3.1	NetLogo parameter values	31
Table 4.1	Carcass data	44
Table 5.1	Model Parameters	54
Table 5.2	Dinosaur carcass sizes	55
Table 5.3	Scavenger mass categories.	55
Table a.1	Description of parameters used in the game theory model.	76
Table b.1	Life history data	84
Table b.2	Avain scavenger reproductive parameters.	85
Table b.3	Avain scavenger mortality parameters - adults.	85
Table b.4	Avain scavenger mortality parameters - immatures.	85
Table b.5	Carrion mass	86
Table b.6	Population density of animals in ecosystem	87
Table b.7	Avain scavenger food requirments.	88
Table b.8	Seasonal changes in the model	88
Table b.9	Description of model parameters	89

List of Figures

Figure 1.1	Comparative home range of birds	4
Figure 2.1	Map of Cape Vulture distribution with home ranges.	12
Figure 2.2	Comparison of the home range of adult and immature birds.	13
Figure 3.1	Arrival times of vultures and raptors to carcasses	22
Figure 3.2	Histogram plot of p-values	24
Figure 3.3	Game theory plot	28
Figure 3.4	Competitive interactions between vultures and raptors	29
Figure 3.5	Results of agent-based model	32
Figure 4.1	Map of African White-backed Vulture foraging radius	38
Figure 4.2	Schematic of P-system cell.	41
Figure 4.3	Flow diagram for PDP system model	43
Figure 4.4	Balance of carrion availability across time in Swaziland	45
Figure 4.5	Avian scavenging guild population dynamics in Swaziland	46
Figure 5.1	<i>T.rex</i> energy balance	57

1.1 The biology of scavengers

Foraging for food is a primary concern for animal life (Danchin et al., 2008) with the diet of a species often apparent from its morphology. Consider carnivorous animals that, in general, have to find, stalk and kill their prey. Take the example of a cheetah which has a series of adaptations that speak to its carnivorous lifestyle such as its canine teeth, agility and acceleration (Bissett and Bernard, 2007). We would expect obligate scavengers, that are completely dependent on carrion resources, to be unusual in their adaptations because, while they too have to be able to consume flesh, they have no need to hunt or subdue prey. Rather, they must cover an area large enough to encounter a sufficient number of carcasses which are, by their very nature, patchily distributed.

As a group, scavengers are understudied (Sekercioglu, 2006; Selva and Fortuna, 2007; Wilson and Wolkovich, 2011). DeVault et al. (2003) propose that this is due to both human disgust at carrion itself and the difficulty in determining if an ingested prey item was killed or scavenged. It is now recognised that scavengers have an important role in keeping energy flows at a higher trophic level in food webs than decomposers because they consume relatively more carrion (DeVault et al., 2003). (Here I consider decomposers as invertebrates and microorganisms whereas scavengers are typically vertebrates.) Scavengers also provide useful ecosystem services by acting as barriers to the spread of disease by quickly consuming rotting carcasses which have often died from contagious illness (Ogada et al., 2012a; DeVault et al., 2003).

Although many terrestrial and marine predators scavenge to some extent (Britton and Morton, 1994; DeVault et al., 2003; Ruxton and Houston, 2004a) the rarity of modern day *obligate* scavengers in the animal kingdom suggests this is a specialised niche to occupy (Ruxton and Houston, 2004a,b). DeVault et al. (2003) argue that competition between scavengers and decomposers acts as the barrier to fully obligate scavenging owing to the high costs involved in detecting and detoxifying carrion. Certainly, scavengers need to be efficient at finding carrion soon after it has been produced (i.e. after the death of the animal from whatever cause) because toxic "products of decomposition" will render the

flesh inedible with time (DeVault et al., 2003). The problem of decomposing resources is also felt by herbivores that have to contest with the microbes that spoil fruit in an effort to monopolise it (Ruxton et al., 2014). Some studies have looked at the theoretical possibility of obligate scavenging in species from ecosystems in the recent and ancient past (Ruxton and Wilkinson, 2013; Ruxton and Houston, 2004b, 2003; Carbone et al., 2011), the latter being particularly revealing of the sorts of species that could inhabit the niche in the absence of vultures. For example, an energetics approach concluded the carnivorous dinosaur *Tyrannosaurus rex* could have existed as an obligate scavenger (Ruxton and Houston, 2003).

Indeed, the convergent groups of Old and New World vultures are the only representatives to inhabit this niche today (Houston, 2001). These birds have a suite of adaptations that allow them to flourish as obligate scavengers. Their efficiency is illustrated by cases of predators like bears and wolves benefiting by taking more carrion in their diet in areas bereft of vultures through competitive release (DeVault et al., 2003). In flight, birds possess a huge advantage over any terrestrial obligate scavenger. Flight affords them the ability to range over a much larger area and detect carrion from an elevated vantage point. Pennycuik (1972) conservatively estimated that a *Gyps* vulture could identify activity at a carcass 4 km away. Further, vultures take advantage of soaring in thermals (Mundy et al., 1992). This economical means of locomotion, whereby the birds circle around pockets of hot air which provide uplift, allows them to cover huge distances at a low energetic cost (figure 1.1). At large body masses flapping flight is prohibitively expensive in energetics terms (Hedenstrom, 1993). These advantages underscore the importance of the environment, in this case an aerial one, in enabling a scavenging lifestyle. Relative to a terrestrial setting, both locomotion and resource detection are easier for aerial scavengers (Tucker, 1975; Ruxton and Houston, 2004b).

Ruxton and Houston (2004b) argue that large body size is another adaptive response to scavenging. Cinereous Vultures (*Aegypius monachus*) and condors (*Vultur gryphus*, *Gymnogyps californianus*) all have body masses that can exceed 10 kg and represent some of the heaviest bird species capable of flight (Ferguson-Lees and Christie, 2001; Donazar et al., 2002). Many of the other 23 species of vulture are at the upper end of the scale in terms of body mass (Ruxton and Houston, 2004b). As carrion generally occurs in large 'packages', bigger birds can stock up and create body reserves which will benefit them during times of insufficiency. Large body mass also confers dominance advantages during agonistic interactions (Kruuk, 1967; Kane et al., 2014).

Social behaviours have been theorised as further adaptations to improve foraging

efficiency because they allow for active and passive information transfer (Dermody et al., 2011; Wakefield et al., 2013; Moleón et al., 2014). Many vulture species, notably those in the genus *Gyps*, display social behaviours such as communal nesting and group foraging (Mundy et al., 1992). By nesting communally the birds are concentrated in space so at the start of the foraging day they will form foraging groups. This may lead to local enhancement effects such that one bird will follow another that descends to a carcass (Dermody et al., 2011).

Some of these adaptations mean vultures are incapable of killing prey themselves; for instance their wing morphology renders them far less agile than a raptorial counterpart (Ruxton and Houston, 2004b). The selective pressures that push mammals and reptiles towards scavenging do not seem to undermine their ability to hunt in the same way, perhaps explaining the absence of obligate scavengers in these groups (Ruxton and Houston, 2004b).

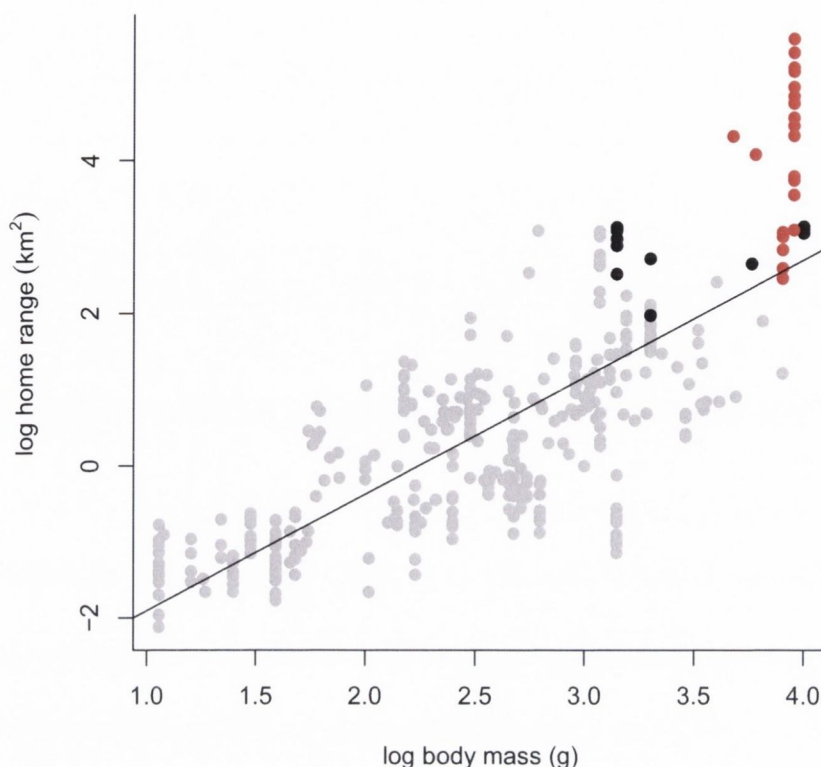


Figure 1.1: Comparative home range of birds (107 species from 11 orders), with *Gyps* vultures highlighted in red, non *Gyps* vultures in black and all other species in grey. The vulture species are *Gyps corprotheres*, *Gyps fulvus*, *Aegypius monachus*, *Cathartes aura*, *Gypaetus barbatus*, *Gyps bengalensis*, *Gyps tenuirostris* and *Neophron percnopterus*. Home range was calculated using minimum convex polygon methods. Data are log transformed (Peery, 2000; García-Ripollés et al., 2011; Gilbert et al., 2007; Krüger et al., 2014; Vasilakis et al., 2005; Dwyer, 2010; Donázar et al., 1996; Stroem and Sonerud, 2001; Buenestado et al., 2008; Gilbert et al., 2005; Nesbitt and Williams, 1990; Pejchar et al., 2005; Springborn and Meyers, 2005; Elchuk and Wiebe, 2003; Rhim, 2006; Legagneux et al., 2009; Rolando, 1998; Hoffman, 1991; Dreitz et al., 2005; Hansbauer et al., 2008; Garza et al., 2005; Vega Rivera et al., 2003; Stober and Kremetz, 2006; Novoa et al., 2006; Holbrook, 2011; Fearer, 1999; Brandt and Cresswell, 2008; Giesen and Braun, 1992).

1.2 Conservation status

Avian scavengers represent an ecologically important guild that has suffered severely from the effects of anthropogenic change (Ogada et al., 2012b) which is not helped by our ignorance of the group. The importance of vultures to ecosystem functioning is best illustrated by the sudden collapse of their numbers in the Indian subcontinent. By feeding on the carcasses of drug-treated cattle, the vultures were poisoned en masse by diclofenac (Oaks et al., 2004). Their absence led to an increase in feral dogs and a resultant

spike in rabies' incidence among humans (Markandya et al., 2008). Aside from poisoning, both targeted and incidental, vultures are endangered by wind turbines, electricity pylons, habitat destruction, food loss and poaching (Monadjem et al., 2003; Virani et al., 2011; Martin et al., 2012). Despite these threats they have proved to be an adaptable group, illustrated by their willingness to feed on the carrion of domesticated animals (Mundy et al., 1992) and their use of electricity pylons as roosting locations which has caused an expansion in their range (Phipps et al., 2013b). Efforts at conserving vultures look to increase the availability of food (Piper, 2005), rehabilitate injured individuals (Monadjem et al., 2014), prevent the spread of poisons (Green et al., 2004), increase public awareness of the group's function etc. (Monadjem et al., 2004). However, the effect of implementing these strategies remains poorly understood (Monadjem et al., 2014). We can take solace in the recent spike in research on vultures which has been brought about by high profile population crashes like that of India (Koenig, 2006). Hopefully, such catastrophes won't be necessary to keep biologists focused on this group in the future.

1.3 Research outline

This thesis draws on a wealth of data collected by field researchers in Africa to answer questions on the foraging ecology of *Gyps* vultures, moving from individual based methods to a study of population dynamics. The possibility of obligate scavengers in past ecosystems is an interesting area because it reveals the adaptations that permit an animal to exist in the niche. As such I use some of the theory and methods from my previous work in describing the feeding ecology of *Tyrannosaurus rex* whose predatory tendencies have been called into question.

Chapter 2: In order to effectively conserve species we must know the extent of their home range and how this can vary across time. Here I describe the home range of 29 Cape Vultures caught, released and tracked in southern Africa. My analysis shows the species range significantly farther as immature birds and, as adults, are constrained by the breeding season. Such variation means there is no easy solution to conservation efforts like supplementary feeding sites which need to be tailored to cater for all life stages.

Chapter 3: As social birds, vultures often rely on each other to find food. They frequently follow the descent of another individual in the hope that it has discovered a carcass. In a Kenyan study site, I show that vultures also take cues from scavenging eagles. I propose that the eagles are used by the vultures in two ways: first they act as indicators of the presence of food; and second the eagles can tear open the hide of a carcass with their relatively stronger beaks, providing a resource that would otherwise be much more difficult for the vultures to access. In each case the larger vultures can then displace the eagles through competitive dominance and monopolise the remaining food. These newly identified social interactions among different species highlight the vital importance of applying integrated management strategies to conserve endangered vulture species.

Chapter 4: Carrion ecology, the fate of animal carcasses, is a crucial component of every ecosystem. Mismanagement can lead to environmental disasters, most notably the decimation of Asian vulture populations which fed on the carrion of drug-treated cattle. Here, I provide data on the carrion ecology of an ecosystem in Swaziland and predict the future trends of its vulture populations. Using novel methods I show that, despite a closure in supplementary feeding sites, these species have enough food from wild carcasses to survive. But only for the time being. Therefore, I recommend a dedicated vulture restaurant initiative to ensure the population survives.

Chapter 5: The feeding ecology of *Tyrannosaurus rex* has long been debated with distinct 'predator versus scavenger' camps. I move away from this polarised debate and explore the effect of the drastic ontogenetic morphological changes the animal underwent. Specifically, I ask whether these changes resulted in it incorporating ever more carrion in its diet. To address my question I created an individual-based model based on the energetics of its movement and the amount of carrion available at the time only to find that the reverse is true. The cost of movement meant searching for patchily-distributed carrion became prohibitively expensive as *T.rex* grew. Instead, my results suggest the dinosaur switched from small prey items to more cumbersome, armoured species as it developed into its robust adult form.

1.4 Additional work

In addition to the chapters enclosed in this thesis, I have also been involved in the following research during my studies:

Healy, K., Finlay, S., Guillerme, T., Kane, A., Kelly, S., McClean, D., Kelly, D., Donohue, I., Jackson, A.L., & Cooper, N. (2014). Ecology and mode-of-life explain lifespan variation in birds and mammals. *Proceedings of the Royal Society B: Biological Sciences* 281.1784: 20140298.

I was involved with the conception, data collection and write-up of this paper.

Wakefield, E.D., Bodey, T.W., Bearhop, S., Blackburn, J., Colhoun, K., Davies, R., Dwyer, R.G., Green, J., Grémillet, D., Jackson, A.L., Jessopp, M.J., Kane, A., Langston, R.H.W., Lescroël, A., Murray, S., Le Nuz, M., Patrick, S.C., Péron, C., Soanes, L., Wanless, S., Votier, S.C., & Hamer, K.C. (2013). Space Partitioning Without Territoriality in Gannets. *Science*. 341, 68-70. doi: 10.1126/science.1236077

I took the lead in developing the individual based models for this paper and taught one of the lead authors (TWB) about the method, working closely with him in developing a suitable model for the gannet system.

Monadjem, A., Wolter, K., Naser, W., & Kane, A. (2013). Effect of rehabilitation on survival rates of endangered Cape vultures. *Animal Conservation*. doi: 10.1111/acv.12054

I was again involved in the data analysis and write-up of this manuscript and forged some links with two vulture conservationists based in South Africa.

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(9), doi: 10.1371/journal.pone.0046434

I was involved in the data analysis and write-up of this manuscript. This was my first full peer-reviewed paper.

Kane, A. (2012). A suggestion on improving mathematically heavy papers. *Proceedings of the National Academy of Sciences*. 109(45) E3058-E3059. doi: 10.1073/pnas.1212310109

This letter was a response to an article highlighting the divide between theoretical and empirical biologists owing to different competencies in mathematics.

chapter 2

Movement ecology of the Cape Vulture

Authors: Adam Kane, Kerri Wolter, Walter Naser, Andrew L Jackson & Ara Monadjem

Author contributions I conceived the idea, analysed the data, interpreted the results and wrote the manuscript; AM supplied data and advised on data analysis; AJ gave feedback on drafts of the manuscript; KW and WN were responsible for the capture and tagging of the birds.

Status: This manuscript is being prepared for publication. Target journal is Bird Conservation International.

2.1 Abstract

Identifying the areas animals use and how this varies across time is vital to conservation efforts especially in the case of wide-ranging vultures that traverse over international borders. Here we conducted a large scale analysis of the movement ecology of 29 Cape Vultures (*Gyps coprotheres*) that were tracked for an average of 311 days over Southern Africa. We describe differences in home range size between adults and immatures as well as seasonal variation. We show that, in line with smaller scale studies, immature birds have larger home ranges than adults. This is likely due to strong competition at feeding sites near colonies and the constraint on adults of having dependent-young. There is also a significant effect of seasonality such that adult birds have smaller home ranges during the dry season. This is also likely a result of breeding birds being constrained by their nests as well as increased food availability provided by higher ungulate death rates. We discuss the conservation implications of these results with special mention given to vulture restaurants. We advocate the use of both frequently stocked restaurants close to colonies to benefit adults and infrequently stocked sites farther away from colonies for the benefit of immature birds.

2.2 Introduction

The Cape Vulture (*Gyps coprotheres*) is a large (9 kg), obligate scavenging vulture known from southern Africa (Mundy et al., 1992). It is IUCN red listed as vulnerable with a declining population. Given their longevity and low reproductive output (clutch size is rarely more than one) Cape vultures are very sensitive to reductions in their survival rates (Phipps et al., 2013b; Monadjem et al., 2014). The bird is known to be a wide-ranging species (Bamford et al., 2007). Indeed *Gyps* vultures (Monsarrat et al., 2013) have a much larger home range than that of closely related members of the Accipitriformes (Peery, 2000) owing to their dependence on patchily distributed carrion (Ruxton and Houston, 2004b). Such large home ranges make conserving these species a challenging task given that they may fly over many countries with different agendas pertaining to wildlife management (Lambertucci et al., 2014). Seasonal and ontogenetic differences in home range have been illustrated before in *Gyps* vultures (Monsarrat et al., 2013; Phipps et al., 2013b). This is significant because specific life stages can have a disproportionate impact on the population growth rate, with the adult stage being most sensitive in the case of the Cape vulture (Monadjem et al., 2012, 2014).

As such, the identification of home range is of great importance in conservation efforts, especially in recognising that home ranges are not static over either long or short periods (Burt, 1943). Here we define home range as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young" (Burt, 1943). We used a large dataset of GPS tracked individuals, to test two intuitive predictions. First, we expected that the home range of immature birds would be larger than that of adults due to adults being constrained by their young (Mundy et al., 1992), the competition suffered by immature birds at feeding sites near colonies which forces them to forage farther afield and, the larger body mass of adults which can hamper ability to take off (Robertson and Boshoff, 1986; Mundy et al., 1992). This is in line with previous studies based on fewer individuals (Mundy et al., 1992; Bamford et al., 2007; Phipps et al., 2013b). Secondly, we hypothesised that adults would have a smaller home range during the breeding season compared to the non-breeding season, again because they have dependants as well as poor flying conditions during this period (Mundy et al., 1992; Monsarrat et al., 2013). The breeding season also coincides with the dry season for Cape vultures, this is a period during which the ungulates suffer an increased death rate and provide more carrion to the scavengers (Mundy et al., 1992). This is another factor that could reduce the home range of the birds given that they would encounter food more often during this period.

Elucidating the movement ecology of these birds at different times, both seasonal and ontogenetic, is important because vulture conservation efforts frequently make use of long-term supplementary feeding sites (Gilbert et al., 2007). The benefits these sites may have could be maximised by knowing when the birds will most often avail of them and which life stages (Monsarrat et al., 2013).

2.3 Methods

In total, we analysed the movements of 29 Cape Vultures. These birds were captured by VulPro, a vulture conservation organisation, at trapping localities in South Africa using a walk-in trap (Diekmann et al., 2004; Phipps et al., 2013b). See Phipps et al. (2013b) for details of their capture and release. Seven of these individuals have been used in a previous study investigating the effects of power lines on Cape Vulture movements (Phipps et al., 2013b). The birds were separated into adult (> 5 years) and immature (< 5 years) categories (?) (Table 2.1). The sex of every bird was not known so we could not include it as an explanatory variable for home range variation; however it should be noted that adult *Gyps* vultures share parental duties and would not be expected to vary much in this respect (Houston, 1976). We calculated the home range for each individual using minimum convex polygon (MCP) (Mohr, 1947) and kernel utilisation distribution methods (KUD) (both set to 95%, such that 5% of the most extreme points were removed)(Worton, 1989). We computed mean and standard deviation summary statistics for these home range areas for the individual birds. Then we used Wilcoxon-Mann-Whitney rank sum tests (the non-parametric alternative to the t-test) to determine if there was a difference in home range size between adult and immature Cape Vultures; and used the same method to test for a difference in home range with season (wet versus dry). The dry season was defined as May-August (Cooper et al., 1988; Mundy et al., 1992). Note that we did not know if a given adult was actually breeding.

For a subset of the birds, namely those that were tracked at a higher temporal resolution (once every 15 minutes cf. the adults who were tracked at 7.00, 11.00 and 15.00 each day), we estimated the distance they covered during a day (Table 2.2). These were all immature individuals. We carried out our analysis using base R and the R package *adehabitatHR* (R Core Team, 2014; Calenge and Fortmann-Roe, 2013).

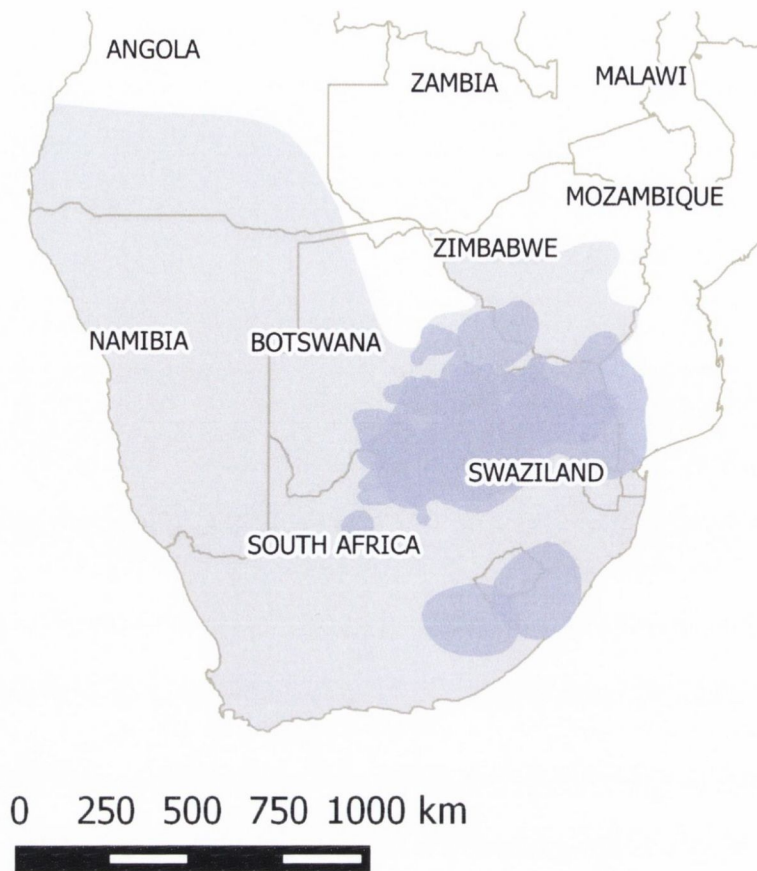


Figure 2.1: Distribution of the Cape Vulture in Southern Africa (data from Bird Life International in grey) and Home Range (KUD 95%) of the 7 immature birds tracked at high resolution.

2.4 Results

Mean KUD home ranges were $282,255 \text{ km}^2$ ($\text{sd} \pm 288,460 \text{ km}^2$) for immature birds and $110,181 \text{ km}^2$ ($\text{sd} \pm 130,464 \text{ km}^2$) for adults (Table 2.1). The Wilcoxon-Mann-Whitney rank sum tests showed this was a significant difference according to the KUD measure ($p = 0.037$). By comparison the MCP difference gave a p -value of 0.057 (figure 2.2). The home ranges of the 7 high resolution birds are shown in figure 2.1.

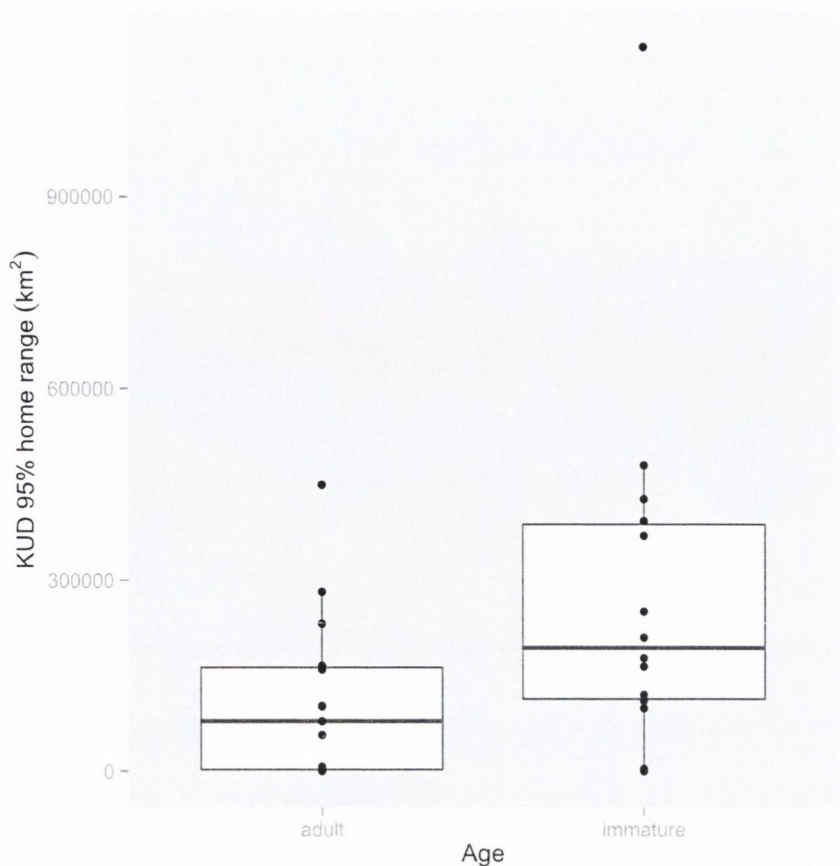


Figure 2.2: Comparison of the home range of adult and immature birds based on KUD. The median is shown by the horizontal bar within the box. The whole box captures the interquartile range of the home ranges i.e. the 25 to 75 percentile. There is an outlier for both the adult and the immature birds.

Mean KUD for adults during wet and dry season were 80,719 km² (sd ±137,799.1 km²) and 36,138 km² (sd ±50,978 km²) respectively. Mean KUD for immatures during wet and dry season were 58,236 km² (sd ±74,593 km²) and 74621 km² (sd ±99,304 km²) respectively. There was a significant difference between wet and dry season for adult birds ($p = 0.03837$) but not for immature birds ($p = 0.5176$) using KUD methods.

Table 2.1: Home range (KUD and MCP) data on the Cape Vultures which were divided into immature and adult birds. Immature values are in the top half of the table, adults the bottom half.

Bird	Start date	Days tracked	HR MCP 95% (km ²)	HR KUD 95% (km ²)
AG313	08-11-09	313	248,982	370,444
AG352	09-12-09	206	344,994	393,788
AG353	17-01-10	557	391,493	427,971
AG382	24-06-10	408	942,236	1,134,326
AM240	15-03-07	77	1,242	637
AM265	28-11-07	505	222,735	165,599
AM295	27-11-07	534	6,269	5,047
Katie	03-04-13	128	88,809	111,645
B604	11-02-13	217	176,980	178,277
B536	30-07-13	71	116,505	99,837
B519	19-05-12	289	507,665	480,431
B516	28-01-13	252	229,341	210,740
B506	08-04-12	549	143,151	121,100
B500	23-03-12	194	222,126	251,735
Total mean			260,181 ($\pm$ 241,304)	282,256 ($\pm$ 288,460)
AG314	08-11-09	477	147,017	79,158
AG329	03-12-09	266	82,475	166,640
AG349	03-12-09	233	50,348	57,728
AG355	19-08-10	301	229,546	282,202
AG522	02-02-11	332	200,849	103,251
AM220	16-02-07	273	330,064	449,835
AM221	14-02-07	469	202,849	160,312
AM222	02-03-07	364	5,558	790
AM226	02-03-07	194	2,279	1,986
AM234a	15-03-07	196	3,569	2,820
AM234b	27-11-07	153	3,970	2,637
AM235	15-03-07	245	2,635	2,465
AM264	29-01-08	484	393,449	232,504
AM267	29-01-08	498	28,801	7,774
AM272	19-12-07	237	69,285	102,625
Total mean			116,846 ($\pm$ 128,112)	110,182 ($\pm$ 130,464)

The average daily distance covered by the 7 high resolution birds was approximately 72 km if we used every relocation (Table 2.2). However when we used only the start and end relocations for a given date, i.e. "as the crow flies", the average was reduced to just over 33 km as a result of the loss of smaller scale movements.

Table 2.2: Average daily distance travelled by the immature birds that were tracked at a high resolution (once per 15 minutes) and the distance "as the crow flies" between the start and end points of the given date.

ID	Mean (km)	SD (km)	Mean "as the crow flies" (km)	SD (km)
B500	82.14	70.41	41.75	47.74
B506	61.09	54.38	27.57	34.37
B516	79.62	66.84	35.96	35.93
B519	64.98	60.71	33.07	41.63
B536	84.93	72.54	40.96	42.6
B604	83.77	68.57	40.58	41.75
Katie	45.68	41.43	13.74	22.27
Total mean	71.74		33.38	

2.5 Discussion

The foraging day of a Cape vulture typically takes place between 10.00 and 18.00 (local time) (JM et al., 2005). They usually fly between an altitude of 250 - 350 m above ground (Mundy et al., 1992). The daily foraging distance reported here (an average of over 70 km) illustrates the impressive abilities of immature Cape Vultures in flight. In contrast, adults of the species have been calculated as covering a radius of 54 km in a day (Mundy et al., 1992). By way of comparison with immature vultures of other species, Phipps et al. (2013a) showed immature African White-backed Vultures (*Gyps africanus*) flew on average 33.39 km per day. Note that those estimates were based on locations recorded three times daily, a much coarser resolution, and thus nearly identical to our "as the crow flies" measure (mean = 33 km). This difference between adults and immatures accounts for the disparity seen in the home range of the Cape Vulture life stages.

Indeed, our large dataset on tracked Cape Vultures demonstrates a significant effect of both age and season on home range size. As mentioned above, these results are most probably the result of adults having to care for dependent young as well as the dominance hierarchy that exists across ontogeny (Duriez et al., 2012; Mundy et al., 1992). We should also consider the effect of weather (Shepard and Lambertucci, 2013). The mass of an adult bird can be prohibitive when cold temperatures result in the formation of weak thermals. These cliff faces deflect wind upwards and are used by the soaring vultures to offset their sink rate (Shepard et al., 2013). This can restrict adult flight time during winter months especially at colony cliffs in open savanna (Mundy et al., 1992). There is also the effect of differential seasonal mortality. The higher death rate of ungulates during the dry season means the vultures will encounter more carrion and won't have to travel as far.

The difference in home range size between Cape Vulture life stages has implications for its conservation. We know from population growth models showing that adults have a disproportionate effect on the growth rate of Cape vulture populations (Monadjem et al., 2014). Habitat fragmentation is known to increase the size of an animal's home range because it causes a reduction in resource density (Haskell et al., 2002). To counter this, conservationists can supply supplementary food (Piper, 2005). However, these sites impact adult and immature birds in different ways depending on how they are run. Duriez et al. (2012) showed that, at artificial feeding sites, close to colonies and regularly stocked with food, adult vultures (*Gyps fulvus*) dominated young individuals who were left to fight over scraps. But "light" feeding sites, located farther from colonies and supplied less regularly, were preferred by immature birds. Conservationists should therefore use a mix

of "light" and "heavy" feeding sites if they are to effectively manage both ontogenetic stages. Komen calculated the energy requirements for this species across its ontogeny, a piece of research that could be put to good use when supplying supplementary feeding sites at different times. We also have excellent data on the population sizes of Cape Vulture colonies in South Africa (Whittington-Jones et al., 2011). By knowing where they forage, how much food they require and variability in the species home range we are well placed to sustain this species. However, conservation actions must be at an international level (Lambertucci et al., 2014) given that Cape Vultures are not impeded by national boundaries.

chapter 3

Vultures acquire information on carcass location from scavenging eagles

Authors: Adam Kane, Andrew L Jackson, Darcy L Ogada, Ara Monadjem & Luke McNally

Author contributions I conceived the idea, analysed the videos for arrival times and competitive interactions, created and ran the IBMs, ran the statistics on these sections, helped LM develop the game theory model and wrote the manuscript; AJ developed the permutation tests and gave input on the manuscript; DO recorded the videos on which this study is based and gave feedback on the manuscript; AM gave feedback on the manuscript; LM created the game theory model, advised on the statistics and gave feedback on the manuscript.

Status: This manuscript has been published at Proceedings of the Royal Society B.

3.1 Abstract

Vultures are recognised as the archetypal scavengers of the natural world. While it is well known that vultures use conspecific social information as they forage, the possibility of inter-guild social information transfer and the resulting multi-species social dilemmas has not been explored. Here we use data on arrival times at carcasses to show that such social information transfer occurs with raptors acting as producers of information and vultures acting as scroungers of information. We develop a game-theoretic model to show that competitive asymmetry, whereby vultures dominate raptors at carcasses, predicts this evolutionary outcome. The eagles, which arrive earlier, benefit from gaining a finder's fee enabling them to exist in a producer role. We support our theoretical prediction using empirical data from competitive interactions at carcasses. Finally, we use an individual based model to show that these producer-scrounger dynamics lead to vultures being vulnerable to declines in raptor populations. Our results show that social information transfer can lead to important non-trophic interactions among species and highlight important potential links among social evolution, community ecology and conservation biology. With vulture populations suffering global declines our study underscores the importance of ecosystem-based management for these endangered keystone species.

3.2 Introduction

Animals base their decisions on both personal and public information (Dall et al., 2005; Schmidt et al., 2010; Sumpter et al., 2008; Couzin, 2009). This is applicable to every facet of an animal's life, be it feeding, movement, mating etc. with high fidelity information allowing an individual to make decisions conducive to its survival (Dall et al., 2005; McNamara and Dall, 2010; Danchin et al., 2004). Public information can be separated into that which is gained from conspecifics and that from heterospecifics (Dall et al., 2005). Conspecific information transfer is essential for basic behavioural functions like sexual reproduction or cooperative hunting (Handegard et al., 2012). But species overlap in the resources they use (Fedriani et al., 2000; Kruuk, 1967), and the environments they inhabit (Fedriani et al., 2000; Kruuk, 1967) which gives the possibility of inter-guild information transfer (Seppänen et al., 2007; Seppänen and Forsman, 2007; Forsman et al., 2009).

Consider the social *Gyps* vultures, a group that is known to forage collectively for carrion. In flight they appear to keep in visual contact with conspecifics (Houston, 1974). Once one vulture discovers and descends to a carcass the information is conveyed to others in the area, this activity can create a local enhancement effect (Jackson et al., 2008). But such social behaviour renders vultures' foraging efficiency susceptible to population declines; with every individual lost, the network is less effective at detecting carrion (Jackson et al., 2008). Although vultures are the most well-known group of avian scavengers there are a number of other species within the family Accipitridae such as eagles (hereafter raptors) that take carrion as a significant proportion of their diet (Mundy et al., 1992). Coexistence among all of these species is possible by both temporal and resource partitioning (Mundy et al., 1992; Houston, 1975). But with any shared resource, direct interactions between them will result, and the possibility of social information transfer among species emerges.

A distinct pattern of arrival of avian scavengers to carrion has been highlighted before (Mundy and Group, 1982; Kendall, 2013; Cortés-Avizanda et al., 2012). Indeed, the African White-backed Vulture (*Gyps africanus*) has been noted in using many other scavengers as a means of local enhancement while foraging (Kruuk, 1967). Yet these heterospecific interactions and their potential for information transfer have not been explored in any detail (Mundy and Group, 1982).

Given the current extreme declines in vulture populations (Ogada et al., 2012b; Green et al., 2004) and their key role in many ecosystems as biomass recyclers (Ogada et al., 2012a; Sekercioglu, 2006), understanding vulture foraging ecology is also of applied rel-

evance. Here we provide evidence for producer-scrouter dynamics among scavenging vulture and raptor species by testing the hypothesis that vultures scrounge information from raptors, and explore its evolutionary underpinnings using a game theoretic model. We conclude by outlining the consequences of this system's properties for vulture conservation.

3.3 Test for producer scrounger dynamics

To test for the occurrence of producer-scrouter dynamics between vultures and raptors we observed arrival times of avian scavengers to a number of experimental carcasses placed out. Our observations were made on 46 videos recorded in the Mpala Research Centre in the Laikipia District of Kenya which had scavenging avifauna (a subset of the videos used in Ogada et al. (2012a)). The carcasses of partially skinned goat and cow carcasses were set out at dawn (06.15 - 07.20) in an open area of the Mpala Ranch which consists of 20,000 ha of savannah. Carrion size ranged from 20 - 340 kg with a mean of 80 kg and did not have a significant effect on the number of avian scavengers present (Ogada et al., 2012a). We focused on the closely related and morphologically similar *Gyps* vultures, the African White-backed Vulture and the Rüppell's Vulture (*Gyps rueppellii*), as well as the congeneric Tawny (*Aquila rapax*) and Steppe Eagles (*Aquila nipalensis*). Some differences between the eagles include the tendency for the Steppes to be slightly larger and more social (Clark, 1992). These four species were by far the most abundant in the recordings (>95%) and formed our vulture and raptor groups respectively (Ogada et al., 2012a). For each video we noted the arrival time and species of every animal. Initially, we compared the probability of producing information on carcass location by looking at which of the two groups, *Gyps* vultures or raptors, landed at the carcass first. A binomial test on the 46 videos showed that the first bird to land at a carcass was significantly more likely to be a raptor than a vulture (Binomial test, 38 successes, 46 trials, expected probability = 0.5, results in observed probability = 0.83, 95% C.I. 0.69-0.92, p-value < 0.001 (figure 3.1)).

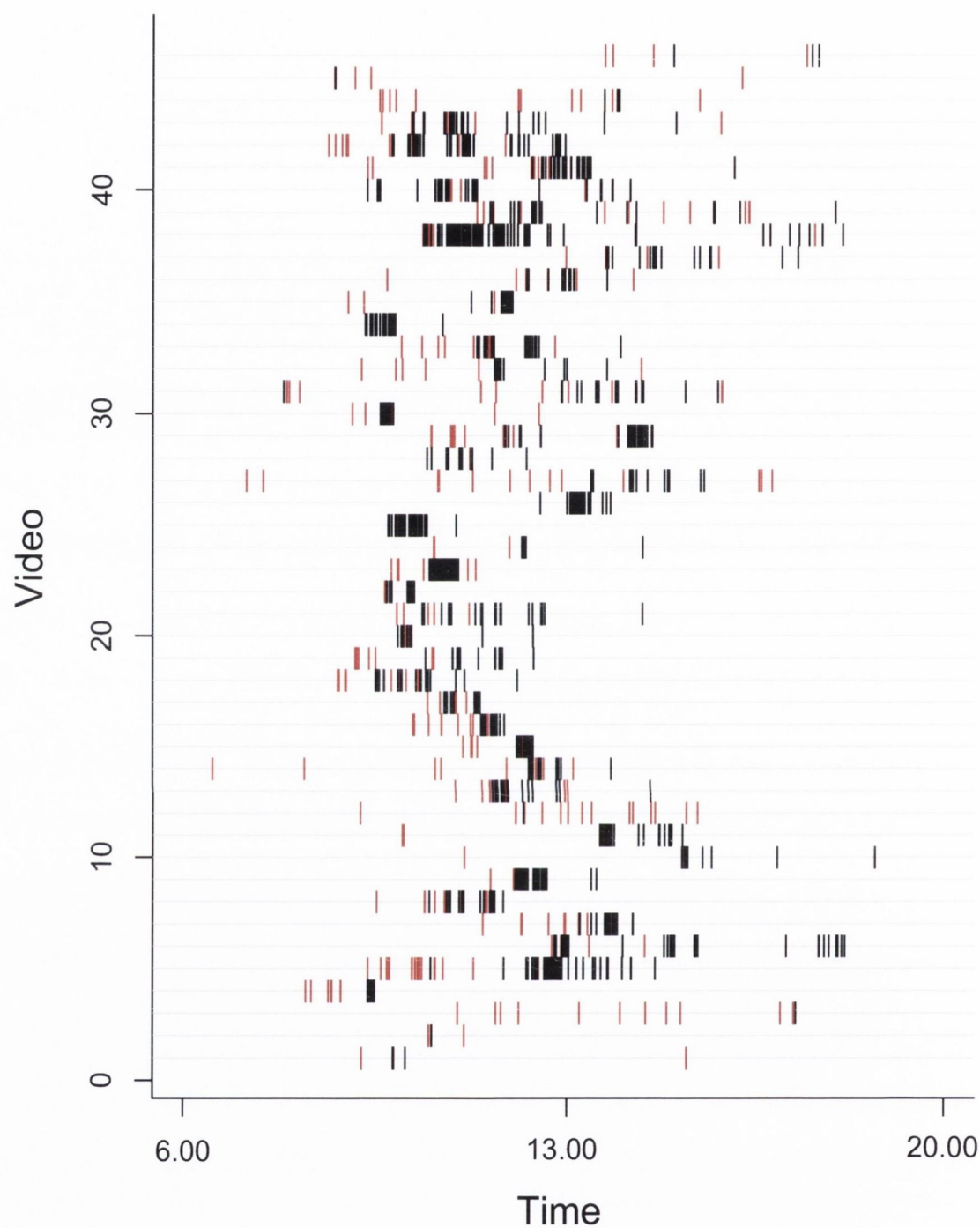


Figure 3.1: Recorded arrival times of individual vultures and raptors at carrion across 46 videos. The red lines are raptors, black are vultures.

We used randomisation tests to test if the birds were following each other rather than simply arriving independently but with different timing to the carcasses. Where a raptor landed first we generated a null distribution of arrival times for the first scrounger (a *Gyps* vulture) over the length of each recording by randomising the arrival times of

the birds. From this distribution we assessed if the first scrounger followed more closely than expected under an assumption of independent foraging. Then, in order to make a population level inference across permutation tests, we use a binomial test where the expected probability of observing a significant result by chance is 0.05 (as per the definition of a p-value where at an alpha of 0.05, we would expect 5% of test results to be significant according to the null model). Vultures were found to follow raptors more closely than expected by chance (i.e. with $p < 0.05$) in 20 of the 38 videos (figure 3.2a) which is significantly more cases of vultures following raptors than expected (Binomial test with 20 successes, 38 trials, expected probability = 0.05 results in an observed probability = 0.53, 95% C.I. 0.36-0.69, p -value < 0.001). Similarly, in six of the eight occasions when vultures landed at the carcass first, raptors followed more closely than expected by chance (figure 3.2b), which is significantly more cases than expected (Binomial test with 6 successes, 8 trials, expected probability = 0.05, results in an observed probability = 0.75, 95% C.I. 0.35-0.97, p -value < 0.001).

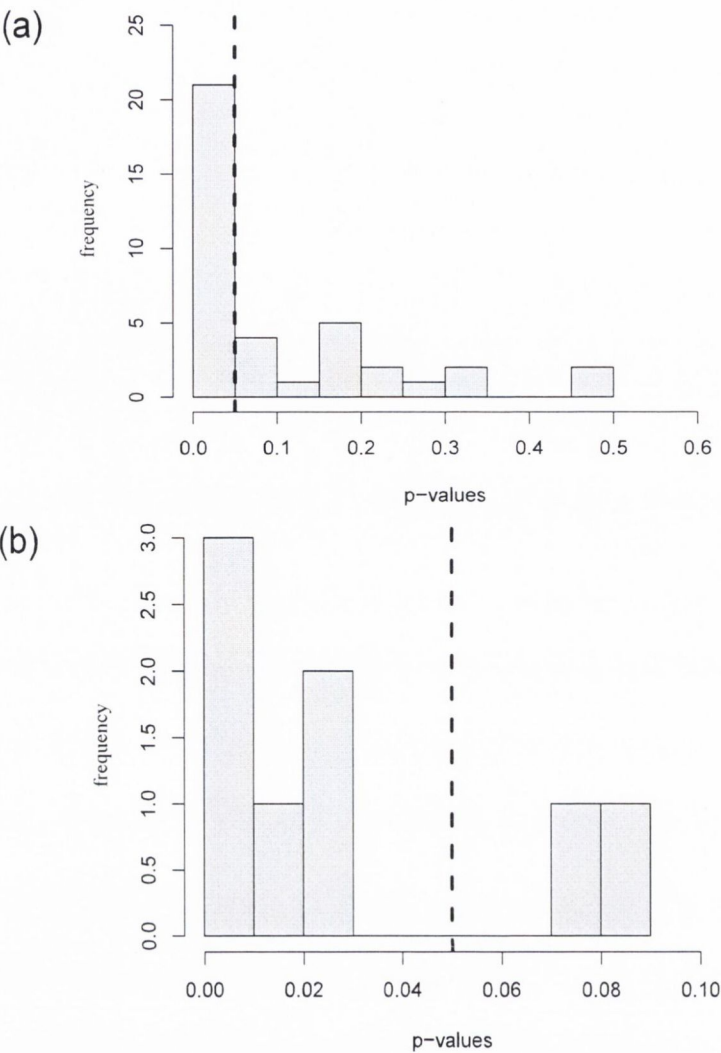


Figure 3.2: Histograms of p-values showing the number of videos where it was significantly probable that (a) the vultures were following the raptors and (b) the raptors were following the vultures. The vertical lines show the level of significance at $p = 0.05$.

3.4 Producer scrounger model

While our analyses suggest that both raptors and vultures follow each other to carcasses, the higher frequency of raptors being the first to land at a carcass leads to raptors acting predominantly in a producing role. This can manifest by raptors providing information on the location of the resource or by engaging in carcass opening whereby the raptor uses its relatively stronger bill to get through an ungulate hide (Kendall, 2013), with vultures acting predominantly as scroungers. This result raises the question of how these divergent roles evolved? We hypothesised that competitive ability may have a strong effect on the strategy typically adopted in each species. If individuals of one species can

competitively dominate those of another this may favour scrounging by the dominant species: producers may gain an exclusive share of the resource by arriving first at the carcass (a "finder's fee") (Vickery et al., 1991), but dominant scroungers may be able to effectively monopolise the remainder of the resource once they arrive, while also gaining information available publically on the locations of carcasses.

We used the game-theoretic framework of the producer-scrounger game to test the evolutionary feasibility of this prediction. In a producer-scrounger game an animal needs to invest either in producing some resource (e.g. information), or exploit the investment from another individual (Morand-Ferron and Giraldeau, 2010). We consider a scenario where vultures and raptors forage in the same area. We assume that time spent feeding at a carcass is small relative to search time (Mundy et al., 1992; Barta and Giraldeau, 1998). Individual vultures and raptors can assume one of two strategies: producer or scrounger. Producers find carcasses at a rate proportional to the carcass density; while all scroungers in a group will follow producers to the carcasses they find, but don't find carcasses for themselves (probabilistic following by scroungers cannot qualitatively affect our results). While in reality vultures and raptors will likely use mixed strategies, this simple scenario allows us to abstract the essential elements of the evolutionary dynamics in a simple framework.

From our assumptions we can write the numbers of vultures and raptors at a carcass found by a vulture as $m_{v,v} = 1 + v_s$ and $m_{v,r} = r_s$, respectively, where v_s and r_s are the numbers of vultures and raptors that are scroungers. Similarly the numbers of vultures and raptors at a carcass found by a raptor are $m_{r,v} = v_s$ and $m_{r,r} = 1 + r_s$, respectively. We assume that new carcasses arrive in the area and decay at fixed rates (both set at 1) and are consumed almost instantaneously when found. Assuming that carcass dynamics occur on a faster timescale than the population dynamics of vultures and raptors the steady-state density of carcasses is then given as $d = 1/(1 + r_p + v_p)$, where v_p and r_p are the numbers of vultures and raptors that are producers. The rates of food consumption for producing and scrounging vultures are:

$$\pi_{v,p} = \left(\frac{1}{1 + r_p + v_p} \right) \left(a + (1 - a) \frac{x}{xm_{v,v} + m_{v,r}} \right) \quad (3.1)$$

and

$$\pi_{v,s} = \left(\frac{1}{1 + r_p + v_p} \right) (1 - a) \left(\frac{v_p x}{xm_{v,v} + m_{v,r}} + \frac{r_p x}{xm_{r,v} + m_{r,r}} \right) \quad (3.2)$$

Similarly the rates of food consumption for producing and scrounging raptors are:

$$\pi_{r,p} = \left(\frac{1}{1 + r_p + v_p} \right) \left(a + (1 - a) \frac{1}{xm_{v,v} + m_{v,r}} \right) \quad (3.3)$$

and

$$\pi_{r,s} = \left(\frac{1}{1 + r_p + v_p} \right) (1 - a) \left(\frac{v_p}{xm_{v,v} + m_{v,r}} + \frac{r_p}{xm_{r,v} + m_{r,r}} \right) \quad (3.4)$$

Here a is the proportion of a carcass that is monopolised by the individual that finds it (the "finder's fee"), and the variable x is the competitive ability of vultures compared to that of raptors, specifically the number of raptors that a vulture is equivalent to in terms of competitive ability. The proportion of the carcass remaining after the finder's fee $(1-a)$ is shared among all birds at the carcass proportionally to their relative competitive ability. For example, at a carcass found by a raptor, a scrounging vulture's share would be $x/(xm_{r,v} + m_{r,r})$. The vulture is competitively equivalent to x raptors so gets a positive weighting of x in the numerator. As other vultures will have a similar competitive ability, the number of vultures at the carcass ($m_{r,v}$) is also weighted by x . This leads to each bird receiving a share proportional to its competitive ability relative to the other birds present at the carcass. The probability that a vulture wins a one-on-one interaction with a raptor is then defined as $x/(1 + x)$. This process could then be seen as a series of competitive interactions over small proportions of the carcass, leading to birds on average receiving a share proportional to their relative competitive ability.

While the equilibrium number of carcasses ($1/(1 + r_p + v_p)$) available declines with the density of producers of both species as more carcasses are found and consumed, the food acquisition rate of scroungers is also positively weighted by producer densities as they are able to follow individuals to carcasses more frequently. This means that, while producers are only affected negatively by other producers (owing to reduction in carcass densities), scroungers are affected both positively (owing to their increasing rate of following to carcasses) and negatively (owing to reduction in carcass density) by producer density. We write the dynamics (Hofbauer and Sigmund, 2003) of producers and scroungers in the vulture and raptor populations as:

$$\frac{dv_p}{dt} = v_p (\pi_{v,p} - \alpha) \quad (3.5)$$

$$\frac{dv_s}{dt} = v_s (\pi_{v,s} - \alpha) \quad (3.6)$$

$$\frac{dr_p}{dt} = r_p \left(\pi_{v,p} - \beta + \frac{\gamma}{1 + r_p + r_s} \right) \quad (3.7)$$

and

$$\frac{dr_s}{dt} = r_s \left(\pi_{r,s} - \beta + \frac{\gamma}{1 + r_p + r_s} \right) \quad (3.8)$$

Here α and β are the mortality rates for vultures and raptors, respectively. The additional term $\gamma / (1 + r_p + r_s)$ captures additional food intake by raptors owing to their additional source of energy through predation. Here we assume that some prey enters the area at rate γ , dies at a fixed rate of 1, and is found by raptors at rate 1 and then instantaneously consumed. Again we assume that the dynamics of the prey population happen on a faster time-scale than the raptor population dynamics so that the steady-state density of prey can be used. Varying the parameter γ then allows us to vary raptor's relative reliance on carcasses as a food source.

Unfortunately no analytical solutions are available for our model, so we examine the evolutionary dynamics of the producer-scrouter interaction using numerical evaluation of steady-state of equations 3.5-3.8. The results of the model displayed in figure 3.3 show the impact of competitive ability, finder's advantage and the availability of prey items to raptors. Notice in plots (a) and (c) that there is a transition from high raptor population densities to high vulture densities as vultures become more dominant over raptors (the switch occurring when the probability a vulture wins is greater than 0.5). The availability of extra food from predation in plot (c) allows the raptors to persist at higher population densities suppressing the increasing vulture numbers relative to plot (a). The effect of increasing relative competitive ability is also realised in driving up the proportion of birds scrounging. The outcome of varying the size of the finder's fee is evident as we can see a lower proportion of scroungers when the amount of food consumed by the producer is high. A competitively dominant species gains a larger share of the resource. It follows that any finder's fee is of less value to them than it is to the competitively inferior species. Thus the competitively dominant species is more likely to forego a finder's fee in order to benefit from the increased rate of information acquisition that can be facilitated by scrounging.

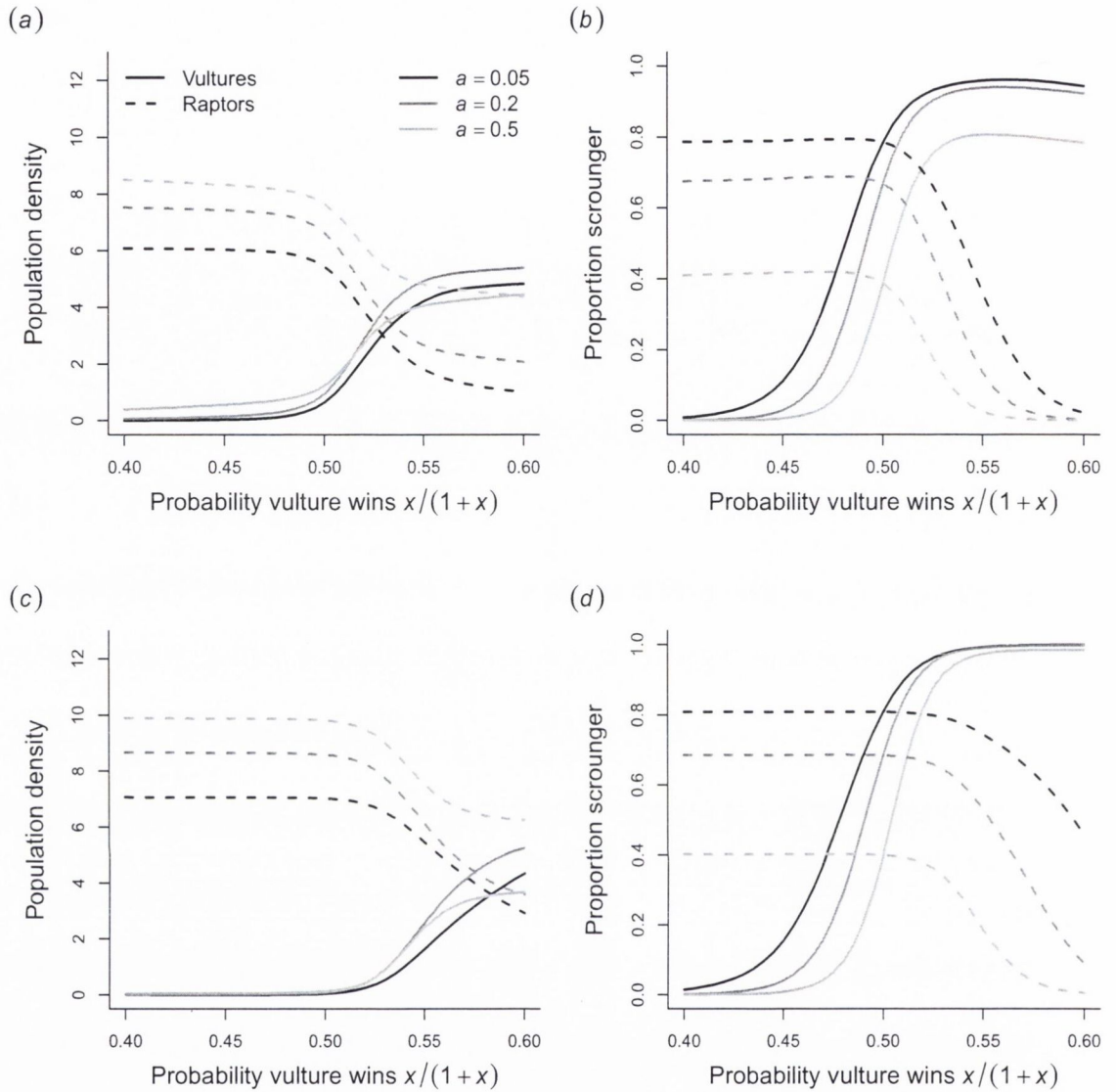


Figure 3.3: Game theory results. Panels on the left (a, c) are the population densities for each species (vultures, solid lines; raptors, dashed lines), panels on the right (b, d) are the frequencies of scroungers in both the vulture and raptor populations. The top panels (a, b) are where raptors rely strongly on carcasses ($\gamma = 0.05$); the bottom panels (c, d) are when they rely more weakly on carcasses ($\gamma = 0.15$). Colours indicate different values for the finder's fee (black, $a = 0.05$; dark grey, $a = 0.2$; light grey, $a = 0.5$). The x-axis is the probability that a vulture wins a one on one interaction, $x/(1+x)$. Mortality rates are $\alpha = 0.1$ and $\beta = 0.1$ for all panels.

3.5 Test of competitive ability

The results of our model demonstrate the potential importance of competitive asymmetry in the evolutionary outcome of inter-guild producer-scrounger dynamics. To test our model prediction of competitive dominance by vultures we analysed competitive interactions between *Gyps* and raptor species at carcasses from our videos. We followed Bamford et al. (2010) in our analysis of agonistic interactions between the birds. In each case of aggression we noted the initiator, the winner and the loser. The loser was defined as a bird spatially displaced by the direct action of another individual. There were 461 interactions in total. We used a binomial generalized linear mixed model with video as a random effect to test the significance of the interactions (figure 3.4).

In support of our theoretical predictions we found vultures are more likely to be the initiator of an aggressive interaction ($n = 274$ Vs 187 , $\beta = 0.7414$, s.e. = 0.1987 , $p < 0.001$, probability = 0.68 , 95% C.I. 0.59 - 0.76 (figure 3.4 a)); vultures are more likely to win when they initiate the contest ($n = 265/274$, $\beta = 3.6942$, s.e. = 0.4134 , $p < 0.001$, probability = 0.98 , 95% C.I. 0.95 - 0.99 (figure 3.4 b)) and raptors are more likely to win when they initiate a contest ($n = 170/187$, $\beta = 2.4893$, s.e. = 0.3473 , $p < 0.001$, probability = 0.92 , 95% C.I. 0.86 - 0.96). The probability that a vulture wins when they initiate a contest is also significantly greater than the probability that a raptor wins when they are the initiator ($\beta = 1.2049$, s.e. = 0.4685 , $p = 0.0101$). Finally, vultures are more likely to win overall ($n = 282$ Vs 179 , $\beta = 0.9567$, s.e. = 0.2303 , $p < 0.001$, probability = 0.72 , 95% C.I. 0.62 - 0.80 (figure 3.4 c)).

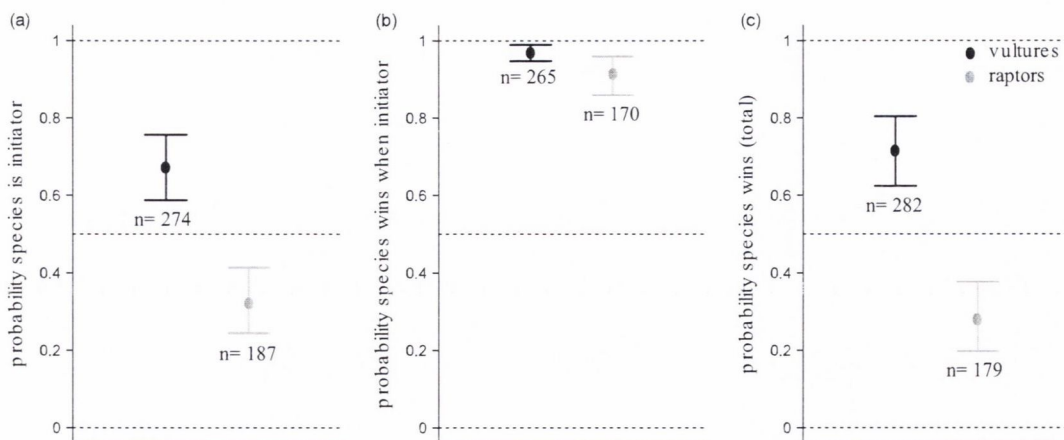


Figure 3.4: The results of the competitive interactions (a) shows the probability that a species was an initiator (b) the probability that an initiator wins a contest and (c) the overall competitive ability. Given are the means with 95% confidence intervals.

3.6 Effect of raptor density on vulture foraging efficiency

The producer-scrourer dynamics that we have illustrated suggest a possible ecological interaction whereby vultures are using raptors to locate carcasses. This would imply that vultures may be vulnerable to declines in raptor populations as their ability to locate food will also decline. To examine this possibility we created an individual based model (IBM) in the program NetLogo (Tisue and Wilensky, 2004) to explore the effect of raptors on the foraging efficiency of the vultures. Our model is a modified version of Jackson et al. (2008) and Dermody et al. (2011), both of which examined vulture foraging behaviour. The main difference is that we include raptors alongside vultures. Our video analysis suggests raptors can find carcasses before vultures. The question is what is it about their biology that allows them to achieve this? A recent study found that Lappet-faced Vultures can discover carrion before African White-backed Vultures despite their smaller population size (Spiegel et al., 2013). We incorporate the changes they deemed likely to impact differential search efficiencies which are applicable to raptors, namely, visual acuity (Howland et al., 2004), flying height, roost departure time and dispersion of the birds at the start of the foraging day owing to different roost arrangements.

The eye of a Tawny Eagle has an axial length of 26.51 mm (c.f. African White-backed Vultures that measure 20.71 mm) (Howland et al., 2004). This gives a measure of visual acuity of 81.5 cycles m^{-1} (again c.f. African White-backed Vultures with a measure 57.5 m^{-1}) (Spiegel et al., 2013; Howland et al., 2004). So this species has better absolute and relative eyesight if we accept these measures, which is further increased by its probable lower flying height (Mundy et al., 1992). Moreover, raptors can depart earlier in the day owing to their lower wing loading relative to the larger *Gyps* vultures (2 kg Vs 5.5 kg) (Mundy et al., 1992). The social *Gyps* are also more densely aggregated at their roost sites (Mundy et al., 1992) relative to the solitary raptors. Vultures are also known to fly at great altitudes (Mundy et al., 1992). It has been noted that "producer individuals may fly low to increase their probability of detecting a patch when they fly over it" (Vickery et al., 1991). By flying above the producing raptors the vultures have the potential to notice any raptor that descends to a carcass. A typical altitude of 350 m and 300 m has been reported for the Rüppell's Vulture and African White-backed Vulture respectively (Mundy et al., 1992). Although the flying height of Tawny and Steppe Eagles is unknown, and despite having different flight styles, these species occupy a similar ecological niche to the Bateleur Eagle (*Terathopius ecaudatus*) which often feeds on carrion (Steyn, 1980). The Bateleur has been recorded cruising at a height of just 50 m above ground (Mundy et al., 1992). We can

justifiably make the assumption that the two raptors that predominate our data fly at a similar altitude while foraging or at least below that of the *Gyps* vultures.

A summary of the model runs can be seen in Table 3.1. At the beginning of the IBM the raptors were randomly allocated in the simulation space that corresponds to a square of 100 x 100 km with periodic boundary conditions so that a bird that flies off the edge of the square will reappear on the opposite side. The vultures are located in a single patch which represents their roost. The raptors forage for seven hours and the vultures five hours (Spiegel et al., 2013). The vultures change direction by 45 degrees once every eight minutes which is based on the time they spend in thermals (Xirouchakis and Andreou, 2009); since raptors are less dependent on thermals they change direction at double this rate. Both have a constant speed as they attempt to find a single randomly located carcass. Both vultures and raptors can find the carrion by themselves. We varied the relative detection distances between the groups such that they are equal; and then that raptors are 2, 3 and 4 times better. For each of these we varied the number of raptors from 1-10 relative to the 90 vultures present in the simulation (Table 3.1). Vultures can detect carrion at 1 km and other scavengers on a carcass at 4 km (Dermody et al., 2011; Pennycuik, 1972), the increase in the latter owing to local enhancement (Jackson et al., 2008). When a vulture discovers a carcass it 'feeds' on it with the model calculating the average amount of food eaten by the vultures at the end of the simulated foraging session. Each simulation was replicated 200 times. We square root transformed our dependent variable data so it would allow us to perform parametric tests and performed the analysis using linear models. Our simulation results show a significant increase in vulture foraging efficiency with raptor density (figure 3.5), indicating that declines in raptor numbers may lead to declines in vulture populations because of a reduced ability to find or open carcasses.

Table 3.1: Parameter values of the individual-based models that were written in NetLogo. The first row represents the case of equal detection distance between raptors and vultures; the second is where raptors can see twice the distance and so on. Enhanced range relates to instances where a local enhancement effect is at play, i.e. the carcass is already occupied by a bird.

No. rap	No. vul	Vul radius	Rap radius	Enhanced radius	Rap day	Vul day
0-10	90	1km	1km	4km	7hrs	5hrs
0-10	90	1km	2km	4km	7hrs	5hrs
0-10	90	1km	3km	4km	7hrs	5hrs
0-10	90	1km	4km	4km	7hrs	5hrs

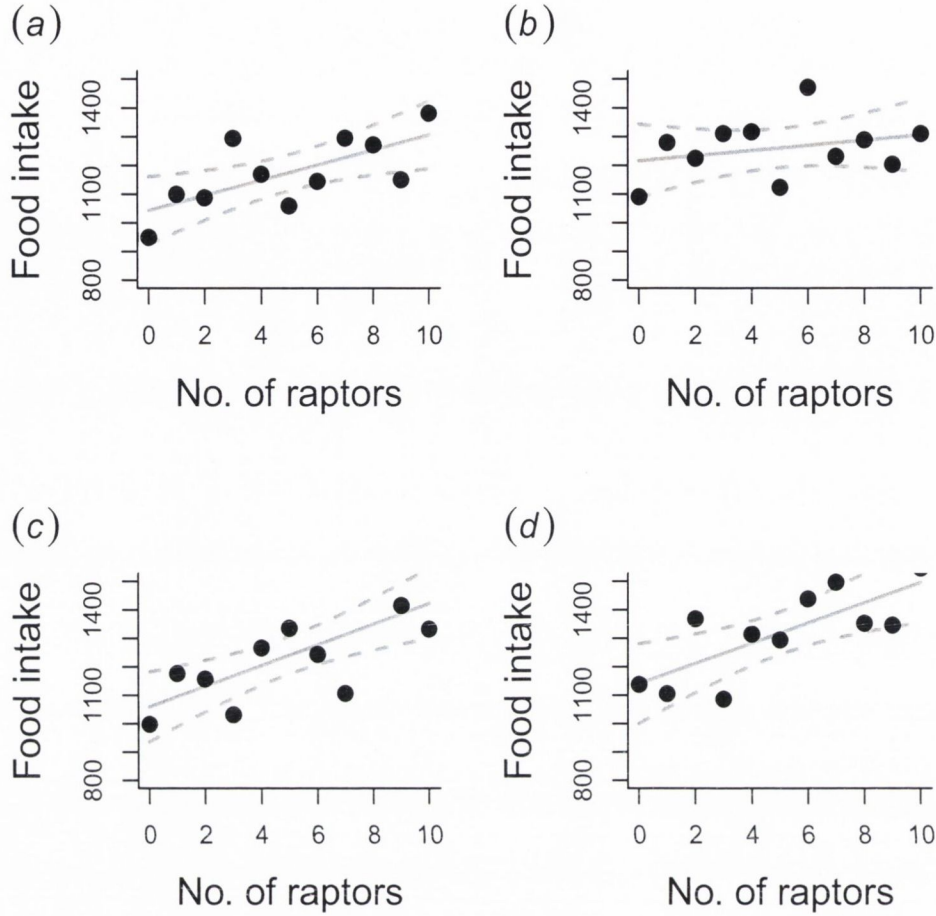


Figure 3.5: Mean vulture food intake (arbitrary units) as a function of raptor number for four scenarios of differing relative detection distance. (a) equal distance (GLM, $\beta = 0.3214$, s.e. = 0.1232, $p = 0.00916$), (b) twice distance (GLM, $\beta = 0.3269$, s.e. = 0.123, $p = 0.00794$), (c) triple distance (GLM, $\beta = 0.5047$, s.e. = 0.1198, $p < 0.001$), (d) quadruple distance (GLM, $\beta = 0.6052$, s.e. = 0.1254, $p < 0.001$).

3.7 Discussion

Our results suggest that there is a producer-scrouter game occurring between *Gyps* vultures and scavenging raptors, with the competitive dominance of vultures favouring a scrouting strategy on their part. The biology of the two groups further lends itself to the evolution of producer-scrouter dynamics. Flapping flight is far more energetically expensive than thermal soaring for large birds (Hedenstrom, 1993) and would prevent vultures from exploring a sufficient area to be effective scavengers (Ruxton and Houston, 2004b). Although raptors do exploit thermals as well, their relatively small size allows them

to use the weaker early-morning thermals compared with the larger vultures (Cone, 1962). Thus they are likely to encounter carrion before the vultures. Kendall (2013) found that, for their abundance, Tawny Eagles were more likely to discover a carcass than African White-backed Vultures, and Rüppell's Vultures were never the first to arrive at a carcass which is consistent with producer-scrounger dynamics. She also reported several cases whereby the African White-backed Vultures would not feed at a carcass until a Tawny Eagle began to eat. As mentioned earlier this may be an instance of carcass opening (Kendall, 2013). The *Gyps* vultures can then dominate the raptor and feed on the previously inaccessible flesh. This would certainly qualify as a producer-scrounger system. A potential follow up to this study would be to include more cameras or observers at the experimental carcasses to note the birds as they arrive from the air. This could be coupled with tracking data to get a better sense of the exact order of arrival of birds in the area. The proposed dynamics are not the result of an abundance of raptors happening upon carcasses more often than the vultures because raptors occur at much lower densities. In the Masai Mara, for instance, *Gyps* species were recorded at an average density of 85.4 species per 100 km compared with 7.4 for Tawny eagles (Virani et al., 2011).

In sum, we show that foraging behaviour in *Gyps* vultures is more complex than previously thought. Social information transfer flows within and among the vulture and raptor species. In conservation terms, the resultant non-trophic interactions (Kéfi et al., 2012) mean we should shift our focus to ecosystem-based management (Slocombe, 1993) instead of centring our attention on one species at a time. As our individual-based model shows, in the ecosystem considered here, scrounging vultures will fare poorly with a decline in producing raptors. With raptor populations on the decline (Ogada and Keesing, 2010), this effect may soon be realised. More generally, we should explore other incidences of socially acquired information transfer between species: inadvertent as it often is, this will be no easy task.

chapter 4

Are vulture restaurants needed to sustain the densest breeding population of the African White-backed Vulture?

Authors: Adam Kane, Andrew L Jackson, Ara Monadjem, M Angels Colomer & Antoni Margalida

Author contributions I conceived the idea, collected the data, incorporated the foraging radius model, helped develop the p-systems model, interpreted the results and wrote the manuscript; AJ gave input on the manuscript; AM supplied some data for carrion availability and gave input on the manuscript; MC created the analytical rules for the p-systems model and ran it; AMar developed the p-systems model and commented on drafts of the manuscript.

Status: This manuscript has been published at Animal Conservation.

4.1 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. By using novel Population Dynamics P-Systems we show that, despite a closure of supplementary feeding stations in Swaziland, carrion provided by wild ungulate biomass is currently enough to sustain this vulture species. However, in light of forecasted vulture population increases, food will become limiting. We discuss the significance of the cessation of the supplementary feeding sites which now forces these birds to forage farther afield, endangering them to poisoning events. We put these results in the context of carcass biomass management and suggest conservation actions to secure the viability of vulture populations and the important ecosystem services they provide. We argue that the reestablishment of vulture restaurants in Swaziland would lessen their exposure to hazards outside of protected areas.

4.2 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 carnivores are probably the group with the most evident adaptive traits to utilise carrion (DeVault et al., 2003; Wilson and 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 and Houston, 2002, 2004b). In sub-Saharan Africa, poisoning, food reduction and habitat loss are key threats to the avian scavenging guild (Monadjem et al., 2003). Thus the practice of providing supplementary resources is a common conservation tool (Piper et al., 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., 2010; 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 (Camiña and Montelio, 2006; Piper, 2005; Zuberogitia 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 and Garcelon, 2005). Historical data show that this AWBV population has increased during the latter part of the 20th century, the reasons for this are unclear (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 90s (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 (Monadjem, 2003). 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. Thus, we hypothesised 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.

4.3 Model building

4.3.1 *Study area and species*

The Hlane-Mlawula-Mbuluzi reserve network in Swaziland (figure 4.1) contains the majority (at least 202 nests) of the country's AWBV breeding population (Monadjem and Garcelon, 2005). Located in the east of Swaziland, the area is characterised as Lowveld Savanna (Acocks, 1988) with Acacia providing suitable nesting trees for the vultures (Monadjem and Garcelon, 2005). The rest of the nesting birds of this species are known from other non-contiguous conservation areas (approx. 12 nests at Mkhaya) and protected cattle ranches (19 nests at the Big Bend Conservancy and 6 at IYSIS) (Monadjem and Garcelon, 2005). AWBVs appear to actively avoid unprotected government ranches in the country for nesting, but their reason for doing so is unclear (Monadjem and Garcelon, 2005). In total, Swaziland is home to six other avian scavenger species (obligate and facultative) which take a considerable portion of their diet as carrion. These are the Cape Vulture (which forages but does not nest in Swaziland), the White-headed Vulture (*Trigonoceps occipitalis*), the Lappet-faced Vulture (*Torgos tracheliotos*), the Marabou Stork (*Leptoptilos crumeniferus*), the Tawny Eagle (*Aquila rapax*) and the Bateleur (*Terathopius ecaudatus*). The majority of the large ungulates in Swaziland (table 4.1) also live in this Hlane-Mlawula-Mbuluzi reserve (Monadjem et al., 2003).

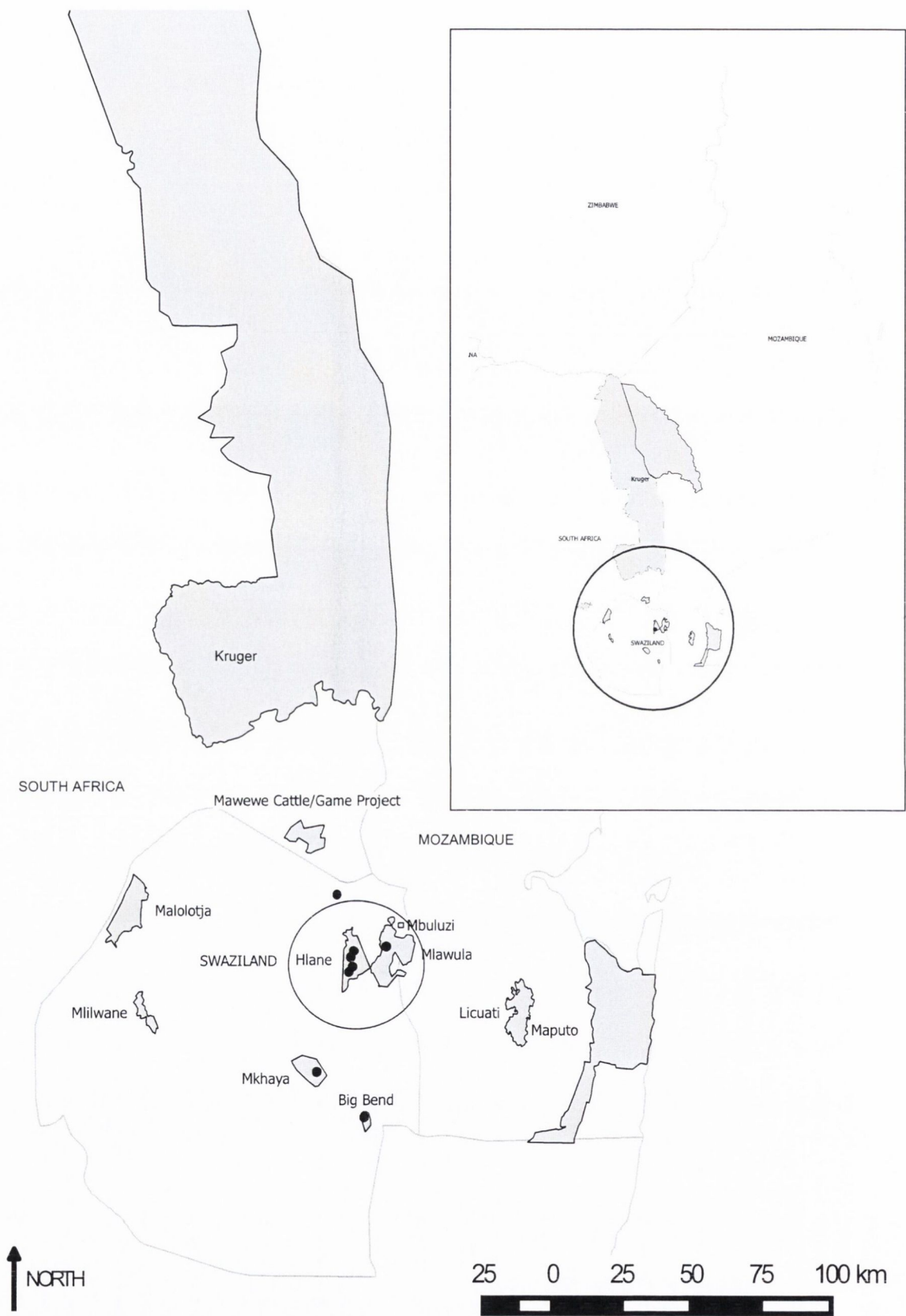


Figure 4.1: Foraging radius (45 km) of African White-backed Vultures when they have dependants on the nest. The points represent recorded nesting sites with Hlane as the origin of the circles. Some major national parks are highlighted. The inset shows the possible feeding range (260 km) when there are no young but the bird is still nesting in Swaziland.

4.3.2 Foraging radius

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 and Norton-Griffiths, 1995). The concept states that every animal is energetically constrained in terms of the spatial range they can cover while foraging (Sinclair and 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 and 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 Rüppell's vulture (*Gyps rueppellii*) which was used to estimate the foraging radius of that species (Ruxton and Houston, 2002):

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

We employed the same model and applied values from our focal species, the African White-backed Vulture where available. Q is the energy density of the carrion (5.2×10^{-6} J) (Ruxton and Houston, 2002); c is the bird's crop capacity (1.2 kg) (Houston and Cooper, 1975); d is the digestion rate ($0.055 \text{ kg hour}^{-1}$) (Ruxton and Houston, 2002); T is the foraging cycle (48 hours) 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 hr^{-1}) (Pennycuick, 1972; Tukcer, 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 hours) (Xirouchakis, 2007); E_{ma} and E_{mc} the adult and chick's metabolic rate respectively (24 Watts and 42 Watts) (Sinclair and Norton-Griffiths, 1995; Houston, 1976). 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.

During the period of nestling dependency the foraging radius of the breeding vultures is estimated at 45 km (figure 4.1). If we remove the cost of provisioning the chick it gives a value of approximately 260 km. Thus the foraging radius the vultures have during the time of nestling dependence restricts them to foraging in the national parks of Swaziland.

4.3.3 *Food requirements of avian scavengers*

The food requirements of individual African White-backed Vultures 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. African White-backed Vultures in Southern Africa typically begin nesting in May-June (Monadjem, 2003) and incubate their single egg for 56-58 days (Mundy et al., 1992). Once hatched the altricial chicks are dependent on their parents for a further four months whereupon they fledge from the nest (Mundy et al., 1992). The adults are therefore constrained as central place foragers for approximately six months of the year and for four of those they must meet with the additional cost of provisioning the chick. An adult African White-backed Vulture requires approximately 400g of food per day (Mundy et al., 1992). The nestling is fed by its parents for approximately four months of the year and consumes a total of 31kg of food during this time (an average of 258g per chick per day) (Mundy et al., 1992). Outside of the breeding season adult birds can range away from their typical nesting sites and may even roost in Kruger National Park (Monadjem pers. comm.). We followed the same approach for the other species in the Swaziland avian scavenging guild (table b.7). We also collected data on relevant life history traits such as age at sexual maturity and longevity (table b.1).

4.3.4 *Model parameters for ungulate carrion*

To determine carrion availability we collected the most recent ungulate population data covering all of Swaziland (Monadjem et al., 2003). Ungulate masses and life history traits such as adult and juvenile mortality were taken from the PanTHERIA database (Jones et al., 2009). We also considered the following: 1) 30% of ungulate mortality is due to direct predation (Sinclair and Norton-Griffiths, 1995), this is significant because vultures very rarely feed on predator kills and most large mammalian predators are absent from Swaziland (Houston, 1974; Monadjem et al., 2003); 2) 55% of a carcass is edible by AWBVs (Sinclair and Norton-Griffiths, 1995) because this species consumes the viscera and soft muscles (Kruuk, 1967); 3) 15% of the edible carcass is consumed by invertebrates and bacteria (Sinclair and Norton-Griffiths, 1995); 4) AWBVs avoid montane environments (cf. Cape Vultures, *Gyps coprotheres*) and as such the ungulate population in the Highveld of Swaziland could be discounted from the total carrion available (A. Monadjem unpubl. data.); 5) the total carrion available annually in Swaziland is not evenly spread throughout the year; the dry season of May to August claims approximately half of the ungulate dead

(Sinclair and Norton-Griffiths, 1995). Therefore, only half of this total is spread over the remaining eight months; and 6) Given that the ungulates are contained within actively managed reserves, where culling takes place, we set the population of each species as constant using the surveyed numbers reported by Monadjem et al. (2003).

4.3.5 Population dynamics P system model

Using this information we developed a population dynamics P system (PDP) model (Colomer et al., 2013). This integrated data on food availability, food requirements and population dynamics of the avian scavenging guild and the ungulate populations of Swaziland 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 (De Magalhaes and Costa, 2009). PDP models are computational methods that are analogous to the machinery of cells (Colomer et al., 2013).

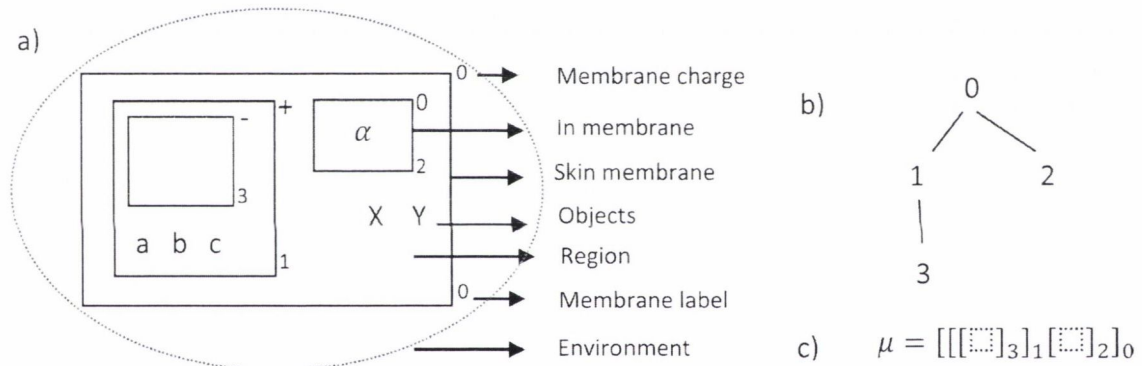


Figure 4.2: Schematic of P-system cell showing a) the cell and its components b) the hierarchy of the membrane structure and c) how this structure is written analytically. Figure is taken from Colomer et al. (2013).

The analogy of a PDP system to a real ecosystem has been drawn before (Colomer et al., 2013, 2011; Margalida et al., 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 (figure 4.2). Animals (which, along with things like 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) so 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 supplementary 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 and Colomer, 2012). The syntax of the model rules take the following form:

$$r \equiv (x)_{e_j} \xrightarrow{p(r)} (y_l)_{e_{jl}}$$

This is an example of a rule describing the movement of an object x (e.g. an animal) from environment e_j to e_{jl} where it becomes object y (e.g. a mature version of an animal). The $p(r)$ element is a function stating the probability of the rule taking place (Colomer et al., 2013). The symbol $\equiv$ means the rule is equal by definition to what follows. The model was implemented in the program MeCoSim (Pérez-Hurtado et al., 2010). Please see the supplementary information for the rules of this model.

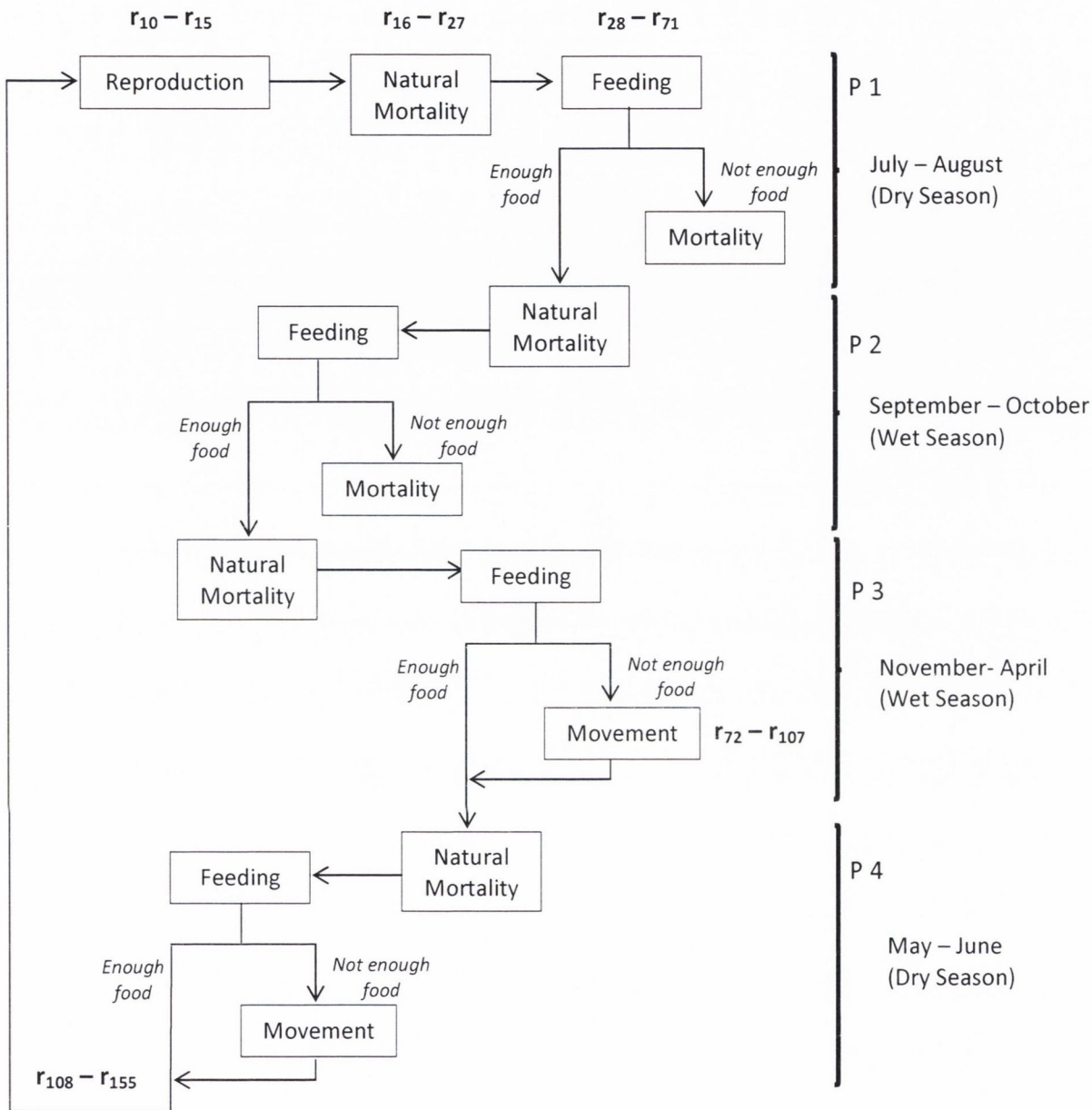


Figure 4.3: Flow diagram representing changes in the status of the avian scavengers over time. The italicised text show conditionals for food availability which determine the path the birds can take. Starting at the 'Reproduction' stage at the upper left hand side this represents the point at which the birds have their young. They 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. Some of the explicit model rules are highlighted at the boxes for movement, reproduction, mortality and feeding. These are described in detail in the supplementary material chapter for this section. Note that not all rules are laid out here such as those involved in the setup and resetting of the model.

Table 4.1: Identity, number of species and average carrion provided per year of the ungulate population of Swaziland.

Species	Initial pop size	Avg carrion/year (kg)	% of total
<i>Aepyceros melampus</i>	16500	48233	32.92
<i>Connochaetes taurinus</i>	1700	18666	12.74
<i>Equus burchellii</i>	1500	13277	9.06
<i>Phacochoerus aethiopicus</i>	2300	12792	8.73
<i>Loxodonta africana</i>	40	11439	7.81
<i>Tragelaphus strepsiceros</i>	1300	10040	6.85
<i>Ceratotherium simum</i>	50	8570	5.85
<i>Giraffa camelopardalis</i>	80	4909	3.35
<i>Tragelaphus angasii</i>	1000	4232	2.89
<i>Kobus ellipsiprymnus</i>	260	4174	2.85
<i>Hippopotamus amphibius</i>	25	3977	2.71
<i>Syncerus caffer</i>	40	1478	1.01
<i>Taurotragus oryx</i>	40	1285	0.88
<i>Tragelaphus scriptus</i>	250	701	0.48
<i>Sylvicapra grimmia</i>	550	564	0.38
<i>Redunca arundinum</i>	120	480	0.33
<i>Hippotragus niger</i>	20	419	0.29
<i>Redunca fulvorufula</i>	200	365	0.25
<i>Hippotragus equinus</i>	7	365	0.25
<i>Damaliscus lunatus</i>	16	209	0.14
<i>Oreotragus oreotragus</i>	200	123	0.08
<i>Raphicerus campestris</i>	140	95	0.06
<i>Cephalophus natalensis</i>	80	55	0.04
<i>Ourebia ourebi</i>	50	52	0.04

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 (figure 4.3). This restricts the birds to game reserves in Swaziland when they have a reduced foraging potential. A bird outside 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, Period 4 = May-June. These periods reflected differences in food availability, in foraging ranges and in food requirements (table b.8).

4.4 Results

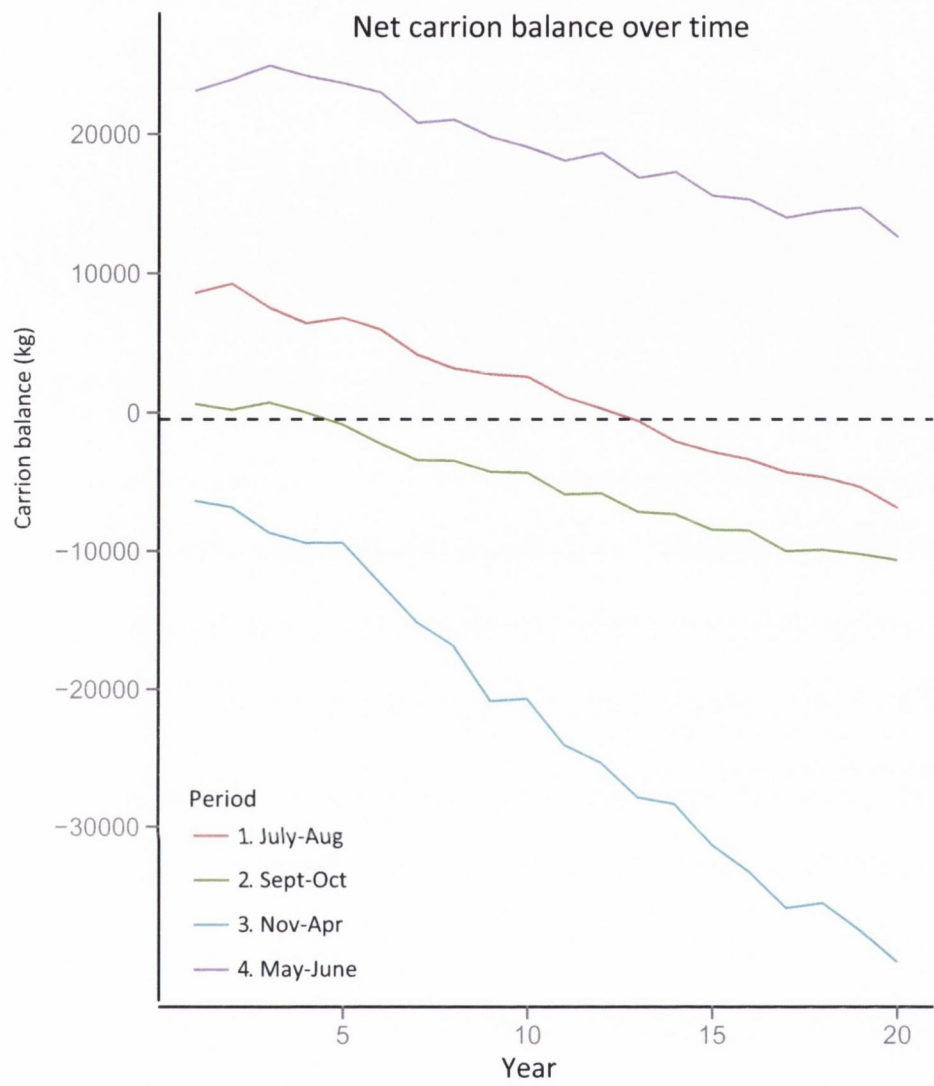


Figure 4.4: Carrion balance across time in the different periods of the year. The horizontal bar represents the point below which the demands of the avian scavenging guild are no longer met by the carrion provided by wildlife in Swaziland. Periods 1 and 2 are the life stages when young are present and food requirements are higher as a result.

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 burchellii*) (9 %) with the remaining 21 species contributing the remaining carrion (table 4.1). Initially, only period 3 (from November to 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 (figure 4.4). 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) (figure 4.5).

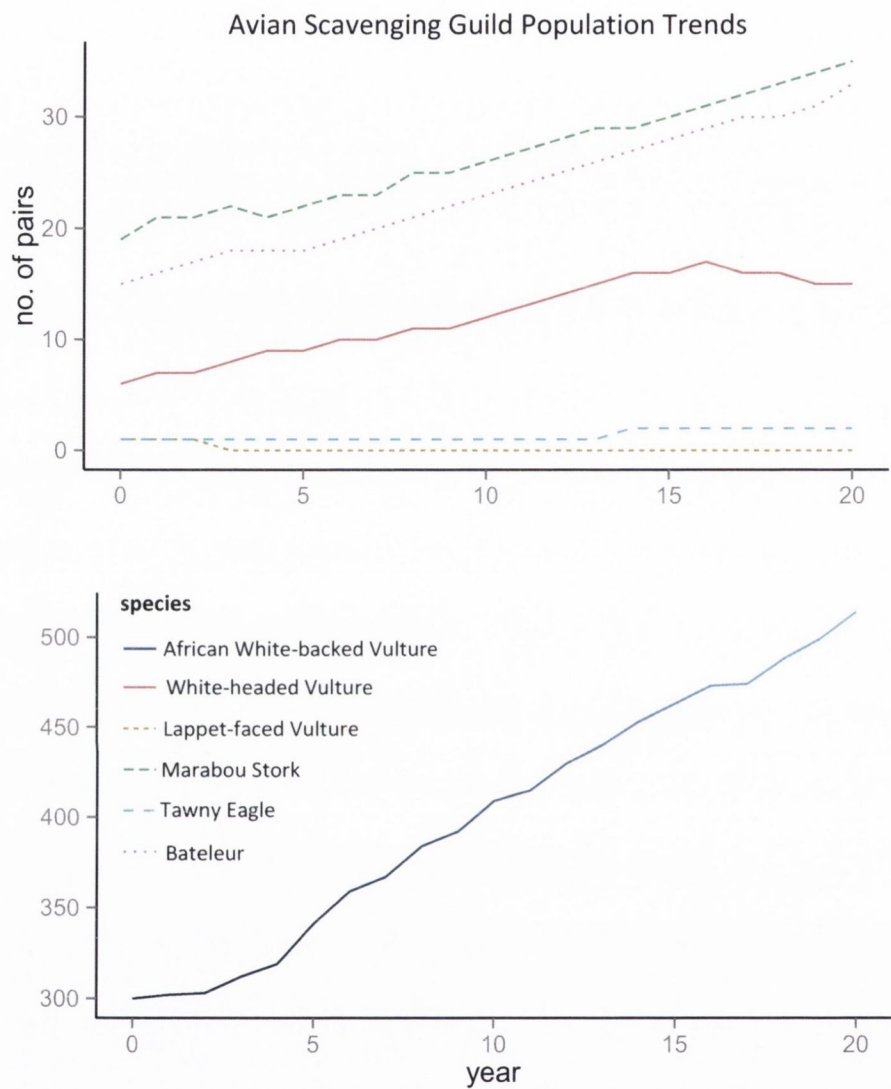


Figure 4.5: Number of pairs of avian scavengers living in Swaziland across time. All species except the Lappet-faced Vulture see a population increase due to the amount of wild carrion available. This one extinction occurs owing to its tiny initial population size. The bottom panel shows the AWBV trend separately for reasons of clarity because of its much larger population size.

4.5 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 (figure 4.5), but only for the time being (figure 4.4). 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-April (figure 4.5). 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, like poisoning, with important consequences on population dynamics if adult survival is affected (Monadjem et al., 2014). 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 authorised 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 et al., 2014a).

We can be confident in our predictions given that 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 AWBVs showed a mean distance travelled per day of 33.39 km (Phipps et al., 2013a). 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 and 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.

This indicates that the original vulture restaurants in Swaziland that have since closed were not necessary in terms of providing food. However this is not to say they are unneeded. Indeed, these findings suggest further intervention, and modification of existing strategies will be required. Vulture 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 system could minimise these issues while maximising the benefits. For instance a study of *Gyps fulvus*, showed "[f]eeding stations were particularly used when resources were scarce (summer) or when flight conditions were poor (winter), limiting long-ranging movements" (Monsarrat et al., 2013). Supplementary feeding can minimise the risk of poisoning (in-

creasing survival) that follows from species foraging outside of protected areas which has been documented in other vulture species (Oro et al., 2008). 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 (figure 4.4) 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 country (Monadjem et al., 2003). Tracking data would improve our knowledge about these issues allowing managers and policy-makers to adopt more objective decisions based on the evidence. The value of theoretical modelling, like PDP P systems, is also underscored by the results generated in this study and others like it (Margalida and Colomer, 2012; Margalida et al., 2011). We should note that any model is only as good as the data used to parameterise 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 are that the carrying capacity of African White-backed Vultures 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.

chapter 5

Did *Tyrannosaurus rex* tend towards scavenging with age?

Authors: Adam Kane, Kevin Healy, Graeme Ruxton & Andrew Jackson

Author contributions I conceived the idea, collected the data used for the scaling relationships, created and ran the IBM, interpreted the results and wrote the manuscript; KH collected the data used for the scaling relationships, calculated their output, helped with interpretation of results and commented on the manuscript; GR supplied data and commented on an early draft of the manuscript; AJ gave feedback on the manuscript.

Status: This manuscript is being prepared for publication. Target journal is *Biology Letters*.

5.1 Abstract

The feeding ecology of *Tyrannosaurus rex* remains controversial, with polarised suggestions of either a predatory or scavenging lifestyle. We move away from this dichotomy and propose the animal incorporated more carrion in its diet as it aged. We hypothesise this to be the case owing to factors related to its drastic morphological change across ontogeny notably an increased availability of carrion through dominance of interspecific competitors at carcasses; by exploiting resources unavailable to its smaller competitors such as skeletal material; and by having a larger capacity to store meat as it grew. We develop an individual based model to address our question. Surprisingly, our results show *T.rex* was very unlikely to have specialised on carrion at any life stage because the cost of movement would have been prohibitively expensive as it increased in mass. In spite of our suggested advantages, scavengers require a more economical model of locomotion while foraging than *T.rex* could have managed.

5.2 Introduction

Animals can avoid direct competition with conspecifics by foraging at different times and locations, or by targeting different resources. This partitioning of resources can occur across ontogeny when the life stages are distinct; so, for example, an agile juvenile may focus on smaller, faster prey than a less nimble adult. Ontogenetic dietary partitioning is known across a diversity of species including crocodiles, insects, fish etc. (Platt et al., 2006; Winemiller, 1989; Steyn, 1980; Hirai, 2002; Knoff et al., 2008) and is often related to changes in body size (Woodward and Hildrew, 2002) but can also arise through other means such as different habitat use patterns (Carrier et al., 2010). Here we suggest that such partitioning may have taken place in the theropod dinosaur *Tyrannosaurus rex*. *T. rex* fits into theropod 'morphotype one' as defined by Weishampel (Weishampel et al., 2004). The carnivorous animals in this category are extremely large, exceeding 10 m in length, have huge skulls, short forelimbs and as such have no living analogues which makes it difficult to draw any conclusions about their mode of life (Weishampel et al., 2004). However, as a species, *T. rex* is atypical because of the large number of fossils available for study (Brusatte et al., 2010). So, for instance, it is known that it exhibited remarkable rate of growth through its development (Brusatte et al., 2010) and underwent dramatic ontogenetic changes in its morphology which has led some researchers to argue for a concomitant change in its ecological habits (Brusatte et al., 2010). For instance, adults had a powerful, deep, robust skull with thick teeth in contrast with the more gracile features of juveniles. One suggested result of this change was a dietary shift from fast prey items to larger more cumbersome herbivores (Brusatte et al., 2010). However, we instead explore whether such marked changes caused an increased tendency towards scavenging given that a scavenging lifestyle has been proposed for the animal in recent times (Horner and Lessem, 1993; Ruxton and Houston, 2004b).

Ruxton and Houston (2004b) argue there is a "a clear evolutionary pressure towards large size for both birds and mammals when they are feeding on large carcasses. This is largely because larger animals can consume more food from each discovered food fall, and carry greater body reserves, than can small ones." A pressure that lends support to our proposal. Indeed, a number of recent studies have looked at the theoretical possibility of obligate scavenging across species including *T. rex* (Ruxton and Houston, 2004a; Ruxton and Wilkinson, 2013; Ruxton and Bailey, 2005; Ruxton and Houston, 2004b, 2003; Carbone et al., 2011). For example, Horner pointed to its slow speed, reduced forearms, large olfactory bulb and incredible bite force, to support this view (Horner, 1994;

Horner and Lessem, 1993). Brown hyenas (*Hyaena brunnea*) can detect carcasses 2 km downwind (Mills, 1984) and the olfactory bulbs of *T. rex* indicate an impressive ability in this respect (Witmer and Ridgely, 2009). Fossil material from a herbivore has also been discovered with bite marks located in a flesh-poor region suggesting a scavenging event after the preferred sections of the animal were consumed (Longrich et al., 2010). Energetic approaches have concluded both for (Ruxton and Houston, 2003) and against (Carbone et al., 2011) *T. rex* being a scavenger. The latter study argued that interspecific competition would undermine the possibility of a scavenging *T. rex* since smaller, more numerous competing species would find and consume any carcass before the larger *T. rex* could benefit. Obligate scavengers are rare among terrestrial vertebrates with even the most common terrestrial example, the brown hyena, displaying a large degree of variation between scavenging behaviour and active predation (DeVault et al., 2003; Sinclair and Norton-Griffiths, 1995). Instead, most carnivores are opportunistic and will take carrion as well as actively hunting prey (DeVault et al., 2003) and mounting evidence suggests that *T. rex* behaved similarly to extant opportunistic predators such as hyenas. The most compelling evidence for a predatory lifestyle comes in the form of a subadult *T. rex* tooth that was found embedded in a hadrosaur tail (DePalma et al., 2013). The wound had healed around the tooth indicating that the prey item escaped and so this was an active predation attempt (DePalma et al., 2013).

In this study we move away from the polarised predator-scavenger debate and look at the possibility that *T. rex* underwent an ontogenetic dietary shift, increasing the proportion of carrion in its diet as it aged. We hypothesise this to be the case on the basis of increased availability of carrion through domination of interspecific competitors at carcasses, by exploiting resources unavailable to its smaller competitors and by having a larger capacity to store meat as it increased in size ontogenetically. This shift would not only see adult *T. rex* avoiding intraspecific competition with younger conspecifics but also with interspecific carnivores of the time. Among contemporary competitors from the Late Maastrichtian Hell Creek formation, the one tonne *Albertosaurus* may have been an immature *T. rex* and *Troodon* and other dromaeosaurids were wolf-sized creatures that would be easily dominated by an adult *T. rex* (Horner et al., 2011; Carr and Williamson, 2004; Farlow and Planka, 2002). Their small size also means they would leave much of the skeletal material of prey/carcasses untouched. However, as alluded to earlier, the morphology of an adult *T. rex* skull suggests an ability to process bone which would be a great boon to a scavenging animal if it were capable of monopolising this resource. Direct evidence comes in the form of distinctive wear marks on its tooth apices (Farlow and

Brinkman, 1994; Schubert and Ungar, 2005). The animal also had an enormous bite force, with one estimate putting it at 57000 Newtons (Bates and Falkingham, 2012). This is noted as being powerful enough to break open skeletal material during feeding (Rayfield et al., 2001). A positive allometric scaling relationship in bite performance during ontogeny has also been recorded (Bates and Falkingham, 2012). This is a similar pattern to that observed in loggerhead sea turtles (*Caretta caretta*) where the bite force exhibits positive allometry across ontogeny allowing adults access to hard benthic prey, a resource inaccessible to other durophagous competitors (Marshall et al., 2012). Further, *T. rex* coprolites were discovered with bone fragments, *prima facie* evidence that it did consume bone (Chin et al., 2003). Osteophagy is known in extant taxa such as the Bearded Vulture (*Gypaetus barbatus*) and hyena species (Hone and Rauhut, 2010). Some fat-rich mammalian bones have an energy density (6.7 kJ/g) comparable with that of muscle tissue (Margalida, 2008; Brown, 1989), making skeletal remains an enticing resource for any scavenger that could process them.

We use an energetics method based on a series of scaling relationships to look at how the energy balance of *T. rex* changed across ontogeny and test whether this could have pushed it towards obligate scavenging. We parameterise an agent-based model which better captures the impact of competition than the numerical approaches of previous studies.

5.3 Methods

5.3.1 Model parameters

We took estimated parameter values from the literature for mass (kg), hip height (cm), detection distance (km), search time (fraction of day), energy content of bone (kJ/kg), energy content of flesh (kJ/kg), density of carcasses (kg/km²/day), the size of competitors and the size of carcasses etc. to estimate several scaling relationships describing theropod foraging behaviour including walking speed (m/s), basal metabolic rate (W) and cost of transport (J/m). This is basically an 'energy in' minus 'energy out' calculation i.e. net energy gain (table 5.1).

Table 5.1: Model parameters and their values for *T.rex* foraging models.

Parameter	Values	Reference
Transport cost (J)	$90.284 \times \text{hip height (cm)}^{-0.77}$	(Pontzer et al., 2009)
Hip height (cm)	Ref. lists hip heights	(Pontzer et al., 2009)
Metabolic type	Mesothermic	(Grady et al., 2014)
Mass (kg)	100-10,000	(Henderson and Snively, 2004)
Walking speed (m/s)	Froude's no. = 0.25	(Pontzer et al., 2009)
Detection distance (m)	500	(Ruxton and Houston, 2003)
Search time (fraction of a day)	0.5	(Ruxton and Houston, 2003)
Bone energy (kJ/kg)	6700	(Brown, 1989)
Flesh energy (kJ/kg)	7000	(Brown, 1989)
Carrion density (kg/km ² /day)	4.38	(Ruxton and Houston, 2003)
Scaling of skeletal to body mass (kg)	$0.065 \times \text{mass}^{1.071}$	(Prange et al., 1979)
Gut capacity (kg)	$0.075 \times \text{mass}^{0.94}$	(Calder, 1996)

The daily costs of theropods of various masses were derived using the scaling relationship of mesothermic dinosaurs from Grady et al. (2014) for basal metabolic rates. We used these for the *T. rex* ontogenetic stages. We then took the scaling relationships outlined in Pontzer et al. (2009) to calculate the cost of searching during foraging. This was estimated using the mass-specific locomotor cost of transport that is based on the hip height of the animal, its mass and its speed to calculate the cost of searching over a 12 hour day (table 5.1). Specifically, the cost of transport, in joules, is the energy required to move 1 kg of mass over 1 metre. From this we can calculate the cost for the whole animal: cost of transport x mass x walking speed (table 5.3).

We used an estimate of energy density of carrion from the Serengeti as an analogue for terrestrial Mesozoic systems (Ruxton and Houston, 2003; Carbone et al., 2011). The amount of food available is derived as a function of the energetics of the food source. The energy available from the carcasses in flesh and bone was calculated using allometric scaling relationships (table 5.1). We used the size bins of a previous study for both the body mass of the prey items and the predators (table 5.2) (Carbone et al., 2011). So for example, 49.3% of carrion mass is packaged up in 75 kg carcasses. Carbone et al. (2011) use mass-abundance relationships (e.g. Damuth's Law) to determine the actual population size of the various species and we followed their approach here.

Table 5.2: Mass categories for carcasses and allometric scaling of bone with body mass across carcass categories. The contribution column defines the percentage of carrion that is made up by a given species category.

Species	Carcass mass (kg)	Bone mass (kg)	Contribution (%)
<i>Thescelosaurus neglectus</i>	75	6.62	49.3
<i>Ornithomimus velox</i>	216	20.56	36.8
<i>Pachycephalosaurus wyomingensis</i>	700	72.45	6
<i>Edmontosaurus annectens</i>	2500	283.21	6.7
<i>Ankylosaurus magniventris</i>	5000	594.99	0.6
<i>Triceratops horridus</i>	8500	1050.32	0.4
<i>Alamosaurus sanjuanensis</i>	25000	3335.09	0.2

Table 5.3: Mass categories, gut capacities, walking speeds and daily energetic cost for the ontogenetic stages of *T. rex* and its competitors as used in the individual-based model.

Species	Mass (kg)	Gut capacity (kg)	Speed (km/hr)	Cost (kJ/day)
<i>Tyrannosaurus.rex</i>	100	6	4.8	28000
<i>Tyrannosaurus.rex</i>	500	26	6.2	110000
<i>Tyrannosaurus.rex</i>	1000	50	6.8	200000
<i>Tyrannosaurus.rex</i>	2000	95	7.6	370000
<i>Tyrannosaurus.rex</i>	4000	182	8.5	670000
<i>Tyrannosaurus.rex</i>	6000	267	9.1	960000
<i>Tyrannosaurus.rex</i>	10000	432	9.8	1500000
<i>Dromaeosaurus albertensis</i>	20	1.25	3.6	N/A
<i>Troodon formosus</i>	50	3	3.6	N/A
<i>Albertosaurus sarcophagus</i>	1100	54	6.8	N/A

5.3.2 Individual-based model

We created a spatially explicit agent-based model using the above calculated parameters to allow us better understand the effect of competition on the ontogenetic stages of *T. rex* if they were restricted to scavenging (table 5.2). Our model was designed in the program NetLogo (Tisue and Wilensky, 2004). The simulation space was a 50x50km square corresponding to a 2500km² landscape. Unfortunately, it is not clear if there was a habitat partitioning across ontogeny in *Tyrannosaurus* which may have implications for factors such as transport costs (Ruxton and Wilkinson, 2014).

The model had a series of mobile agent types which corresponded to *T. rex* ontogenetic stages and its competitors (table 5.3). There was one *T. rex* ontogenetic stage per run e.g.

a 100 kg individual. The initial state of the model had all dinosaurs and carcasses located randomly in the environment. The dinosaurs then set off in a random direction at their assigned speed searching for carrion (table 5.3). They maintained the same walking speed for the duration of the model and had a constant turning rate. Upon finding a carcass in its visual field (500 m) the *T.rex* walked towards it and started to feed, extracting energy until sated as defined by its gut capacity (table 5.1) or until the carcass was consumed. The competitors behaved similarly only they were incapable of feeding on the bones of carcasses. If nothing remained for the animals to eat and they were not entirely sated they began to forage again. If they were full they moved away from the carcass and wandered until the next day whereupon their gut capacity went back to 0. The gut passage time of *T.rex* is difficult to ascertain but we know it was relatively quick given the state of consumed material in its coprolites (Chin et al., 1998, 2003). Without being fed upon, a carcass decayed down to bone and then to nothing because of mammalian scavengers, invertebrates, bacteria etc. (Sinclair and Norton-Griffiths, 1995). This process took seven days (Carbone et al., 2011). Competition in our model followed a simple, 'if bigger than me, then avoid' rule, and applied to the interaction between the *T.rex* life stages and their competitors. A foraging day in our model was 12 hours. At the end of the day the 'energy in' of the *T.rex* was subtracted from the 'energy out' (table 5.3). We ran the model for 200 days for each of the seven *T.rex* life stages.

5.4 Results

Our results show that under the conditions of our model *T.rex* was in negative energy balance if it were an obligate scavenger. We can see from figure 5.1 that, in contrast to our hypothesis, the net energy intake of *T.rex* from scavenging decreases with their body mass. The horizontal dashed line represents the point where the energy out is balanced by the energy in. Even the average of the smallest ontogenetic stage (a 100 kg individual), falls below this line.

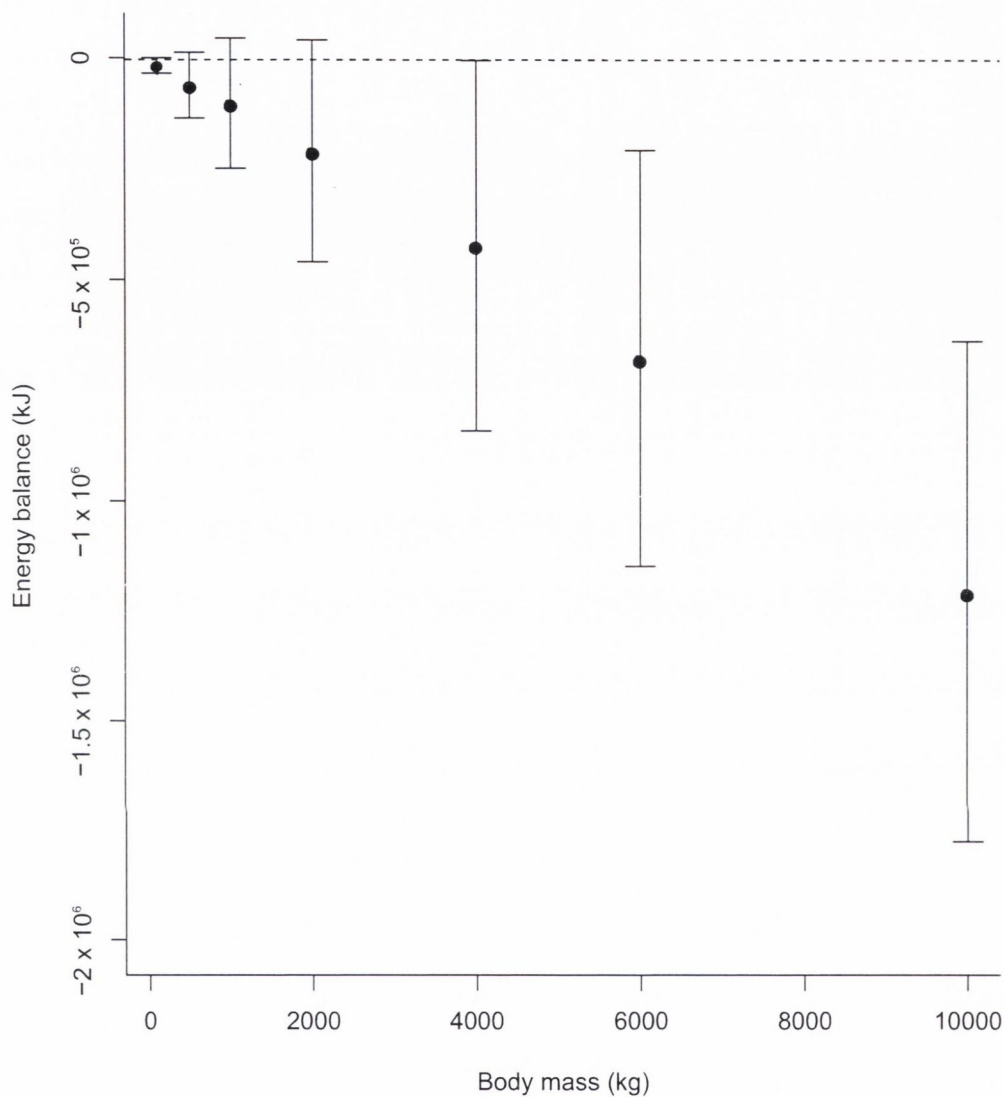


Figure 5.1: The energy balance of the *T. rex* ontogenetic stages. The dashed horizontal line represents the point, below which, the animal has a negative energy balance. Each point in the figure is the mean of the 200 day model run for the given body size with its standard deviation.

5.5 Discussion

In order to be an effective terrestrial vertebrate scavenger an animal must be able to traverse huge distances at low cost (Ruxton and Houston, 2004b). This is why soaring flight allows vultures to occupy the obligate scavenger niche. The cost of locomotion seems to be one of the main barriers precluding *T. rex* from being an obligate scavenger.

A lot of energy would have been required to propel an eight tonne adult around its habitat in search of a patchily distributed resource. The increasing variation in energy balance seen in figure 5.1 is a result of gut capacity and carcass size distributions. The smaller individuals can fill their gut to capacity every time they encounter a carcass; by contrast the larger animals will only rarely encounter a carcass of sufficient mass to sate them entirely. As such it would be interesting to investigate the effect of different carcass mass distributions on *T.rex* scavenging behaviour. Our model is limited in depending on data from long extinct ecosystems. Consequently there are many unknowns. We do not know how carrion was distributed for instance or if there was habitat partitioning across the ontogeny of *T.rex*. The costs of movement for the *T.rex* stages are based on the most recent studies of dinosaur metabolism (Grady et al., 2014) but it is unlikely that we will ever know the species level adaptations that some animals had such as the ability of vultures to decrease their metabolic rate at night (Ruxton and Houston, 2002). However, the model is flexible and sensitivity analyses can be readily performed to account for the large margin of error when dealing with prehistoric systems. A development of the model could allow for differing detection radii and turning rates for example.

Ecologically, *T.rex* was unusual. Census records show it to have had a population higher than would be expected for a typical apex predator suggesting that its mode of life was atypical with Horner and colleagues positing a hyena-like niche for the animal (Horner et al., 2011; Mills, 1984). The radical change in morphology with ontogeny would then appear to represent a dietary niche shift which has been suggested previously (Brusatte et al., 2010). The change from a gracile to robust form may have allowed the animal to switch its targets from small prey items to the huge armoured herbivores of the time (table 5.2). Species such as *Triceratops* and *Ankylosaurus* would have made formidable opponents for a predaceous *T.rex*. To be able to dispatch such prey items quickly with its enormous bite force would be of great advantage. It has been suggested that an ambush strategy seems the most probable gambit it used to hunt (Krauss and Robinson, 2013). It could rush from cover and use its arms to hold a prey item while biting it (Krauss and Robinson, 2013). This is not to discount scavenging entirely. Such was its likely competitive dominance *T. rex* may well have been an effective kleptoparasite. Spotted hyenas (*Crocuta crocuta*) can get over a quarter of their carcasses by stealing from other predators (Curio, 1976). Although we have framed our study such that it focuses on *T.rex*, the same energetic barriers likely prevented other theropods in the morphotype one category (Weishampel et al., 2004) from evolving into scavenging specialists.

6.1 How the environment selects for scavengers

The resource environment of a scavenger is a patchily distributed one, because it is difficult to predict both when and where a carcass is produced. As a result of this, any animal existing as a scavenger must maximise its detection capabilities and minimise its locomotory costs. The ease with which natural selection pushes an animal towards these optima is dependent on the environment the species is in. Land-based scavengers can be thought of as existing in a 2-dimensional plane while foraging for carrion directly. The range at which they can detect carcasses is thus defined by the radius of their sensory organs, usually the visual and olfactory senses which is further modulated by the habitat type. By flying, vultures have effectively added an extra spatial dimension, i.e. the vertical component, to their sensory environment. This allows them to look down on a landscape where they are unencumbered by obstacles that would obstruct the view of a terrestrial scavenger. Interestingly, animals like hyenas can and do take advantage of the directed flight of vultures because it indicates they have discovered a carcass (Sinclair and Norton-Griffiths, 1995). But this is an indirect method of detection and, as I showed in chapter 2, scrounging is also utilised by vultures. Vultures have a further advantage in improving their encounter rate in terms of cost of movement. In general, flight is a cheaper means of locomotion than running (Tucker, 1975), but vultures extend this advantage further by engaging in soaring instead of flapping flight, which is even cheaper energetically (Hedenstrom, 1993). Thus, as we saw from the results of chapter 1, they can cover huge distances over the course of a day, something I showed was impossible for *T.rex* in chapter 4.

In ancient ecosystems, the volant pterosaurs have also been postulated as occupying a vulture-like niche (Witton and Naish, 2008). These animals could reach enormous sizes and look to have engaged in soaring flight (Witton and Naish, 2008). So they certainly existed in an environment that can support scavengers. However, the inflexibility of their necks and straight, rather than hooked jaw morphology argues against their existing as obligate scavengers (Witton and Naish, 2008). As yet, no one has ever attempted an

energetics approach for this group. This is likely due to the many uncertainties over their biology (Witton and Habib, 2010); which is even more difficult to predict than that of the dinosaurs.

It is worth noting that the existence of an obligate scavenger in a marine setting also remains hypothetical (Britton and Morton, 1994; Ruxton and Houston, 2004a). Carrion in this environment is produced by dead fish and marine mammals when their carcasses descend to the sea floor. This low-light environment means animals detect resources through chemo- and mechanoreception (Ruxton and Houston, 2004a). Detection distances are far lower than they would be in the air (< 100 m) as a result. However, water is a medium that is conducive to low-cost movement (Tucker, 1975) and so may be able to support a small obligate scavenging fish which would gain the further benefit of low-cost ectothermic metabolism (Ruxton and Houston, 2004a). Although, for the time being this remains conjectural.

In sum, it seems that aerial foraging allows for a better medium for locomotion and grants access to more information on the location of resources. Natural selection has driven vultures to occupy a niche in which only the most specialised of species could exist.

6.2 All models are wrong

My thesis has a variety of models, which focus on different biological scales, from the individual to the population. I would like to discuss my philosophy of modelling in light of these methods. Norgaard (1989) argues the case for methodological pluralism when we are dealing with complex systems. And this seems to me to be the right approach for ecology which is clearly a study of complexity. Of course no one person can be an expert in all methods but the collaborative nature of science means this is easily compensated for. The statistician George Box wrote "essentially, all models are wrong, but some are useful" (Box and Draper, 1987). What he meant by this is when we model a system, we necessarily abstract and simplify so we can get at the question we seek to address. A one to one representation of a system would be the system itself!

That we can address questions on the feeding ecology of long extinct dinosaurs speaks to the advantages of modelling. By drawing sensible analogies to modern day systems and carrying out a sanity check on the model parameters we can come to a reasonable conclusion that *T.rex* was not an obligate scavenger. The complexity needed in a model is dependent on the hypothesis one is looking to explore. So the question

of the necessity of supplementary feeding for vultures in chapter 3 called for a relatively complex model because there is an applied relevance. That said, we should always invoke the principle of parsimony when selecting the most suitable method for the question at hand. This is especially important for papers with an application outside of pure theoretical advancement of the field, like in conservation, where we want as many people to understand the implications of the research as possible (Kane, 2012).

6.3 The value of data

It still remains that a model is only as good as the data used to create it. 'Garbage in garbage out' is worth remembering. This is an issue given some of the most fundamental biological data on scavengers are still missing such as their life expectancies or metabolic rates. In general, scavengers are often discounted from descriptions of ecosystems (DeVault et al., 2003) with Wilson and Wolkovich (2011) calculating a 16 fold underestimation of scavenging in food-web research. Specific to this work, information on the life history of many vulture species are still unknown (De Magalhaes and Costa, 2009) and there is a geographical bias in that most studies on vulture systems are based in Africa (Moleón et al., 2014). This has to be reversed if we are to have any success in conserving them. Indeed, in India there has been a move to build population viability models in order to determine if the *Gyps* species are recovering now that diclofenac has been prohibited (Baral et al., 2013). Yet, we do not have data on age-specific survival rates for the birds limiting the scope of the models that have been created (Baral et al., 2013). The authors of that study have called on others to establish vulture banding projects to improve on this deficiency (Baral et al., 2013).

I was fortunate that data of such quality were available to populate the models in chapter 3. The creation of similar models for threatened vulture populations would be a great boon to their conservation. The steady advance of technology does give us reason to be hopeful. Trackers can now record spatial data at a temporal and spatial scale impossible ten years ago. So, for example, it is now feasible to retrieve information on the behaviour of the animals remotely (Nathan et al., 2012; Tomkiewicz et al., 2010) allowing us to investigate interesting questions such as use of supplementary feeding sites (Monsarrat et al., 2013). We can also monitor biodiversity by means of satellite remote sensing (Pettorelli et al., 2014). Though there is still plenty of room for field work to ground truth these observations. The digital age with its big data should see the gaps in our basic understanding of these species being filled.

6.4 Conservation prospects

The identification and description of the producer-scrounger system in chapter 2 highlights the problem of focusing on one species in a study system. I would argue that this is a clear example of why conservation needs to take place at the level of the ecosystem. We are dealing with systems whose individual components interact, creating an emergent complexity. A species does not exist in isolation and consequently the best way to sustain it is to maintain its environment. Of the 23 vulture species, 14 are in danger of extinction (Ogada et al., 2012b). Although there are many causes of their decline (Mundy et al., 1992), poisoning, both accidental and from direct persecution, has been identified as the main agent responsible. It is their very nature that renders vultures particularly susceptible to poisoning given they forage and feed communally (Ogada et al., 2012b). A single poisoned carcass can wipe out over a 100 birds (Mundy et al., 1992). The clear cut case in India of the effect of diclofenac makes the recent authorisation of its use in Spain all the more exasperating (Margalida et al., 2014b). As I mentioned earlier the conservation of such a wide ranging species has to occur internationally but this is predicated on sensible national decisions. In addition to direct human-caused threats such as poisoning, climate change may add another threat to obligate scavengers. Of particular note is the increase in decomposition rate of carrion with temperature which could result in a seasonal reduction of carrion availability given predicted warming trends (Moleón et al., 2014). Unfortunately the low reproductive rates of these birds means their populations are particularly sensitive to increased mortality (Ogada et al., 2012b).

6.5 Future directions

The idea of having a big picture also applies to the science of scavenger ecology in general. Moleón et al. (2014) call attention to the inter-specific interactions linking predators, live prey, vultures and carrion production in terrestrial ecosystems. Such is their efficiency at consuming carrion, vultures may indirectly affect ungulate populations in forcing carnivores to hunt i.e. by denying them an easy meal. A relationship that was revealed in India only after the crash of its vulture population (Moleón et al., 2014). But vultures could also reduce pressure on potential prey items by acting as producers of carcass location to mammalian scroungers. And yet, there has never been a quantitative study examining the effect vultures have on ungulate numbers (Moleón et al., 2014; Elbroch and Wittmer, 2013). All of this is to emphasise the connectedness of species interactions in an ecosystem from which vultures are no exception.

Supposing we can maintain their numbers, I want to expand here on one of the most important questions in vulture behavioural ecology. That is *how do vultures forage as a group?* Because of their dependence on thermals for flight, vultures are often concentrated in relatively tight clusters around these hot air pockets (Xirouchakis and Andreou, 2009). This means one bird can track the descent of another to a carcass i.e. a local enhancement effect is at play. However Houston (1974) argued that the directed movement of this second bird would cause a third to follow it and so on, causing a chain reaction that could pull in birds from up to 35 km away. He suggested that this would explain the sudden arrival of so many individuals to the carcass in a short space of time. By contrast Cortés-Avizanda et al. (2014) found the numbers of birds arriving at a carcass were better explained by the initial local enhancement effect. By tagging a large group of the birds during their breeding season so they would forage from the same location and tracking them at high resolution we could properly address how the birds find carrion. As Cortés-Avizanda et al. (2014) note these hypotheses have different implications for conservation management because if birds form a chain they will be far more sensitive to population declines. Hopefully with the cost of such technology decreasing this will be achievable in the near future. These studies focus on the highly social *Gyps* vultures but there is considerable variation in foraging behaviour outside of this genus. A large scale comparative analysis of vulture foraging behaviour is lacking. In addition to improving our understanding of vultures a cross species comparison of habitat use would mean we could more easily conserve these species. Behavioural differences within vultures are only recently being discovered but there does seem to be a significant variability in the search efficiencies of species (Spiegel et al., 2013). Again, the conservation implications of this is significant. Notably, supplementary feeding will impact birds that intensely forage in relatively small areas (e.g. Lappet-faced Vultures) differently to non-territorial wide-ranging species (e.g. African White-backed Vultures) (Spiegel et al., 2013).

It seems to me that vultures are well-placed to benefit from citizen science (Silvertown, 2009). Public campaigns are often run in southern Africa to encourage people to report on resightings, creating data which can be used to ascertain the health of the bird population (Monadjem et al., 2014). That some section of the public are interested in supporting and being involved in science is beyond dispute. One need only look to the huge sums of money donated to crowd-sourcing initiatives where the incentive to donate is little more than pure interest in the study. Including an interested lay public in science has the effect of promoting awareness about the species too. In the case of vultures this would be

a tremendous boon for their PR, often reviled as they are for the most superficial of reasons.

Bibliography

- Acoccks JPH (1988) Veld types of South Africa. 57, Ed. 3.
- Bamford AJ, Diekmann M, Monadjem A, Mendelsohn J (2007) Ranging behaviour of Cape Vultures *Gyps coprotheres* from an endangered population in Namibia. *Bird Conservation International* 17: 331–339.
- Bamford AJ, Monadjem A, Hardy IC (2010) Associations of avian facial flushing and skin colouration with agonistic interaction outcomes. *Ethology* 116: 1163–1170.
- Baral N, Nagy C, Crain BJ, Gautam R (2013) Population viability analysis of Critically Endangered white-rumped vultures *Gyps bengalensis*. *Endangered Species Research* 21: 65–76.
- Barta Z, Giraldeau LA (1998) The effect of dominance hierarchy on the use of alternative foraging tactics: a phenotype-limited producing-scrounging game. *Behavioral Ecology and Sociobiology* 42: 217–223.
- Barton PS, Cunningham SA, Lindenmayer DB, Manning AD (2013) The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. *Oecologia* 171: 761–772.
- Bates K, Falkingham P (2012) Estimating maximum bite performance in *Tyrannosaurus rex* using multi-body dynamics. *Biology Letters* 8: 660–664.
- Bissett C, Bernard R (2007) Habitat selection and feeding ecology of the cheetah (*Acinonyx jubatus*) in thicket vegetation: is the cheetah a savanna specialist? *Journal of Zoology* 271: 310–317.
- Box GE, Draper NR (1987) Empirical model-building and response surfaces. John Wiley & Sons.
- Brandt MJ, Cresswell W (2008) Breeding behaviour, home range and habitat selection in Rock Firefinches *Lagonosticta sanguinodorsalis* in the wet and dry season in central Nigeria. *Ibis* 150: 495–507.
- Britton JC, Morton B (1994) Marine carrion and scavengers. *Oceanography and Marine Biology: an annual review* 32: 369–434.
- Brown C (1991) Declining martial *Polemaetus bellicosus* and tawny *Aquila rapax* eagle populations and causes of mortality on farmlands in central Namibia. *Biological Conservation* 56: 49–62.
- Brown CJ (1989) A study of the Bearded Vulture *Gypaetus barbatus* in southern Africa. Ph.D. thesis, University of Natal (Pietermaritzburg).
- Brusatte SL, Norell MA, Carr TD, Erickson GM, Hutchinson JR, et al. (2010) Tyrannosaur paleobiology: new research on ancient exemplar organisms. *Science* 329: 1481–1485.
- Buenestado F, Ferreras P, Delibes-Mateos M, Tortosa F, Blanco-Aguilar VR JA (2008) Habitat selection and home range size of red-legged partridges in Spain. *Agriculture, Ecosystems & Environment* 126: 158–162.
- Burt WH (1943) Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24: 346–352.
- Calder WA (1996) Size, function, and life history. Courier Dover Publications.

- Calenge C, Fortmann-Roe S (2013) adehabitatHR: home range estimation. R package version 04 7.
- 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 Ornithologica* 41: 7–13.
- Carbone C, Turvey ST, Bielby J (2011) Intra-guild competition and its implications for one of the biggest terrestrial predators, *Tyrannosaurus rex*. *Proceedings of the Royal Society B: Biological Sciences* 278: 2682–2690.
- Carr TD, Williamson TE (2004) Diversity of late Maastrichtian Tyrannosauridae (Dinosauria: Theropoda) from western North America. *Zoological Journal of the Linnean Society* 142: 479–523.
- Carrier JC, Musick JA, Heithaus MR (2010) *Sharks and their relatives II: biodiversity, adaptive physiology, and conservation*. CRC Press.
- Chin K, Eberth DA, Schweitzer MH, Rando TA, Sloboda WJ, et al. (2003) Remarkable preservation of undigested muscle tissue within a Late Cretaceous tyrannosaurid coprolite from Alberta, Canada. *Palaios* 18: 286–294.
- Chin K, Tokaryk TT, Erickson GM, Calk LC (1998) A king-sized theropod coprolite. *Nature* 393: 680–682.
- Clark W (1992) The taxonomy of Steppe and Tawny Eagles, with criteria for separation of museum specimens and live eagles. *Bulletin of the British Ornithological Club* 112: 150–157.
- Colomer M, Margalida A, Sanuy D, Pérez-Jiménez MJ (2011) A bio-inspired computing model as a new tool for modeling ecosystems: the avian scavengers as a case study. *Ecological Modelling* 222: 33–47.
- Colomer MÀ, Margalida A, Pérez-Jiménez MJ (2013) Population dynamics p system (pdp) models: A standardized protocol for describing and applying novel bio-inspired computing tools. *PLOS ONE* 8: e60698.
- Cone CD (1962) Thermal soaring of birds. *American Scientist* 50: 180–209.
- Cooper SM, Owen-Smith N, Bryant JP (1988) Foliage acceptability to browsing ruminants in relation to seasonal changes in the leaf chemistry of woody plants in a South African savanna. *Oecologia* 75: 336–342.
- Cortés-Avizanda A, Jovani R, Carrete M, Donázar JA (2012) Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: a field experiment. *Ecology* 93: 2570–2579.
- Cortés-Avizanda A, Jovani R, Donázar JA, Grimm V (2014) Bird sky networks: How do avian scavengers use social information to find carrion? *Ecology* 95: 1799–1808.
- Couzin ID (2009) Collective cognition in animal groups. *Trends in Cognitive Sciences* 13: 36–43.
- Curio E (1976) *Ethology of predation*. Springer.
- Dall SR, Giraldeau LA, Olsson O, McNamara JM, Stephens DW (2005) Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution* 20: 187–193.
- Danchin É, Giraldeau LA, Cézilly F (2008) *Behavioural Ecology*, vol. 610. Oxford University Press Oxford.
- Danchin E, Giraldeau LA, Valone TJ, Wagner RH (2004) Public information: from nosy neighbors to cultural evolution. *Science* 305: 487–491.

- De Magalhaes J, Costa J (2009) A database of vertebrate longevity records and their relation to other life-history traits. *Journal of Evolutionary Biology* 22: 1770–1774.
- DePalma RA, Burnham DA, Martin LD, Rothschild BM, Larson PL (2013) Physical evidence of predatory behavior in *Tyrannosaurus rex*. *Proceedings of the National Academy of Sciences* 110: 12560–12564.
- Dermody B, Jackson A, Tanner C (2011) The evolutionary pathway to obligate scavenging in *Gyps* vultures. *PLOS ONE* 6: e24635.
- DeVault TL, Rhodes Jr OE, Shivik JA (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. *Behavioral Ecology* 21: 1131–1139.
- Diekmann M, Scott A, Scott M, Diekmann J (2004) Capture and fitting of satellite-and radio-telemetry equipment onto Cape Griffon vulture *Gyps coprotheres*, African white-backed vulture *Gyps africanus* and Lappet-faced vulture *Torgos tracheliotos* in the Waterberg area, Namibia in 2004. *Vulture News* 51: 34–45.
- Donazar JA, Blanco G, Hiraldo F, Soto-Largo E, Oria J (2002) Effects of forestry and other land-use practices on the conservation of cinereous vultures. *Ecological Applications* 12: 1445–1456.
- Donazar JA, Ceballos O, Tella JL (1996) Communal roost of Egyptian vultures (*Neophron percnopterus*): dynamics and implications for the species conservation. *Biology and Conservation of Mediterranean Raptors Monograph* 4: 189–202.
- Dreitz VJ, Wunder MB, Knopf FL (2005) Movements and home ranges of Mountain Plovers raising broods in three Colorado landscapes. *The Wilson Bulletin* 117: 128–132.
- Duriez O, Herman S, Sarrazin F (2012) Intra-specific competition in foraging Griffon Vultures *Gyps fulvus*: 2. The influence of supplementary feeding management. *Bird Study* 59: 193–206.
- Dwyer JF (2010) Ecology of non-breeding and breeding Crested Caracaras (*Caracara cheriway*) in Florida. Ph.D. thesis, Virginia Polytechnic Institute and State University.
- Elbroch LM, Wittmer HU (2013) Nuisance ecology: do scavenging condors exact foraging costs on pumas in Patagonia? *PLOS ONE* 8: e53595.
- Elchuk C, Wiebe K (2003) Home-range size of northern flickers (*Colaptes auratus*) in relation to habitat and parental attributes. *Canadian Journal of Zoology* 81: 954–961.
- Farlow J, Brinkman D (1994) Wear surfaces on the teeth of tyrannosaurs. In: *Dino Fest: Proceedings of a Conference for the General Public*. Palaeontological Society Special Publications, vol. 7, pp. 165–175.
- Farlow JO, Planka ER (2002) Body size overlap, habitat partitioning and living space requirements of terrestrial vertebrate predators: implications for the paleoecology of large theropod dinosaurs. *Historical Biology* 16: 21–40.
- Fearer TM (1999) Relationship of ruffed grouse home range size and movement to landscape characteristics in southwestern Virginia. Ph.D. thesis, Virginia Polytechnic Institute and State University.
- Fedriani JM, Fuller TK, Sauvajot RM, York EC (2000) Competition and intraguild predation among three sympatric carnivores. *Oecologia* 125: 258–270.
- Ferguson-Lees J, Christie DA (2001) *Raptors of the world*. Houghton Mifflin Harcourt.

- Forsman JT, Hjernquist MB, Gustafsson L (2009) Experimental evidence for the use of density based interspecific social information in forest birds. *Ecography* 32: 539–545.
- García-Ripollés C, López-López P, Urios V (2011) Ranging behaviour of non-breeding Eurasian Griffon Vultures *Gyps fulvus*: a GPS-telemetry study. *Acta Ornithologica* 46: 127–134.
- Garza V, Suárez F, Herranz J, Traba J, De la Morena ELG, et al. (2005) Home range, territoriality and habitat selection by the Dupont's lark *Chersophilus duponti* during the breeding and post-breeding periods. *Ardeola* 52: 133–146.
- Giesen KM, Braun CE (1992) Winter home range and habitat characteristics of white-tailed ptarmigan in Colorado. *The Wilson Bulletin* 104: 263–272.
- Gilbert G, Tyler G, Smith KW (2005) Behaviour, home-range size and habitat use by male Great Bittern *Botaurus stellaris* in Britain. *Ibis* 147: 533–543.
- Gilbert M, Watson RT, Ahmed S, Asim M, Johnson JA (2007) Vulture restaurants and their role in reducing diclofenac exposure in Asian vultures. *Bird Conservation International* 17: 63–77.
- Grady JM, Enquist BJ, Dettweiler-Robinson E, Wright NA, Smith FA (2014) Evidence for mesothermy in dinosaurs. *Science* 344: 1268–1272.
- Green RE, Newton I, Shultz S, Cunningham AA, Gilbert M, et al. (2004) Diclofenac poisoning as a cause of vulture population declines across the Indian subcontinent. *Journal of Applied Ecology* 41: 793–800.
- Handegard NO, Boswell KM, Ioannou CC, Leblanc SP, Tjøstheim DB, et al. (2012) The dynamics of coordinated group hunting and collective information transfer among schooling prey. *Current Biology* 22: 1213–1217.
- Hansbauer MM, Storch I, Pimentel RG, Metzger JP (2008) Comparative range use by three Atlantic Forest understorey bird species in relation to forest fragmentation. *Journal of Tropical Ecology* 24: 291–299.
- Haskell JP, Ritchie ME, Olff H (2002) Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. *Nature* 418: 527–530.
- Hedenstrom A (1993) Migration by soaring or flapping flight in birds: the relative importance of energy cost and speed. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences* 342: 353–361.
- Henderson DM, Snively E (2004) Tyrannosaurus en pointe: allometry minimized rotational inertia of large carnivorous dinosaurs. *Proceedings of the Royal Society of London Series B: Biological Sciences* 271: S57–S60.
- Hirai T (2002) Ontogenetic change in the diet of the pond frog, *Rana nigromaculata*. *Ecological Research* 17: 639–644.
- Hofbauer J, Sigmund K (2003) Evolutionary game dynamics. *Bulletin of the American Mathematical Society* 40: 479–519.
- Hoffman RW (1991) Spring movements, roosting activities, and home-range characteristics of male Merriam's wild turkey. *The Southwestern Naturalist* 36: 332–337.
- Holbrook KM (2011) Home range and movement patterns of toucans: implications for seed dispersal. *Biotropica* 43: 357–364.
- Hone DW, Rauhut OW (2010) Feeding behaviour and bone utilization by theropod dinosaurs. *Lethaia* 43: 232–244.

- Horner J (1994) Steak knives, beady eyes, and tiny little arms (a portrait of *T. rex* as a scavenger). *Dino Fest Paleontological Society Special Publication* 7: 157–164.
- Horner JR, Goodwin MB, Myhrvold N (2011) Dinosaur census reveals abundant *Tyrannosaurus* and rare ontogenetic stages in the Upper Cretaceous Hell Creek Formation (Maastrichtian), Montana, USA. *PLOS ONE* 6: e16574.
- Horner JR, Lessem D (1993) The complete *T. rex*. Simon & Schuster.
- Houston D (1974) Food searching in griffon vultures. *African Journal of Ecology* 12: 63–77.
- Houston D (1975) Ecological isolation of African scavenging birds. *Ardea* 63: 55–64.
- Houston D (1976) Breeding of the White-backed and Rüppell's griffon vultures, *Gyps africanus* and *G. rueppellii*. *Ibis* 118: 14–40.
- Houston DC (2001) Condors and vultures, vol. 68. Voyageur Press.
- Houston DC, Cooper J (1975) The digestive tract of the whiteback griffon vulture and its role in disease transmission among wild ungulates. *Journal of Wildlife Diseases* 11: 306–313.
- Howland HC, Merola S, Basarab JR (2004) The allometry and scaling of the size of vertebrate eyes. *Vision research* 44: 2043–2065.
- Jackson AL, Ruxton GD, Houston DC (2008) The effect of social facilitation on foraging success in vultures: a modelling study. *Biology Letters* 4: 311–313.
- JM M, CJ B, M M, M D (2005) Observations on the movement of adult Cape Vultures in central Namibia. *Lanioturdus* 38: 16–20.
- Jones KE, Bielby J, Cardillo M, Fritz SA, O'Dell J, et al. (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090-184. *Ecology* 90: 2648–2648.
- Kane A (2012) A suggestion on improving mathematically heavy papers. *Proceedings of the National Academy of Sciences of the United States of America* 109: E3056.
- Kane A, Jackson AL, Ogada DL, Monadjem A, McNally L (2014) Vultures acquire information on carcass location from scavenging eagles. *Proceedings of the Royal Society of London B: Biological Sciences* 281.
- Kéfi S, Berlow EL, Wieters EA, Navarrete SA, Petchey OL, et al. (2012) More than a meal... integrating non-feeding interactions into food webs. *Ecology letters* 15: 291–300.
- Kendall CJ (2013) Alternative strategies in avian scavengers: how subordinate species foil the despotic distribution. *Behavioral Ecology and Sociobiology* 67: 383–393.
- Knoff A, Hohn A, Macko S (2008) Ontogenetic diet changes in bottlenose dolphins (*Tursiops truncatus*) reflected through stable isotopes. *Marine Mammal Science* 24: 128–137.
- Koenig R (2006) Vulture research soars as the scavengers' numbers decline. *Science* 312.
- Komen J (????) Energy requirements of nestling Cape Vultures. *Condor* 93: 153–158.
- Krauss DA, Robinson JM (2013) The Biomechanics of a Plausible Hunting Strategy for *Tyrannosaurus rex*. *Tyrannosaurid Paleobiology* pp. 251–265.
- Krüger SC, Allan DG, Jenkins AR, Amar A (2014) Trends in territory occupancy, distribution and density of the Bearded Vulture *Gypaetus barbatus meridionalis* in southern Africa. *Bird Conservation International* 24: 162–177.
- Kruuk H (1967) Competition for food between vultures in East Africa. *Ardea* 55: 171–193.
- Lambertucci SA, Alarcón PA, Hiraldo F, Sanchez-Zapata JA, Blanco G, et al. (2014) Apex scavenger movements call for transboundary conservation policies. *Biological Conservation* 170: 145–150.

- Legagneux P, Blaize C, Latraube F, Gautier J, Bretagnolle V (2009) Variation in home-range size and movements of wintering dabbling ducks. *Journal of Ornithology* 150: 183–193.
- Longrich NR, Horner JR, Erickson GM, Currie PJ (2010) Cannibalism in *Tyrannosaurus rex*. *PLOS ONE* 5: e13419.
- Margalida A (2008) Bearded vultures (*Gypaetus barbatus*) prefer fatty bones. *Behavioral Ecology and Sociobiology* 63: 187–193.
- Margalida A, Colomer MÀ (2012) Modelling the effects of sanitary policies on European vulture conservation. *Scientific reports* 2.
- Margalida A, Colomer MÀ, Oro D (2014a) Man-induced activities modify demographic parameters in a long-lived species: effects of poisoning and health policies. *Ecological Applications* 24: 436–444.
- Margalida A, Colomer MÀ, 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, Donazar JA, Carrete M, Sánchez-Zapata JA (2010) Sanitary versus environmental policies: fitting together two pieces of the puzzle of European vulture conservation. *Journal of Applied Ecology* 47: 931–935.
- Margalida A, Sánchez-Zapata JA, Blanco G, Hiraldo F, Donazar JA (2014b) Diclofenac Approval as a Threat to Spanish Vultures. *Conservation Biology* 28: 631–632.
- Markandya A, Taylor T, Longo A, Murty M, Murty S, et al. (2008) Counting the cost of vulture decline - An appraisal of the human health and other benefits of vultures in India. *Ecological Economics* 67: 194–204.
- Marshall CD, Guzman A, Narazaki T, Sato K, Kane EA, et al. (2012) The ontogenetic scaling of bite force and head size in loggerhead sea turtles (*Caretta caretta*): implications for durophagy in neritic, benthic habitats. *The Journal of Experimental Biology* 215: 4166–4174.
- Martin GR, Portugal SJ, Murn CP (2012) Visual fields, foraging and collision vulnerability in Gyps vultures. *Ibis* 154: 626–631.
- McNamara JM, Dall SR (2010) Information is a fitness enhancing resource. *Oikos* 119: 231–236.
- Mills M (1984) The comparative behavioural ecology of the brown hyaena *Hyaena brunnea* and the spotted hyaena *Crocuta crocuta* in the southern Kalahari. *Koedoe* 27: 237–247.
- Mohr CO (1947) Table of equivalent populations of North American small mammals. *American midland naturalist* 37: 223–249.
- Moleón M, Sánchez-Zapata JA, Selva N, Donazar JA, Owen-Smith N (2014) Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. *Biological Reviews* .
- Monadjem A (2003) Nesting distribution and status of vultures in Swaziland. *Vulture News* 48: 12–19.
- Monadjem A, Anderson M, Piper S, Boshoff A (2004) The vultures of southern Africa—quo vadis. In: *Proceedings of a workshop on vulture research and conservation in southern Africa*. Birds of Prey Working Group. Endangered Wildlife Trust. Johannesburg.
- Monadjem A, Botha A, Murn C (2013) Survival of the African white-backed vulture *Gyps africanus* in north-eastern South Africa. *African Journal of Ecology* 51: 87–93.

- Monadjem A, Boycott R, 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, Garcelon DK (2005) Nesting distribution of vultures in relation to land use in Swaziland. *Biodiversity & Conservation* 14: 2079–2093.
- 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, Naser W, Kane A (2014) Effect of rehabilitation on survival rates of endangered Cape vultures. *Animal Conservation* 17: 52–60.
- Monsarrat S, Benhamou S, Sarrazin F, Bessa-Gomes C, Bouten W, et al. (2013) How predictability of feeding patches affects home range and foraging habitat selection in avian social scavengers? *PLOS ONE* 8: e53077.
- Morand-Ferron J, Giraldeau LA (2010) Learning behaviorally stable solutions to producer–scrounger games. *Behavioral Ecology* 21: 343–348.
- Mundy PJ, Butchart D, Ledger J, Piper S (1992) The vultures of Africa. Academic Press London.
- Mundy PJ, Group VS (1982) The comparative biology of southern African vultures, vol. 1. Vulture Study Group Johannesburg.
- Nathan R, Spiegel O, Fortmann-Roe S, Harel R, Wikelski M, et al. (2012) Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *The Journal of Experimental Biology* 215: 986–996.
- Nesbitt SA, Williams KS (1990) Home range and habitat use of Florida sandhill cranes. *The Journal of Wildlife Management* 54: 92–96.
- Norgaard RB (1989) The case for methodological pluralism. *Ecological Economics* 1: 37–57.
- Novoa C, Dumas S, Resseguier J (2006) Home-range size of Pyrenean grey partridges *Perdix perdix hispaniensis* during the breeding season. *Wildlife Biology* 12: 11–18.
- Oaks JL, Gilbert M, Virani MZ, Watson RT, Meteyer CU, et al. (2004) Diclofenac residues as the cause of vulture population decline in Pakistan. *Nature* 427: 630–633.
- Ogada D, Torchin M, Kinnaird M, Ezenwa V (2012a) Effects of vulture declines on facultative scavengers and potential implications for mammalian disease transmission. *Conservation biology* 26: 453–460.
- Ogada DL, Keesing F (2010) Decline of raptors over a three-year period in Laikipia, central Kenya. *Journal of Raptor Research* 44: 129–135.
- Ogada DL, Keesing F, Virani MZ (2012b) Dropping dead: causes and consequences of vulture population declines worldwide. *Annals of the New York Academy of Sciences* 1249: 57–71.
- Oro D, Margalida A, Carrete M, Heredia R, Donazar JA (2008) Testing the goodness of supplementary feeding to enhance population viability in an endangered vulture. *PLOS ONE* 3: e4084.
- Peery MZ (2000) Factors affecting interspecies variation in home-range size of raptors. *The Auk* 117: 511–517.
- Pejchar L, Holl KD, Lockwood JL (2005) Hawaiian honeycreeper home range size varies with habitat: implications for native *Acacia koa* forestry. *Ecological Applications* 15: 1053–1061.

- Pennycuik C (1972) Soaring behaviour and performance of some East African birds, observed from a motor-glider. *Ibis* 114: 178–218.
- Pennycuik C (1976) Breeding of the lappet-faced and white-headed vultures (*Torgos tracheliotus* Forster and *Trigonoceps occipitalis* Burchell) on the Serengeti Plains, Tanzania. *African Journal of Ecology* 14: 67–84.
- Pérez-Hurtado I, Valencia-Cabrera L, Pérez-Jiménez MJ, Colomer MA, Riscos-Nulñez A (2010) MeCoSim: A general purpose software tool for simulating biological phenomena by means of P Systems. In: *Bio-Inspired Computing: Theories and Applications (BIC-TA)*, 2010 IEEE Fifth International Conference on, pp. 637–643, IEEE.
- Pettorelli N, Laurance WF, O'Brien TG, Wegmann M, Nagendra H, et al. (2014) Satellite remote sensing for applied ecologists: opportunities and challenges. *Journal of Applied Ecology* 51: 839–848.
- Phipps WL, Willis SG, Wolter K, Naidoo V (2013a) Foraging ranges of immature African white-backed vultures (*Gyps africanus*) and their use of protected areas in southern Africa. *PLOS ONE* 8: e52813.
- Phipps WL, Wolter K, Michael MD, MacTavish LM, Yarnell RW (2013b) Do Power Lines and Protected Areas Present a Catch-22 Situation for Cape Vultures (*Gyps coprotheres*)? *PLOS ONE* 8: e76794.
- Piper SE (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* pp. 41–50.
- Piper SE, Boshoff AF, Scott HA (1999) Modelling survival rates in the Cape Griffon *Gyps coprotheres*, with emphasis on the effects of supplementary feeding. *Bird Study* 46: S230–S238.
- Platt SG, Rainwater TR, Finger AG, Thorbjarnarson JB, Anderson TA, et al. (2006) Food habits, ontogenetic dietary partitioning and observations of foraging behaviour of Morelet's crocodile (*Crocodylus moreletii*) in northern Belize. *The Herpetological Journal* 16: 281–290.
- Pontzer H, Allen V, Hutchinson JR (2009) Biomechanics of running indicates endothermy in bipedal dinosaurs. *PLOS ONE* 4: e7783.
- Prange HD, Anderson JF, Rahn H (1979) Scaling of skeletal mass to body mass in birds and mammals. *American Naturalist* 113: 103–122.
- R Core Team (2014) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, URL <http://www.R-project.org>.
- Rayfield EJ, Norman DB, Horner CC, Horner JR, Smith PM, et al. (2001) Cranial design and function in a large theropod dinosaur. *Nature* 409: 1033–1037.
- Rhim SJ (2006) Home range and habitat selection of hazel grouse *Bonasa bonasia* in a temperate forest of South Korea. *Forest ecology and management* 226: 22–25.
- Robb GN, McDonald RA, Chamberlain DE, Bearhop S (2008) Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Frontiers in Ecology and the Environment* 6: 476–484.
- Robertson A, Boshoff A (1986) The feeding ecology of cape vultures *Gyps coprotheres* in a stock-farming area. *Biological Conservation* 35: 63–86.
- Rolando A (1998) Factors affecting movements and home ranges in the jay (*Garrulus glandarius*). *Journal of Zoology* 246: 249–257.

- 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. *African Journal of Ecology* 40: 260–266.
- Ruxton GD, Bailey DM (2005) Searching speeds and the energetic feasibility of an obligate whale-scavenging fish. *Deep Sea Research Part I: Oceanographic Research Papers* 52: 1536–1541.
- Ruxton GD, Houston DC (2003) Could *Tyrannosaurus rex* have been a scavenger rather than a predator? An energetics approach. *Proceedings of the Royal Society of London Series B: Biological Sciences* 270: 731–733.
- Ruxton GD, Houston DC (2004a) Energetic feasibility of an obligate marine scavenger. *Marine ecology Progress series* 266: 59–63.
- Ruxton GD, Houston DC (2004b) Obligate vertebrate scavengers must be large soaring fliers. *Journal of Theoretical Biology* 228: 431–436.
- Ruxton GD, Wilkinson DM (2013) Endurance running and its relevance to scavenging by early Hominins. *Evolution* 67: 861–867.
- Ruxton GD, Wilkinson DM (2014) Energetic arguments predict larger-bodied animals will be increasingly confined to flat environments. *Journal of theoretical biology* 335: 236–238.
- Ruxton GD, Wilkinson DM, Schaefer HM, Sherratt TN (2014) Why fruit rots: theoretical support for Janzen's theory of microbe–macrobe competition. *Proceedings of the Royal Society B: Biological Sciences* 281: 20133320.
- Schmidt KA, Dall SR, Van Gils JA (2010) The ecology of information: an overview on the ecological significance of making informed decisions. *Oikos* 119: 304–316.
- Schubert BW, Ungar PS (2005) Wear facets and enamel spalling in tyrannosaurid dinosaurs. *Acta Palaeontologica Polonica* 50: 93–99.
- Sekercioglu CH (2006) Increasing awareness of avian ecological function. *Trends in Ecology & Evolution* 21: 464–471.
- Selva N, Fortuna MA (2007) The nested structure of a scavenger community. *Proceedings of the Royal Society B: Biological Sciences* 274: 1101–1108.
- Seppänen JT, Forsman JT (2007) Interspecific social learning: novel preference can be acquired from a competing species. *Current Biology* 17: 1248–1252.
- Seppänen JT, Forsman JT, Mönkkönen M, Thomson RL (2007) Social information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology* 88: 1622–1633.
- Shepard EL, Lambertucci SA (2013) From daily movements to population distributions: weather affects competitive ability in a guild of soaring birds. *Journal of The Royal Society Interface* 10: 20130612.
- Shepard EL, Wilson RP, Rees WG, Grundy E, Lambertucci SA, et al. (2013) Energy landscapes shape animal movement ecology. *The American Naturalist* 182: 298–312.
- Silvertown J (2009) A new dawn for citizen science. *Trends in Ecology & Evolution* 24: 467–471.
- Sinclair ARE, Norton-Griffiths M (1995) *Serengeti: dynamics of an ecosystem*. University of Chicago Press.
- Slocombe DS (1993) Implementing ecosystem-based management. *BioScience* 43: 612–622.

- Spiegel O, Getz WM, Nathan R (2013) Factors influencing foraging search efficiency: why do scarce lappet-faced vultures outperform ubiquitous white-backed vultures? *The American Naturalist* 181: E102–E115.
- Springborn EG, Meyers JM (2005) Home range and survival of breeding painted buntings on Sapelo Island, Georgia. *Wildlife Society Bulletin* 33: 1432–1439.
- Steyn P (1980) Breeding and food of the bateleur in Zimbabwe (Rhodesia). *Ostrich* 51: 168–178.
- Stober JM, Krementz DG (2006) Variation in Bachman's Sparrow home-range size at the Savannah River site, South Carolina. *The Wilson Journal of Ornithology* 118: 138–144.
- Stroem H, Sonerud G (2001) Home range and habitat selection in the Pygmy Owl *Glaucidium passerinum*. *Ornis Fennica* 78: 145–158.
- Sumpter D, Buhl J, Biro D, Couzin I (2008) Information transfer in moving animal groups. *Theory in Biosciences* 127: 177–186.
- Tisue S, Wilensky U (2004) Netlogo: A simple environment for modeling complexity. In: *International Conference on Complex Systems*, pp. 16–21.
- Tomkiewicz SM, Fuller MR, Kie JG, Bates KK (2010) Global positioning system and associated technologies in animal behaviour and ecological research. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 2163–2176.
- Tucker VA (1975) The Energetic Cost of Moving About: Walking and running are extremely inefficient forms of locomotion. Much greater efficiency is achieved by birds, fish and bicyclists. *American Scientist* 63: 413–419.
- Tucker VA (1988) Gliding birds: descending flight of the whitebacked vulture, *Gyps africanus*. *Journal of Experimental Biology* 140: 325–344.
- Vasilakis D, Poirazidis K, Elorriaga J (2005) Breeding season range use of a Eurasian Black Vulture *Aegypius monachus* population in Dadia National Park and the adjacent areas, Thrace, NE Greece. *Conservation and Management of Vulture Populations* 42: 355–373.
- Vega Rivera JH, Ayala D, Haas CA (2003) Home-range size, habitat use, and reproduction of the Ivory-billed Woodcreeper (*Xiphorhynchus flavigaster*) in dry forest of western Mexico. *Journal of Field Ornithology* 74: 141–151.
- Vickery WL, Giraldeau LA, Templeton JJ, Kramer DL, Chapman CA (1991) Producers, scroungers, and group foraging. *American Naturalist* pp. 847–863.
- Virani MZ, 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. *Biological Conservation* 144: 746–752.
- Wakefield ED, Bodey TW, Bearhop S, Blackburn J, Colhoun K, et al. (2013) Space partitioning without territoriality in gannets. *Science* 341: 68–70.
- Weishampel DB, Dodson P, Osmólska H (2004) *The dinosaurs*. University of California Press.
- Whittington-Jones C, Wolter K, West S (2011) Monitoring of Cape Vulture (*Gyps coprotheres*) breeding colonies in the Magaliesberg, South Africa: 2007–2009. *Vulture News* 60: 6–12.
- Wilson EE, Wolkovich EM (2011) Scavenging: how carnivores and carrion structure communities. *Trends in Ecology & Evolution* 26: 129–135.
- Winemiller KO (1989) Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan llanos. *Environmental Biology of Fishes* 26: 177–199.

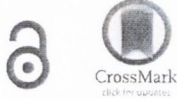
- Witmer LM, Ridgely RC (2009) New insights into the brain, braincase, and ear region of tyrannosaurs (Dinosauria, Theropoda), with implications for sensory organization and behavior. *The Anatomical Record* 292: 1266–1296.
- Witton MP, Habib MB (2010) On the size and flight diversity of giant pterosaurs, the use of birds as pterosaur analogues and comments on pterosaur flightlessness. *PLOS ONE* 5: e13982.
- Witton MP, Naish D (2008) A reappraisal of azhdarchid pterosaur functional morphology and paleoecology. *PLOS ONE* 3: e2271.
- Woodward G, Hildrew AG (2002) Body-size determinants of niche overlap and intraguild predation within a complex food web. *Journal of Animal Ecology* 71: 1063–1074.
- Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70: 164–168.
- Xirouchakis SM (2007) Seasonal and daily activity pattern in Griffon Vulture (*Gyps fulvus*) colonies on the island of Crete (Greece). *Ornis Fennica* 84: 39.
- Xirouchakis SM, Andreou G (2009) Foraging behaviour and flight characteristics of Eurasian griffons *Gyps fulvus* in the island of Crete, Greece. *Wildlife Biology* 15: 37–52.
- Zuberogoitia I, Martínez JE, Margalida A, Gómez I, Azkona A, et al. (2010) Reduced food availability induces behavioural changes in Griffon Vulture *Gyps fulvus*. *Ornis Fennica* 87: 52–60.

appendix a

Vultures acquire information on carcass location from scavenging eagles - Supplementary information

Table a.1: Description of parameters used in the game theory model

Model variables	Definition
v_s	No. of scrounger vultures
v_p	No. of producer vultures
r_s	No. of scrounger raptors
r_p	No. of producer raptors
$m_{v,v}$	No. of vultures found at a vulture-produced carcass
$m_{v,r}$	No. of raptors found at a vulture-produced carcass
$m_{r,v}$	No. of vultures found at a raptor-produced carcass
$m_{r,r}$	No. of raptors found at a raptor-produced carcass
π	Rate of food consumption
d	Steady state density of carcasses
a	Finder's fee
x	The competitive ability of vultures compared to that of raptors
α	Vulture mortality rate
β	Raptor mortality rate
γ	Food gained by raptors through predation



Cite this article: Kane A, Jackson AL, Ogada DL, Monadjem A, McNally L. 2014 Vultures acquire information on carcass location from scavenging eagles. *Proc. R. Soc. B* **281**: 20141072.
<http://dx.doi.org/10.1098/rspb.2014.1072>

Received: 2 May 2014
Accepted: 13 August 2014

Subject Areas:
ecology, evolution, behaviour

Keywords:
inter-guild interactions, producer–scrounger game, scavengers, social information, vultures

Author for correspondence:
Adam Kane
e-mail: kanead@tcd.ie

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2014.1072> or via <http://rspb.royalsocietypublishing.org>.

Vultures acquire information on carcass location from scavenging eagles

Adam Kane^{1,2}, Andrew L. Jackson^{1,2}, Darcy L. Ogada^{3,4}, Ara Monadjem⁵ and Luke McNally^{6,7}

¹Department of Zoology, School of Natural Sciences, and ²Centre for Biodiversity Research, Trinity College Dublin, Dublin 2, Republic of Ireland

³The Peregrine Fund, 5668 West Flying Hawk Lane, Boise, ID 83709, USA

⁴National Museums of Kenya, Ornithology Section, PO Box 40658, Nairobi 00100, Kenya

⁵All Out Africa Research Unit, Department of Biological Sciences, University of Swaziland, Private Bag 4, Kwaluseni, Swaziland

⁶Centre for Immunity, Infection and Evolution, School of Biological Sciences, and ⁷Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Edinburgh EH9 3JT, UK

© AK, 0000-0002-2830-5338; ALJ, 0000-0001-7334-0434; LMcn, 0000-0002-1928-6235

Vultures are recognized as the scroungers of the natural world, owing to their ecological role as obligate scavengers. While it is well known that vultures use intraspecific social information as they forage, the possibility of inter-guild social information transfer and the resulting multi-species social dilemmas has not been explored. Here, we use data on arrival times at carcasses to show that such social information transfer occurs, with raptors acting as producers of information and vultures acting as scroungers of information. We develop a game-theoretic model to show that competitive asymmetry, whereby vultures dominate raptors at carcasses, predicts this evolutionary outcome. We support this theoretical prediction using empirical data from competitive interactions at carcasses. Finally, we use an individual-based model to show that these producer–scrounger dynamics lead to vultures being vulnerable to declines in raptor populations. Our results show that social information transfer can lead to important non-trophic interactions among species and highlight important potential links among social evolution, community ecology and conservation biology. With vulture populations suffering global declines, our study underscores the importance of ecosystem-based management for these endangered keystone species.

1. Introduction

Animals base their decisions on both personal and public information [1–4]. This is applicable to every facet of an animal's life, be it feeding, movement, mating, etc., with high fidelity information allowing an individual to make decisions conducive to its survival [1,5,6]. Public information can be separated into that which is gained from intraspecifics and that from interspecifics [1]. Intraspecific information transfer is essential for basic behavioural functions such as sexual reproduction or cooperative hunting [7]. But species overlap in the resources they use [8,9] and the environments they inhabit [8,9], which gives the possibility of inter-guild information transfer [10–12].

Consider the social *Gyps* vultures, a group that is known to forage collectively for carrion. In flight, they appear to keep in visual contact with conspecifics [13]. Once one vulture discovers and descends to a carcass, the information is conveyed to others in the area; this activity can create a local enhancement effect [14]. But such social behaviour renders vultures' foraging efficiency susceptible to population declines; with every individual lost, the network is less effective at detecting carrion [14].

Although vultures are the most well-known group of avian scavengers, there are a number of other species within the family Accipitridae, such as eagles (hereafter raptors), that take carrion as a significant proportion of their diet [15]. Coexistence among all of these species is possible by both temporal and resource niche partitioning [15,16]. But with any shared resource, direct interactions between them will result, and the possibility of social information transfer among species emerges. A distinct pattern of arrival of avian scavengers to carrion has been highlighted before [17–19]. Indeed, the African white-backed vulture has been noted in using many other scavengers as a means of local enhancement while foraging [9]. Yet, these hetero-specific interactions and their potential for information transfer have not been explored in any detail [17]. Given the current extreme declines in vulture populations [20,21] and their key role in many ecosystems as biomass recyclers [22,23], understanding vulture foraging ecology is also of applied relevance. Here, we provide evidence for producer–scrounger dynamics among scavenging vulture and raptor species by testing the hypothesis that vultures scrounge information from raptors and explore its evolutionary underpinnings using a game-theoretic model. We conclude by outlining the consequences of this system's properties for vulture conservation.

2. Test for producer–scrounger dynamics

To test for the occurrence of producer–scrounger dynamics between vultures and raptors, we observed arrival times of avian scavengers at a number of carcasses placed out (see the electronic supplementary material). Our observations were made on 46 videos recorded in the Mpala Research Centre in the Laikipia District of Kenya which had scavenging avifauna (a subset of the videos used in [22]). We focused on the closely related and morphologically similar *Gyps* vultures, the African white-backed vulture (*Gyps africanus*) and the Rüppell's vulture (*Gyps rueppellii*), as well as the congeneric tawny (*Aquila rapax*) and steppe eagles (*Aquila nipalensis*). These four species were by far the most abundant in the recordings (more than 95%) and formed our vulture and raptor groups, respectively [22].

For each video, we noted the arrival time and species of every animal. Initially, we compared the probability of producing information on carcass location by looking at which of the two groups, *Gyps* vultures or raptors, landed at the carcass first. A binomial test on the 46 videos showed that the first bird to land at a carcass was significantly more likely to be a raptor than a vulture (binomial test, 38 successes, 46 trials, expected probability = 0.5, results in observed probability = 0.83, 95% CI 0.69–0.92, p -value < 0.001; figure 1).

We used randomization tests to test whether the birds were following each other rather than simply arriving independently but with different timing to the carcasses. Where a raptor landed first, we generated a null distribution of arrival times for the first scrounger (a *Gyps* vulture) over the length of each recording by randomizing the arrival times of the birds. From this distribution, we assessed whether the first scrounger followed more closely than expected under an assumption of independent foraging. Then, in order to make a population-level inference across permutation tests, we used a binomial test where the expected probability of observing a significant result by chance is 0.05 (as per the definition of a p -value, where at an α of 0.05, we would expect 5% of test results to be significant according to the null model). Vultures

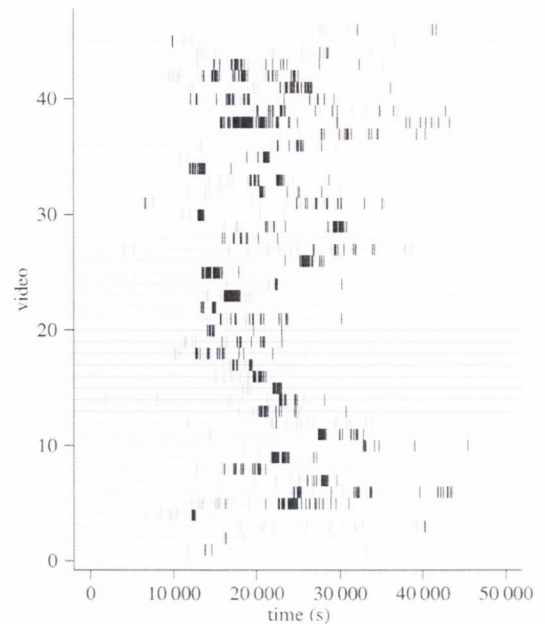


Figure 1. Recorded arrival times of individual vultures and raptors at carrion across 46 videos. The grey lines are the raptors and the black are the vultures.

were found to follow raptors more closely than expected by chance (i.e. with $p < 0.05$) in 20 of the 38 videos (figure 2a), which is significantly more cases of vultures following raptors than expected (binomial test with 20 successes, 38 trials, expected probability = 0.05 results in an observed probability = 0.53, 95% CI 0.36–0.69, p -value < 0.001).

Similarly, on six of the eight occasions when vultures landed at the carcass first, raptors followed more closely than expected by chance (figure 2b), which is significantly more cases than expected (binomial test with six successes, eight trials, expected probability = 0.05 results in an observed probability = 0.75, 95% CI 0.35–0.97, p -value < 0.001).

3. Producer–scrounger model

While our analyses indicate that both raptors and vultures follow each other to carcasses, the higher frequency of raptors being the first to land at a carcass leads to raptors acting predominantly in a producing role. This can manifest by raptors providing information on the location of the resource or by engaging in carcass opening whereby the raptor uses its relatively stronger bill to get through an ungulate hide [18], with vultures acting predominantly as scroungers. This result raises the question of how did these divergent roles evolve? We hypothesized that competitive ability may have a strong effect on the strategy typically adopted in each species. If individuals of one species can competitively dominate those of another, this may favour scrounging by the dominant species: producers may gain an exclusive share of the resource by arriving first at the carcass (a 'finder's fee'), but dominant scroungers may be able to effectively monopolize the remainder of the resource once they arrive, while also gaining information available publically on the locations of carcasses.

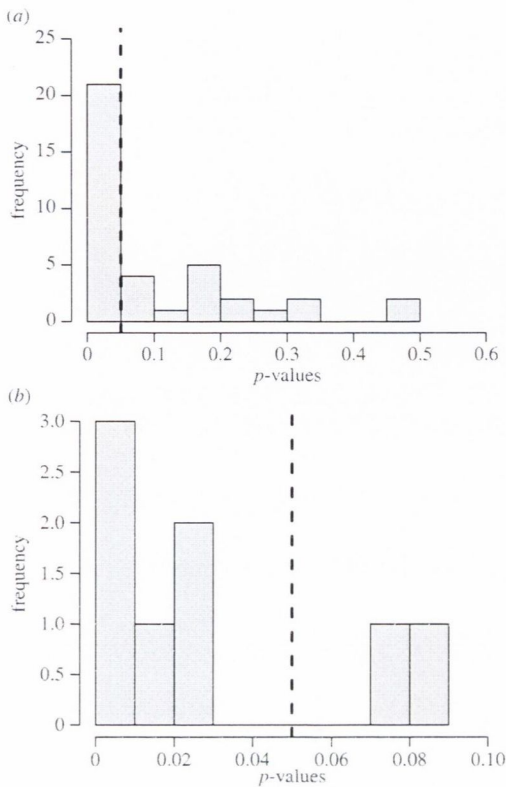


Figure 2. Histograms of p -values showing the number of videos where it was significantly probable that (a) the vultures were following the raptors and (b) the raptors were following the vultures. The vertical lines show the level of significance at $p = 0.05$.

We used the game-theoretic framework of the producer–scrounger game to test the evolutionary feasibility of this prediction. In a producer–scrounger game, an animal needs to either invest in producing some resource (typically information) or exploit the investment from another individual [24]. We consider a scenario where vultures and raptors forage in the same area. We assume that time spent feeding at a carcass is small relative to search time [15,25]. Individual vultures and raptors can assume one of two strategies: producer or scrounger. Producers find carcasses at a rate proportional to the carcass density, while all scroungers in a group will follow producers to the carcasses they find, but do not find carcasses for themselves (probabilistic following by scroungers cannot qualitatively affect our results). While, in reality, vultures and raptors will likely use mixed strategies, this simple scenario allows us to abstract the essential elements of the evolutionary dynamics in a simple framework.

From our assumptions, we can write the numbers of vultures and raptors at a carcass found by a vulture as $m_{v,v} = 1 + v_s$ and $m_{v,r} = r_s$, respectively, where v_s and r_s are the numbers of vultures and raptors that are scroungers. Similarly, the numbers of vultures and raptors at a carcass found by a raptor are $m_{r,v} = v_s$ and $m_{r,r} = 1 + r_s$, respectively. We assume that new carcasses arrive in the area and decay at fixed rates (both set at 1) and are consumed almost instantaneously when found. Assuming that carcass dynamics occur on a

faster timescale than the population dynamics of vultures and raptors, the steady-state density of carcasses is then given as $d = 1/(1 + r_p + v_p)$, where v_p and r_p are the numbers of vultures and raptors that are producers. The rates of food consumption for producing and scrounging vultures are

$$\pi_{v,p} = \left(\frac{1}{1 + r_p + v_p} \right) \left(a + (1 - a) \frac{x}{xm_{v,v} + m_{v,r}} \right) \quad (3.1)$$

and

$$\pi_{v,s} = \left(\frac{1}{1 + r_p + v_p} \right) (1 - a) \left(\frac{v_p x}{xm_{v,v} + m_{v,r}} + \frac{r_p x}{xm_{r,v} + m_{r,r}} \right). \quad (3.2)$$

Similarly, the rates of food consumption for producing and scrounging raptors are

$$\pi_{r,p} = \left(\frac{1}{1 + r_p + v_p} \right) \left(a + (1 - a) \frac{1}{xm_{v,v} + m_{v,r}} \right) \quad (3.3)$$

and

$$\pi_{r,s} = \left(\frac{1}{1 + r_p + v_p} \right) (1 - a) \left(\frac{v_p}{xm_{v,v} + m_{v,r}} + \frac{r_p}{xm_{r,v} + m_{r,r}} \right). \quad (3.4)$$

Here, a is the proportion of a carcass that is monopolized by the individual that finds it (the ‘finder’s fee’), and x is the competitive ability of vultures compared with that of raptors, specifically the number of raptors that a vulture is equivalent to in terms of competitive ability. The proportion of the carcass remaining after the finder’s fee ($1 - a$) is shared among all birds at the carcass proportionally to their relative competitive ability. For example, at a carcass found by a raptor, a scrounging vulture’s share would be $x/(xm_{r,v} + m_{r,r})$. The vulture is competitively equivalent to x raptors so gets a positive weighting of x in the numerator. As other vultures will have a similar competitive ability, the number of vultures at the carcass ($m_{r,v}$) is also weighted by x . This leads to each bird receiving a share proportional to its competitive ability relative to the other birds present at the carcass. The probability that a vulture wins a one-on-one interaction with a raptor is then defined as $x/(1 + x)$. This process could then be seen as a series of competitive interactions over small proportions of the carcass, leading to birds on average receiving a share proportional to their relative competitive ability.

While the equilibrium number of carcasses ($1/(1 + r_p + v_p)$) available declines with the density of producers of both species as more carcasses are found and consumed, the food acquisition rate of scroungers is also positively weighted by producer densities as they are able to follow individuals to carcasses more frequently. This means that, while producers are only affected negatively by other producers (owing to reduction in carcass densities), scroungers are affected both positively (owing to their increasing rate of following to carcasses) and negatively (owing to reduction in carcass density) by producer density.

We write the dynamics [26] of producers and scroungers in the vulture and raptor populations as

$$\frac{dv_p}{dt} = v_p(\pi_{v,p} - \alpha), \quad (3.5)$$

$$\frac{dv_s}{dt} = v_s(\pi_{v,s} - \alpha), \quad (3.6)$$

$$\frac{dr_p}{dt} = r_p \left(\pi_{r,p} - \beta + \frac{\gamma}{1 + r_p + r_s} \right) \quad (3.7)$$

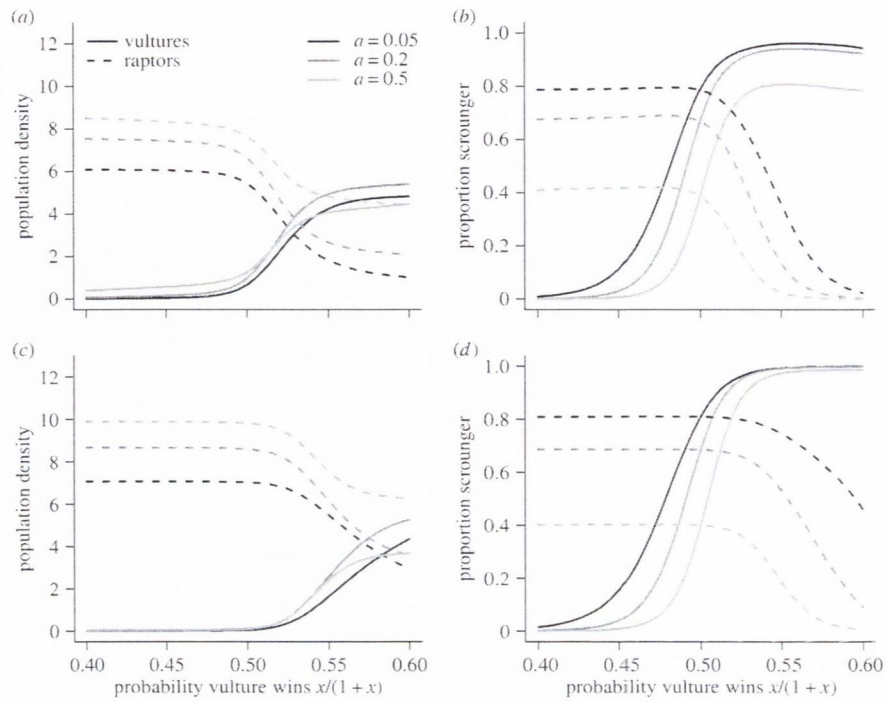


Figure 3. Game theory results. (a,c) Population densities for each species (vultures, solid lines; raptors, dashed lines), and (b,d) frequencies of scroungers in both the vulture and raptor populations. (a,b) Raptors rely strongly on carcasses ($\gamma = 0.05$); (c,d) they rely more weakly on carcasses ($\gamma = 0.15$). Line shades indicate different values for the finder's fee (black, $a = 0.05$; dark grey, $a = 0.2$; light grey, $a = 0.5$). The x-axis is the probability that a vulture wins a one-on-one interaction, $x/(1+x)$. Mortality rates are $\alpha = 0.1$ and $\beta = 0.1$ for all panels.

$$\text{and } \frac{dr_s}{dt} = r_s \left(\pi_{r,s} - \beta + \frac{\gamma}{1 + r_p + r_s} \right). \quad (3.8)$$

Here, α and β are the mortality rates for vultures and raptors, respectively. The additional term $\gamma/(1 + r_p + r_s)$ captures additional food intake by raptors owing to their additional source of energy through predation. Here, we assume that some prey enters the area at rate γ , dies at a fixed rate of 1 and is found by raptors at rate 1 and then instantaneously consumed. Again we assume that the dynamics of the prey population happen on a faster timescale than the raptor population dynamics so that the steady-state density of prey can be used. Varying the parameter γ then allows us to vary raptor's relative reliance on carcasses as a food source.

Unfortunately, no analytical solutions are available for our model, so we examine the evolutionary dynamics of the producer–scrounger interaction using numerical evaluation of steady-state of equations (3.5)–(3.8). The results of the model displayed in figure 3 show the impact of competitive ability, finder's advantage and the availability of prey items to raptors. Note that in figure 3a,c, there is a transition from high raptor population densities to high vulture densities as vultures become more dominant over raptors (the switch occurring when the probability a vulture wins is greater than 0.5). The availability of extra food from predation in figure 3c allows the raptors to persist at higher population densities, suppressing the increasing vulture numbers relative to figure 3a. The effect of increasing relative competitive ability is also realized in driving up the proportion of birds scrounging. The outcome of varying the size of the finder's fee is

evident as we can see a lower proportion of scroungers when the amount of food consumed by the producer is high. A competitively dominant species gains a larger share of the resource. It follows that any finder's fee is of less value to them than it is to the competitively inferior species. Thus the competitively dominant species is more likely to forego a finder's fee in order to benefit from the increased rate of information acquisition that can be facilitated by scrounging.

4. Test of competitive ability

The results of our model demonstrate the potential importance of competitive asymmetry in the evolutionary outcome of inter-guild producer–scrounger dynamics. To test our model prediction of competitive dominance by vultures, we analysed competitive interactions between *Gyps* and raptor species at carcasses from our videos. We followed Bamford *et al.* [27] in our analysis of agonistic interactions between the birds. In each case of aggression, we noted the initiator and the winner. The loser was defined as a bird spatially displaced by the direct action of another individual.

There were 461 interactions in total. We used a binomial generalized linear mixed model with video as a random effect to test the significance of the interactions (figure 4). In support of our theoretical predictions, we found vultures are more likely to be the initiator of an aggressive interaction ($n = 274$ versus 187, figure 4a, $\beta = 0.7414$, s.e. = 0.1987, $p < 0.001$, probability = 0.68, 95% CI 0.59–0.76); vultures are more likely to win when they initiate the contest ($n = 265/274$, figure 4b,

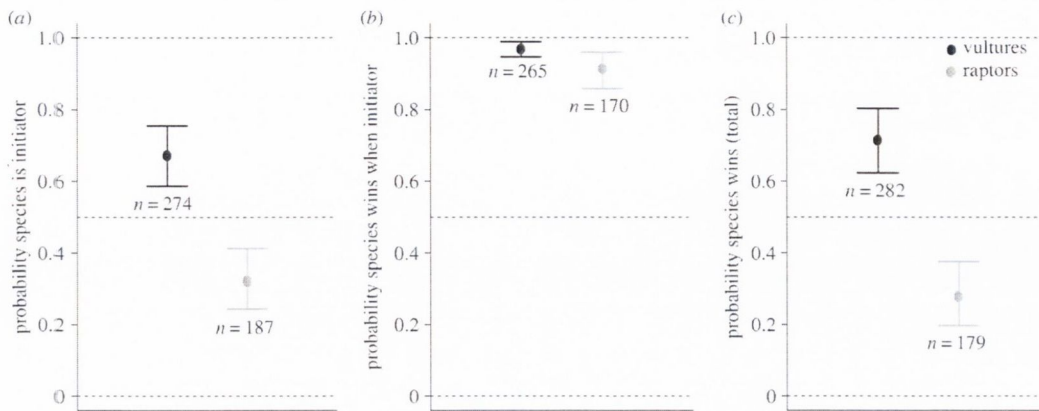


Figure 4. The results of the competitive interactions show (a) the probability that a species was an initiator, (b) the probability that an initiator wins a contest, and (c) the overall competitive ability. Given are the means with 95% CIs.

$\beta = 3.6942$, s.e. = 0.4134, $p < 0.001$, probability = 0.98, 95% CI 0.95–0.99) and raptors are more likely to win when they initiate the contest ($n = 170/187$, $\beta = 2.4893$, s.e. = 0.3473, $p < 0.001$, probability = 0.92, 95% CI 0.86–0.96). The probability that a vulture wins when it initiates a contest is also significantly greater than the probability that a raptor wins when it is the initiator ($\beta = 1.2049$, s.e. = 0.4685, $p = 0.0101$). Finally, vultures are more likely to win overall ($n = 282$ versus 179, figure 4c, $\beta = 0.9567$, s.e. = 0.2303, $p < 0.001$, probability = 0.72, 95% CI 0.62–0.80).

5. Effects of raptor density on vulture foraging efficiency

The producer–scrounger dynamics that we have illustrated suggest a possible ecological interaction whereby vultures are using raptors to locate carcasses. This would imply that vultures may be vulnerable to declines in raptor populations as their ability to locate food will also decline. To examine this possibility, we created an individual-based model (IBM) in the program NETLOGO [28] to explore the effect of raptors on the foraging efficiency of the vultures. Our model is a modified version of Jackson *et al.* [14] and Dermody *et al.* [29], both of which examined vulture foraging behaviour. The main difference is that we include raptors alongside vultures.

Our video analysis suggests raptors can find carcasses before vultures. The question is what is it about their biology that allows them to achieve this? A recent study found that lappet-faced vultures can discover carrion before white-backed vultures despite their smaller population size [30]. We incorporate the changes they deemed likely to impact differential search efficiencies applicable to raptors, namely, visual acuity [31], flying height, roost departure time and dispersion of the birds at the start of the foraging day owing to different roost arrangements (see the electronic supplementary material).

At the beginning of the IBM, the raptors were randomly allocated in the simulation space that corresponds to a square of 100×100 km with periodic boundary conditions so that a bird that flies off the edge of the square will reappear on the opposite side. The vultures are located in a single patch which represents their roost. The raptors forage for

7 h and the vultures 5 h [30]. The vultures change direction by 45° once every 8 min, which is based on the time they spend in thermals [32]; as raptors are less dependent on thermals, they change direction at double this rate. Both have a constant speed as they attempt to find a single randomly located carcass [29]. Both vultures and raptors can find the carrion by themselves. We varied the relative detection distances between the groups such that they are equal; and then that raptors are two, three and four times better. For each of these, we varied the number of raptors from 1 to 10 relative to the 90 vultures present in the simulation (see the electronic supplementary material, table S2).

In the model, vultures can detect carrion at 1 km and can detect other scavengers on a carcass at 4 km [29], the increase in the latter owing to local enhancement [14]. In the version of the model whereby raptors have double the detection distance they can detect carrion at 2 km, which gives a fourfold increase in search area. When a vulture discovers a carcass, it ‘feeds’ on it, with the model calculating the average amount of food eaten by the vultures at the end of the simulated foraging session. Each simulation was replicated 200 times. We square-root transformed our data and analysed it using generalized linear models (GLMs).

Our simulation results show a significant increase in vulture foraging efficiency with raptor density (figure 5), indicating that declines in raptor numbers may lead to declines in vulture populations because of a reduced ability to find or open carcasses.

6. Discussion

Our results suggest that there is a producer–scrounger game occurring between *Gyps* vultures and scavenging raptors, with the competitive dominance of vultures favouring a scrounging strategy on their part.

The biology of the two groups further lends itself to the evolution of producer–scrounger dynamics. *Gyps* vultures are dependent on thermals to fly [33]. Flapping flight is far more energetically expensive than thermal soaring [34] and would prevent vultures from exploring a sufficient area to be effective scavengers [33]. Although raptors do exploit thermals as well, their relatively small size allows them to use the

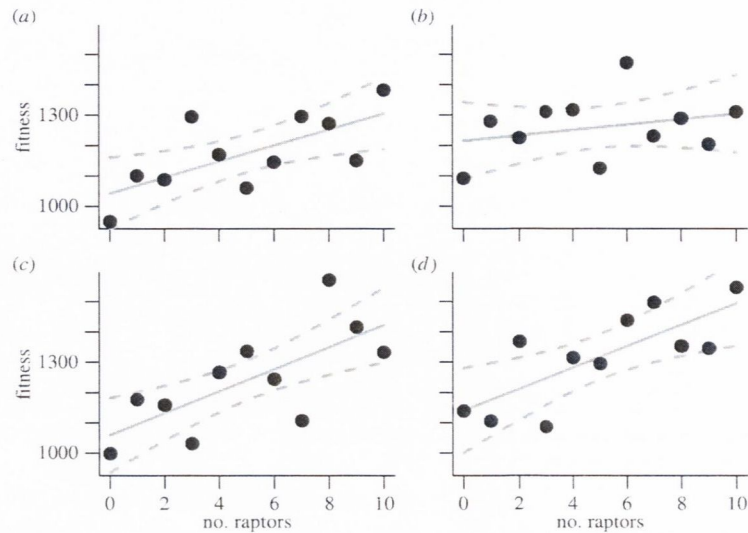


Figure 5. Mean vulture food intake (arbitrary units) as a function of raptor number for four scenarios of differing relative detection distance. (a) Equal distance (GLM, $\beta = 0.3214$, s.e. = 0.1232, $p = 0.00916$), (b) twice distance (GLM, $\beta = 0.3269$, s.e. = 0.123, $p = 0.00794$), (c) triple distance (GLM, $\beta = 0.5047$, s.e. = 0.1198, $p < 0.001$) and (d) quadruple distance (GLM, $\beta = 0.6052$, s.e. = 0.1254, $p < 0.001$).

weaker early morning thermals compared with the larger vultures [35]. Thus they are likely to encounter carrion before the vultures. Kendall [18] found that, for their abundance, tawny eagles were more likely to discover a carcass than African white-backed vultures, and Ruppell's vultures were never the first to arrive at a carcass, which is consistent with producer-scrounger dynamics. She also reported several cases whereby the African white-backed vultures would not feed at a carcass until a tawny eagle began to eat. As mentioned earlier, this may be an instance of carcass opening [18]. The *Gyps* vultures can then dominate the raptor and feed on the previously inaccessible flesh. This would certainly qualify as a producer-scrounger system.

The proposed dynamics are not the result of an abundance of raptors happening upon carcasses more often than the vultures because raptors occur at much lower densities. In the Masai Mara, for instance, *Gyps* species were recorded at an average density of 85.4 species per 100 km compared with 7.4 for tawny eagles [36].

In sum, we show that foraging behaviour in *Gyps* vultures is more complex than previously thought. Social information

transfer flows within and among the vulture and raptor species. In conservation terms, the resultant non-trophic interactions [37] mean that we should shift our focus to ecosystem-based management [38,39] instead of centring our attention on one species at a time. As our IBM shows, scrounging vultures will fare poorly with a decline in producing raptors. With raptor populations on the decline [40], this effect may soon be realized. More generally, we should explore other incidences of socially acquired information transfer between species: inadvertent as it often is, this will be no easy task.

Data accessibility. Some of the data used in the analyses are available in the electronic supplementary material.

Acknowledgements. Thanks to the anonymous reviewers for suggesting improvements to our manuscript. Thanks also to Deirdre McClean for her help in running the IBMs. We thank Munir Virani and T. de Roy for permission to use their images.

Funding statement. A.K. was funded by Trinity College Dublin. L.M. was supported by a Research Fellowship as part of a Wellcome Trust Strategic grant to the Centre for Immunity, Infection and Evolution (grant reference no. 095831).

References

- Dall SRX, Giraldeau LA, Olsson O, McNamara JM, Stephens DW. 2005 Information and its use by animals in evolutionary ecology. *Trends Ecol. Evol.* **20**, 187–193. (doi:10.1016/j.tree.2005.01.010)
- Schmidt KA, Dall SR, Van Gils JA. 2010 The ecology of information: an overview on the ecological significance of making informed decisions. *Oikos* **119**, 304–316. (doi:10.1111/j.1600-0706.2009.17573.x)
- Sumpter D, Buhl J, Biro D, Couzin I. 2008 Information transfer in moving animal groups. *Theor. Biosci.* **127**, 177–186. (doi:10.1007/s12064-008-0040-1)
- Couzin ID. 2009 Collective cognition in animal groups. *Trends Cogn. Sci.* **13**, 36–43. (doi:10.1016/j.tics.2008.10.002)
- McNamara JM, Dall SR. 2010 Information is a fitness enhancing resource. *Oikos* **119**, 231–236. (doi:10.1111/j.1600-0706.2009.17509.x)
- Danchin É, Giraldeau L-A, Valone TJ, Wagner RH. 2004 Public information: from nosy neighbors to cultural evolution. *Science* **305**, 487–491. (doi:10.1126/science.1098254)
- Handegard NO, Boswell KM, Ioannou CC, Leblanc SP, Tjøstheim DB, Couzin ID. 2012 The dynamics of coordinated group hunting and collective information transfer among schooling prey. *Curr. Biol.* **22**, 1213–1217. (doi:10.1016/j.cub.2012.04.050)
- Fedriani JM, Fuller TK, Sauvajot RM, York EC. 2000 Competition and intraguild predation among three sympatric carnivores. *Oecologia* **125**, 258–270. (doi:10.1007/s004420000448)
- Kruuk H. 1967 Competition for food between vultures in East Africa. *Ardea* **55**, 171–193.

10. Seppänen J-T, Forsman JT, Monkkonen M, Thomson RL. 2007 Social information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology* **88**, 1622–1633. (doi:10.1890/06-1757.1)
11. Seppänen J-T, Forsman JT. 2007 Interspecific social learning: novel preference can be acquired from a competing species. *Curr. Biol.* **17**, 1248–1252. (doi:10.1016/j.cub.2007.06.034)
12. Forsman JT, Hjernquist MB, Gustafsson L. 2009 Experimental evidence for the use of density based interspecific social information in forest birds. *Ecography* **32**, 539–545. (doi:10.1111/j.1600-0587.2008.05635.x)
13. Houston D. 1974 Food searching in griffon vultures. *Afr. J. Ecol.* **12**, 63–77. (doi:10.1111/j.1365-2028.1974.tb00107.x)
14. Jackson AL, Ruxton GD, Houston DC. 2008 The effect of social facilitation on foraging success in vultures: a modelling study. *Biol. Lett.* **4**, 311–313. (doi:10.1098/rsbl.2008.0038)
15. Mundy PJ, Butchart D, Ledger J, Piper S. 1992 *The vultures of Africa*. London, UK: Academic Press.
16. Houston D. 1975 Ecological isolation of African scavenging birds. *Ardea* **63**, 55–64.
17. Mundy PJ. 1982 *The comparative biology of southern African vultures*. Johannesburg, South Africa: Vulture Study Group.
18. Kendall CJ. 2013 Alternative strategies in avian scavengers: how subordinate species foil the despotic distribution. *Behav. Ecol. Sociobiol.* **67**, 383–393. (doi:10.1007/s00265-012-1458-5)
19. Cortés-Avizanda A, Jovani R, Carrete M, Donazar JA. 2012 Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: a field experiment. *Ecology* **93**, 2570–2579. (doi:10.1890/12-0221.1)
20. Ogada DL, Keesing F, Virani MZ. 2012 Dropping dead: causes and consequences of vulture population declines worldwide. *Ann. NY Acad. Sci.* **1249**, 57–71. (doi:10.1111/j.1749-6632.2011.06293.x)
21. Green RE *et al.* 2004 Diclofenac poisoning as a cause of vulture population declines across the Indian subcontinent. *J. Appl. Ecol.* **41**, 793–800. (doi:10.1111/j.0021-8901.2004.00954.x)
22. Ogada D, Torchin M, Kinnaird M, Ezenwa V. 2012 Effects of vulture declines on facultative scavengers and potential implications for mammalian disease transmission. *Conserv. Biol.* **26**, 453–460. (doi:10.1111/j.1523-1739.2012.01827.x)
23. Sekercioglu CH. 2006 Increasing awareness of avian ecological function. *Trends Ecol. Evol.* **21**, 464–471. (doi:10.1016/j.tree.2006.05.007)
24. Morand-Ferron J, Giraldeau LA. 2010 Learning behaviorally stable solutions to producer–scrounger games. *Behav. Ecol.* **21**, 343–348. (doi:10.1093/beheco/arp195)
25. Barta Z, Giraldeau LA. 1998 The effect of dominance hierarchy on the use of alternative foraging tactics: a phenotype-limited producing-scrounging game. *Behav. Ecol. Sociobiol.* **42**, 217–223. (doi:10.1007/s002650050433)
26. Hofbauer J, Sigmund K. 2003 Evolutionary game dynamics. *Bull. Am. Math. Soc.* **40**, 479–519. (doi:10.1090/S0273-0979-03-00988-1)
27. Bamford AJ, Monadjem A, Hardy ICW. 2010 Associations of avian facial flushing and skin colouration with agonistic interaction outcomes. *Ethology* **116**, 1163–1170. (doi:10.1111/j.1439-0310.2010.01834.x)
28. Wilensky U. 1999 *NetLogo center for connected learning and computer-based modeling*. Evanston, IL: Northwestern University. See <http://ccl.northwestern.edu/netlogo>.
29. Dermody BJ, Tanner CJ, Jackson AL. 2011 The evolutionary pathway to obligate scavenging in *Gyps* vultures. *PLoS ONE* **6**, e24635. (doi:10.1371/journal.pone.0024635)
30. Spiegel O, Getz WM, Nathan R. 2013 Factors influencing foraging search efficiency: why do scarce lappet-faced vultures outperform ubiquitous white-backed vultures? *Am. Nat.* **181**, E102–E115. (doi:10.1086/670009)
31. Howland CH, Merola S, Basarab JR. 2004 The allometry and scaling of the size of vertebrate eyes. *Vis. Res.* **44**, 2043–2065. (doi:10.1016/j.visres.2004.03.023)
32. Xirouchakis SM, Andreou G. 2009 Foraging behaviour and flight characteristics of Eurasian griffons *Gyps fulvus* in the island of Crete, Greece. *Wildlife Biol.* **15**, 37–52. (doi:10.2981/07-090)
33. Ruxton GD, Houston DC. 2004 Obligate vertebrate scavengers must be large soaring fliers. *J. Theor. Biol.* **228**, 431–436. (doi:10.1016/j.jtbi.2004.02.005)
34. Hedenstrom A. 1993 Migration by soaring or flapping flight in birds: the relative importance of energy cost and speed. *Phil. Trans. R. Soc. Lond. B* **342**, 353–361. (doi:10.1098/rstb.1993.0164)
35. Cone CD. 1962 Thermal soaring of birds. *Am. Sci.* **50**, 180–209.
36. Virani MZ, 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. (doi:10.1016/j.biocon.2010.10.024)
37. Kefi S *et al.* 2012 More than a meal... integrating non-feeding interactions into food webs. *Ecol. Lett.* **15**, 291–300. (doi:10.1111/j.1461-0248.2011.01732.x)
38. Slocumbe DS. 1993 Implementing ecosystem-based management. *BioScience* **43**, 612–622. (doi:10.2307/1312148)
39. Layzer JA. 2012 The purpose and politics of ecosystem-based management. In *Sustainability science: the emerging paradigm and the urban environment* (eds MP Weinstein, RE Turner), pp. 177–197. New York: Springer.
40. Ogada DL, Keesing F. 2010 Decline of raptors over a three-year period in Laikipia, central Kenya. *J. Raptor Res.* **44**, 129–135. (doi:10.3356/JRR-09-49.1)

appendix b

Are vulture restaurants needed to sustain the densest breeding population of the African White-backed Vulture? - Supplementary information

Table b.1: Life history parameters for all of the species in the community under study, values are in years Brown (1991); Pennycuick (1976); Jones et al. (2009); Monadjem et al. (2012); Piper et al. (1999); De Magalhaes and Costa (2009).

Species	Adult age	Fertile age	End of fertility	Life expectancy
<i>Gyps africanus</i>	1	5	19	20
<i>Trigonoceps occipitalis</i>	1	5	29	30
<i>Torgos tracheliotos</i>	1	5	39	40
<i>Leptoptilos crumeniferus</i>	1	5	24	25
<i>Aquila rapax</i>	1	5	15	16
<i>Terathopius ecaudatus</i>	1	5	29	30
<i>Aepyceros melampus</i>	1	1	17	17
<i>Connochaetes taurinus</i>	1	2	22	22
<i>Equus burchellii</i>	1	2	40	40
<i>Phacochoerus aethiopicus</i>	1	1	19	19
<i>Loxodonta africana</i>	10	12	50	80
<i>Tragelaphus strepsiceros</i>	1	1	23	23
<i>Ceratotherium simum</i>	5	6	50	50
<i>Giraffa camelopardalis</i>	3	4	36	36
<i>Tragelaphus angasii</i>	1	2	16	16
<i>Kobus ellipsiprymnus</i>	3	4	20	20
<i>Hippopotamus amphibius</i>	4	5	55	55
<i>Syncerus caffer</i>	3	4	30	30
<i>Taurotragus oryx</i>	1	2	24	24
<i>Tragelaphus scriptus</i>	1	1	13	13
<i>Sylvicapra grimmia</i>	1	1	14	14
<i>Redunca arundinum</i>	1	1	17	17
<i>Hippotragus niger</i>	1	2	22	22
<i>Redunca fulvorufula</i>	1	1	12	12
<i>Hippotragus equinus</i>	1	2	20	20
<i>Damaliscus lunatus</i>	1	2	18	18
<i>Oreotragus oreotragus</i>	1	1	17	17
<i>Raphicerus campestris</i>	1	1	14	14
<i>Cephalophus natalensis</i>	1	1	15	15
<i>Ourebia ourebi</i>	1	1	16	16

Table b.2: Reproductive parameters for species of the avian scavenging guild (number of descendants corresponds to the number of fledglings for the following species) Mundy et al. (1992); Monadjem and Garcelon (2005); Mundy and Group (1982); Margalida and Colomer (2012).

Species	Proportion female	Fertility ratio	No. of descendants
<i>Gyps africanus</i>	0.7	0.8	1
<i>Trigonoceps occipitalis</i>	0.7	0.65	1
<i>Torgos tracheliotos</i>	0.7	0.7	1
<i>Leptoptilos crumeniferus</i>	0.7	0.7	1
<i>Aquila rapax</i>	0.7	0.7	1
<i>Terathopius ecaudatus</i>	0.7	0.7	1

Table b.3: Mortality values for adults of the avian scavenging guild over a year Brown (1991); Pennycuick (1976); Monadjem et al. (2012); Piper et al. (1999); Monadjem et al. (2013).

Species	July-Aug	Sept-Oct	Nov-Apr	May-June
<i>Gyps africanus</i>	0.0002	0.0002	0.0005	0.0002
<i>Trigonoceps occipitalis</i>	0.0002	0.0002	0.005	0.0002
<i>Torgos tracheliotos</i>	0.0002	0.0002	0.005	0.0002
<i>Leptoptilos crumeniferus</i>	0.01333	0.01333	0.04	0.01333
<i>Aquila rapax</i>	0.0002	0.0002	0.005	0.0002
<i>Terathopius ecaudatus</i>	0.0002	0.0002	0.005	0.0002

Table b.4: Mortality values for immatures of the avian scavenging guild over a year Brown (1991); Pennycuick (1976); Monadjem et al. (2012); Piper et al. (1999); Monadjem et al. (2013).

Species	July-Aug	Sept-Oct	Nov-Apr	May-June
<i>Gyps africanus</i>	0.096	0.096	0.29	0.096
<i>Trigonoceps occipitalis</i>	0.1	0.1	0.3	0.1
<i>Torgos tracheliotos</i>	0.1	0.1	0.3	0.1
<i>Leptoptilos crumeniferus</i>	0.06	0.06	0.178	0.06
<i>Aquila rapax</i>	0.096	0.096	0.29	0.096
<i>Terathopius ecaudatus</i>	0.096	0.096	0.29	0.096

Table b.5: Meat available for scavengers from carrion providing species Jones et al. (2009); Sinclair and Norton-Griffiths (1995).

Species	Meat from juveniles (kg)	Meat from adults (kg)
<i>Aepyceros melampus</i>	14.7	19.6
<i>Connochaetes taurinus</i>	53.025	70.7
<i>Equus burchellii</i>	60.9	81.2
<i>Phacochoerus aethiopicus</i>	23.625	31.5
<i>Loxodonta africana</i>	1490.25	1987
<i>Tragelaphus strepsiceros</i>	53.55	71.4
<i>Ceratotherium simum</i>	876.75	1169
<i>Giraffa camelopardalis</i>	417	556
<i>Tragelaphus angasii</i>	24.675	32.9
<i>Kobus ellipsiprymnus</i>	56.7	75.6
<i>Hippopotamus amphibius</i>	650.25	867
<i>Syncerus caffer</i>	192.75	257
<i>Taurotragus oryx</i>	152.25	203
<i>Tragelaphus scriptus</i>	12.6	16.8
<i>Sylvicapra grimmia</i>	4.2	5.6
<i>Redunca arundinum</i>	17.85	23.8
<i>Hippotragus niger</i>	56.7	75.6
<i>Redunca fulvorufula</i>	6.825	9.1
<i>Hippotragus equinus</i>	64.05	85.4
<i>Damaliscus lunatus</i>	28.875	38.5
<i>Oreotragus oreotragus</i>	3.15	4.2
<i>Raphicerus campestris</i>	3.15	4.2
<i>Cephalophus natalensis</i>	3.15	4.2
<i>Ourebia ourebi</i>	4.2	5.6

Table b.6: Initial and maximum density of all the species considered in the ecosystem/ model. For the birds we calculated the area potentially available to each species in Swaziland and then used recorded density estimates to determine the maximum number we would expect in such an area. Initial is equivalent to max density for the ungulates given our model assumptions mentioned above. The birds are in pairs, the ungulates are individuals (Monadjem et al., 2003).

Species	Initial density	Maximum density
<i>Gyps africanus</i>	300	1000
<i>Trigonoceps occipitalis</i>	6	20
<i>Torgos tracheliotos</i>	1	66
<i>Leptoptilos crumeniferus</i>	19	100
<i>Aquila rapax</i>	1	20
<i>Terathopius ecaudatus</i>	15	30
<i>Gyps coprotheres</i>	15	15
<i>Aepyceros melampus</i>	16500	16500
<i>Connochaetes taurinus</i>	1700	1700
<i>Equus burchellii</i>	1500	1500
<i>Phacochoerus aethiopicus</i>	2300	2300
<i>Loxodonta africana</i>	40	40
<i>Tragelaphus strepsiceros</i>	1300	1300
<i>Ceratotherium simum</i>	50	50
<i>Giraffa camelopardalis</i>	80	80
<i>Tragelaphus angasii</i>	1000	1000
<i>Kobus ellipsiprymnus</i>	260	260
<i>Hippopotamus amphibius</i>	25	25
<i>Syncerus caffer</i>	40	40
<i>Taurotragus oryx</i>	40	40
<i>Tragelaphus scriptus</i>	250	250
<i>Sylvicapra grimmia</i>	550	550
<i>Redunca arundinum</i>	120	120
<i>Hippotragus niger</i>	20	20
<i>Redunca fulvorufula</i>	200	200
<i>Hippotragus equinus</i>	7	7
<i>Damaliscus lunatus</i>	16	16
<i>Oreotragus oreotragus</i>	200	200
<i>Raphicerus campestris</i>	140	140
<i>Cephalophus natalensis</i>	80	80
<i>Ourebia ourebi</i>	50	50

Table b.7: Daily Food Requirements for the avian scavenging guild. Marabou Stork food requirements are taken to be the same as the similarly sized Cape Griffon Mundy et al. (1992); Mundy and Group (1982); Calder (1996).

Species	Daily food requirements (g)
<i>Gyps africanus</i>	400
<i>Gyps coprotheres</i>	520
<i>Trigonoceps occipitalis</i>	350
<i>Torgos tracheliotos</i>	500
<i>Leptoptilos crumeniferus</i>	520
<i>Aquila rapax</i>	160
<i>Terathopius ecaudatus</i>	160

Table b.8: A summary of the changes in ungulate mortality, vulture food requirements and, foraging radius throughout the year and according to the periods considered.

Month	Season	Young	Food requirements	Foraging radius	Period
Jan	Wet	N/A	Low	N/A	3
Feb	Wet	N/A	Low	N/A	3
Mar	Wet	N/A	Low	N/A	3
Apr	Wet	N/A	Low	N/A	3
May	Dry	Incubating	Low	Reduced	4
June	Dry	Incubating	Low	Reduced	4
July	Dry	Hatched	High	Reduced	1
Aug	Dry	Hatched	High	Reduced	1
Sept	Wet	Hatched	High	Reduced	2
Oct	Wet	Hatched	High	Reduced	2
Nov	Wet	N/A	Low	N/A	3
Dec	Wet	N/A	Low	N/A	3

Table b.9: Parameters and definitions used in the model.

Parameter	Concept
$g_{i,2}$	Is equal 1 if the species i is facultative otherwise it is equal 0.
$g_{i,2}$	Age animals of species i get to adult size.
$g_{i,3}$	Age females of species i start to be fertile.
$g_{i,4}$	Age females of species i end their fertile period.
$g_{i,5}$	Life expectancy of species i
$m_{i,1,c}$	Probability of death of young animals of species i in the period c .
$m_{i,2,c}$	Probability of death of adult animals of species i in the period c .
$k_{i,1}$	Sex ratio of species i .
$k_{i,2}$	Probability to reproduce a female of species i .
$f, l_{i,1}$	Biomass (meat) of young animals of species i leave when they die.
$f, l_{i,2}$	Biomass (meat) of adult animals of species i leave when they die.
$f, u_{i,1}$	Amount of useful biomass of young animals of species i .
$f, u_{i,2}$	Amount of useful biomass of adult animals of species i .
$f, f_{i,1,c}$	Necessary biomass for young animals of species i in the period c .
$f, f_{i,2,c}$	Necessary biomass for adult animals of species i in the period c .
$p_{i,c}$	Probability that animals of species i move when the resources are insufficient in period c
$q_{i,j}$	Number of animals of species i and age j .
$N_{i,2}$	Floating population of species i .
d_i	maximum population (carrying capacity) of the species i .

PDP Model Components

Following Colomer et al. (2013), there are four main components to the model: 1) A set of environments that are connected according to some prefixed relation, and which can be formally described by a network; 2) a membrane structure that provides the hierarchy among the different membranes that constitute the cell contained in each environment; 3) objects involved in the system under study (individuals, resources etc.) are represented by alphabetic characters; 4) A set of rules that specify the behaviour of the objects in the model and a set of rules for the model environments which define how individuals can move between the environments as well as generating values for the variables correlated between environments.

PDP Systems Full Model

Membrane structure

$$\mu = [[]_1 []_2 []_3 \cdots []_P]_0$$

μ is the membrane structure of the model. Internal membranes of the membrane skin are associated with the four periods considered. The p represents the number of membranes.

Initial objects

$$\mu_0 = \{X_{i,j}^{q_{i,j}}, 1 \leq i \leq N, 1 \leq j \leq g_{i,5}\} \cup \{XF_i^{N_{i,2}}, DY_i, 1 \leq i \leq CNY\} \cup \{co_1\}.$$

$$\mu_i = \{R\}, 1 \leq i \leq P.$$

Each animal that has its territory in the ecosystem is associated with an object $X_{i,j}$, i and j indicate the species and the age respectively, $q_{i,j}$ is the number of animals of the species i and age j . Each animal that belongs to the floating population is associated with an object XF_i , $N_{i,2}$ is the number of floating animals of species i . These floating species are animals that normally live outside of the environment in question i.e. Swaziland but can interact with it by feeding on the carrion resources there. In this instance the Cape vulture is our important floating population. DY_i is an object that controls the maximum density of scavenger species (carrying capacity). CNY is the number of different species in the ecosystem. The population of the "prey" species has been assumed as constant.

The object co_1 , controls the seasonality of the model and the object R is a counter that allows synchronization of the model.

Step 1

The membrane is activated for the period to simulate changing its polarization.

$$r_1 \equiv co_c []_c \rightarrow []_c^+, 1 \leq c \leq P.$$

Step 2

The counter R of the activated membrane begins to evolve and this counter allows for synchronization of the model.

$$r_2 \equiv [R]_c^+ \rightarrow [R_1]_c, 1 \leq c \leq P.$$

The objects associated with the animals enter the activated membrane

$$r_3 \equiv X_{i,j} []_c^+ \rightarrow [X_{i,j}]_c, 0 \leq j \leq g_{i,5}, 1 \leq c \leq P, 1 \leq i \leq N.$$

The XF'_i component is a copy of XF_i necessary for the next step.

$$r_4 \equiv XF_i []_c^+ \rightarrow [XF_i, XF'_i]_c, 1 \leq c \leq P, 1 \leq i \leq CNY.$$

represents the dissolution of the objects in the model. This rule ensures that any object with 100 in the second index disappears.

$$r_5 \equiv X_{i,100} []_c^+ \rightarrow [\#]_c, 1 \leq c \leq P, 1 \leq i \leq N.$$

There is an object DY for each species of avian scavenger, these objects evolve, creating objects of type a and e that allow control of the maximum load of each species. Objects a and their superscripts are used to control the maximum load capacity whereas objects e and their superscripts are used to generate randomness in the load of the animals. The parameter d_i represents the carrying capacity of species i .

$$r_6 \equiv DY_i[]_c^+ \rightarrow [DY_i, a_i^{0.9 \cdot d_i}, e_i^{0.2 \cdot d_i}]_c, 1 \leq c \leq P, 1 \leq i \leq CNY.$$

Step 3

Evolution of the counter and the object e allows small random variations in load.

$$r_7 \equiv [R_1 \rightarrow R_2]_c, 1 \leq c \leq P.$$

$$r_8 \equiv [e_i \xrightarrow{0.5} a_i]_c, 1 \leq c \leq P, 1 \leq i \leq N.$$

$$r_9 \equiv [e_i \xrightarrow{0.5} \#]_c, 1 \leq c \leq P, 1 \leq i \leq N.$$

The objects associated with the animals start the reproduction process that is performed in period 1 (Membrane 1), can reproduce fertile females (when these reach the age of maturity they are able to have a first breeding attempt) creating new objects.

Evolution of the objects $Y_{i,j}$ associated with fertile females that reproduce.

$$r_{10} \equiv [X_{i,j} \xrightarrow{k_{i,2} \cdot k_{i,1}} Y_{i,j}, Y_{i,0}^{k_{i,3}}]_1, g_{i,3} \leq j \leq g_{i,4}, 1 \leq i \leq N.$$

Evolution of the objects associated with fertile females that do not reproduce.

$$r_{11} \equiv [X_{i,j} \xrightarrow{1 - k_{i,2} \cdot k_{i,1}} Y_{i,j}]_1, g_{i,3} \leq j \leq g_{i,4}, 1 \leq i \leq N.$$

Evolution of the objects associated with infertile adult animals.

$$r_{12} \equiv [X_{i,j} \rightarrow Y_{i,j}]_1, g_{i,4} < j \leq g_{i,5}, 1 \leq i \leq N.$$

Evolution of the objects associated with infertile young animals.

$$r_{13} \equiv [X_{i,j} \rightarrow Y_{i,j}]_1, 0 \leq j < g_{i,3}, 1 \leq i \leq N.$$

In the remaining periods no reproduction occurs, therefore the objects evolve but these do not generate new objects.

$$r_{14} \equiv [X_{i,j} \rightarrow Y_{i,j}]_c, 0 \leq j < g_{i,5}, 1 \leq i \leq N, 2 \leq c \leq P.$$

$$r_{15} \equiv [XF_i \rightarrow YF_i]_c, 1 \leq i \leq CNY, 1 \leq c \leq P.$$

Step 4

$$r_{16} \equiv [R_2 \rightarrow R_3]_c, 1 \leq c \leq P.$$

Begins the process of mortality, the scavengers are separated from other animals whose biomass is left in meat.

Young scavengers survive generating objects $Z_{i,j}$.

$$r_{17} \equiv \left[Y_{i,j} \xrightarrow{1-m_{i,1,c}} Z_{i,j} \right]_c, 0 \leq j < g_{i,2}, 1 \leq i \leq CNY, 1 \leq c \leq P.$$

Young scavengers die.

$$r_{18} \equiv \left[Y_{i,j} \xrightarrow{m_{i,1,c}} \# \right]_c, 0 \leq j < g_{i,2}, 1 \leq i \leq CNY, 1 \leq c \leq P.$$

Young animals that are not scavengers who survive

$$r_{19} \equiv \left[Y_{i,j} \xrightarrow{1-m_{i,1,c}} Z_{i,j} \right]_c, 0 \leq j < g_{i,2}, CNY + 1 \leq i \leq N, 1 \leq c \leq P.$$

young animals that are not scavengers who die leaving biomass. The model takes into account that the population of animals that are not scavengers remains constant; therefore the object associated with the animal evolves but does not disappear.

$$r_{20} \equiv \left[Y_{i,j} \xrightarrow{m_{i,1,c}} C_i^{fl_{i,1} \cdot fu_i}, M_i^{fl_{i,1} \cdot fu_i}, Z_{i,j} \right]_c, 0 \leq j < g_{i,2}, CNY + 1 \leq i \leq N, 1 \leq c \leq P.$$

Adult scavengers who survive.

$$r_{21} \equiv \left[Y_{i,j} \xrightarrow{1-m_{i,2,c}} Z_{i,j} \right]_c, g_{i,2} \leq j < g_{i,5}, 1 \leq i \leq CNY, 1 \leq c \leq P.$$

Adult scavengers who die.

$$r_{22} \equiv \left[Y_{i,j} \xrightarrow{m_{i,2,c}} \# \right]_c, g_{i,2} \leq j < g_{i,5}, 1 \leq i \leq CNY, 1 \leq c \leq P.$$

Adult animals that are not scavengers who survive.

$$r_{23} \equiv \left[Y_{i,j} \xrightarrow{1-m_{i,2,c}} Z_{i,j} \right]_c, g_{i,2} \leq j < g_{i,5}, CNY + 1 \leq i \leq N, 1 \leq c \leq P.$$

Adult animals that are not scavengers who die.

$$r_{24} \equiv \left[Y_{i,j} \xrightarrow{m_{i,2,c}} C_i^{fl_{i,2} \cdot fu_i}, M_i^{fl_{i,2} \cdot fu_i}, Z_{i,j} \right]_c, g_{i,2} \leq j < g_{i,5}, CNY + 1 \leq i \leq N, 1 \leq c \leq P.$$

Flotant population

$$r_{25} \equiv [YF_i \rightarrow ZF_i]_c, 1 \leq i \leq CNY, 1 \leq c \leq P.$$

The animals when they reach life expectancy will disappear from the ecosystem; it is assumed that in each period 25% die.

$$r_{26} \equiv \left[Y_{i,g_{i,5}} \xrightarrow{0.25} C_i^{fl_{i,2} \cdot fu_i}, M_i^{fl_{i,2} \cdot fu_i}, Z_{i,g_{i,5}} \right]_c, 1 \leq i \leq N, 1 \leq c \leq P.$$

$$r_{27} \equiv \left[Y_{i,g_{i,5}} \xrightarrow{0.75} Z_{i,g_{i,5}} \right]_c, 1 \leq i \leq N, 1 \leq c \leq P.$$

Step 5

$$r_{28} \equiv [R_3]_c \rightarrow [R_4]_c^+, 1 \leq c \leq P.$$

There are no limitations on food for animals that are not scavengers, therefore all evolve

$$r_{29} \equiv [Z_{i,j}]_c \rightarrow [W_{i,j}]_c^+, 0 \leq j < g_{i,5}, CNY + 1 \leq i \leq N, 1 \leq c \leq P.$$

There are priorities for food available to scavengers in the simulator; species are entered according to this criterion, so after species 1 eats species 2 will eat and so on. This is achieved by Znumber (Z1,...Z7) and ZFnumber (ZF1,... ZF7). The hierarchy in our model is, in order of arrival, 1) Bateleur, 2) Tawny Eagle, 3) White-backed Vulture, 4) Lappet-faced Vulture, 5) White-headed Vulture, 6) Cape Vulture, and 7) Marabou Stork ^[1]

$$r_{30} \equiv [Z_{i,j}]_c \rightarrow [Z1_{i,j}]_c^+, 0 \leq j < g_{i,5}, 1 \leq i \leq CNY, 1 \leq c \leq P.$$

$$r_{31} \equiv [ZF_i]_c \rightarrow [ZF1_i]_c^+, 1 \leq i \leq CNY, 1 \leq c \leq P.$$

Step 6

$$r_{32} \equiv [R_4 \rightarrow R_5]_c^+, 1 \leq c \leq P.$$

If there are sufficient resources all the animals of species 1 will eat.

$$r_{33} \equiv [Z1_{1,j}, M^{ff_{1,1,c}} \rightarrow W_{1,j}]_c^+, 0 \leq j < g_{1,3}, 1 \leq c \leq P.$$

$$r_{34} \equiv [Z1_{1,j}, a_2, M^{ff_{1,2,c}} \rightarrow W_{1,j}]_c^+, g_{1,3} \leq j \leq g_{1,5}, 1 \leq c \leq P.$$

$$r_{35} \equiv [ZF1_1, M^{ff_{1,2,c}} \rightarrow \#]_c^+, 1 \leq c \leq P.$$

The other objects associated with the remaining species evolve Z2 type objects.

$$r_{36} \equiv [Z1_{i,j} \rightarrow Z2_{i,j}]_c^+, 0 \leq j \leq g_{i,5}, 2 \leq i \leq CNY, 1 \leq c \leq P.$$

$$r_{37} \equiv [ZF1_i \rightarrow ZF2_i]_c^+, 2 \leq i \leq CNY, 1 \leq c \leq P.$$

Step 7

$$r_{38} \equiv [R_5 \rightarrow R_6]_c^+, 1 \leq c \leq P.$$

If resources are left over animals of species 2 eat.

$$r_{39} \equiv [Z2_{2,j}, M^{ff_{2,1,c}} \rightarrow W_{2,j}]_c^+, 0 \leq j < g_{2,3}, 1 \leq c \leq P.$$

$$r_{40} \equiv [Z2_{2,j}, a_2, M^{ff_{2,2,c}} \rightarrow W_{2,j}]_c^+, g_{2,3} \leq j \leq g_{2,5}, 1 \leq c \leq P.$$

$$r_{41} \equiv [ZF2_2, M^{ff_{2,2,c}} \rightarrow \#]_c^+, 1 \leq c \leq P.$$

The remaining animals evolve

$$r_{42} \equiv [Z2_{i,j} \rightarrow Z3_{i,j}]_c^+, 0 \leq j \leq g_{i,5}, 3 \leq i \leq CNY, 1 \leq c \leq P.$$

$$r_{43} \equiv [ZF2_i \rightarrow ZF3_i]_c^+, 3 \leq i \leq CNY, 1 \leq c \leq P.$$

Step 8

$$r_{44} \equiv [R_6 \rightarrow R_7]_c^+, 1 \leq c \leq P.$$

If resources are left over, the animals of species 3 will eat.

$$r_{45} \equiv [Z3_{3,j}, M^{ff_{3,1,c}} \rightarrow W_{3,j}]_c^+, 0 \leq j < g_{3,3}, 1 \leq c \leq P.$$

$$r_{46} \equiv [Z3_{3,j}, a_3, M^{ff_{3,2,c}} \rightarrow W_{3,j}]_c^+, g_{3,3} \leq j \leq g_{3,5}, 1 \leq c \leq P.$$

$$r_{47} \equiv [ZF3_3, M^{ff_{3,2,c}} \rightarrow \#]_c^+, 1 \leq c \leq P.$$

The remaining animals evolve

$$r_{48} \equiv [Z3_{i,j} \rightarrow Z4_{i,j}]_c^+, 0 \leq j \leq g_{i,5}, 4 \leq i \leq CNY, 1 \leq c \leq P.$$

$$r_{49} \equiv [ZF3_i \rightarrow ZF4_i]_c^+, 4 \leq i \leq CNY, 1 \leq c \leq P.$$

Step 9

$$r_{50} \equiv [R_7 \rightarrow R_8]_c^+, 1 \leq c \leq P.$$

If resources are left over, the animals of species 4 will eat.

$$r_{51} \equiv [Z4_{4,j}, M^{ff_{4,1,c}} \rightarrow W_{4,j}]_c^+, 0 \leq j < g_{4,3}, 1 \leq c \leq P.$$

$$r_{52} \equiv [Z4_{4,j}, a_4, M^{ff_{4,2,c}} \rightarrow W_{4,j}]_c^+, g_{4,3} \leq j \leq g_{4,5}, 1 \leq c \leq P.$$

$$r_{53} \equiv [ZF4_4, M^{ff_{4,2,c}} \rightarrow \#]_c^+, 1 \leq c \leq P.$$

The remaining animals evolve

$$r_{54} \equiv [Z4_{i,j} \rightarrow Z5_{i,j}]_c^+, 0 \leq j \leq g_{i,5}, 5 \leq i \leq CNY, 1 \leq c \leq P.$$

$$r_{55} \equiv [ZF4_i \rightarrow ZF5_i]_c^+, 5 \leq i \leq CNY, 1 \leq c \leq P.$$

Step 10

$$r_{56} \equiv [R_8 \rightarrow R_9]_c^+, 1 \leq c \leq P.$$

If resources are left over, the animals of species 5 will eat.

$$r_{57} \equiv [Z5_{5,j}, M^{ff_{5,1,c}} \rightarrow W_{5,j}]_c^+, 0 \leq j < g_{5,3}, 1 \leq c \leq P.$$

$$r_{58} \equiv [Z5_{5,j}, a_5, M^{ff_{5,2,c}} \rightarrow W_{5,j}]_c^+, g_{5,3} \leq j \leq g_{5,5}, 1 \leq c \leq P.$$

$$r_{59} \equiv [ZF5_5, M^{ff_{5,2,c}} \rightarrow \#]_c^+, 1 \leq c \leq P.$$

The remaining animals evolve

$$r_{60} \equiv [Z5_{i,j} \rightarrow Z6_{i,j}]_c^+, 0 \leq j \leq g_{i,5}, 6 \leq i \leq CNY, 1 \leq c \leq P.$$

$$r_{61} \equiv [ZF5_i \rightarrow ZF6_i]_c^+, 6 \leq i \leq CNY, 1 \leq c \leq P.$$

Step 11

$$r_{62} \equiv [R_9 \rightarrow R_{10}]_c^+, 1 \leq c \leq P.$$

If resources are left over, the animals of species 6 will eat.

$$r_{63} \equiv [Z6_{6,j}, M^{ff_{6,1,c}} \rightarrow W_{6,j}]_c^+, 0 \leq j < g_{6,3}, 1 \leq c \leq P.$$

$$r_{64} \equiv [Z6_{6,j}, a_6, M^{ff_{6,2,c}} \rightarrow W_{6,j}]_c^+, g_{6,3} \leq j \leq g_{6,5}, 1 \leq c \leq P.$$

$$r_{65} \equiv [ZF6_6, M^{ff_{6,2,c}} \rightarrow \#]_c^+, 1 \leq c \leq P.$$

The remaining animals evolve

$$r_{66} \equiv [Z6_{i,j} \rightarrow Z7_{i,j}]_c^+, 0 \leq j \leq g_{i,5}, 7 \leq i \leq CNY, 1 \leq c \leq P.$$

$$r_{67} \equiv [ZF6_i \rightarrow ZF7_i]_c^+, 7 \leq i \leq CNY, 1 \leq c \leq P.$$

Step 12

$$r_{68} \equiv [R_{10}]_c^+ \rightarrow [R_{11}]_c^-, 1 \leq c \leq P.$$

If resources are left over, the animals of species 7 will eat.

$$r_{69} \equiv [Z7_{7,j}, M^{ff_{7,1,c}}]_c^+ \rightarrow [W_{7,j}]_c^-, 0 \leq j < g_{7,3}, 1 \leq c \leq P.$$

$$r_{70} \equiv [Z7_{7,j}, a_7, M^{ff_{7,2,c}}]_c^+ \rightarrow [W_{7,j}]_c^-, g_{7,3} \leq j \leq g_{7,5}, 1 \leq c \leq P.$$

$$r_{71} \equiv [ZF7_7, M^{ff_{7,2,c}}]_c^+ \rightarrow [\#]_c^-, 1 \leq c \leq P.$$

Step 13

$$r_{72} \equiv [R_{11}]_c^- \rightarrow [R]_c, 1 \leq c \leq P.$$

The objects that are associated with the floating population disappear; the floating population without access to food resources goes to another area.

$$r_{73} \equiv [ZF1_1]_c^- \rightarrow [\#]_c, 1 \leq c \leq P.$$

$$r_{74} \equiv [ZF2_2]_c^- \rightarrow [\#]_c, 1 \leq c \leq P.$$

$$r_{75} \equiv [ZF3_3]_c^- \rightarrow [\#]_c, 1 \leq c \leq P.$$

$$r_{76} \equiv [ZF4_4]_c^- \rightarrow [\#]_c, 1 \leq c \leq P.$$

$$r_{77} \equiv [ZF5_5]_c^- \rightarrow [\#]_c, 1 \leq c \leq P.$$

$$r_{78} \equiv [ZF6_6]_c^- \rightarrow [\#]_c, 1 \leq c \leq P.$$

$$r_{79} \equiv [ZF7_7]_c^- \rightarrow [\#]_c, 1 \leq c \leq P.$$

Scavengers with insufficient food resources in the area, depending on the time of year can move to other areas to eat the necessary food and return to their territory. So objects can evolve and not necessarily to disappear. Objects associated with some non facultative animals ($g_{i,1} = 0$) can disappear from the ecosystem.

$$r_{80} \equiv [Z1_{1,j}]_c^- \xrightarrow{p_{1,c}} X'_{1,j}[\]_c, 0 \leq j \leq g_{1,3}, 1 \leq c \leq P-1.$$

$$r_{81} \equiv [Z1_{1,j}]_c^- \xrightarrow{1-p_{1,c}} X'^{g_{1,1}}_{1,j}[\]_c, 0 \leq j < g_{1,3}, 1 \leq c \leq P-1.$$

$$r_{82} \equiv [Z1_{1,j}, a_1]_c^- \xrightarrow{p_{1,c}} X_{1,j}[\]_c, g_{1,3} \leq j \leq g_{1,5}, 1 \leq c \leq P-1.$$

$$r_{83} \equiv [Z1_{1,j}, a_1]_c^- \xrightarrow{1-p_{1,c}} X^{g_{1,1}}_{1,j}[\]_c, g_{1,3} \leq j \leq g_{1,5}, 1 \leq c \leq P-1.$$

$$r_{84} \equiv [Z2_{2,j}]_c^- \xrightarrow{p_{2,c}} X'_{2,j}[\]_c, 0 \leq j \leq g_{2,3}, 1 \leq c \leq P-1.$$

$$r_{85} \equiv [Z2_{2,j}]_c^- \xrightarrow{1-p_{2,c}} X'^{g_{2,1}}_{2,j}[\]_c, 0 \leq j < g_{2,3}, 1 \leq c \leq P-1.$$

$$r_{86} \equiv [Z2_{2,j}, a_2]_c^- \xrightarrow{p_{2,c}} X_{2,j}[\]_c, g_{2,3} \leq j \leq g_{2,5}, 1 \leq c \leq P-1.$$

$$r_{87} \equiv [Z2_{2,j}, a_2]_c^- \xrightarrow{1-p_{2,c}} X^{g_{2,1}}_{2,j}[\]_c, g_{2,3} \leq j \leq g_{2,5}, 1 \leq c \leq P-1.$$

$$r_{88} \equiv [Z3_{3,j}]_c^- \xrightarrow{p_{3,c}} X'_{3,j}[\]_c, 0 \leq j \leq g_{3,3}, 1 \leq c \leq P-1.$$

$$r_{89} \equiv [Z3_{3,j}]_c^- \xrightarrow{1-p_{3,c}} X'^{g_{3,1}}_{3,j}[\]_c, 0 \leq j < g_{3,3}, 1 \leq c \leq P-1.$$

$$r_{90} \equiv [Z3_{3,j}, a_3]_c^- \xrightarrow{p_{3,c}} X_{3,j}[\]_c, g_{3,3} \leq j \leq g_{3,5}, 1 \leq c \leq P-1.$$

$$r_{91} \equiv [Z3_{3,j}, a_3]_c^- \xrightarrow{1-p_{3,c}} X^{g_{3,1}}_{3,j}[\]_c, g_{3,3} \leq j \leq g_{3,5}, 1 \leq c \leq P-1.$$

$$r_{92} \equiv [Z4_{4,j}]_c^- \xrightarrow{p_{4,c}} X'_{4,j}[\]_c, 0 \leq j \leq g_{4,3}, 1 \leq c \leq P-1.$$

$$r_{93} \equiv [Z4_{4,j}]_c^- \xrightarrow{1-p_{4,c}} X'^{g_{4,1}}_{4,j}[\]_c, 0 \leq j < g_{4,3}, 1 \leq c \leq P-1.$$

$$r_{94} \equiv [Z4_{4,j}, a_4]_c^- \xrightarrow{p_{4,c}} X_{4,j}[\]_c, g_{4,3} \leq j \leq g_{4,5}, 1 \leq c \leq P-1.$$

$$r_{95} \equiv [Z4_{4,j}, a_4]_c^- \xrightarrow{1-p_{4,c}} X^{g_{4,1}}_{4,j}[\]_c, g_{4,3} \leq j \leq g_{4,5}, 1 \leq c \leq P-1.$$

$$r_{96} \equiv [Z5_{5,j}]_c^- \xrightarrow{p_{5,c}} X'_{5,j}[\]_c, 0 \leq j \leq g_{5,3}, 1 \leq c \leq P-1.$$

$$r_{97} \equiv [Z5_{5,j}]_c^- \xrightarrow{1-p_{5,c}} X'^{g_{5,1}}_{5,j}[\]_c, 0 \leq j < g_{5,3}, 1 \leq c \leq P-1.$$

$$r_{98} \equiv [Z5_{5,j}, a_5]_c^- \xrightarrow{p_{5,c}} X_{5,j}[\]_c, g_{5,3} \leq j \leq g_{5,5}, 1 \leq c \leq P-1.$$

$$r_{99} \equiv [Z5_{5,j}, a_5]_c^- \xrightarrow{1-p_{5,c}} X^{g_{5,1}}_{5,j}[\]_c, g_{5,3} \leq j \leq g_{5,5}, 1 \leq c \leq P-1.$$

$$r_{100} \equiv [Z6_{6,j}]_c^- \xrightarrow{p_{6,c}} X'_{6,j}[\]_c, 0 \leq j \leq g_{6,3}, 1 \leq c \leq P-1.$$

$$r_{101} \equiv [Z6_{6,j}]_c^- \xrightarrow{1-p_{6,c}} X'^{g_{6,1}}_{6,j}[\]_c, 0 \leq j < g_{6,3}, 1 \leq c \leq P-1.$$

$$r_{102} \equiv [Z6_{6,j}, a_6]_c^- \xrightarrow{p_{6,c}} X_{6,j}[\]_c, g_{6,3} \leq j \leq g_{6,5}, 1 \leq c \leq P-1.$$

$$r_{103} \equiv [Z6_{6,j}, a_6]_c^- \xrightarrow{1-p_{6,c}} X^{g_{6,1}}_{6,j}[\]_c, g_{6,3} \leq j \leq g_{6,5}, 1 \leq c \leq P-1.$$

$$r_{104} \equiv [Z7_{7,j}]_c^- \xrightarrow{p_{7,c}} X'_{7,j}[\]_c, 0 \leq j \leq g_{7,3}, 1 \leq c \leq P-1.$$

$$r_{105} \equiv [Z7_{7,j}]_c^- \xrightarrow{1-p_{7,c}} X'^{g_{7,1}}_{7,j}[\]_c, 0 \leq j < g_{7,3}, 1 \leq c \leq P-1.$$

$$r_{106} \equiv [Z7_{7,j}, a_7]_c^- \xrightarrow{p_{7,c}} X_{7,j}[\]_c, g_{7,3} \leq j \leq g_{7,5}, 1 \leq c \leq P-1.$$

$$r_{107} \equiv [Z7_{7,j}, a_7]_c^- \xrightarrow{1-p_{7,c}} X^{g_{7,1}}_{7,j}[\]_c, g_{7,3} \leq j \leq g_{7,5}, 1 \leq c \leq P-1.$$

In the last of the four periods, the second index is increased by 1 (a year has passed), so the animals will move into the next year.

$$r_{108} \equiv [Z1_{1,j}]_p^- \xrightarrow{p_{1,P}} X'_{1,j+1}[\]_p, 0 \leq j < g_{1,3} - 1.$$

$$r_{109} \equiv [Z1_{1,j}]_p^- \xrightarrow{1-p_{1,P}} X'^{g_{1,1}}_{1,j+1}[\]_p, 0 \leq j < g_{1,3} - 1.$$

$$r_{110} \equiv [Z1_{1,j}, a_1]_p^- \xrightarrow{p_{1,P}} X_{1,j+1}[\]_p, g_{1,3} \leq j \leq g_{1,5}.$$

$$r_{111} \equiv [Z1_{1,j}, a_1]_p^- \xrightarrow{1-p_{1,P}} X^{g_{1,1}}_{1,j+1}[\]_p, g_{1,3} \leq j \leq g_{1,5}.$$

$$r_{112} \equiv [Z2_{2,j}]_p^- \xrightarrow{p_{2,P}} X'_{2,j+1}[\]_p, 0 \leq j < g_{2,3} - 1.$$

$$r_{113} \equiv [Z2_{2,j}]_p^- \xrightarrow{1-p_{2,P}} X'^{g_{2,1}}_{2,j+1}[\]_p, 0 \leq j < g_{2,3} - 1.$$

$$r_{114} \equiv [Z2_{2,j}, a_2]_p^- \xrightarrow{p_{2,P}} X_{2,j+1}[\]_p, g_{2,3} \leq j \leq g_{2,5}.$$

$$r_{115} \equiv [Z2_{2,j}, a_2]_p^- \xrightarrow{1-p_{2,P}} X^{g_{2,1}}_{2,j+1}[\]_p, g_{2,3} \leq j \leq g_{2,5}.$$

$$r_{116} \equiv [Z3_{3,j}]_p^- \xrightarrow{p_{3,P}} X'_{3,j+1}[\]_p, 0 \leq j < g_{3,3} - 1.$$

$$r_{117} \equiv [Z3_{3,j}]_p^- \xrightarrow{1-p_{3,P}} X'^{g_{3,1}}_{3,j+1}[\]_p, 0 \leq j < g_{3,3} - 1.$$

$$r_{118} \equiv [Z3_{3,j}, a_3]_p^- \xrightarrow{p_{3,P}} X_{3,j+1}[\]_p, g_{3,3} \leq j \leq g_{3,5}.$$

$$r_{119} \equiv [Z3_{3,j}, a_3]_c^- \xrightarrow{1-p_{3,P}} X_{3,j+1}^{g_{3,1}} []_c, g_{3,3} \leq j \leq g_{3,5}.$$

$$r_{120} \equiv [Z4_{4,j}]_p^- \xrightarrow{p_{4,P}} X'_{4,j+1} []_p, 0 \leq j < g_{4,3} - 1.$$

$$r_{121} \equiv [Z4_{4,j}]_p^- \xrightarrow{1-p_{4,P}} X_{4,j+1}^{g_{4,1}} []_p, 0 \leq j < g_{4,3} - 1.$$

$$r_{122} \equiv [Z4_{4,j}, a_4]_p^- \xrightarrow{p_{4,P}} X_{4,j+1} []_p, g_{4,3} \leq j \leq g_{4,5}.$$

$$r_{123} \equiv [Z4_{4,j}, a_4]_c^- \xrightarrow{1-p_{4,P}} X_{4,j+1}^{g_{4,1}} []_c, g_{4,3} \leq j \leq g_{4,5}.$$

$$r_{124} \equiv [Z5_{5,j}]_p^- \xrightarrow{p_{5,P}} X'_{5,j+1} []_p, 0 \leq j < g_{5,3} - 1.$$

$$r_{125} \equiv [Z5_{5,j}]_p^- \xrightarrow{1-p_{5,P}} X_{5,j+1}^{g_{5,1}} []_p, 0 \leq j < g_{5,3} - 1.$$

$$r_{126} \equiv [Z5_{5,j}, a_5]_p^- \xrightarrow{p_{5,P}} X_{5,j+1} []_p, g_{5,3} \leq j \leq g_{5,5}.$$

$$r_{127} \equiv [Z5_{5,j}, a_5]_c^- \xrightarrow{1-p_{5,P}} X_{5,j+1}^{g_{5,1}} []_c, g_{5,3} \leq j \leq g_{5,5}.$$

$$r_{128} \equiv [Z6_{6,j}]_p^- \xrightarrow{p_{6,P}} X'_{6,j+1} []_p, 0 \leq j < g_{6,3} - 1.$$

$$r_{129} \equiv [Z6_{6,j}]_p^- \xrightarrow{1-p_{6,P}} X_{6,j+1}^{g_{6,1}} []_p, 0 \leq j < g_{6,3} - 1.$$

$$r_{130} \equiv [Z6_{6,j}, a_6]_p^- \xrightarrow{p_{6,P}} X_{6,j+1} []_p, g_{6,3} \leq j \leq g_{6,5}.$$

$$r_{131} \equiv [Z6_{6,j}, a_6]_c^- \xrightarrow{1-p_{6,P}} X_{6,j+1}^{g_{6,1}} []_c, g_{6,3} \leq j \leq g_{6,5}.$$

$$r_{132} \equiv [Z7_{7,j}]_p^- \xrightarrow{p_{7,P}} X'_{7,j+1} []_p, 0 \leq j < g_{7,3} - 1.$$

$$r_{133} \equiv [Z7_{7,j}]_p^- \xrightarrow{1-p_{7,P}} X_{7,j+1}^{g_{7,1}} []_p, 0 \leq j < g_{7,3} - 1.$$

$$r_{134} \equiv [Z7_{7,j}, a_7]_p^- \xrightarrow{p_{7,P}} X_{7,j+1} []_p, g_{7,3} \leq j \leq g_{7,5}.$$

$$r_{135} \equiv [Z7_{7,j}, a_7]_c^- \xrightarrow{1-p_{7,P}} X_{7,j+1}^{g_{7,1}} []_c, g_{7,3} \leq j \leq g_{7,5}.$$

Young animals are recorded individually, while adults in pairs, as they reach their reproductive age, new breeding pairs are generated from two young individuals.

$$r_{136} \equiv [Z1_{1,g_{1,3}-1}^2, a_1]_p^- \xrightarrow{p_{1,P}} X_{1,g_{1,3}} []_p.$$

$$r_{137} \equiv [Z1_{1,g_{1,3}-1}^2, a_1]_p^- \xrightarrow{1-p_{1,P}} X_{1,g_{1,3}}^{g_{1,1}} []_P.$$

$$r_{138} \equiv [Z2_{2,g_{2,3}-1}^2, a_2]_p^- \xrightarrow{p_{2,P}} X_{2,g_{2,3}} []_P.$$

$$r_{139} \equiv [Z2_{2,g_{2,3}-1}^2, a_2]_p^- \xrightarrow{1-p_{2,P}} X_{2,g_{2,3}}^{g_{2,1}} []_P.$$

$$r_{140} \equiv [Z3_{3,g_{3,3}-1}^2, a_3]_p^- \xrightarrow{p_{3,P}} X_{3,g_{3,3}} []_P.$$

$$r_{141} \equiv [Z3_{3,g_{3,3}-1}^2, a_3]_p^- \xrightarrow{1-p_{3,P}} X_{3,g_{3,3}}^{g_{3,1}} []_P.$$

$$r_{142} \equiv [Z4_{4,g_{4,3}-1}^2, a_4]_p^- \xrightarrow{p_{4,P}} X_{4,g_{4,3}} []_P.$$

$$r_{143} \equiv [Z4_{4,g_{4,3}-1}^2, a_4]_p^- \xrightarrow{1-p_{4,P}} X_{4,g_{4,3}}^{g_{4,1}} []_P.$$

$$r_{144} \equiv [Z5_{5,g_{5,3}-1}^2, a_5]_p^- \xrightarrow{p_{5,P}} X_{5,g_{5,3}} []_P.$$

$$r_{145} \equiv [Z5_{5,g_{5,3}-1}^2, a_5]_p^- \xrightarrow{1-p_{5,P}} X_{5,g_{5,3}}^{g_{5,1}} []_P.$$

$$r_{146} \equiv [Z6_{6,g_{6,3}-1}^2, a_6]_p^- \xrightarrow{p_{6,P}} X_{6,g_{6,3}} []_P.$$

$$r_{147} \equiv [Z6_{6,g_{6,3}-1}^2, a_6]_p^- \xrightarrow{1-p_{6,P}} X_{6,g_{6,3}}^{g_{6,1}} []_P.$$

$$r_{148} \equiv [Z7_{7,g_{7,3}-1}^2, a_7]_p^- \xrightarrow{p_{7,P}} X_{7,g_{7,3}} []_P.$$

$$r_{149} \equiv [Z7_{7,g_{7,3}-1}^2, a_7]_p^- \xrightarrow{1-p_{7,P}} X_{7,g_{7,3}}^{g_{7,1}} []_P.$$

Finally the objects associated with animals that have had enough food resources evolve, the young to X' and adults to X .

$$r_{150} \equiv [W_{i,j}]_c^- \longrightarrow X'_{i,j} []_c, 0 \leq j < g_{i,3}, 1 \leq i \leq CNY, 1 \leq c \leq P-1.$$

$$r_{151} \equiv [W_{i,j}]_c^- \longrightarrow X_{i,j} []_c, g_{i,3} \leq j \leq g_{i,5}, 1 \leq i \leq CNY, 1 \leq c \leq P-1.$$

$$r_{152} \equiv [W_{i,j}]_p^- \longrightarrow X'_{i,j} []_p, 0 \leq j < g_{i,3}, 1 \leq i \leq CNY.$$

$$r_{153} \equiv [W_{i,g_{i,3}-1}^2, a_i]_p^- \longrightarrow X_{i,g_{i,3}} []_p, 1 \leq i \leq CNY.$$

$$r_{154} \equiv [W_{i,j}]_p^- \longrightarrow X_{i,j+1} []_p, g_{i,3} \leq j \leq g_{i,5}, 1 \leq i \leq CNY.$$

$$r_{155} \equiv [W_{i,j}]_c^- \longrightarrow X_{i,j} []_c, 0 \leq j \leq g_{i,5}, CNY+1 \leq i \leq N, 1 \leq c \leq P.$$

The objects associated with uneaten food are dissolved.

$$r_{156} \equiv [M]_c^- \longrightarrow []_c, 1 \leq c \leq P.$$

C_i object stores information about the food generated by each of the species, these objects go out into the skin membrane, which dissolve after being registered in the model.

$$r_{157} \equiv [C_i]_c^- \longrightarrow C_i[]_c, 1 \leq i \leq N, 1 \leq c \leq P.$$

a_i left over objects are dissolved.

$$r_{158} \equiv [a_i]_c^- \longrightarrow []_c, 1 \leq i \leq N, 1 \leq c \leq P.$$

DY' object evolves to object DY . When the above rules have been executed the period is completed and the object co_i must record the new period in its index.

$$r_{159} \equiv [DY'_i]_c^- \longrightarrow DY_i[]_c, 1 \leq i \leq N, 1 \leq c \leq P.$$

$$r_{160} \equiv [co_i]_c^- \longrightarrow co_{i+1}[]_c, 1 \leq i \leq 3, 1 \leq c \leq P.$$

$$r_{161} \equiv [co_4]_c^- \longrightarrow co_1[]_c, 1 \leq c \leq P.$$

$$r_{162} \equiv [XF'_i]_c^- \longrightarrow X_{i,100}, XF_i[]_c, 1 \leq i \leq CNY, 1 \leq c \leq P.$$

Step1 = Step 14

Registered resources provided by each of the species in the simulated period, objects dissolve.

$$r_{163} \equiv [C_i \longrightarrow \#]_0, 1 \leq i \leq N.$$

Young animals evolve to restart a new loop.

$$r_{164} \equiv [X'_{i,j} \longrightarrow X_{i,j}]_0, 0 \leq j < g_{i,3}, 1 \leq i \leq CNY.$$

Dissolve the objects that have not evolved.

$$r_{165} \equiv [Z1_{1,j} \longrightarrow \#]_c, g_{1,3} \leq j \leq g_{1,5}, 1 \leq c \leq P.$$

$$r_{166} \equiv [Z2_{2,j} \longrightarrow \#]_c, g_{2,3} \leq j \leq g_{2,5}, 1 \leq c \leq P.$$

$$r_{167} \equiv [Z3_{3,j} \longrightarrow \#]_c, g_{3,3} \leq j \leq g_{3,5}, 1 \leq c \leq P.$$

$$r_{168} \equiv [Z4_{4,j} \longrightarrow \#]_c, g_{4,3} \leq j \leq g_{4,5}, 1 \leq c \leq P.$$

$$r_{169} \equiv [Z5_{5,j} \longrightarrow \#]_c, g_{5,3} \leq j \leq g_{5,5}, 1 \leq c \leq P.$$

$$r_{170} \equiv [Z6_{6,j} \longrightarrow \#]_c, g_{6,3} \leq j \leq g_{6,5}, 1 \leq c \leq P.$$

$$r_{171} \equiv [Z7_{7,j} \longrightarrow \#]_c, g_{7,3} \leq j \leq g_{7,5}, 1 \leq c \leq P.$$

ORIGINAL MANUSCRIPT

Carriion 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. Colomer⁵ & A. Margalida^{6,7}¹ Department of Zoology, School of Natural Sciences, Trinity College Dublin, Dublin, Ireland² Centre for Biodiversity Research, Trinity College Dublin, Dublin, Ireland³ All Out Africa Research Unit, Department of Biological Sciences, University of Swaziland, Kwaluseni, Swaziland⁴ Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, Pretoria, South Africa⁵ Department of Mathematics, University of Lleida, Lleida, Spain⁶ Department of Animal Production (Division of Wildlife), University of Lleida, Lleida, Spain⁷ Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Bern, Switzerland**Keywords**

Carriion; *Gyps africanus*; PDP-Systems; population dynamics; scavengers; supplementary feeding; Swaziland; vultures.

Correspondence

Adam Kane, Department of Zoology, School of Natural Sciences, Trinity College Dublin, Dublin 2, Ireland. Tel: +353 877731665
Email: kanead@tcd.ie

Editor: Darren Evans

Associate Editor: Vincenzo Penteriani

Received 11 March 2014; accepted 27 August 2014

doi:10.1111/acv.12169

Abstract

As obligate scavengers, vultures are entirely dependent on carriion resources. In this study, we model the carriion 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 carriion 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

Carriion 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 carriion, 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 carriion 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 Pennycuik (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):

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

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) (Pennycuik, 1972), V is the flight speed (45 km h⁻¹) (Pennycuik, 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) (Pennycuik, 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'.)

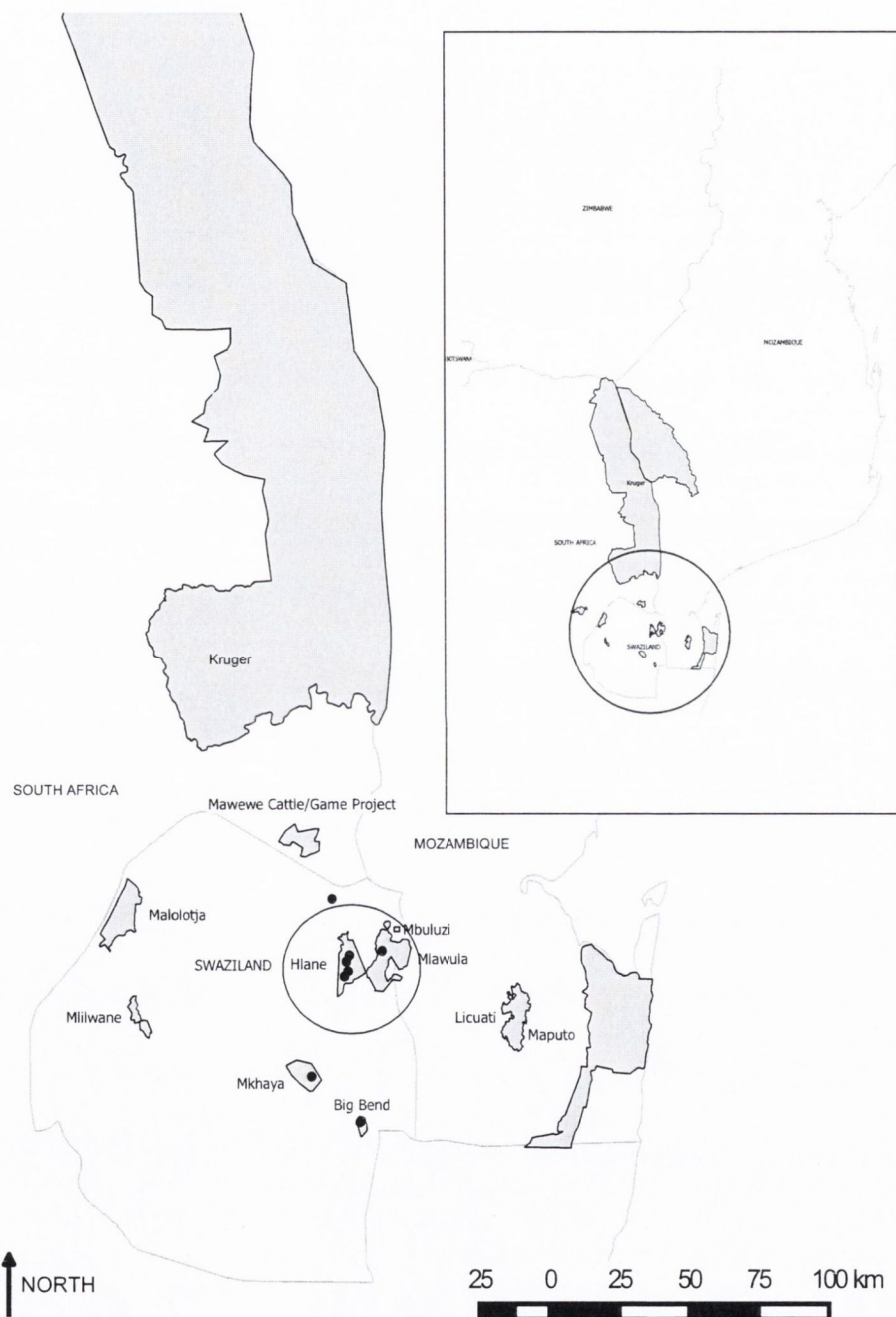


Figure 1 Foraging radius (45 km) of African white-backed vultures when they have dependants on the nest. The points represent recorded nesting sites with Hlane as the origin of the circles. Some major national parks are highlighted. The inset shows the possible feeding range (260 km) when there are no 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
<i>Aepyceros melampus</i>	16 500	48 233.35	32.92
<i>Connochaetes taurinus</i>	1700	18 666.35	12.74
<i>Equus burchelli</i>	1500	13 276.95	9.06
<i>Phacochoerus aethiopicus</i>	2300	12 791.8	8.73
<i>Loxodonta africana</i>	40	11 439.45	7.81
<i>Tragelaphus strepsiceros</i>	1300	10 039.95	6.85
<i>Ceratotherium simum</i>	50	8570.25	5.85
<i>Giraffa camelopardalis</i>	80	4909.35	3.35
<i>Tragelaphus angasii</i>	1000	4231.5	2.89
<i>Kobus ellipsiprymnus</i>	260	4174.25	2.85
<i>Hippopotamus amphibius</i>	25	3976.75	2.71
<i>Syncerus caffer</i>	40	1478.4	1.01
<i>Taurotragus oryx</i>	40	1284.95	0.88
<i>Tragelaphus scriptus</i>	250	700.9	0.48
<i>Sylvicapra grimmia</i>	550	563.65	0.38
<i>Redunca arundinum</i>	120	480.3	0.33
<i>Hippotragus niger</i>	20	419.4	0.29
<i>Redunca fulvorufula</i>	200	364.65	0.25
<i>Hippotragus equinus</i>	7	364.5	0.25
<i>Damaliscus lunatus</i>	16	208.55	0.14
<i>Oreotragus oreotragus</i>	200	122.85	0.08
<i>Raphicerus campestris</i>	140	95.15	0.06
<i>Cephalophus natalensis</i>	80	55.05	0.04
<i>Ourebia ourebi</i>	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

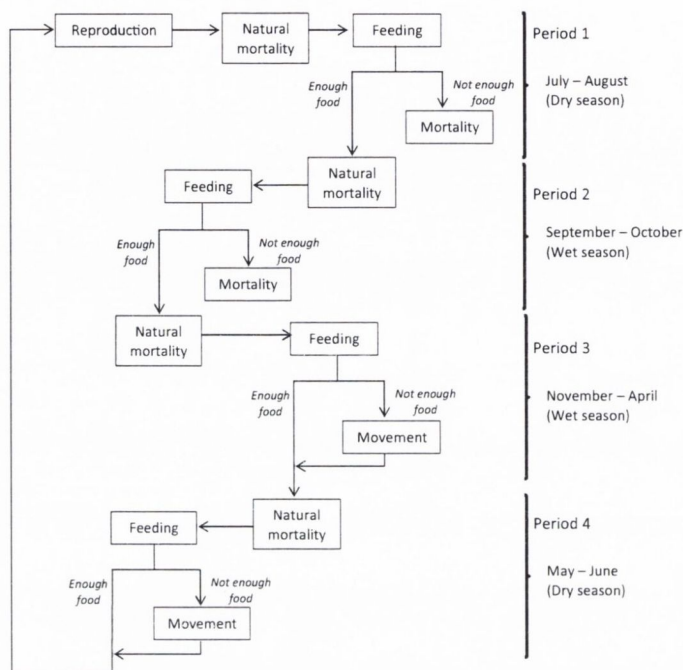


Figure 2 Flow diagram representing the changes in the status of the avian scavengers through time (Periods 1–4). The italicized text show conditionals for food availability which determine the path the birds can take. If we start at the 'Reproduction' stage, at the upper left hand side, this represents 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

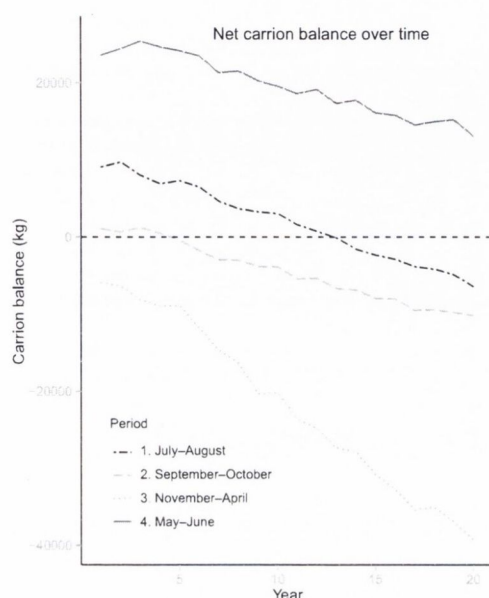


Figure 3 Carrion balance across time in the different periods of the year. The horizontal bar represents the point at which the demands of the avian scavenging guild are no longer met by the carrion provided by wildlife in Swaziland. Periods 1 and 2 are the life stages when young are present and food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

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).

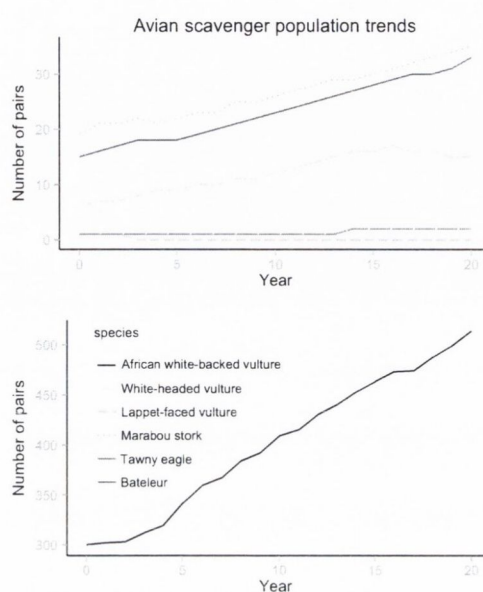


Figure 4 Number of pairs of avian scavengers living in Swaziland across time. All species, except the Lappet-faced vulture, see a population increase because of the amount of wild carrion available. The one extinction occurs owing to its tiny initial population size. The bottom panel shows the African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

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

Thanks to Seán Kelly, Deirdre McClean, Campbell Murn, Morgan Pfeiffer, Álvaro Soutullo and two anonymous reviewers for their valuable comments on the paper. A.K. was funded by TCD. An.M. was supported by a Ramón y Cajal research contract from the Ministerio de Economía y Competitividad (RYC-2012-11867).

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. & Montelio, 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.Á., 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. & Donazar, J.A. (2014). Apex scavenger movements call for transboundary conservation policies. *Biol. Conserv.* **170**, 145–150.
- Margalida, A. & Colomer, M.Á. (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.Á. & 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. & Donazar, 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.Á. & 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. & Donazar, J.A. (2008). Testing the goodness of supplementary feeding to enhance population viability in an endangered vulture. *PLoS ONE* **3**, e4084.
- Pennycuik, C. (1972). Soaring behaviour and performance of some East African birds, observed from a motor-glider. *Ibis* **114**, 178–218.
- Pennycuik, 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., Martinez, J.E., Margalida, A., Gómez, I., Azkona, A. & Martinez, 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.

appendix c

Other Publications

LETTER

A suggestion on improving mathematically heavy papers

C. P. Snow spoke of the split of the “two cultures” of science and art, bemoaning the lack of crosstalk between the two. It seems that something similar has happened between the worlds of theoretical and empirical biology, and mathematics is the barrier. The findings of Fawcett and Higginson are a cause for concern (1), but they offer up a number of potential solutions. The authors note the risks of moving the majority of the equations to an appendix, where they are more likely to be skipped over. Continuity is hugely important when trying to grasp a new idea. Certainly, jumping to a new page in search of further explanation is jarring. I would suggest the adoption of an in-text drop-down box whereby a reader can reveal more of the detail as (s)he reads the paper if (s)he chooses. These text boxes could contain

the information in the appendix with perhaps some more explanation of the derivations. Surely, in the age of Web 2.0, this would be something trivially easy to implement. It would also remove the problem of limited journal space. A link to the appendix that opens in-text while you are reading adds nothing more to the word count, and, importantly, there is no disruption to the flow of the text. I believe this would cater to all readers; for instance, mathematically fluent readers simply do not click on the extra explanation. Every effort should be made to create papers that can be understood by as wide an audience as possible.

Adam Kane¹

Theoretical Ecology Research Group, School of Natural Science, Trinity College Dublin, Dublin 2, Ireland

1. Fawcett TW, Higginson AD (2012) Heavy use of equations impedes communication among biologists. *Proc Natl Acad Sci USA* 109:11735–11739.

Author contributions: A.K. wrote the paper.

The author declares no conflict of interest.

¹E-mail: kanead@tcd.ie.

Survival and Population Dynamics of the Marabou Stork in an Isolated Population, Swaziland

Ara Monadjem^{1*}, Adam Kane², Andre Botha³, Desire Dalton^{4,5}, Antoinette Kotze^{4,5}

1 All Out Africa Research Unit, Department of Biological Sciences, University of Swaziland, Kwaluseni, Swaziland, **2** Department of Zoology, School of Natural Sciences, Trinity College Dublin, Dublin, Ireland, **3** Birds of Prey Programme, Endangered Wildlife Trust, Modderfontein, South Africa, **4** National Zoological Gardens of South Africa, Pretoria, South Africa, **5** Genetics Department, University of the Free State, Bloemfontein, South Africa

Abstract

Investigating the ecology of long lived birds is particularly challenging owing to the time scales involved. Here an analysis is presented of a long term study of the survival and population dynamics of the marabou stork (*Leptoptilos crumeniferus*), a wide ranging scavenging bird from Sub-Saharan Africa. Using resightings data of tagged nestlings and free flying birds we show that the stork population can be divided into three general life stages with unique survival probabilities and fecundities. Fecundity of the storks is inversely related to rainfall during their breeding season. Corroborative evidence for a metapopulation structure is discussed highlighting the impact of the Swaziland birds on the ecology of the species in the broader region. The importance of tag loss or illegibility over time is highlighted. Clearly, any attempt at conserving a species will require a detailed understanding of its population structure, of the sort examined here.

Citation: 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(9): e46434. doi:10.1371/journal.pone.0046434

Editor: Matt Hayward, Australian Wildlife Conservancy, Australia

Received: June 29, 2012; **Accepted:** August 29, 2012; **Published:** September 28, 2012

Copyright: © 2012 Monadjem et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Funding: The authors have no funding or support to report.

Competing Interests: The authors have declared that no competing interests exist.

* E-mail: ara@unisw.sz

Introduction

Survival estimates are critical parameters for various ecological models, particularly population dynamics, which in turn inform conservation [1]. This is particularly important for long-lived vertebrates which may take several years to mature into breeding adults [2], [3]. However, survival estimates are often not available for long-lived birds such as storks; the only species for which robust estimates of both subadults and adults are available is the white stork *Ciconia ciconia* [4], [5], [6]. Survival in the marabou stork *Leptoptilos crumeniferus* has been crudely estimated by comparing the proportion of immature to adult birds [7], however robust estimates of survival must be based on following marked individuals through time [8].

The marabou stork is a widespread scavenging bird occurring in savanna habitats throughout sub-Saharan Africa [9]. Despite its extensive distributional range, this species breeds at a rather limited number of localities [10]. For example, despite having been recorded across most of eastern, central and northern South Africa, it has not yet successfully bred in that country [11]. In fact, in all of southern Africa, this species breeds at just one site in Swaziland [12] (Figure 1), one site in Botswana [13] and less than a dozen scattered sites in Zimbabwe [14]. Hence this species has a metapopulation structure [15] with breeding birds concentrated in discrete colonies (Figure 2). This raises the possibility that the breeding populations act as sources for the South African sink. Dispersing birds can cover extensive distances of up to 1500 km thus allowing for dynamics of this sort to occur [10].

One way to infer a metapopulation structure for this species would be through a population dynamics model. Such models require a number of parameters for them to have any predictive

power, notably probability of survival and fecundity rates [16]. Moreover, in most species these parameters will change as they age; a first year marabou stork, for instance, is not going to be involved in reproduction [17]. This is the shortcoming of exponential or geometric decay models of population growth which treat all life stages equally, resulting in a serious oversimplification [18]. An extensive knowledge of the breeding ecology and demographics of marabou storks is therefore necessary before such population dynamics modelling can be conducted.

The aim of this paper is to elucidate the population ecology of the marabou stork in southern Africa. It is hypothesized that survival is age dependent and that this species has a positive population growth rate. The objectives of this paper are to:

- 1) Relate fecundity of marabou storks breeding in Swaziland over a nine year period with climatic conditions,
- 2) Estimate survival rates based on resightings of tagged nestlings and free-flying marabou storks in southern Africa,
- 3) Use the breeding data and survival estimates of the breeding population in Swaziland to model the population dynamics of this species.

Materials and Methods

Study area

The collection of breeding data and the tagging of nestlings was conducted in the 16 000 ha Hlane National Park (31°53'S, 26°18'E), Swaziland. The vegetation is dominated by knobthorn *Acacia nigrescens* woodland interspersed with riverine forest. The

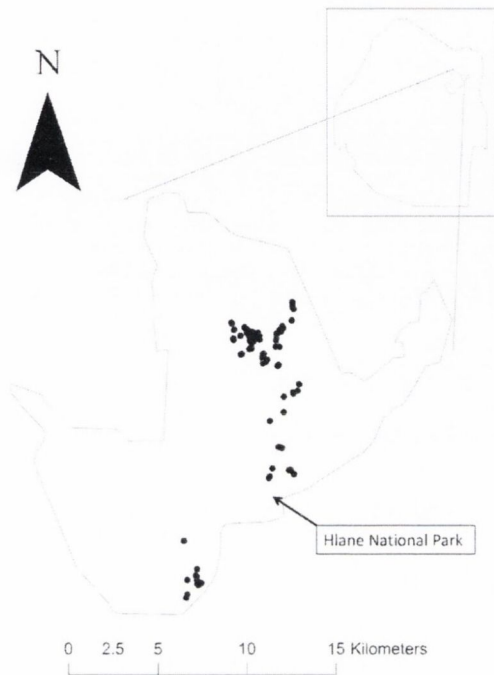


Figure 1. Map showing the distribution of marabou stork nests (black circles) at Hlane National Park. The inset shows the location of Hlane National Park within Swaziland.
doi:10.1371/journal.pone.0046434.g001

climate is subtropical [see [12], [19] for more details on topography and climate]. The marabou stork breeding season covers the austral winter: 2–3 eggs are laid in May or June; eggs hatch after approximately 30 d incubation, usually in June or July, which is the coldest time of year; and the chicks fledge in October [20], [10], [19], [21].

Free-flying marabou storks were captured and tagged at the Moholoholo Wildlife Rehabilitation Centre (24°30'S; 30°54'E, 600 m above sea level), north-eastern South Africa. The site is situated in low-lying savanna, to the west of the Kruger National Park.

There is no Ethics Committee at the University of Swaziland to oversee the compliance of biological studies. However, the current study was conducted under a permit from the Swaziland National Trust Commission to Ara Monadjem. As outlined in our methods, the only contact we had with the study animals was tagging 210 birds based on a standard technique applicable throughout the World. Furthermore, we did not harm or compromise the health of any species during this study.

Patagial tagging was implemented as the preferred method of colour-marking for large raptors, vultures and storks by the Birds of Prey Programme of the Endangered Wildlife Trust in 2006. An extensive review and assessment process of a range of methods was conducted over a period of 18 months before the members and associates of the Programme agreed on and approved the tagging protocol for the use of this method at its Annual Conference [22]. The review included a clinical assessment of the condition of captive and recaptured free-flying tagged birds by independent

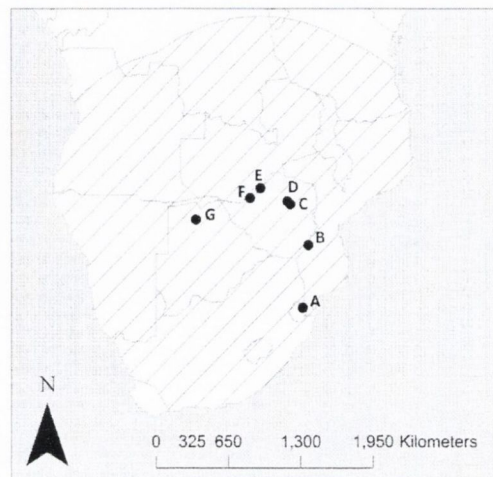


Figure 2. Map showing the distribution of marabou stork nesting colonies known to be active since 1990 in southern Africa (south of the Zambezi and Cunene rivers). The nesting colonies are represented by black circles and are as follows: (A) Hlane National Park, Swaziland [12]; (B) Gonarezhou National Park, Zimbabwe [14]; (C) Imbgwa Farm, Zimbabwe [14]; (D) Carswell Farm, Zimbabwe [14]; (E) Matusadona National Park, Zimbabwe [14]; (F) Binga, Zimbabwe [14]; (G) Okavango Delta, Botswana. The hatching represents all areas within 1500 km of these nesting colonies and therefore within dispersal distance of recently fledged chicks (see Discussion).
doi:10.1371/journal.pone.0046434.g002

veterinarians after tagging and no signs of infection or other potentially negative symptoms resulting from the tagging have to date been found [22]. Based on the results of the survival and movements of tagged birds, the method also does not seem to have a detrimental effect on the mobility and foraging ability of other large birds e.g. vultures [23].

Data collection

Breeding marabou storks were monitored regularly between 2003 and 2011 at Hlane National Park. Originally nests were located on foot, but from 2008 we used a microlight to search for nests from the air once per year in July. Active nests (a nest on which eggs were found or adult activity was observed) were visited twice weekly until the chicks hatched or the nest failed. Fledging date was taken as the date of the last visit on which the chick was still on the nest. The mass and wing length was measured during each visit.

Free-flying birds were captured in a specially designed walk-in trap for vultures [24], [25] that was erected alongside the vulture restaurant at Moholoholo Wildlife Rehabilitation Centre. Captured birds were aged and had their mass and wing length measured. Ageing was based on plumage characteristics [26] and birds were assigned to one of three age classes: juvenile (1st year bird), subadult (2–4 years old) and five years old or older. 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 [22]. 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 [22]. All tagged marabou storks were released unharmed and within 120 min of capture.

A dedicated resightings programme was established using radio and television broadcasts, newspaper and magazine articles, and posters in Kruger National Park rest camps. A significant proportion of resightings was submitted by the staff at Moholoholo who kept a daily watch at the vulture restaurant, at which the marabou storks were frequently observed. Resightings were also reported inter alia by managers of other vulture restaurants, game ranchers, farmers and tourists.

Sexing

Only nestlings were sexed. DNA extraction was conducted using the QiagenDNeasy® Blood and Tissue Kit. The extraction protocol as outlined in the manufacturer protocol was followed. CHD1 gene amplification was conducted using the 2550F/2718R [27] primer set at the National Zoological Gardens of South Africa. Amplification was carried out using 25 µl reaction volume and polymerase chain reaction was conducted with PromegaGo-Taq® Flexi DNA polymerase (Promega Corporation) which has a 1× buffer containing 10 milli molar (mM) Tris®-HCl (pH 9.0), 50 mM potassium chloride (KCl) and 0.1% Triton® X-100. The final reaction conditions were as follows: 1 X PCR buffer, 1.5 mM MgCl2, 200 micro molar (µM) of each 2'-deoxynucleotide triphosphate (dNTP), 5 picomol (pmol) of each of the forward and reverse primer, 0.25 unit (U) Taq DNA polymerase and 10–20 nano gram (ng) genomic DNA template. A no template control as well as positive controls for a male and female bird of known sex was included. The conditions for PCR amplification were as follows: 2 min at 95°C initial denaturation, 30 cycles for 30 s at 95°C, 30 s at 50°C and 2 min at 72°C, followed by extension at 72°C for 10 min. The PCR reaction was carried out in the BOECO TC-PRO Thermal Cycler. PCR products mixed with tracking dye were separated by electrophoresis in a 2% agarose gel for 45 min at 100 V in 1× Tris-borate- EDTA buffer.

Data analysis

Fecundity is a measure of reproductive success and was defined as the number of fledglings successfully raised per pair per annum [28]. A Pearson's correlation was used to test whether fecundity was related to rainfall in the preceding summer (October to March, inclusive) and rainfall during the winter breeding season (May to September), as these variables had previously been shown to be important for marabou stork breeding [19].

The program MARK was used to estimate survival and recapture of marabou storks using the standard Cormack-Jolly-Seber model [29], [30]. A variety of models that included time dependence, sex and age were developed. Models were ranked using Akaike's Information Criterion corrected for small sample size (AICc) [31]. The model with the lowest AICc was deemed the best model; where ΔAICc for any two (or more) models was <2.0, they were both deemed to be equally good.

Survival was estimated separately for the birds tagged as nestlings from those tagged as free-flying. A subset (n = 100, tagged between 2008 and 2011) of those tagged as nestlings were sexed, and were used to test for the role of sex in survival of marabou storks. Models which included sex performed poorly compared with those that did not (ΔAICc>2.9) and hence sex was removed as a factor. Subsequently, the data for the sexes of the nestlings were pooled and only age and time dependence were included.

To test for violations of the assumptions of homogeneity of survival and recaptures, GOF (goodness of fit) tests were conducted in the program Release [32]. Test 2 tests the

assumption of equal catchability (in our case, resightings) of marked individuals. Test 3 tests the assumption that all individuals have equal probability of survival independent of when they were marked.

Model Building

Leslie Matrices are used to chart the development of a population over time by separating the given group into distinct age classes, with matrix elements representing probability of survival and fecundity of these classes [33]. A variation of a Leslie Matrix was developed to investigate the population dynamics of a marabou stork population. The model used information from females only as they are responsible for reproduction in the population [34] and assumes that the above parameters are constant for each age class. The number of females in each class is given by a column vector **N**_t such that the number determined at time t+1 is given by **N**_{t+1} = **L****N**_t, where **L** represents the Leslie Matrix. This process is repeated for each time step. In this case **t** represents one year. This gives the following general equation:

$$\begin{bmatrix} n_1(t+1) \\ n_2(t+1) \\ \vdots \\ n_k(t+1) \end{bmatrix} = \begin{bmatrix} f_1 & f_2 & \cdots & f_k \\ s_1 & 0 & \cdots & 0 \\ 0 & s_2 & 0 & \vdots \\ 0 & 0 & s_{k-1} & 0 \end{bmatrix} \begin{bmatrix} n_1(t) \\ n_2(t) \\ \vdots \\ n_k(t) \end{bmatrix}$$

where "f" is fecundity and "s" is the probability of survival from one age class to the next. The dominant eigenvalue of the matrix is the λ value and represents the growth rate of the population. If λ>1, the population is growing, 0<λ<1, it is decreasing and λ=1, the population is stable. The right eigenvector of a given matrix represents the stable age distribution of the group i.e. the proportion of birds in each stage. This is a measure of the contribution the life stages have to overall population growth [35]. So although juveniles do not reproduce they still make a contribution here.

A variation of the Leslie Matrix known as the Lefkovich Matrix was used in order to separate the storks into distinct life stages [16]: juveniles, subadults and adults,

$$\begin{bmatrix} P_1 & F_2 & F_3 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \\ 0 & 0 & 0 & G_4 \end{bmatrix}$$

Gx (on the subdiagonal) is the probability of surviving for a year and moving into the next stage; Px (on the diagonal) is the probability of surviving for a year and remaining in the same stage; Fx represents fecundity. The model did not take into account density dependent effects. The matrix was created in MS Excel using a variation of a template developed by Spangenberg and Jungck [33] (see results section for the values used to parameterize the model). Seeing as subadult and adult birds can remain in their respective stages for more than a single year this was corrected for accordingly with the following equations,

$$P_i = \left[\frac{1 - (s_i)^{d_i - 1}}{1 - (s_i)^{d_i}} \right] \cdot s_i$$

$$q_i = \frac{(s_i)^{d_i} \cdot (1 - s_i)}{1 - (s_i)^{d_i}}$$

The probability of remaining in an age class at next year is given by p_i and q_i is the probability of moving up an age class at next year. S_i is the survivor rate for i^{th} year and d_i is the length of time spent in this i^{th} stage (taken from [16]).

The below matrix was developed using the values from our results which corrected the original parameters for stage duration and fecundity,

$$\begin{bmatrix} 0 & 0 & 0.525 & 0 \\ 0.644 & 0.587 & 0 & 0 \\ 0 & 0.205 & 0.865 & 0 \\ 0 & 0 & 0.008 & 0 \end{bmatrix}$$

This matrix has the three defined age classes i.e. the columns (there is a small non-zero probability that the birds will live past the third stage and fall into a fourth category but any individuals here have zero probability of surviving to the next time step). Subadult birds spend years two to four in their stage and adults spend from age five to 25 in their stage. This assumes a life expectancy of 25 years for wild marabou storks [36], [11]. The fecundity value shown here was taken as an average from 2003–2011 (see Figure 3). The model was run with a varying starting population of three to 10 adult females; the lower number represents a minimum estimate of the nesting population in

Swaziland during the early 1960s [37]. However, seeing that nesting sites can easily be overlooked by observers on the ground we also ran the model with a starting population of up to 10 females.

Results

Between 19 and 31 pairs of marabou storks bred annually at Hlane National Park that fledged between 11 and 43 chicks. The fecundity of marabou storks breeding at Hlane National Park differed greatly between years (Figure 3), with a mean of 1.05 fledged offspring per pair per annum. There was no correlation between fecundity and rainfall in the previous summer ($r = 0.401$, $df = 7$, $P = 0.284$), however, there was a significant inverse correlation with rainfall during the breeding season ($r = -0.785$, $df = 9$, $P = 0.012$).

A total of 193 nestlings and 17 free-flying marabou storks have been tagged since 2005 and which have been resighted 811 and 834 times, respectively. On fledging, male marabou storks had significantly larger mean ($\pm$ SE) wing lengths (663.1 ± 4.63 mm vs 596.1 ± 5.85 mm; $t = 8.98$, $P < 0.0001$, $DF = 98$) and heavier mean ($\pm$ SE) masses (7437 ± 110 g vs 6155 ± 114 g; $t = 8.09$, $P < 0.0001$, $DF = 98$) than females. Free-flying birds had mean ($\pm$ SE) wing length of 700.7 ± 7.88 mm ($n = 17$), and mean ($\pm$ SE) mass of 5038 ± 291 mm ($n = 13$).

In the nestling analysis covering the seven years between 2005 and 2011, survival of nestlings post-fledging was age-dependent. The best model for survival had three age classes, 1st year birds, 2nd–4th year birds and $\geq 5^{\text{th}}$ year birds (Table 1). The next model had $\Delta AIC_c < 2$ compared with the best model, and had survival separated into five age classes. For both of these models recapture rates were age and time independent (Table 1). The next three

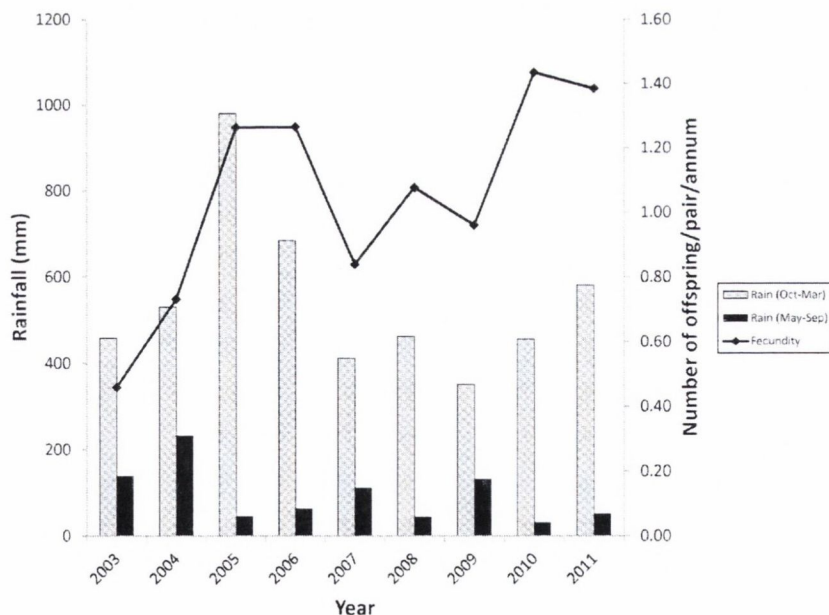


Figure 3. The relationship between fecundity of marabou storks and rainfall between 2003 and 2011 in Swaziland.
doi:10.1371/journal.pone.0046434.g003

Table 1. The candidate models used to estimate survival in nestling marabou storks tagged in Swaziland between 2005 and 2011, and resighted across southern Africa.

Model	AICc	Delta AICc	AICc Weights	N
phi(age1, 2–4, ≥5) p(.)	489.751	0	0.13917	4
phi(age1, 2, 3, 4, ≥5) p(.)	490.1439	0.3928	0.11435	5
phi(age1, 2, 3, 4, ≥5) p(age1, ≥2)	492.1082	2.3572	0.04282	6
phi(age1, 2, 3, 4, ≥5) p(t)	494.1198	4.3688	0.01566	10
phi(age1, ≥2) p(.)	494.3246	4.5736	0.01414	3
phi(t) p(.)	495.4601	5.7091	0.00801	7
phi(age1, 2, ≥3) p(.)	496.0157	6.2647	0.00607	4
phi(t) p(t)	496.0794	6.3284	0.00588	10
phi(age1, ≥2) p(age1, ≥2)	496.2424	6.4914	0.00542	4
phi(age1, 2, 3, 4, ≥5) p(.)	497.811	8.0600	0.00247	5
phi(age1, ≥2+t) p(.)	500.4836	10.7326	0.00065	11
phi(age1–2, ≥3+t) p(.)	502.8863	13.1353	0.0002	11
phi(age1, 2, ≥3+t) p(.)	505.8063	16.0553	0.00005	15

Estimates of survival (phi) and recapture (p) were modelled with time (t), and/or age class of the birds (age). Age1–5 refers to age classes of 1st year birds through to 5th year birds. The number of parameters is indicated by “n”. The models are arranged from best (top of table) to worst (bottom). doi:10.1371/journal.pone.0046434.t001

models all had survival being age dependent. The first model to have survival independent of age had a ΔAIC_c>5 (Table 1). All the test 2 and test 3 results were statistically not significant (chi-square test, P>0.05), showing that the assumptions tested had not been violated.

In the analysis of the free-flying birds, the best model had survival separated into two age classes (Table 2). In this model, the two age classes were 1st year birds, and subadult/adult birds (i.e. no difference in survival of subadults and adults). The next three best models all had ΔAIC_c<2, suggesting that they were not statistically distinguishable from the best model. In all three of

Table 2. The candidate models used to estimate survival in free-flying marabou storks tagged in South Africa between 2007 and 2011, and resighted across southern Africa.

Model	AICc	Delta AICc	AICc Weights	n
phi(age1, ≥2) p(age1, ≥2)	52.0191	0	0.29804	3
phi(age1, 2, ≥3) p(age1, 2, ≥3)	52.554	0.5349	0.22810	4
phi(age1, 2, ≥3) p(age1, ≥2)	52.5604	0.5413	0.22737	4
phi(age1, 2, ≥3) p(.)	53.2647	1.2456	0.15988	4
phi(age1, 2, ≥3) p(t)	59.7627	7.7436	0.00621	6
phi(age1, 2, ≥3+t) p(age1, 2, ≥3+t)	66.2284	14.2093	0.00024	8
phi(age1, 2, ≥3 *t) p(age1, 2, ≥3 *t)	79.696	27.6769	0	11

Estimates of survival (phi) and recapture (p) were modeled with time (t), and/or age class of the birds (age). Age1 refers to age classes of 1st year birds, age2 to subadults (2nd to 4th year birds) and age3 to adults (≥5th year birds). 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). doi:10.1371/journal.pone.0046434.t002

Table 3. Survival and recapture (resightings) rates of marabou storks tagged as nestlings and free-flying adults in South Africa between 2005 and 2011.

Analysis	Estimated parameter	rate	SD
Nestlings	Survival of 1 st year birds	0.6440	0.0765
Nestlings	Survival of 2 nd –4 th year birds	0.7917	0.0597
Nestlings	Survival of ≥5 th year birds	0.2193	0.1459
Nestlings	Recapture rate	0.4226	0.0523
Free-flying	Survival of 1 st year birds	0.2500	0.2165
Free-flying	Survival of ≥ subadult birds	0.8727	0.2483
Free-flying	Recapture of 1 st year birds	0.9999	0.0004
Free-flying	Recapture of ≥ subadult birds	0.2545	0.1559

The analysis refers to the specific dataset used for the estimates: nestlings = all nestlings tagged and resighted between 2005 and 2011; free-flying = all free-flying birds tagged and resighted between 2007 and 2011. See Methods for further details. doi:10.1371/journal.pone.0046434.t003

these models survival was separated into three age classes. In the top three models, recapture rates were age dependent, whereas in the fourth best model recaptures were independent of both age and time (Table 2). Again, the test 2 and test 3 results were statistically not significant (chi-square test, P>0.05), showing that the assumptions tested had not been violated.

The survival rates of marabou storks varied considerably between age classes and the datasets analysed (Table 3). Typically, first year survival was lower than that of older birds. Based on the analysis of birds tagged as nestlings, survival to the end of the first year was 0.6440. However, based on the analysis of free-flying birds, the survival of 1st year birds was only 0.2500. Survival of older age classes (subadults and adults) was generally high ranging from 0.7917 to 0.8727 (Table 4). The only exception was ≥5th year birds tagged as nestlings where survival dropped to 0.2193, suggesting loss or fading of tags.

The resulting λ value was 1.0212 indicating a population increase over time (see Figure 4). The population in this model developed from exclusively adults to an age structure which stabilizes at 43.8% adults, 33.4% subadults and 22.5% juveniles (Table 5). The reproductive value increases with age in marabou storks with the adult stage being the highest (see Table 5).

The final population in the model is clearly dependent on the initial number of founding individuals and the fecundity of the storks. Starting with three females a total population of 26 birds is produced over the 50 year time frame; 10 females resulted in 86 birds (Figure 4). The total number of adult females was six and 19 respectively (Figure 4).

Table 4. Parameters used in matrix.

Stage	Fx	Px	Gx
Juveniles	0	0	0.644
Subadults	0	0.587	0.205
Adults	0.525	0.865	0.008

Fx = Fecundity; Px = Probability of remaining in age class at next year; Gx = Probability of moving up an age class at next year. doi:10.1371/journal.pone.0046434.t004

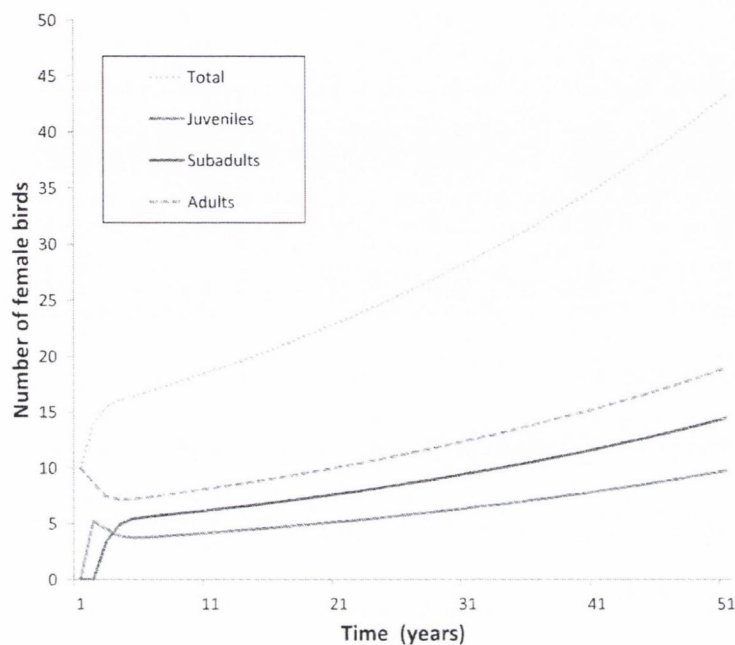


Figure 4. Graph showing the growth of the total population and each component stage over a 50 year period commencing in 1962. The initial population was set to 10 females in this case. $\lambda = 1.0212$.
doi:10.1371/journal.pone.0046434.g004

Discussion

This study presents the first estimates of survival for the marabou stork based on resightings of tagged individuals that also accounts for recapture (resightings) probability. A previous study estimated the survival of marabou storks based on the proportion of immature birds to adult birds, yielding survival rates of 28% for first year birds, 72% for subadults and 92% for adults [7], [38]. Our estimates are lower than these for adults but higher for juvenile and subadult birds. Our estimate for sub-adult survival mentioned above also matches those for the wood stork, *Mycteria americana* [39]. From the tagging of nestlings, our estimate of 1st year mean survival is 64%. This is higher than survival rates for 1st year white storks estimated at 47% [40], 48% [4] and 33–42% [41], and for 1st year wood storks at 44% [42]. This is not surprising since the marabou stork is larger than these two species and survival rates are directly related to size [38]. However, the estimate of 1st year survival based on the tagging of free-flying

birds was exceptionally low (25%), lower than that reported for the white or wood storks. Undoubtedly, this estimate suffers from small sample sizes as only four free-flying 1st year birds were captured and tagged compared with 193 nestlings.

Adult survival was higher, but the specific value depended on the dataset that was used. Based on the free-flying birds the survival rate was 87% and apparently did not differ between subadults and adults. Subadult (2nd–4th year birds) mean survival rates based on resightings of tagged nestlings was 79%, with adult ($\geq 5^{\text{th}}$ year birds) survival rate dropping to 22%. This clearly is not an accurate reflection of adult survival, where captive marabou storks may live to 31 years [11], but may be related to tag loss (see below). The annual survival of adult white storks in Europe exhibited considerable inter-annual variation over a 19-year period ranging from a low of about 70% to almost 100% [41]. By contrast, mean annual survival rates in declining populations of white storks in Europe ranged between 58% and 75% [4].

Survival rates of the marabou stork were not time-dependent. In contrast, the variation in survival rates of the white stork has been linked to rainfall in the Sahel where this species migrates to in the northern winter [40]. The marabou stork is not a migrant [11] which may explain the lack of time-dependence in this species. The lack of time-dependent survival, however, is still surprising in the marabou stork, especially since reproductive success of this species is strongly related to rainfall [19]. The current study corroborated the findings of a previous study [19] showing fecundity to be negatively related to rainfall during the breeding season. The reasons for this have previously been argued to be related to food availability and foraging efficiency of the parents [19] rather than due to the inability of the chicks to thermoreg-

Table 5. Values for the stable age distribution and the reproductive value of the life stages as given by the right and left eigenvectors of the matrix respectively.

Stage	Stable Age Distribution	Reproductive Value
Juveniles	0.2251	1.00
Subadults	0.3337	1.59
Adults	0.4378	3.36

doi:10.1371/journal.pone.0046434.t005

ulate in cold and cloudy conditions [43]. Marabou storks are scavengers feeding on a wide range of food resources including carrion from large mammal carcasses, aquatic vertebrates and human waste [7], [17], [44]. The exact nature of the relationship between rainfall, food and marabou stork fecundity remains unclear, but we suggest the following. Since rainfall is necessarily linked with cloud cover, increased rainfall during the breeding season represents increased cloud cover during this period of food stress when parents need to fend for themselves as well as growing chicks. However, marabou storks require thermals for foraging [17], which are only available on sunny days, and hence increased cloud cover may result in less soaring time and less efficient foraging.

There are a number of hypotheses that have been put forward to explain the relationship between rainfall and breeding success. One suggestion is that high rainfall impedes the formation of thermals on which the Marabous soar while they forage [19]. Another is that rainfall impacts on breeding success indirectly by influencing food availability for the storks. During the breeding season freshwater fishes make up a significant portion of the storks' diet [44]. Indeed the nestlings were observed to regurgitate fish on which they had recently been fed [19]. Low rainfall would grant the birds easier access to fish stocks as they waded through rivers and streams with lower water levels [19].

There was no apparent difference in the survival of male and female marabou storks. A similar result has been reported for the white stork [4]. However, female wood stork fledglings had survival rates of up to five times higher than in the larger males [41]. In line with a previous study [21], male marabou storks had larger masses and wing lengths than female storks. Larger size may be correlated with larger mortality, especially under difficult environmental conditions [45]. This, however, was not the case in this study.

Tag loss or fading is a serious violation of the assumptions of capture-mark-recapture studies [46], [47]. In our study, tag loss seems to have been a factor in the older age classes ($\geq 5^{\text{th}}$ year birds). A similar resightings study of African white-backed vultures fitted with the same tags showed that they were fading and become illegible from about 5–6 years of age and older [23]. In this study, we report a sudden and significant drop in survival rate from the age of 5 years and above, suggesting that the same fate befell these tags. Hence our survival estimates are only applicable up to the 5th year of a bird carrying the tags. We suggest that future studies investigate the possibility of using more durable tags for tagging of marabou storks.

Pastor [18] proposes that source and sink dynamics could be explored using stage-structured models like the one used here. If two subpopulations are linked one would expect opposite lambda values because one population is supplying the other. Given the proposal here that Swaziland is the source, an investigation of the Kruger population could confirm this hypothesis. The fact that marabou storks have yet to breed successfully within the Kruger area [48] supports this statement. A positive correlation between breeding success and colony size for marabou storks has been reported [17]. Birds that bred successfully were typically in close proximity to other breeding pairs, often in the same tree [17]. So there may be Allee effects [49] at play in marabou nesting sites.

References

1. Tucker AD, Gibbons JW, Greene JL (2001) Estimates of adult survival and migration for diamondbacked turtles: conservation insight from local extirpation within a metapopulation. *Can J Zool* 79: 2199–2209.
2. Heppell SS (1998) Application of life-history theory and population model analysis to turtle conservation. *Copeia* 1998: 367–375.

This may explain the number of reported failed nests in Kruger National Park where breeding attempts involved single breeding pairs.

The lambda value from the matrix produced a population that either underestimated the modern day population completely or hit the lower range of the known breeding population encountered today of 19 pairs. This is with three and 10 breeding females respectively.

In general, this may be indicative of a metapopulation structure for marabou storks whereby more birds must be recruited to the local population in order to produce the numbers seen today [50]. The only data required to determine this are a local census and the λ [50]. So this is a potential way of predicting metapopulations with relatively little information. As noted above, one proviso is the sensitivity the model shows to the fecundity value, which varies year on year.

Specifically the lambda values reported here show that the Swaziland population of marabou storks is increasing. The metapopulation structure of marabou storks in southern Africa could explain the presence of a large population (300–400 individuals) of non-breeding birds in the Kruger National Park, South Africa [51]. The rate of increase seen in Swaziland is not enough to account for an assemblage of this size over a reasonable time period but if the breeding sites in Botswana and Zimbabwe are considered alongside (assuming similar population dynamics) the South African numbers could be explained. Juvenile marabou storks are capable of dispersing up to 1500 km after fledging, easily allowing them to cover the relatively short distance (<100 km) between the study site in Swaziland and Kruger National Park in South Africa [10] (see Figure 2).

The high reproductive value of adult marabou storks is worth highlighting. This value represents the contribution that birds at any stage make to population growth. Our analysis showed that adults contributed twice as much as subadults and over three times as much as juveniles to the growth of the population. The population growth of wood storks was similarly shown to be highly sensitive to adult survivorship [39]. Clearly, this is an important point to recognize for conservation efforts targeting long-lived species [52]. The inverse relationship between survival and reproductive value means that the emphasis should be on ensuring the survival of adults.

Acknowledgments

We thank Mickey Reilly for permission to study marabou storks at Hlane National Park and for logistical support. Mduduzi Ngwenya, Martha Surridge, Elaine Franklin, Marie Dahl Gydesen and various All Out Africa volunteers assisted with the finding of nests and processing of the chicks. Dave Ducasse has flown various assistants annually over the study area in a microlight in search of marabou stork nests since 2008.

Author Contributions

Conceived and designed the experiments: AM AB. Performed the experiments: AM AB. Analyzed the data: AM A. Kane. Contributed reagents/materials/analysis tools: AM AB DD A. Kotze. Wrote the paper: AM A. Kane.

5. Sæther B-E, Grotan V, Tryjanowski P, Barbraud C, Engen S, et al. (2006) Climate and spatio-temporal variation in the population dynamics of long distance migrant, the white stork. *J Anim Ecol* 75: 80–90.
6. Nevoux M, Barbraud J-M, Barbraud C (2008) Nonlinear impact of climate on survival in a migratory white stork population. *J Anim Ecol* 77: 1143–1152.
7. Pomeroy DE (1977) The biology of marabou storks in Uganda. 1. Some characteristics of the species, and the population structure. *Ardea* 65: 1–24.
8. Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62: 67–118.
9. Brown LH, Urban EK, Newman K (1982) *The Birds of Africa*, Vol. 1. Academic Press, London.
10. Monadjem A, Bamford AJ, Rasmussen M (2008) Dispersal of juvenile Marabou Storks *Leptoptilos crumeniferus* as determined by resightings. *Ostrich* 79: 187–189.
11. Anderson MD (2005). Marabou Stork *Leptoptilos crumeniferus*. Pp 626–627. In: Hockey, PAR, Dean, WRJ, Ryan, PG (eds). *Roberts – Birds of Southern Africa*. VII th ed. The Trustees of the John Voelcker Bird Book Fund, Cape Town.
12. Monadjem A (2005) Breeding biology of the Marabou Stork (*Leptoptilos crumeniferus*) in Swaziland. *Ostrich* 76: 90–94.
13. Tarboton W (2001) A guide to the nests and eggs of southern African birds. Struik, Cape Town.
14. Mundy PJ (2003) Breeding of Marabou Storks. *Honeyguide* 49: 148–150.
15. Hanski I (1998) Metapopulation dynamics. *Nature* 396: 41–49.
16. Grouse DT, Crowder LB, Caswell H (1987) A Stage-Based Population Model for Loggerhead Sea Turtles and Implications for Conservation. *Ecology* 68: 1412–1423.
17. Pomeroy DE (1978) The biology of marabou storks in Uganda. 2. Breeding biology and general review. *Ardea* 66: 1–23.
18. Pastor J (2008) Mathematical ecology of populations and ecosystems: Wiley-Blackwell. 65–77 p.
19. Monadjem A, Bamford AJ (2009) Influence of rainfall on timing and success of reproduction in Marabou Storks *Leptoptilos crumeniferus*. *Ibis* 151: 344–351.
20. Monadjem A, Garcelon DK (2005) Nesting distribution of vultures in relation to land use in Swaziland. *Biodiversity and Conservation* 14: 2079–2093.
21. Monadjem A, Bamford AJ, Hardy ICW, Earnshaw JK, Franklin E, et al. (2010) Temporal and sex-specific variation in growth rates of Marabou Stork *Leptoptilos crumeniferus* chicks. *Ostrich* 81: 83–91.
22. Botha A (2007) A review of colour-marking techniques used on vultures in southern Africa. *Vulture News* 56:52–63.
23. Monadjem A, Botha A, Murn C (2012) Survival of the African white-backed vulture *Gyps africanus* in north-eastern South Africa. *Afr J Ecol*. doi: 10.1111/aje.12009
24. 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 tracheliotus* vultures in the Waterberg area, Namibia. in 2004 *Vulture News* 51: 34–45.
25. Bamford AJ, Diekmann M, Monadjem A, Hardy ICW (2009) Development of non-explosive based methods for mass capture of vultures. *S Afr J Wildlife Res* 39: 202–208.
26. Mundy PJ, Butchart D, Ledger JA, Piper SE (1992) The vultures of Africa. Acorn Books & Russel Friedman Books, Randburg & Halfway House, South Africa.
27. Fridolfsson AK, Ellegren H (1999) A simple and universal method for molecular sexing of non-ratite birds. *J Avian Biol*. 20: 116–121.
28. Postupalsky S (1973) Raptor reproductive success: some problems with methods, criteria, and terminology. In: Hamerstrom FN, Harrell BE and Olendorf RR (eds) *Management of Raptors*. Proceedings of the Conference on Raptor Conservation Techniques. pp 21–31. Fort Collins, Colorado.
29. White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* 46: S120–S139.
30. White GC (2008) Closed population estimation models and their extensions in Program MARK. *Environ Ecol Stat* 15: 89–99.
31. Burnham KP, Anderson DR (2002) Model selection and multimodel inference. A practical information-theoretic approach. Second edition. Springer-Verlag, New York, USA.
32. Burnham KP, Anderson DR, White GC, Brownie C, Pollock KH (1987) Analysis and design methods for fish survival experiments based on release-recapture. *Am Fish Soc Monogr* 5.
33. Leslie PH (1945) On the Use of Matrices in Certain Population Mathematics. *Biometrika* 33: 183–212.
34. Spangenberg JA, and Jungck JR (2005) Leslie/Lefkovich Matrix Models for Age or Stage-structured Populations 1.0, BioQUEST Curriculum Consortium, Beloit College. http://bioquest.org/esteem/esteem_details.php?product_id=210
35. Crowder LB, Grouse DT, Heppell SS, Martin TH (1994) Predicting the Impact of Turtle Excluder Devices on Loggerhead Sea Turtle Populations. *Ecological Applications* 4: 437–445.
36. Campbell B. (1974). *The Dictionary of Birds in Color*. The Viking Press.
37. Reilly T, Wasdell B (1965) Marabou Stork *Leptoptilos crumeniferus* (Lesson) breeding in Swaziland. *Ostrich* 36: 96.
38. Brown LH, Pomeroy DE (1984) The age structure of populations of wild birds in tropical Africa, as demonstrated by plumage characteristics and marking techniques. *Proc V Pan-Afr orn Congr* 97–119.
39. Borkhataria RR, Frederick PC, Hylton K, Bryan Jr AL, Rodgers JA (2008) A Preliminary Model of Wood Stork Population Dynamics in the Southeastern United States. *Waterbirds* 31: 42–49.
40. Kanyambwa S, Schierer A, Pradel R, Lebreton J-D (1990) Changes in adult annual survival rates in a western European population of the white stork *Ciconia ciconia*. *Ibis* 132: 27–35.
41. Schaub M, Kania W, Koppen U (2005) Variation in primary production during winter induces synchrony in survival rates in migratory white storks *Ciconia ciconia*. *J Anim Ecol* 74: 656–666.
42. Hylton RA, Frederick PC, de la Fuente TE, Spalding MG (2006) Effects of nestling health on postfledging Survival of wood storks. *Condor* 108: 97–106.
43. Jovani R, Tella JL (2004) Age-related environmental sensitivity and weather mediated nestling mortality in White Storks *Ciconia ciconia*. *Ecography* 27: 611–618.
44. Kahl MP (1966) A contribution to the ecology and reproductive biology of the Marabou Stork in East Africa. *J Zool, Lond* 148: 289–311.
45. Clutton-Brock TH, Albon SD, Guinness FE (1983) Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* 313: 131–133.
46. Seber GAF, Felton R (1981) Tag loss and the Petersen mark-recapture experiment. *Biometrika* 68: 211–219.
47. Rotella JJ, Hines JE (2005) Effects of tag loss on direct estimates of population growth rate. *Ecology* 86: 821–827.
48. Whyte JJ, Otto JPA du T, Barton B (1993) Marabou nesting in the Kruger National Park. *Ostrich* 64: 186.
49. Stephens PA, Sutherland WJ, Freckleton RP (1999) What is the Allee effect? *Oikos* 87: 185–190.
50. Carroll C, Miquelle DG (2006) Spatial viability analysis of Amur tiger *Panthera tigris altaica* in the Russian Far East: the role of protected areas and landscape matrix in population persistence. *J Appl Ecol* 43: 1056–1068.
51. Barnes K (1998) The important bird areas of southern Africa. Johannesburg: BirdLife South Africa.
52. Sarrazin F, Bagnolini C, Pinna JL, Danchin E, Clobert J (1994) High survival estimates of griffon vultures (*Gyps fulvus fulvus*) in a reintroduced population. *Auk* 111: 853–862.

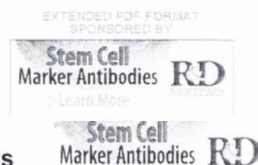


Space Partitioning Without Territoriality in Gannets

Ewan D. Wakefield *et al.*

Science **341**, 68 (2013);

DOI: 10.1126/science.1236077



This copy is for your personal, non-commercial use only.

If you wish to distribute this article to others, you can order high-quality copies for your colleagues, clients, or customers by [clicking here](#).

Permission to republish or repurpose articles or portions of articles can be obtained by following the guidelines [here](#).

The following resources related to this article are available online at www.sciencemag.org (this information is current as of August 28, 2013):

Updated information and services, including high-resolution figures, can be found in the online version of this article at:

<http://www.sciencemag.org/content/341/6141/68.full.html>

Supporting Online Material can be found at:

<http://www.sciencemag.org/content/suppl/2013/06/05/science.1236077.DC1.html>

A list of selected additional articles on the Science Web sites **related to this article** can be found at:

<http://www.sciencemag.org/content/341/6141/68.full.html#related>

This article **cites 42 articles**, 3 of which can be accessed free:

<http://www.sciencemag.org/content/341/6141/68.full.html#ref-list-1>

This article has been **cited by** 1 articles hosted by HighWire Press; see:

<http://www.sciencemag.org/content/341/6141/68.full.html#related-urls>

This article appears in the following **subject collections**:

Ecology

<http://www.sciencemag.org/cgi/collection/ecology>

Science (print ISSN 0036-8075; online ISSN 1095-9203) is published weekly, except the last week in December, by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005. Copyright 2013 by the American Association for the Advancement of Science; all rights reserved. The title *Science* is a registered trademark of AAAS.

Space Partitioning Without Territoriality in Gannets

Ewan D. Wakefield,^{1,*,†} Thomas W. Bodey,^{2,†} Stuart Bearhop,^{2,*} Jez Blackburn,³ Kendrew Colhoun,⁴ Rachel Davies,¹ Ross G. Dwyer,² Jonathan A. Green,⁵ David Grémillet,^{6,7} Andrew L. Jackson,⁸ Mark J. Jessopp,⁹ Adam Kane,⁸ Rowena H. W. Langston,¹⁰ Amélie Lescroël,^{6,11} Stuart Murray,¹² Mélanie Le Nuz,¹³ Samantha C. Patrick,^{14,‡} Clara Péron,⁶ Louise M. Soanes,⁵ Sarah Wanless,¹⁵ Stephen C. Votier,^{16,*} Keith C. Hamer^{1*}

Colonial breeding is widespread among animals. Some, such as eusocial insects, may use agonistic behavior to partition available foraging habitat into mutually exclusive territories; others, such as breeding seabirds, do not. We found that northern gannets, satellite-tracked from 12 neighboring colonies, nonetheless forage in largely mutually exclusive areas and that these colony-specific home ranges are determined by density-dependent competition. This segregation may be enhanced by individual-level public information transfer, leading to cultural evolution and divergence among colonies.

Colonial animals are constrained by their colony locations, which are ultimately limited by resource availability (1). However, within species, potential colony home ranges often overlap, implying that competition among colonies may also be limiting (2). In eusocial central-place foragers, the spatial effects of direct competition among colonies are well understood (2). By contrast, the spatial influences of indirect competition and information transfer on nonterritorial species (e.g., seals, swallows, and seabirds), where levels of relatedness are much lower, remain conjectural. For example, the hinterland model (3) predicts that breeding seabirds segregate along colonial lines, because of inequalities in travel costs from each colony. Predicted home ranges therefore comprise Voronoi

polygons (Fig. 1A), as seen in some territorial animals (2). Food availability is assumed to be proportional to polygon area, limiting colony size. An alternative model proposes that density-dependent competition among colony members is limiting (4). As colonies grow, local prey depletion or disturbance requires birds to travel further to provision their young. However, this model ("Ashmole's halo") does not consider interactions among colonies and tacitly assumes that adjacent colonies' home ranges overlap (5).

Indirect evidence exists to support both models (3, 6, 7), and recent tracking studies suggest that seabirds and pinnipeds segregate along colonial lines (8–12). However, these studies proved inconclusive on the causes and ubiquity of segregation, largely because few colonies were sampled or tracking resolution was low. Here we used high-resolution satellite tracks of the foraging movements of 184 chick-rearing northern gannets, *Morus bassanus* (hereafter gannets), from 12 of the 26 colonies fringing the British Isles (median 17 birds/colony), representing ~80% of the area's breeding population (Fig. 1A and table S1), to test whether among-colony segregation occurs in a model colonial nonterritorial central-place forager. We then used population- and individual-level models to explore potential mechanisms underlying spatial segregation.

Gannets are wide-ranging (maximum foraging range ~700 km) pelagic seabirds that forage in patches of enhanced production, primarily on shoaling, mesotrophic fish and to a lesser extent, fisheries discards (13–15). In almost all cases, we tracked birds from adjacent colonies simultaneously (16). Individual gannet tracks (Fig. 1B and fig. S1) and percentage utilization distributions (UDs) (Fig. 2A and fig. S2) showed a distinctive pattern of between-colony variation and spatial segregation, within and across years (fig. S3). The size of 95% foraging UD was strongly dependent ($F_{1,8} = 149.7$, $P < 0.001$, $R^2 = 0.94$; fig. S4) on square-root colony size (N). Likewise, maximum foraging range and trip duration were dependent on $N^{0.5}$ [linear mixed-effects (LME)

models, $P = 0.002$ and < 0.001 ; tables S2 and S3]. Birds from colonies of all sizes divided their time equally between foraging and chick attendance (LME, $P = 0.191$; table S4), and the number of foraging trips per day was negatively dependent on $N^{0.5}$ (LME, $P = 0.024$; table S5). Prey delivery rate, for which we assume trips per day is a proxy, is therefore negatively dependent on $N^{0.5}$, supporting the prediction that colony size is limited by density-dependent competition (4, 6). Contrary to the hinterland model (3), we found no relationship between colony Voronoi polygon area and colony size ($F_{1,35} < 0.01$, $P = 0.699$, $R^2 < 0.01$; fig. S5).

Using empirical relationships between colony size and foraging area, we devised a population-level null model of the distribution of foraging gannets, assuming negligible competition between birds from neighboring colonies (16). This successfully explains among-colony segregation when colonies are far apart but predicts extensive overlap between several study colonies, particularly in the Celtic Sea (Fig. 2A). However, observed UD were largely mutually exclusive (fig. S2), overlapping markedly less than predicted (fig. S6). For example, the null population overlap index (POI) [the number of potential pairwise interactions between birds from adjacent colonies (16)] for Little Skellig and Bull Rock (populations ~29,700 and 3700 pairs; separation distance 27 km) was 105,000, whereas the empirical estimate was 6000, largely because foraging trips were directed away from closely neighboring colonies (Fig. 1B). This pattern differs from the hinterland model in two key respects: Segregation was not absolute, and divisions between the UD of unequally sized colonies were not equidistant between the two (Fig. 1B and fig. S2) but typically occurred closer to the smaller colony, a phenomenon also observed in penguins (9). Hence, the predictive performance of the hinterland model (log-likelihood, $L = -0.54$, AIC 3691; table S6) was poor in comparison to that of the null model [$L = -0.30$, Akaike information criterion (AIC) = 2231].

Given the inability of existing models to explain gannet distribution when colonies are close together, we propose a multicolony extension of Ashmole's halo (4), which we term the density-dependent hinterland (DDH) model. As adjacent colonies grow, foraging ranges increase as a result of prey depletion or disturbance (6) until their home ranges overlap. At low densities, birds from different colonies may forage together, but as prey availability decreases, populations respond by spreading down conspecific density gradients to the nearest areas subject to a lower rate of exploitation (6). As a first approximation, we assume a simple inverse relationship between the exploitation by conspecifics from adjacent colonies and the likelihood of new birds foraging in an area (16). However, the trade-off between transport and competition costs means that birds favor areas close to their own colonies, so density declines with colony distance d (10). Hence,

¹School of Biology, University of Leeds, Leeds LS2 9JT, UK. ²Centre for Ecology and Conservation, University of Exeter, Penryn, Cornwall TR10 9EZ, UK. ³British Trust for Ornithology, The Nunnery, Thetford IP24 2PU, UK. ⁴The Royal Society for the Protection of Birds, Northern Ireland Headquarters, Belfour Park Forest, Belfast BT8 4QT, UK. ⁵School of Environmental Sciences, University of Liverpool, Environmental Sciences, Liverpool L69 3GP, UK. ⁶CEFE-CNRS, 1919 Route de Mende, F-34293 Montpellier Cedex 5, France. ⁷FitzPatrick Institute, Department of Science and Technology—National Research Foundation Centre of Excellence, University of Cape Town, Rondebosch 7701, South Africa. ⁸Department of Zoology, School of Natural Sciences, Trinity College Dublin, Dublin 2, Ireland. ⁹Coastal and Marine Research Centre, University College Cork, Cork, Ireland. ¹⁰The Royal Society for the Protection of Birds, Sandy, Bedfordshire SG19 2DL, UK. ¹¹Biodiversité et gestion des territoires, Université de Rennes 1—UMR 7204, Muséum National d'Histoire Naturelle, 35042 Rennes Cedex, France. ¹²Easter Craigie Dhu, Dunkeld, Perthshire PH8 0EY, UK. ¹³Reserve naturelle des Sept-Îles, Ligue pour la Protection des Oiseaux, F-22560 Pleumeur Bodou, France. ¹⁴Marine Biology and Ecology Research Centre, Plymouth University, Plymouth PL4 8AA, UK. ¹⁵Centre for Ecology and Hydrology, Penicuik EH26 0QB, UK. ¹⁶Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall TR10 9EZ, UK.

*Corresponding author. E-mail: e.d.wakefield@leeds.ac.uk (E.D.W.); t.w.bodey@exeter.ac.uk (T.W.B.); s.bearhop@exeter.ac.uk (S.B.); stephen.votier@plymouth.ac.uk (S.C.V.); k.c.hamer@leeds.ac.uk (K.C.H.).

†These authors contributed equally to this work.

‡Present address: Centre d'Études Biologiques de Chizé, CNRS-UPR1934, Villiers en Bois, France.

when colonies are large or close together, segregation between home ranges may become absolute. Using these assumptions, we modeled the development of spatial segregation as colonies grow (16). We aim to replicate colony growth at the onset of the breeding season (9) but note that historical colony growth patterns may also influence spatial segregation (6) and that colony sizes are unlikely to be in equilibrium (6, 14). Initial comparisons with our tracking data showed that weighting the relative rate of exploitation by $d^{-0.5}$ improved this model, implying a decline in competitive fitness with distance. The DDH model

proved a better fit to the tracking data ($L = -0.58$, $AIC = 25440$) than the null ($L = -0.61$, $AIC = 27015$; table S7; compare Fig. 2, A and B). Furthermore, unlike the null, the DDH model successfully predicted the POI (fig. S6) and the angular displacement of the center of gravity of the 75% UD from their colonies (circular correlation, observed versus predicted directions, null model, $r = 0.214$, $P = 0.463$, $n = 12$; DDH model, $r = 0.761$, $P = 0.020$, $n = 12$). The shapes of the UDs predicted by the DDH model were closer to those observed (Dice's similarity coefficient $s = 0.57$, table S8) than the null model's predictions ($s =$

0.45) (16). The DDH model's greater predictive strength was most marked for colonies with close neighbors (Fig. 2 and table S8). Notably, the DDH model predicts greater foraging ranges than the null model (paired t test, square-root mean distance $t_{24} = 4.542$, $P < 0.001$), which implies that indirect competition from neighboring colonies diminishes chick provisioning rates, limiting colony size (5).

Like Ashmole's halo and the hinterland model, the DDH model assumes that gannets are ideal free foragers. However, seabird prey occurs in widely dispersed, partially predictable

Fig. 1. Gannet colony foraging ranges. (A) Gannets tracked from colonies around the British Isles forage in largely mutually exclusive areas, despite their potential home ranges overlapping (red, study colonies; yellow, others). Home ranges predicted by the hinterland model (3) form Voronoi polygons, bounded by lines of equidistance between colonies (black lines). (B) Satellite tracks from 184 individuals show that foraging birds direct their movements away from neighboring colonies (colors correspond to different colonies). Data were collected in 2011, except for St Kilda (SK), which were collected in 2010. Gray lines, 200- and 1000-m isobaths; LS, Little Skellig; TB, Bull Rock (mentioned in the text; see table S1 for colony details).

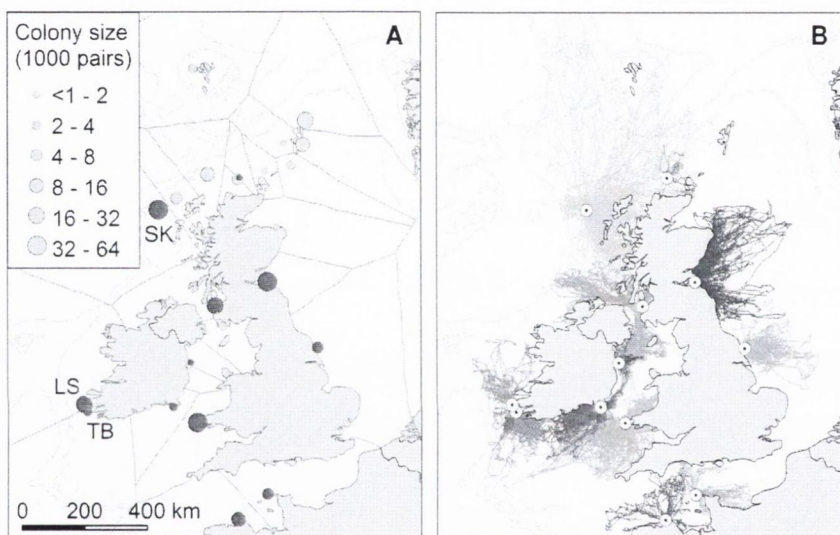
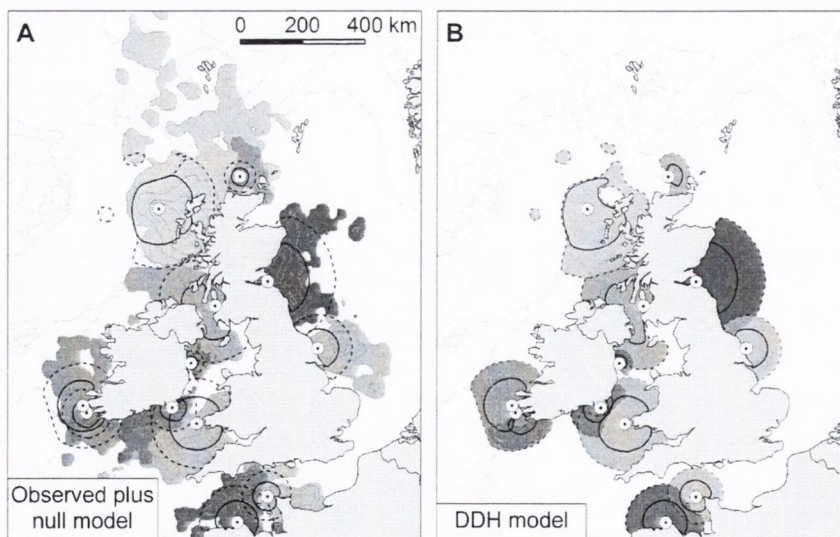


Fig. 2. Density-dependent competition and colony segregation. Density-dependent competition within and between colonies explains large-scale among-colony segregation. (A) Observed colony utilization distributions (colored polygons plus 95, 75, 50, and 25% UD contours) are largely mutually exclusive. This is at odds with the null model (predicted 75 and 95% UDs, solid and dashed lines), which assumes density-dependent competition only within colonies, predicting broad overlap between some UDs. (B) The density-dependent hinterland (DDH) model additionally assumes competition between colonies, providing a better fit to the tracking data.



patches (17). Thus, seabirds may not base foraging decisions on personal information (memory) alone but may also exploit public information (8, 18), gained by observing conspecifics at the colony (19–21) or at sea (22, 23), although empirical evidence remains limited (24). To examine these hypotheses, we developed a range of two-dimensional individual-based models of gannets foraging from two colonies (30 and 300 individuals), constrained by energy reserves (Table 1), to determine whether segregation emerges through information sharing (16). Only one model, incorporating memory and public information transfer at sea and at the colony, produced a significant reduction in overlap between colony UD's (Fig. 3 and fig. S7). Between-colony segregation rapidly became established and then persisted (fig. S8), a pattern consistent at multiple food patch densities and most marked when colonies were close (figs. S9 and S10).

Public information is probably transmitted unintentionally, as in other colonial species (18, 21, 23, 25, 26). Several traits make this likely: Specifically, on arrival and departure from the nest, gannets signal visually and audibly. Before beginning foraging trips they land on the sea, near the colony, frequently departing in groups (14). These behaviors may allow conspecifics to

follow or copy successful birds (20, 21), channeling information from the population to the individual, thereby allowing birds to efficiently select foraging locations where they are competitively advantaged over conspecifics from other colonies. Although these mechanisms are likely to operate over temporal scales of minutes to weeks, gannets have overlapping generations and a long prebreeding period (≥ 4 years), during which they attend colonies with increasing regularity (14, 27). This is thought to allow young birds to learn about prey distribution. If this involves public information acquisition, the preconditions exist for cultural evolution of foraging behavior over much longer time scales (8, 28).

Our results suggest that density-dependent competition, rather than territoriality, causes spatial segregation in a model colonial central-place forager. Although the mechanisms remain unclear, there is increasing recognition that nonterritorial colonial central-place foragers utilize public information to inform decisions (18, 21, 23, 25, 26, 28). Contrary to the prevailing view, we predict that between-colony segregation is the norm when aggregations of animals such as bats, seals, bumblebees, and birds occur at high densities (i.e., when colonies are clustered or large), forcing a

reexamination of our understating of their foraging ecology.

References and Notes

1. J. F. Wittenberger, G. L. J. Hunt Jr., in *Avian Biology*, D. S. Farner, J. R. King, K. C. Parkes, Eds. (Academic Press, New York, 1985), vol. 8, pp. 1–78.
2. E. S. Adams, *Annu. Rev. Ecol. Syst.* **32**, 277–303 (2001).
3. D. K. Cairns, *Am. Nat.* **134**, 141 (1989).
4. N. P. Ashmole, *Ibis* **103b**, 458–473 (1963).
5. R. W. Furness, T. R. Birkhead, *Nature* **311**, 655–656 (1984).
6. S. Lewis, T. N. Sherratt, K. C. Hamer, S. Wanless, *Nature* **412**, 816–819 (2001).
7. K. H. Elliott et al., *Auk* **126**, 613–625 (2009).
8. D. Grémillat et al., *Mar. Ecol. Prog. Ser.* **268**, 265–279 (2004).
9. D. G. Ainley et al., *Ecol. Monogr.* **74**, 159–178 (2004).
10. E. D. Wakefield et al., *Ecol. Monogr.* **81**, 141–167 (2011).
11. S. Wanless, M. P. Harris, *Colon. Waterbirds* **16**, 176 (1993).
12. A. M. M. Baylis, B. Page, S. D. Goldsworthy, *Mar. Ecol. Prog. Ser.* **361**, 279–290 (2008).
13. K. C. Hamer et al., *Mar. Ecol. Prog. Ser.* **338**, 295–305 (2007).
14. B. Nelson, *The Atlantic Gannet* (Fenix Books, Great Yarmouth, UK, ed. 2, 2001).
15. S. C. Votier et al., *J. Appl. Ecol.* **47**, 487–497 (2010).
16. Information on materials and methods is available on Science Online.
17. P. Fauchald, *Mar. Ecol. Prog. Ser.* **391**, 139–151 (2009).
18. T. J. Valone, *Behav. Ecol. Sociobiol.* **62**, 1–14 (2007).
19. P. Ward, A. Zahavi, *Ibis* **115**, 517–534 (1973).
20. A. E. Burger, *Colon. Waterbirds* **20**, 55 (1997).
21. H. Weimerskirch, S. Bertrand, J. Silva, J. C. Marques, E. Goya, *PLoS ONE* **5**, e9928 (2010).
22. N. J. Buckley, *Am. Nat.* **149**, 1091–1112 (1997).
23. E. D. Silverman, R. R. Veit, G. A. Nevitt, *Mar. Ecol. Prog. Ser.* **277**, 25–36 (2004).
24. H. Richner, P. Heeb, *Adv. Stud. Behav.* **24**, 1–45 (1995).
25. M. Baude, E. Danchin, M. Mugabo, I. Dajoz, *Proc. Biol. Sci.* **278**, 2806–2813 (2011).
26. D. K. N. Dechmann et al., *Proc. Biol. Sci.* **276**, 2721–2728 (2009).
27. S. C. Votier, W. J. Grecian, S. Patrick, J. Newton, *Mar. Biol.* **158**, 355–362 (2011).
28. E. Danchin, L. A. Giraldeau, T. J. Valone, R. H. Wagner, *Science* **305**, 487–491 (2004).

Acknowledgments: Funding was provided by the Natural Environment Research Council (Standard Grant NE/H007466/1 to K.C.H., S.B., and S.C.V.), the UK Department of Energy and Climate Change, the Centre for Ecology and Hydrology, the Centre National de la Recherche Scientifique, the Ligue pour la Protection des Oiseaux, the Alderney Commission for Renewable Energy, the Beaufort Marine Research Award, and the European Union INTERREG projects CHARM III and FAME. We acknowledge use of www.seaturtle.org and their analysis tools. Data reported in this paper are tabulated in the supplementary materials and archived by BirdLife International (www.seabirdtracking.org).

Supplementary Materials

www.sciencemag.org/cgi/content/full/science.1236077/DC1
Materials and Methods
Supplementary Text
Figs. S1 to S13
Tables S1 to S10
R model algorithm and supporting data
References (29–50)

4 February 2013; accepted 10 May 2013
Published online 6 June 2013;
10.1126/science.1236077

Table 1. Rules governing information use in individual-based models of foraging gannets (see table S10 for details).

Foraging rules	Description
Null	Birds forage randomly during each trip
Memory (ME)	Birds return to previously successful locations (private information)
Local enhancement (ME + LE)	ME + uninformed birds may follow informed birds at sea (private and public information)
Information centre (ME + IC)	ME + uninformed birds may follow informed birds from their colony (private and public information)
All sources combined (ME + LE + IC)	ME + uninformed birds may follow informed birds from the colony and at sea (public and private information)

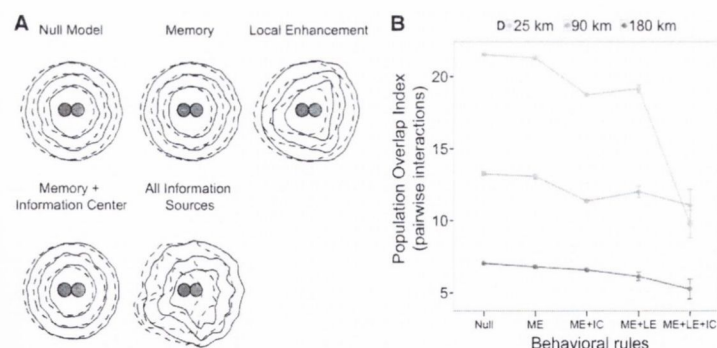


Fig. 3. Utilization distribution overlaps. Individual-based simulations show that overlap between the utilization distributions (UDs) of two hypothetical colonies (A) (solid lines/blue circle, large colony; dashed lines/red circle, small colony) reduces (B) only when birds use private information and gain public information before departure and during foraging trips (see Table 1 for model rules). Isopleths: 50, 75, and 95% UD's. Results shown for 25 prey patches. Error bars show 95% confidence intervals.

Research



Cite this article: Healy K *et al.* 2014 Ecology and mode-of-life explain lifespan variation in birds and mammals. *Proc. R. Soc. B* **281**: 20140298.
<http://dx.doi.org/10.1098/rspb.2014.0298>

Received: 5 February 2014
Accepted: 24 March 2014

Subject Areas:
evolution, ecology

Keywords:
longevity, extrinsic mortality, MCMCglmm,
volant, non-volant

Author for correspondence:
Kevin Healy
e-mail: healyke@tcd.ie

[†]Zoology Building, Trinity College Dublin, Dublin 2, Republic of Ireland.

[‡]These authors contributed equally to this study.

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2014.0298> or via <http://rspb.royalsocietypublishing.org>.

Ecology and mode-of-life explain lifespan variation in birds and mammals

Kevin Healy^{1,2,†}, Thomas Guillaume^{1,2}, Sive Finlay^{1,2,‡}, Adam Kane^{1,2,‡},
Seán B. A. Kelly^{1,2,‡}, Deirdre McClean^{1,2,‡}, David J. Kelly^{1,2}, Ian Donohue^{1,2},
Andrew L. Jackson^{1,2} and Natalie Cooper^{1,2}

¹School of Natural Sciences, and ²Trinity Centre for Biodiversity Research, Trinity College Dublin, Dublin 2, Republic of Ireland

AJ, 0000-0001-7334-0434

Maximum lifespan in birds and mammals varies strongly with body mass such that large species tend to live longer than smaller species. However, many species live far longer than expected given their body mass. This may reflect interspecific variation in extrinsic mortality, as life-history theory predicts investment in long-term survival is under positive selection when extrinsic mortality is reduced. Here, we investigate how multiple ecological and mode-of-life traits that should reduce extrinsic mortality (including volancy (flight capability), activity period, foraging environment and fossoriality), simultaneously influence lifespan across endotherms. Using novel phylogenetic comparative analyses and to our knowledge, the most species analysed to date ($n = 1368$), we show that, over and above the effect of body mass, the most important factor enabling longer lifespan is the ability to fly. Within volant species, lifespan depended upon when (day, night, dusk or dawn), but not where (in the air, in trees or on the ground), species are active. However, the opposite was true for non-volant species, where lifespan correlated positively with both arboreality and fossoriality. Our results highlight that when studying the molecular basis behind cellular processes such as those underlying lifespan, it is important to consider the ecological selection pressures that shaped them over evolutionary time.

1. Introduction

Lifespan, or longevity, is a fundamental life-history trait that exhibits considerable variation both within and among species. Maximum lifespan in vertebrates, for example, ranges from up to 211 years in the bowhead whale (*Balaena mysticetus*; [1]), down to just eight weeks in the pygmy goby (*Eviota sigillata*; [2]). Like most other life-history traits, lifespan varies strongly with body size such that large species tend to live longer than smaller species [3–6]. However, many species have far longer, or indeed shorter, lives than expected given their body mass (figure 1). Understanding the mechanisms underlying these deviations from predicted lifespan may reveal the secrets to treating and combating human ageing [7,8].

One explanation for species living longer than expected, given their body size, is that low extrinsic mortality (i.e. low risk of death owing to external causes such as disease, predation, food shortages or accidents) will, on average, select for longer lifespans than when extrinsic mortality is high [9,10]. This is because when untimely death is more likely, investment in early and frequent reproduction is favoured rather than investment in long-term maintenance and survival. Therefore, species with adaptations that reduce the risks of extrinsic mortality should live longer than expected, given their body mass [11]. These ideas have led to myriad, taxon-specific hypotheses about traits that may reduce extrinsic mortality and result in increased lifespan (reviewed in [7]). However, there is little consensus about the general drivers of increased lifespan across clades.

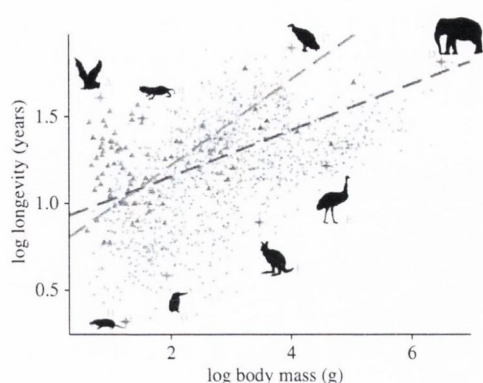


Figure 1. Relationships between body mass and maximum lifespan in birds and mammals. Silhouettes highlight a selection of species with much longer or shorter lifespans than expected given their body size. These species are (A) *Myotis brandtii*, Brandt's bat; (B) *Heterocephalus glaber*, naked mole rat; (C) *Vultur gryphus*, Andean condor; (D) *Loxodonta Africana*, African elephant; (E) *Dromaius novaehollandiae*, emu; (F) *Dorcopsulus macleayi*, Papuan forest-wallaby; (G) *Ceryle rudis*, pied kingfisher and (H) *Myosorex varius*, forest shrew. Blue points and line represent volant birds and mammals ($n = 662$; slope = 0.25, intercept = 0.73). Red points and line represent non-volant birds and mammals ($n = 706$; slope = 0.13, intercept = 0.89). Blue triangles represent bat species and red triangles represent non-volant bird species. Estimates of slopes and intercepts represent back transformed values from mean centred values given in table 1. (Online version in colour.)

The ability to fly, and thus more easily escape predation and unfavourable conditions, is perhaps the most effective way a terrestrial species can evolve to reduce its extrinsic mortality and increase its lifespan [11–13]. This is supported strongly by striking differences in the lifespan of volant (flying) and non-volant (non-flying) vertebrates; on average, bats live 3.5 times longer than similar-sized non-volant placental mammals [14,15], whereas birds live up to four times longer than similar-sized mammals [3,16]. However, flight may not be the only route to reducing extrinsic mortality and thereby increasing lifespan. Ecological factors may also be important. Previous studies have investigated the relationship between lifespan and various ecological variables, but most only investigated select groups of species and few considered multiple traits simultaneously (e.g. [17]).

Here, we investigate how multiple ecological and mode-of-life traits simultaneously influence maximum lifespan across birds and mammals. We generate clear, testable hypotheses (see below) about the relationships among lifespan and ecological and mode-of-life traits known to influence extrinsic mortality risk; including flight capability (volant or non-volant), activity period (diurnal, crepuscular (i.e. active at dawn and dusk), nocturnal or cathemeral (i.e. active both day and night)), foraging environment (terrestrial, semi-arboreal, arboreal, aerial or aquatic) and fossoriality (i.e. living in burrows; fossorial, semi-fossorial, non-fossorial). We then test these hypotheses across birds and mammals using, to our knowledge, the largest number of species to date ($n = 589$ birds and 779 mammals) and state-of-the-art phylogenetic comparative analyses (including using a distribution of 500 combined bird and mammal phylogenies) to control for the phylogenetic autocorrelation introduced by shared ancestry [18] and body mass [3]. Together, these novel features of our analyses

allow unprecedented testing of these key hypotheses that underpin life-history evolution in endotherms.

We predict that, after controlling for body mass: (i) volant species will live longer than non-volant species, because they can more easily evade predators and unfavourable conditions [11–13]; (ii) nocturnal, crepuscular or cathemeral species will live longer than diurnal species, because species that are active at night or dusk are likely to be harder for predators to detect [12,19]; (iii) species which forage in non-terrestrial environments (i.e. species which feed in trees, water or aerially) will live longer than terrestrial foragers, because they will be more capable of escaping from predators than species that feed on the ground [13,17,20]; and (iv) fossorial (i.e. species that live in permanent burrows) and semi-fossorial species will live longer than purely terrestrial species, because they possess means to escape predation and unfavourable conditions through refuge [21].

We expect that the ecological factors which influence lifespan will vary among volant and non-volant species, because sources of extrinsic mortality will differ in these two groups. We therefore split species into volant (most birds and all bats) and non-volant (some birds and most mammals) subgroups, to discover general, broad-scale correlates of lifespan in endotherms, rather than separate correlates for birds and mammals. We then tested our hypotheses on volant and non-volant species separately. We find that, as predicted, after controlling for body mass and phylogeny, the most important factor enabling longer lifespan is the ability to fly. In addition, ecological correlates of lifespan varied among volant and non-volant species such that the longest lived volant species are nocturnal, cathemeral or diurnal, whereas the longest lived non-volant species are arboreal or fossorial.

2. Material and methods

(a) Data

We used maximum longevity as our measure of lifespan as it is thought to be the best available estimator of a species' ageing rate [5] and because of the amount of high-quality longevity data available. We obtained data on maximum longevity (years) and adult body mass (g) from the AnAge database [1,22]. In our main analysis, we excluded species with maximum longevity estimates based on fewer than 10 longevity records, or with low or questionable data quality as defined in the AnAge database [5]. As maximum values are dependent on sample size, we also ran a sensitivity analysis excluding species with maximum longevity estimated from fewer than 100 longevity records. This should show whether data quantity has a strong influence on our results, though it is worth remembering that data quality in a database such as AnAge is highly heterogeneous, and increasing sample size may not necessarily correlate with increased data quality. Note that longevity records for non-volant mammals tend to come from captive individuals, whereas data for bats and birds tend to come from wild caught individuals. Although we expect captive individuals to live longer than wild individuals, on average maximum longevity tends to remain unchanged between captive and wild populations [23]. Further, given that bats and birds live longer than non-volant mammals, this should make our analyses more conservative.

To test our hypotheses concerning the relationships between lifespan, mode-of-life and ecological traits, we collected data on the flight capability (volant or non-volant), activity period (diurnal, crepuscular, nocturnal or cathemeral), foraging environment

Table 1. Relationship between maximum longevity (years), body mass (g) and flight capability (volant or non-volant) in 1368 birds and mammals. (Estimates are modal estimates from 500 models. Lower CI = lower 95% confidence interval from 500 models. Upper CI = upper 95% confidence interval from 500 models. Posterior distribution = distribution of estimates from 500 models. Body mass : flight capability = interaction between body mass and flight capability. Notes: 24 000 000 iterations with 4 000 000 burn-in and thinning interval of 10 000.)

	estimate (β)	lower CI	upper CI	posterior distribution
fixed terms				
intercept	-0.145	-1.544	1.260	
body mass	0.554	0.467	0.639	
flight capability volant	0.507	0.033	0.981	
body mass : flight capability	0.456	0.302	0.613	
random terms				
residual variance	0.107	0.090	0.127	
phylogenetic variance	1.542	1.264	1.871	

(terrestrial, semi-arboreal, arboreal, aerial or aquatic) and fossoriality (fossorial, semi-fossorial or non-fossorial) of each species using *Walker's Mammals of the World* [24], the *Handbook of Birds of the World* series [25], the *Handbook of the Birds of Europe*, the Middle East and North Africa series [26] and some additional sources (electronic supplementary material, appendix 1, [27–29]). These categories are described in detail in the electronic supplementary material, appendix 1. We used the taxonomy of Wilson & Reeder [30] for mammals and Jetz *et al.* [31] for birds. We excluded purely aquatic mammals (Cetacea and Sirenia) from the analyses, because we expect selection pressures to be very different in these groups. We also excluded gliding mammals, because there were too few species ($n = 9$) to run a separate analysis and because this group could equally fit into either the volant or non-volant subgroups.

Rather than basing our analyses on just a single phylogenetic tree and assuming this tree was known without error, we instead used a distribution of trees. We extracted 500 bird trees from the posterior distribution of a recent bird phylogeny generated under a Bayesian inference framework [31], and used the 10 000 mammal trees constructed by Kuhn *et al.* [32]. Each individual mammal tree comprises one resolution of the polytomies of a previously published supertree [33]. We treat these as equivalent to a Bayesian posterior distribution of trees, because no such tree analysis exists for all mammals. As we needed a distribution of phylogenies containing both birds and mammals, we randomly selected one bird tree and one mammal tree (without replacement) and bound them to make a combined tree. The trees were bound with a root age of 315 million years, corresponding to the fossil calibration for all amniotes, i.e. *Archaeopteryx lithographica* (electronic supplementary material, appendix 1; [34]). We repeated this procedure 500 times to generate a distribution of 500 combined bird and mammal trees.

Many studies on vertebrate ageing have noted a strong correlation between maximum longevity and metabolic rate. Opinion is divided as to whether this is a causative relationship or merely confounded with the strong correlation between body mass and metabolic rate [7]. To determine whether our conclusions hold when we include metabolic rate in our models, we also compiled mass-specific basal metabolic rate (BMR; Wg^{-1}) data (see the electronic supplementary material, appendix 1).

In total, our analyses used data from 589 birds (579 volant and 10 non-volant) and 779 mammals (83 volant and 696 non-volant; see the electronic supplementary material, appendix 3: table A1 for more details and appendix 2 for the complete dataset). This was reduced to 112 birds and 330 mammals when we include BMR in our models, and 474 birds and 435 mammals in the sensitivity analysis using only species with 100 or more longevity records.

(b) Analyses

To test our hypotheses, we fitted the following three models, with maximum longevity and *body mass* incorporated as continuous variables; *flight capability*, *foraging environment*, *activity period* and *fossoriality* as factors and with *body mass : flight capability* representing the interaction between body mass and flight capability.

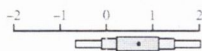
- (1) For all species ($n = 1368$):
maximum longevity = $f(\text{body mass} + \text{flight capability} + \text{body mass : flight capability})$.
- (2) For volant species only ($n = 662$):
maximum longevity = $f(\text{body mass} + \text{foraging environment} + \text{activity period})$.
- (3) For non-volant species only ($n = 706$):
maximum longevity = $f(\text{body mass} + \text{foraging environment} + \text{fossoriality} + \text{activity period})$.

All analyses were carried out in R v. 3.0.2 [35]. Maximum longevity and body mass (and BMR, see below) were $\log_{10}$ transformed to correct inherent skewness before being mean centred and expressed in units of standard deviation.

We fitted our models using Bayesian phylogenetic mixed models from the MCMCglmm package [36], to account for non-independence in species traits introduced as a result of common ancestry [18]. MCMCglmm uses a Markov chain Monte Carlo (MCMC) estimation approach and accounts for non-independence among closely related species by including the phylogenetic relationships among species as a random variable. We determined the number of iterations, thinning and the burn-in period for each model run across all trees using diagnostics in the coda package [37] and we checked for convergence between model chains using the Gelman-Rubin statistic, the potential scale reduction factor (PSR), with all models required to have a PSR below 1.1 [38]. Following the recommendations of Hadfield [36], we used an uninformative inverse-Wishart distribution (with variance, V , set to 0.5 and belief parameter, ν , set to 0.002) and a parameter expanded prior, with a half-Cauchy distribution (described by the parameters $V = 0.5$, $\nu = 1$, the prior mean $\alpha.\mu = 0$, and $\alpha.V = 10^2$, which represents the prior standard deviation with a scale of 10), for the random factor to improve mixing and decrease autocorrelation among iterations.

As noted earlier, rather than using one phylogenetic tree and assuming this tree was error free, we instead used a distribution of 500 combined bird and mammal trees and fitted each of our models to each of these trees. We then combined the resulting model outputs to give model estimates which incorporate the

Table 2. Relationship between maximum longevity (years), body mass (g), foraging environment and activity period in 662 volant birds and mammals. (Estimates are modal estimates from 500 models. Column heads explained same as given in table 1. Notes: 12 000 000 iterations with 2 000 000 burn-in and thinning interval of 5000.)

	estimate (β)	lower CI	upper CI	posterior distribution
fixed terms				
intercept	0.668	-0.664	2.028	
body mass	1.035	0.899	1.172	
foraging environment				
aerial	0.116	-0.119	0.354	
arboreal	0.068	-0.119	0.258	
semi-arboreal	0.124	-0.056	0.301	
aquatic	-0.166	-0.383	0.049	
activity period				
cathemeral	0.085	-0.088	0.261	
crepuscular	-0.479	-0.772	-0.182	
nocturnal	-0.131	-0.385	0.122	
random terms				
residual variance	0.184	0.151	0.223	
phylogenetic variance	1.155	0.789	1.693	

error across the 500 trees. As the posterior outputs of MCMC models are combinable, coefficient distributions were created by amalgamating each coefficient posterior.

Finally, to determine whether our conclusions held when we excluded species with fewer than 100 longevity records or when metabolic rate was included in our models, we repeated models 1–3 with either the reduced dataset of species with 100 or more longevity records or with BMR as an additional linear covariate. We also repeated models 2 and 3 for birds and mammals (rather than volant and non-volant species) separately to ensure that differences between the volant and non-volant subgroups were owing to differences in flight capability and were not simply representing the difference between mammals and birds. We calculated the deviance information criteria (DIC), a hierarchical generalization of the Akaike information criteria, for each bird and mammal paired models and compared it to the paired volant and non-volant models to compare model ‘fit’ of each approach.

3. Results

We found that volant species live longer than non-volant species of a similar body mass (table 1 and figure 1). In addition, for a given increase in body mass, the lifespans of volant species (modal slope estimate (after converting from mean-centred values) = 0.25; table 1) increase significantly more than the lifespans of non-volant species (modal slope estimate (after converting from mean-centred values) = 0.13; table 1).

The relationships among our ecological variables and lifespan differed between the volant and non-volant subgroups. Within volant taxa, crepuscular species (i.e. those active at dusk and dawn) had significantly shorter lifespans than both diurnal and nocturnal species (table 2). By contrast, activity period was not associated with lifespan in non-volant species (table 3). Foraging environment did not influence lifespan significantly in volant species; bats and birds that forage on the ground do not have shorter lifespans than species that forage in the air or in trees (table 2). Within non-volant species,

however, those foraging arboreally have longer lifespans than those foraging terrestrially, and fossorial (i.e. burrowing) species live longer than non-fossorial ones (table 3).

In the supplementary analysis with maximum longevity estimates based on 100 or more records, the models showed qualitatively comparable results to the findings in the main analysis (electronic supplementary material, appendix 3: tables A2–A4). When we included BMR as an additional linear covariate into models 1–3, the results showed similar general trends as those without BMR except with no significant effect of crepuscularity in volant species, no effect of semi-arboreality in non-volant species and a negative correlation between BMR and longevity in non-volant species (electronic supplementary material, appendix 3: tables A5–A7). We also repeated models 2 and 3 for birds and mammals (rather than volant and non-volant species) separately. The results were qualitatively identical apart from a predictable reduction in the phylogenetic residual term and also a lower combined DIC value for models 2 and 3 (modal volant and non-volant DIC = 1184) in comparison to a taxonomically split model (modal birds and mammals DIC = 1227) (electronic supplementary material, appendix 3: tables A8–A9). The phylogenetic residual term was high in all of our models (model 1: 1.542; model 2: 1.555; model 3: 1.627; tables 1–3) but was much lower in the taxonomically split bird and mammal models, as expected given their more restricted phylogenetic scope (birds: 0.371; mammals: 0.936; electronic supplementary material, appendix 3: table A10).

4. Discussion

As predicted, we found that volant species live longer than non-volant species of a similar body mass after accounting for phylogenetic relatedness. However, the effects of body mass on lifespan in the two groups differed: similar increases in body mass resulted in disproportionately greater increases

Table 3. Relationship between maximum longevity (years), body mass (g), foraging environment, fossoriality and activity period in 706 non-volant birds and mammals. (Estimates are modal estimates from 500 models. Column heads explained same as given in table 1. Notes: 24 000 000 iterations with 4 000 000 burn-in and thinning interval of 10 000.)

	estimate (β)	lower CI	upper CI	posterior distribution
fixed terms				
intercept	0.013	-1.433	1.467	
body mass	0.531	0.449	0.614	
foraging environment				
arboreal	0.213	0.070	0.358	
semi-arboreal	0.148	0.022	0.274	
aquatic	0.064	-0.220	0.341	
fossoriality				
fossorial	0.437	0.088	0.785	
semi-fossorial	0.035	-0.081	0.149	
activity period				
catemeral	0.060	-0.056	0.173	
crepuscular	-0.050	-0.194	0.096	
nocturnal	0.038	-0.075	0.153	
random terms				
residual variance	0.042	0.031	0.059	
phylogenetic variance	1.627	1.319	1.985	

in lifespan for volant compared with non-volant species. Additionally, after accounting for phylogeny and body size, the lifespans of volant species depended upon when species are active but not where that activity occurs, whereas the opposite was true for non-volant species. Thus, the longest-lived volant birds and mammals tended to be either diurnal or nocturnal, and the longest-lived non-volant species tended to be arboreal, semi-arboreal or fossorial.

The link between flight and long lifespan in vertebrates is well known. Among birds, flightless or weakly flying species (i.e. game birds) have the shortest lifespans [6,11,14]. Among mammals, bats live far longer than similar-sized non-volant mammals and gliding species also have greater lifespans than expected given their body mass [12]. This probably reflects the ability of flying species to escape sources of extrinsic mortality such as predation and unfavourable conditions, allowing greater investment in increased lifespan [11–13].

The relationships among our ecological variables and lifespan differed between the volant and non-volant subgroups, as expected given the different sources of extrinsic mortality they experience. Activity period was important in volant species, with crepuscular species possessing the shortest lifespans. This suggests that being crepuscular is a poor strategy for volant species, perhaps because they are exposed to both diurnal and nocturnal predators, resulting in higher extrinsic mortality. The scarcity of crepuscular volant species ($n = 16$) in our dataset also suggests that specialization to be active between nocturnal and diurnal periods is a relatively unsuccessful strategy. However, activity period was not related to lifespan in non-volant species, counter to our initial prediction that nocturnal, crepuscular and catemeral species would be more long-lived, which assumed that diurnal species would be easier for predators to detect. However, there are many additional ways to avoid predation (see

below) and many alternative reasons for becoming nocturnal, crepuscular or catemeral. For example, many large mammals are crepuscular or catemeral in order to avoid the intense heat of the day in tropical areas, while species such as wolves and hyenas may have become nocturnal to access more prey. Consequently, although nocturnality may decrease extrinsic mortality for some species, it may actually increase it for others.

Foraging environment did not influence lifespan significantly in volant species, but it was important in non-volant species where arboreal, semi-arboreal and fossorial species had longer lifespans than terrestrial species. The relationship between arboreality and extended lifespan in mammals has been shown previously [17], but to the best of our knowledge this is the first comparative analysis of lifespan in fossorial versus non-fossorial species. Our results may, therefore, offer a partial explanation for the exceptional longevity of naked mole rats (*Heterocephalus glaber*) which are completely fossorial and live 10 times longer than expected, given their body size [21].

Across all our models, body size was correlated strongly with lifespan, which is consistent with previous studies (e.g. [3,5,6]). However, our study is the first, to our knowledge, to demonstrate the general importance of body size in both volant and non-volant species concurrently (as opposed to traditional taxonomic groupings of birds, bats and terrestrial mammals separately). Large species are expected to live longer than small species, in part, because they should experience lower rates of extrinsic mortality and therefore invest more in long-term maintenance and survival. For example, large species are expected to suffer lower predation risk, and be better able to cope with temporary food shortages, climatic fluctuations and extreme weather compared with smaller species [15,39]. Also following from Peto’s paradox, that

cancer incidence does not correlate with body size despite the larger number of cells from which it can potentially develop [40], the increased lifespan afforded through decreased extrinsic mortality in large species can increase selection for molecular controls on senescence related diseases [11].

Previous studies generated similar slopes for the relationship between log lifespan and log body mass in birds (slope = 0.20) and mammals (slope = 0.22), but the bird slope had a much higher intercept [3,39]. By contrast, we found that, for a given increase in body mass, the lifespans of volant species (modal slope estimate (after converting from mean-centred values) = 0.25) increase significantly more than the lifespans of non-volant species (modal slope estimate (after converting from mean-centred values) = 0.13). This suggests that the similarities in bird and mammal slopes seen previously may have been the result of splitting species into taxonomic rather than ecological groups. The explanation for the steeper slope in volant species is unclear. However, we suggest that increasing body mass in volant species reduces their extrinsic mortality much more markedly than it does in non-volant species, favouring greater investment in long-term survival. Alternatively, this may reflect constraints on life-history optimization, particularly in bats, where the energetic and biomechanical requirements of flight restrict females to raising small litters [24]. This leaves few options for the optimization of life history in bats other than increasing lifespan, thereby increasing lifetime opportunities for reproduction.

For birds and mammals, the most important factor in reducing extrinsic mortality and allowing investment in a longer lifespan, after controlling for body size and phylogeny, is the ability to fly. This effect is so strong that it overshadows all other ecological variables explaining lifespan variation in volant species. However, there is still residual variation in all of our models. Much of this is related to phylogeny, particularly in volant species because this group contains a fairly even number of mammals (bats) and birds. On the other hand, owing to the paucity of lifespan data resulting in so few non-volant birds in our dataset ($n = 10$), the phylogenetic residuals in the non-volant model are unlikely to be attributed to the inclusion of birds species in the mammal dominated non-volant models. But even accounting for phylogeny (as we do in all our models), there is still substantial unexplained variation in the model for volant species (residual error = 0.18 in the model for volant species compared with 0.042 in the model for non-volant species; tables 2 and 3). We anticipated such unexplained variation would be related to bats because of their

reputed extreme lifespans [14], yet, of the 32 species with the top 5% of residuals in our models of maximum lifespan against body size, foraging environment and activity period, less than half are bats. Instead, flying foxes (Pteropodidae) are scattered among the birds and fit the volant species regression line well, as do most microchiropteran bats. This suggests that the prolonged lifespans of most bats are not exceptional, given their volant mode-of-life. In our models, the exceptionally long-lived bats are mostly Vespertilionidae (*Barbastella barbastellus*, *Myotis blythii*, *Myotis brandtii*, *Myotis daubentonii*, *Myotis evotis*, *Myotis lucifugus*, *Myotis myotis*, *Myotis mystacinus*, *Myotis nattereri*, *Myotis volans*, *Plecotus auritus* and *Plecotus austriacus*) plus *Desmodus rotundus*, *Rhinolophus ferrumequinum* and *Rhinolophus hipposideros*. However, the species in the top 5% of residuals also include pelagic seabirds (*Alca torda*, *Uria aalge*, *Pelecanus erythrorhynchos*, *Pelecanus occidentalis*, *Pelecanus onocrotalus*, *Diomedea epomophora*, *Diomedea exulans*, *Phoebastria immutabilis*, *Phoebastria nigripes*, *Thalassarche chrysostoma*, *Thalassarche melanophrys*, *Fulmarus glacialis*, *Puffinus puffinus*, *Fregata minor* and *Haliaeetus albicilla*), parrots (*Cacatua leadbeateri*), flamingos (*Phoenicopterus roseus*), swans (*Cygnus olor*) and even diving ducks (*Aythya fuligula*). The mechanisms underlying the exceptional lifespans of these species are likely to be idiosyncratic, given the broad array of ecologies these birds exhibit. Thus, if we want to uncover the secrets of long life, we may need to expand our search beyond bats and naked mole rats [8,41]. When studying the molecular basis behind cellular processes such as those underlying longevity, it is important to consider the selection pressures that shaped them over evolutionary time.

Acknowledgements. We thank the members of NERD club for insightful discussions, Gavin Thomas for assistance with the bird phylogeny, Luke McNally for suggestions on the analysis and the anonymous reviewers for their helpful suggestions.

Data accessibility. All data used in these analyses are available in the electronic supplementary material, appendix 2.

Funding statement. Funding was provided by the Earth and Natural Sciences (ENS) Doctoral Studies Programme, funded by the Higher Education Authority (HEA) through the Programme for Research at Third Level Institutions, Cycle 5 (PRTL-5), co-funded by the European Regional Development Fund (ERDF) (K.H.); IRC Embark Initiative Postgraduate Scholarship (S.F.); Trinity College Dublin (T.G., A.K., S.K.), the EU INTERREG IVA Cross-border Programme-funded DOLMANT Project (ref. no: 002862; D.M.) and European Commission CORDIS Seventh Framework Programme (FP7) Marie Curie CIG grant (proposal no: 321696; N.C.). All calculations were performed on the Lonsdale cluster maintained by the Trinity Centre for High Performance Computing. This cluster was funded through grants from Science Foundation Ireland.

References

- de Magalhães JP, Costa J. 2009 A database of vertebrate longevity records and their relation to other life-history traits. *J. Evol. Biol.* **22**, 1770–1774. (doi:10.1111/j.1420-9101.2009.01783.x)
- Depczynski M, Bellwood DR. 2005 Shortest recorded vertebrate lifespan found in a coral reef fish. *Curr. Biol.* **15**, R288–R289. (doi:10.1016/j.cub.2005.04.016)
- Lindstedt S, Calder III W. 1981 Body size, physiological time, and longevity of homeothermic animals. *Q. Rev. Biol.* **56**, 1–16. (doi:10.1086/412080)
- Promislow DEL. 1993 On size and survival: progress and pitfalls in the allometry of life span. *J. Gerontol.* **48**, B115–B123. (doi:10.1093/geronj/48.4.B115)
- de Magalhães JP, Costa J, Church GM. 2007 An analysis of the relationship between metabolism, developmental schedules, and longevity using phylogenetic independent contrasts. *J. Gerontol. Series A: Biol. Sci. Med. Sci.* **62**, 149–160. (doi:10.1093/gerona/62.2.149)
- Ricklefs RE. 2010 Life-history connections to rates of aging in terrestrial vertebrates. *Proc. Natl Acad. Sci. USA* **107**, 10 314–10 319. (doi:10.1073/pnas.1005862107)
- Ricklefs RE. 2010 Insights from comparative analyses of aging in birds and mammals. *Aging Cell* **9**, 273–284. (doi:10.1111/j.1474-9726.2009.00542.x)
- Zhang G *et al.* 2013 Comparative analysis of bat genomes provides insight into the evolution of flight and immunity. *Science* **339**, 456–460. (doi:10.1126/science.1230835)
- Stearns SC. 1992 *The evolution of life histories*. Oxford, UK: Oxford University Press.

10. Williams GC. 1957 Pleiotropy, natural selection, and the evolution of senescence. *Evolution* **11**, 398–411. (doi:10.2307/2406060)
11. Partridge L, Barton NH. 1993 Optimality, mutation and the evolution of ageing. *Nature* **362**, 305–311. (doi:10.1038/362305a0)
12. Holmes DJ, Austad SN. 1994 Fly now, die later: life-history correlates of gliding and flying in mammals. *J. Mammal.* **75**, 224–226. (doi:10.2307/1382255)
13. Pomeroy D. 1990 Why fly? The possible benefits for lower mortality. *Biol. J. Linnean Soc.* **40**, 53–65. (doi:10.1111/j.1095-8312.1990.tb00534.x)
14. Wilkinson GS, South JM. 2002 Life history, ecology and longevity in bats. *Aging Cell* **1**, 124–131. (doi:10.1046/j.1474-9728.2002.00020.x)
15. Austad SN, Fischer KE. 1991 Mammalian aging, metabolism, and ecology: evidence from the bats and marsupials. *J. Gerontol.* **46**, B47–B53. (doi:10.1093/geronj/46.2.B47)
16. Holmes D, Ottinger M. 2003 Birds as long-lived animal models for the study of aging. *Exp. Gerontol.* **38**, 1365–1375. (doi:10.1016/j.exger.2003.10.018)
17. Shattuck MR, Williams SA. 2010 Arboreality has allowed for the evolution of increased longevity in mammals. *Proc. Natl Acad. Sci. USA* **107**, 4635–4639. (doi:10.1073/pnas.0911439107)
18. Harvey PH, Pagel MD. 1991 *The comparative method in evolutionary biology*. Oxford, UK: Oxford University Press.
19. Promislow DEL, Harvey PH. 1990 Living fast and dying young: a comparative analysis of life-history variation among mammals. *J. Zool.* **220**, 417–437. (doi:10.1111/j.1469-7998.1990.tb04316.x)
20. Byrnes G, Spence AJ. 2011 Ecological and biomechanical insights into the evolution of gliding in mammals. *Integr. Comp. Biol.* **51**, 991–1001. (doi:10.1093/icb/icc069)
21. Buffenstein R, Jarvis JUM. 2002 The naked mole rat: a new record for the oldest living rodent. *Sci. Aging Knowl. Environ.* **2002**, pe7. (doi:10.1126/sageke.2002.21.pe7)
22. Tacutu R, Craig T, Budovsky A, Wuttke D, Lehmann G, Taranukha D, Costa J, Fraifeide VE, de Magalhães JP. 2013 Human ageing genomic resources: integrated databases and tools for the biology and genetics of ageing. *Nucleic Acids Res.* **41**, D1027–D1033. (doi:10.1093/nar/gks1155)
23. Ricklefs RE, Scheuerlein A. 2001 Comparison of aging-related mortality among birds and mammals. *Exp. Gerontol.* **36**, 845–857. (doi:10.1016/S0531-5565(00)00245-X)
24. Nowak RM. 1999 *Walker's mammals of the world*. Baltimore, MD: The Johns Hopkins University Press.
25. del Hoyo J, Elliott A, Sargatal J. 1992 *Handbook of the birds of the world*, vol. 1: *ostrich to ducks*. Barcelona, Spain: Lynx Edicions.
26. Cramp S. 1977 *Handbook of the birds of Europe, the Middle East, and North Africa: the birds of the Western Palearctic*, vol. 1, *ostrich to ducks*. Oxford, UK: Oxford University Press.
27. Fry HC, Fry K. 2010 *Kingfishers, bee-eaters and rollers: a handbook*. London, UK: A & C Black.
28. Juniper T, Parr M. 2003 *Parrots: a guide to parrots of the world*. London, UK: A&C Black.
29. Williams TD. 1995 *The penguins: Spheniscidae*. Oxford, UK: Oxford University Press.
30. Wilson DE, Reeder DAM. 2005 *Mammal species of the world: a taxonomic and geographic reference*, 3rd edn. Washington, DC: Smithsonian Institution Press.
31. Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012 The global diversity of birds in space and time. *Nature* **491**, 444–448. (doi:10.1038/nature11631)
32. Kuhn TS, Mooers AO, Thomas GH. 2011 A simple polytomy resolver for dated phylogenies. *Methods Ecol. Evol.* **2**, 427–436. (doi:10.1111/j.2041-210X.2011.00103.x)
33. Bininda-Emonds ORP *et al.* 2007 The delayed rise of present-day mammals. *Nature* **446**, 507–512. (doi:10.1038/nature05634)
34. Reisz RR, Müller J. 2004 Molecular timescales and the fossil record: a paleontological perspective. *Trends Genet.* **20**, 237–241. (doi:10.1016/j.tig.2004.03.007)
35. R Development Core Team. 2012 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
36. Hadfield JD. 2010 MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J. Stat. Softw.* **33**, 1–22.
37. Plummer M, Best N, Cowles K, Vines K. 2006 CODA: convergence diagnosis and output analysis for MCMC. *R News* **6**, 7–11.
38. Gelman A, Rubin DB. 1992 Inference from iterative simulation using multiple sequences. *Statist. Sci.* **7**, 457–472. (doi:10.1214/ss/1177011136)
39. Hulbert A, Pamplona R, Buffenstein R, Buttemer W. 2007 Life and death: metabolic rate, membrane composition, and life span of animals. *Physiol. Rev.* **87**, 1175–1213. (doi:10.1152/physrev.00047.2006)
40. Peto R, Roe F, Lee P, Levy L, Clack J. 1975 Cancer and ageing in mice and men. *Br. J. Cancer* **32**, 411–426. (doi:10.1038/bjc.1975.242)
41. Tian X *et al.* 2013 High-molecular-mass hyaluronan mediates the cancer resistance of the naked mole rat. *Nature* **499**, 346–349. (doi:10.1038/nature12234)

Effect of rehabilitation on survival rates of endangered Cape vultures

A. Monadjem^{1,2}, K. Wolter³, W. Naser³ & A. Kane^{4,5}

¹ All Out Africa Research Unit, Department of Biological Sciences, University of Swaziland, Kwaluseni, Swaziland

² Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa

³ VulPro, Skerpoort, North West Province, South Africa

⁴ Department of Zoology, School of Natural Sciences, Trinity College Dublin, Dublin, Ireland

⁵ Trinity Centre for Biodiversity Research, Trinity College Dublin, Dublin, Ireland

Keywords

Cape vulture; MARK; population dynamics; rehabilitation; survival.

Correspondence

Ara Monadjem, UNISWA, Private Bag 4, Kwaluseni M202, Swaziland. Tel: +268(0)25184011; Fax: +268(0)25185276 Email: ara@uniswa.sz

Editor: Todd Katzner

Received 26 November 2012; accepted 17 April 2013

doi:10.1111/acv.12054

Abstract

The rehabilitation of injured or poisoned birds, including raptors, is widely practiced even though its conservation value is not well understood. In this study, the survival rate of rehabilitated Cape vultures (*Gyps coprotheres*) released back into the wild was compared with that of wild-caught birds at a breeding colony in South Africa. The program MARK was used to model survival based on age, sex and whether they were rehabilitated or wild-caught for 405 individual birds. Despite receiving treatment, rehabilitated birds suffered significantly lower survival rates when compared with wild conspecifics of identical age. Annual survival rates ($\pm$ SE) of rehabilitated and wild-caught birds were 74.8% ($\pm$ 8.1%) and 91.3% ($\pm$ 6.3%), respectively. In addition, a population dynamics model was developed to predict future trends based on varying proportions of rehabilitated and wild-caught birds. The population growth rate (λ) for a wild population (i.e. without any rehabilitated individuals) was greater than one or increasing, whereas that for an entirely rehabilitated population was less than one or declining. A stable growth rate, $\lambda = 1$, occurred when approximately 50% of the adults were rehabilitated. Together, our results underscore the importance of tackling the causes of these injuries to Cape vultures before rehabilitation becomes necessary.

Introduction

The number of bird species facing the threat of extinction has been increasing in the past few decades (Butchart *et al.*, 2010), placing pressure on successful implementation of conservation activities. A major problem is that the effectiveness of many conservation actions has yet to be assessed. One such conservation activity that is particularly widely practiced for birds is rehabilitation of injured, poisoned or otherwise harmed birds, which are then released back into the wild. Although rehabilitation of compromised birds as a conservation tool may be appealing (Naidoo *et al.*, 2011; Finkelstein *et al.*, 2012), few studies have actually tested the efficacy of the technique. After all, if rehabilitated birds are unable to survive in the wild, then the technique can hardly be called a conservation tool (Sharp, 1996).

The impact of rehabilitation on birds has best been examined in oiled seabirds, where survival of rehabilitated birds typically is significantly lower than that of non-oiled birds (Anderson, Gress & Fry, 1996; Sharp, 1996; Goldsworthy *et al.*, 2000; Golightly *et al.*, 2002). Notable exceptions are African penguins (*Spheniscus demersus*; Underhill *et al.*,

1999; Whittington, 1999) and Cape gannets (*Morus capensis*; Altwegg *et al.*, 2008). In contrast, very few studies have compared survival rates of rehabilitated raptors with wild (non-rehabilitated) birds (Sweeney, Redig & Tordoff, 1997).

Captive-bred Mauritius kestrels (*Falco punctatus*) had similar survival rates compared with wild-bred birds (Nicoll, Jones & Norris, 2004). Similarly, survival of captive-bred adult Griffon vultures (*Gyps fulvus*) after 1 year post-release was similar to that of wild-born adults (Sarrazin *et al.*, 1994). However, in general, captive-bred birds will not have experienced a traumatic or injurious event, in contrast to rehabilitated birds. The effects of rehabilitation on raptor survival are poorly understood and the handful of existing studies either suffer from very small sample size (e.g. Hamilton, Zwank & Olsen, 1988) and/or did not conduct robust survival analysis (e.g. Sweeney *et al.*, 1997; Fajardo, Babiloni & Miranda, 2000) where recaptures and survival are separately estimated such as is done in the program MARK (White & Burnham, 1999).

Many vulture and raptor populations have experienced serious declines (Thiollay, 2007; Pain *et al.*, 2008; Virani *et al.*, 2011) and most Old World vulture species are now

listed on the IUCN Red List (IUCN, 2012). Factors contributing to these declines include poisoning, electrocution, persecution and collision with power lines, and bush encroachment affecting their foraging ability (Anderson, 2000; Piper, 2005; Bamford, Monadjem & Hardy, 2009a). The Cape vulture (*G. coprotheres*) is a southern African endemic that has been declining in range (Robertson *et al.*, 1998; Boshoff, Piper & Michael, 2009) as well as numbers of breeding pairs (Benson, 2004), and is currently considered 'endangered' (IUCN, 2012) owing to the above causes. Individual birds range over large areas (Bamford *et al.*, 2007), making them susceptible to deliberate (Ogada, Keesing & Virani, 2012), indirect [notably from consumption of lead ammunition (Finkelstein *et al.*, 2012)] and accidental (e.g. see Swarup *et al.*, 2007) poisoning, even if the poisons are used at only a few localities (Green *et al.*, 2004). Poisoned and injured birds regularly show up at rehabilitation centers in South Africa (Naidoo *et al.*, 2011), where they receive medical attention and, if they recover, may be released. Previously, the efficacy of such treatments has been quantified on whether the birds have recovered from the injury or poisoning (Naidoo *et al.*, 2011). However, the longer term effects on the survival of these rehabilitated individuals have not been assessed.

This study aims to compare the survival rates of rehabilitated Cape vultures with wild-captured individuals in the Magaliesberg, South Africa. We predict that rehabilitated birds will have survival rates lower than those of healthy wild-captured birds since we suspect that the injury or poisoning that brought the bird into a rehabilitation center may occasionally (or even frequently) cause permanent damage to the animal. We also develop a population dynamics model by investigating the effect different proportions of rehabilitated birds will have on the future trends of the Magaliesberg colony.

Materials and methods

Study site and species

Vultures were captured and tagged at 12 localities, 10 of which are in close proximity to each other (Fig. 1a). These 10 sites are all situated in the Magaliesberg mountain range and are covered by savanna, much of it recently transformed by humans. Vulture restaurants (*sensu* Piper, 2007) were established at some of these localities. Carcasses or parts thereof were put out for vultures several times a week at VulPro and the Rhino and Lion Park restaurants. The amount varied according to availability, but vultures were generally observed each day. In the past decade, approximately 300–400 pairs of Cape vultures have bred annually at the three colonies in the Magaliesberg range (Wolter, Whittington-Jones & West, 2007), which is slightly down from the maximum of 436 breeding pairs recorded in 1983 (Tarboton & Allan, 1984).

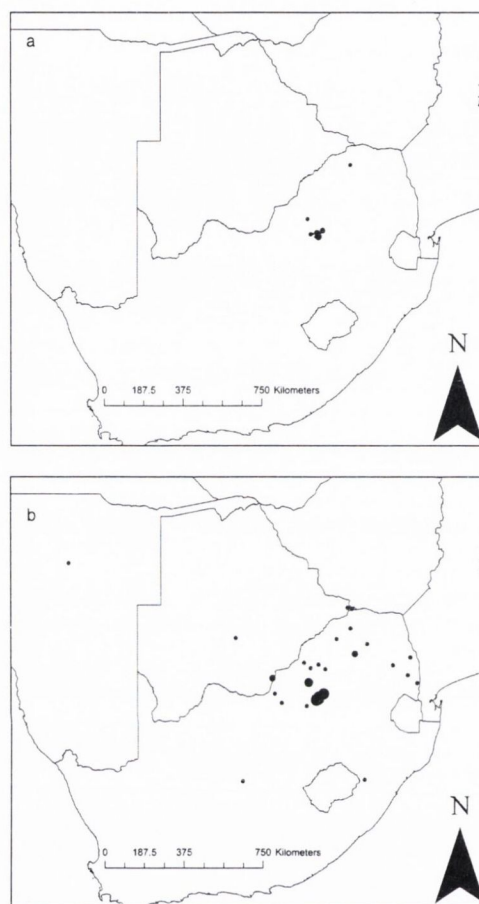


Figure 1 (a) The distribution localities where Cape vultures (*Gyps coprotheres*) were captured, tagged and released. The size of the circle is proportional to the numbers of birds released at each locality. (b) The distribution of localities where Cape vultures, tagged during this study, were resighted. The size of the circle is proportional to the numbers of birds resighted at each locality.

Data collection

Vultures were captured in a specially designed walk-in trap (Diekmann *et al.*, 2004; Bamford *et al.*, 2009b) that was built at the vulture restaurant at VulPro and the Rhino and Lion Park. Sick, injured or poisoned birds were either brought in to the center or collected by a staff member. Birds were captured and released, or rehabilitated birds released, between November 2005 and May 2012. A total of 163 rehabilitated birds were tagged and released. Rehabilitated birds were generally brought in singly and were released once fully recovered throughout the study period.

A total of 242 wild caught birds were captured, tagged and released. Wild birds were captured on 22 occasions where on average 9.0 birds (range, 1–32) were caught, tagged and released per capture session.

Captured birds were aged and had their wing length measured. Ageing was based on plumage characteristics (based on Piper, Mundy & Vernon, 1989; Mundy *et al.*, 1992) and birds were assigned to one of three age classes: juveniles (1st year birds), immatures (2nd–4th year birds), and adults (≥ 5 th year birds). Although sexing of Cape vultures is possible on external features (Naidoo *et al.*, 2011), not all the birds were assigned a sex in the field, and therefore, sex was dropped 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), which involves the use of a double set of standard cattle tags engraved with a unique number, which was fitted to the patagium 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 immediately after processing each individual, which took, on average, 6 min per bird.

Injured and sick birds brought in for rehabilitation were examined closely to allow the cause of the injury to be determined. However, in most cases, it was not possible to establish the actual cause, even though the injury was evident. The number of days that each bird spent in captivity was recorded for some, but not all birds.

A dedicated resightings program was established, specifically at known vulture restaurants with hides and/or camera traps which are frequently visited by Cape vultures in the Gauteng and North West Provinces of South Africa. Media, both written and verbal, were also used to get buy-in and support from the general public, landowners, vulture restaurant managers and bird clubs to encourage them to report their tagged resightings to VulPro. In addition, a vulture restaurant monitoring protocol was also developed to standardize monitoring at the various vulture restaurants. The majority of the resightings came from vulture restaurants, which may lead to biases. For example, rehabilitated and wild-caught birds (or birds of different ages) may use these restaurants in different proportions and therefore have different resighting rates. However, the fact that all tagged birds in this study were released at vulture restaurants should reduce this resighting bias. In support of this assertion, the proportion of rehabilitated and wild-caught birds that were resighted at vulture restaurants (as opposed to being resighted away from the restaurants) was similar. For rehabilitated birds, 187 resightings were at restaurants compared with 18 elsewhere ($n = 62$ tagged birds); for wild-caught birds, 711 resightings were at restaurants compared with 32 elsewhere ($n = 172$ tagged birds).

Data analysis

Model selection and estimation of demographic parameters

Survival and recapture were computed, using a combined 'live encounter-dead recovery' approach (Burnham, 1993; Lebreton *et al.*, 1995) in the program MARK (White & Burnham, 1999; White, 2008) using resightings (alive) and recoveries (dead) of Cape vultures. This model is appropriate since some tagged vultures were recovered dead. The model calculates '*S*' (the probability of surviving the interval), '*r*' (the probability of being found dead and reported), '*F*' (the probability of remaining in the sample), and '*P*' (the probability of recapture, conditional on being alive and in the sampling region). A goodness-of-fit test was used to test whether the general model (full-time dependence for all parameters) violated the underlying assumptions of MARK, using the median $\hat{c}$ procedure and the bootstrap method, both implemented in MARK. The goodness-of-fit test showed that (at least) one of the four basic assumptions of MARK had been violated, $\hat{c} = 1.371$, $SE = 0.0194$ ($P = 0.003$). These assumptions are: (1) every marked animal present in the population at time (*i*) has the same probability of recapture (*pi*); (2) every marked animal in the population immediately after time (*i*) has the same probability of surviving to time (*i* + 1); (3) marks are not lost or missed; (4) all samples are instantaneous, relative to the interval between occasion (*i*) and (*i* + 1), and each release is made immediately after the sample. The loss of tags from birds have been reported from other recent studies using similar patagial tags (Monadjem, Botha & Murn, 2012a; Monadjem *et al.*, 2012b), and this is thought to be the case in this study as well. Since there is no reason to suspect that the rate of tag loss would differ between rehabilitated and wild-caught birds, any errors in estimation of survival rates should equally affect both groups.

A variety of survival models that included rehabilitation, time dependence and age were developed. These models were developed on the basis of biological sensibility and were hypothesis driven as opposed to ones derived from a data dredge. 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.

Projection of population growth rate

We created an age-based deterministic population dynamics model to explore the effect that different proportions of rehabilitated birds would have on the population trend of the Cape vultures. All of our population dynamics models were created and analyzed in the statistical programming language R. Statistical analyses were carried out in R 2.13.1 (R Development Core Team, Vienna; <http://www.r-project.org>) using the popbio package (Stubben, Milligan &

Nantel, 2012). Specifically, the model used here is based on a Leslie Matrix. The top row represents the fecundity values and the other values show survival probabilities from fledgling, s_0 to adult, s_{4+} , together these values are the so called vital rates of the matrix (Borkhtaria *et al.*, 2008).

$$\begin{bmatrix} 0 & 0 & 0 & f_3 & f_{4+} \\ s_0 & 0 & 0 & 0 & 0 \\ 0 & s_1 & 0 & 0 & 0 \\ 0 & 0 & s_2 & 0 & 0 \\ 0 & 0 & 0 & s_3 & s_{4+} \end{bmatrix}$$

The matrix assumes a birth pulse, post-breeding census. This is suitable for birds because they typically have a set breeding season. We used the mean value of fecundity (0.69) based on 29 studies on Cape vultures contained in Piper (1994). Such a model only takes females into account, so fecundity values were halved accordingly. Further, given this is based on a post-breeding census, the survival probabilities of the birds at stage x are multiplied by the fecundity values of the stage $x + 1$ because they must survive the year in order to reproduce (see Beissinger *et al.*, 2006 for details). In our matrix, this is moving from stage 4 to stage 5 and above.

The completed matrix is multiplied by a vector, which contains the numbers of the birds for each stage present at time zero. This is iterated over a specified period of time, in this case, years, upon which the population growth rate can be determined. These values are the dominant eigenvalue and dominant eigenvector respectively. The growth rate is designated as lambda λ ; a value >1 signifies a population increase, a value <1 a decrease and when $\lambda = 1$, the population is stable.

We created models that assumed a best-case scenario whereby there were no rehabilitated adults in the population and a worst-case scenario whereby all the adults were rehabilitated. Then, we considered the intermediate case which had a 50:50 split of wild and rehabilitated adults. The new values for the survival rates were a function of this new proportion. For instance, a survival rate for adults in a 50:50 mix population would be $(0.7479 + 0.9130)/2 = 0.83045$. The fecundity values were updated concomitantly. We used the mean survival rate and the upper and lower confidence intervals in our models. The proportion that gave a lambda approximately equal to one could be considered the tipping point below which the population would decline. Our survival data for first year birds far exceeds the estimates of Piper, Boshoff & Scott (1999). Considering our sample size for this age class was relatively small, we decided to incorporate the survival rate from Piper *et al.* (1999) into this matrix. We feel that this is a better estimate of first year survival especially since the latter study reported an increase in first year survival rate when supplementary feeding sites became available to the vultures (Piper *et al.*, 1999), a situation similar to that of the Magaliesberg colony.

The initial population vector contained 400 individuals for the adult stage, the upper estimate from Wolter *et al.* (2007) and the models were iterated for 40 years, the life

expectancy of the closely related Eurasian griffon (Carey & Judge, 2000; note this is maximum life expectancy, data are unavailable for wild species but may be shorter).

Sensitivity and elasticity analyses

We then performed sensitivity and elasticity analyses to explore how changes in each vital rate value in our matrix (i.e. fecundity and survival rates) affected the population growth rate, λ . These analyses measure the absolute and relative impact, respectively (see Caswell, 2001).

Statistical analysis

An analysis of variance was used to test whether the length of time rehabilitated birds spent in captivity differed based on the injuries for which they were originally admitted into the rehabilitation center.

The location of resightings was plotted using ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, CA, USA). All mean values are quoted with $\pm$ SE.

Results

A total of 405 Cape vultures was fitted with patagial tags and released, of which 163 were rehabilitated birds. The causes of injuries were mostly unknown (Table 1). Of the 19 vultures with known causes of injury poisoning accounted for eight of them, followed by poaching (four birds), collision (two birds) and electrocution (two birds). The length of time spent in captivity was known for 92 of the rehabilitated birds and averaged 68 days, and did not differ statistically between birds with different injuries, that is, poisoning, poached, collision and electrocution ($F = 1.603$, $P = 0.194$, d.f. = 3, 8).

The age classes of these birds are shown in Table 2. Of these, 234 birds (58%) were resighted a total of 952 times between January 2006 and May 2012 (mean of 2.4 times per bird, range: 0–29). The locations of the capture sites and resightings are shown in Fig. 1. A summary of the dead recoveries and live recaptures is shown in Table 3.

Model selection and estimation of demographic parameters

The best model was represented by differential survival for rehabilitated and wild-caught birds and time dependence for

Table 1 The causes of injuries of the 163 rehabilitated Cape vultures (*Gyps coprotheres*) in this study

Cause of injury	# individuals
Poisoning	8
Poaching	4
Power line collision	2
Power line electrocution	2
Other	3
Unknown-grounded	38
Unknown-other	106

the parameters ‘*r*’, ‘*F*’ and ‘*P*’ (Table 4). The next two models had a $\Delta AIC_c \leq 0.2525$ and were hence indistinguishable from the best model. One was represented by differential survival and recapture rates based on condition (rehabilitated vs. wild-caught), whereas the other was represented by both differential survival for condition (rehabilitated vs. wild-caught) and age, with other parameters being time dependent (Table 4). The remaining models had $\Delta AIC_c \geq 2.0$ with declining AIC_c weights (Table 4), and were therefore discounted as best candidate models. Based on the best model, the survival estimates for rehabilitated

and wild-caught birds were 0.7479 ± 0.08189 and 0.9130 ± 0.06327 , respectively.

Projection of population growth rate

This matrix (below) contains vital rates of a wild population without any rehabilitated individuals,

0	0	0	0.314985	0.314985
0.689	0	0	0	0
0	0.913	0	0	0
0	0	0.913	0	0
0	0	0	0.913	0.913

The projected population changes of the five matrix models are summarized in Fig. 2. The population growth rate for a wild population (i.e. without any rehabilitated individuals) is greater than one. By contrast the growth rate for an entirely rehabilitated population (i.e. with only rehabilitated individuals) indicates a decline. In our model, $\lambda = 1$, that is,

Table 2 The number of juvenile, immature and adult Cape vultures (*Gyps coprotheres*) marked and released in this study, either as rehabilitated or wild-caught birds

Age class	Rehabilitated	Wild-caught	Total
Juvenile (1st year)	37	39	76
Immature (2nd–4th year)	66	114	180
Adult (≥ 5 th year)	60	89	149
Total	163	242	405

Table 3 Number of Cape vultures (*Gyps coprotheres*) tagged in South Africa and subsequently resighted (alive) or recovered (dead) (in parentheses), by year

Year of ringing	Number ringed	Number of resightings (recoveries)							
		2005	2006	2007	2008	2009	2010	2011	2012
2005	2	0 (0)	0 (1)	1 (0)	0 (0)	1 (0)	0 (0)	0 (0)	0 (0)
2006	36		5 (3)	5 (0)	5 (0)	5 (0)	2 (0)	0 (0)	0 (0)
2007	117			65 (2)	39 (1)	59 (0)	38 (0)	14 (0)	3 (0)
2008	17				5 (0)	9 (0)	8 (0)	3 (0)	4 (1)
2009	95					26 (0)	29 (0)	14 (1)	9 (0)
2010	50						5 (0)	11 (0)	5 (0)
2011	39							12 (0)	7 (2)
2012	49								21 (0)

Table 4 The candidate models used to estimate survival in rehabilitated and wild-caught Cape vultures (*Gyps coprotheres*) captured in South Africa

Model	AICc	Delta AICc	AICc weights	<i>n</i>
<i>S</i> (condition), <i>P</i> (<i>t</i>), <i>r</i> (<i>t</i>), <i>F</i> (<i>t</i>)	1187.1064	0	0.43742	22
<i>S</i> (condition), <i>P</i> (condition), <i>r</i> (<i>t</i>), <i>F</i> (<i>t</i>)	1187.2139	0.1075	0.28152	18
<i>S</i> (condition + age2), <i>P</i> (<i>t</i>), <i>r</i> (<i>t</i>), <i>F</i> (<i>t</i>)	1187.3589	0.2525	0.26171	24
<i>S</i> (age2), <i>P</i> (<i>t</i>), <i>r</i> (<i>t</i>), <i>F</i> (<i>t</i>)	1190.0874	2.9810	0.09853	22
<i>S</i> (condition + age3), <i>P</i> (<i>t</i>), <i>r</i> (<i>t</i>), <i>F</i> (<i>t</i>)	1191.2596	4.1532	0.05198	26
<i>S</i> (condition), <i>P</i> (.), <i>r</i> (<i>t</i>), <i>F</i> (<i>t</i>)	1191.9462	4.8398	0.0389	17
<i>S</i> (age3), <i>P</i> (<i>t</i>), <i>r</i> (<i>t</i>), <i>F</i> (<i>t</i>)	1192.2037	5.0973	0.0342	23
<i>S</i> (condition), <i>P</i> (condition), <i>r</i> (condition), <i>F</i> (<i>t</i>)	1197.0221	9.9157	0.00209	12
<i>S</i> (condition + <i>t</i>), <i>P</i> (<i>t</i>), <i>r</i> (<i>t</i>), <i>F</i> (<i>t</i>)	1199.6142	12.5078	0.00084	33
<i>S</i> (<i>t</i>), <i>P</i> (.), <i>r</i> (.), <i>F</i> (.)	1199.8801	12.7737	0.00050	11
<i>S</i> (condition), <i>P</i> (.), <i>r</i> (.), <i>F</i> (<i>t</i>)	1199.9394	12.8330	0.00049	11
<i>S</i> (condition), <i>P</i> (condition), <i>r</i> (condition), <i>F</i> (condition)	1245.8147	58.7083	0	6
<i>S</i> (condition), <i>P</i> (.), <i>r</i> (.), <i>F</i> (.)	1247.4331	60.3267	0	5
<i>S</i> (.), <i>P</i> (.), <i>r</i> (.), <i>F</i> (.)	1270.3358	83.2294	0	4

Estimates of survival (*S*), recovery rate (*r*), site fidelity (*F*) and recapture (*P*) were modeled with time (*t*), and age class (age) and whether rehabilitated or wild-caught (condition). ‘age2’ refers to two age classes (1st years vs. and all other age classes), and ‘age3’ refers to three age classes (1st years, 2nd–4th years, and ≥ 5 years). The number of parameters is indicated by ‘*n*’. The models are arranged from best (top of table) to worst (bottom).

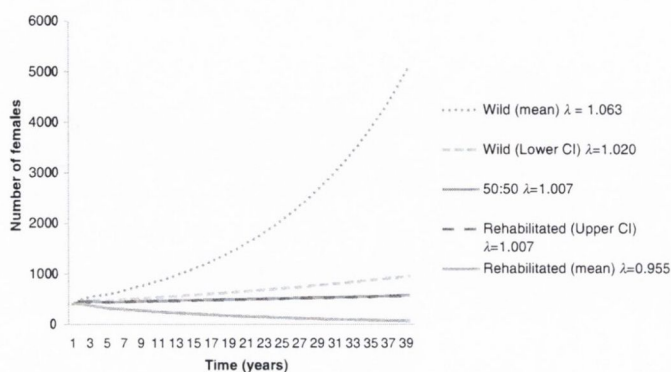


Figure 2 Graph showing predicted population trends over time for the various mixtures of wild and rehabilitated birds in a colony of Cape vultures (*Gyps coprotheres*). Only the upper CI for rehabilitated birds and the lower CI for wild birds are graphed for ease of viewing. The 50–50 proportion and the upper CI for rehabilitated birds exhibit a similar trend.

Table 5 Elasticity and sensitivity values for the various vital rates in the Leslie Matrices. $s_{0,s_{4+}}$ are the stage-specific survival rates, f_3, f_{4+} are the stage-specific fecundities

Vital rate		Elasticity	Sensitivity
s_0	Wild	0.099	0.153
	Rehab	0.131	0.182
	50:50	0.115	0.168
s_1	Wild	0.099	0.116
	Rehab	0.131	0.138
	50:50	0.115	0.128
s_2	Wild	0.099	0.116
	Rehab	0.131	0.138
	50:50	0.115	0.127
s_3	Wild	0.085	0.099
	Rehab	0.102	0.108
	50:50	0.094	0.105
s_{4+}	Wild	0.517	0.603
	Rehab	0.371	0.474
	50:50	0.445	0.540
f_3	Wild	0.014	0.047
	Rehab	0.029	0.087
	50:50	0.020	0.065
f_{4+}	Wild	0.085	0.288
	Rehab	0.103	0.381
	50:50	0.095	0.333

a stable growth rate, occurs when approximately 50% of the adults are rehabilitated.

Sensitivity and elasticity analyses

These analyses showed that for all models the survival rate of the adult stage was the most important component of the populations' life histories (see Table 5).

Discussion

Our study demonstrates that the survival rate of rehabilitated Cape vultures was lower than that of wild-caught birds. This is a significant finding because it shows that, despite treatment received, the survival rate of rehabilitated

birds does not recover to the level of non-injured, wild birds. The difference in survival rates between rehabilitated and wild-caught birds is large enough to have serious conservation implications. It should be noted, however, that artificial feeding sites (such as vulture restaurants) may act to counter this to some extent. For example, Oro *et al.* (2008) showed that artificial feeding sites buffered the effects of illegal poisoning on the survival of immature and juvenile Bearded vultures (*Gypaetus barbatus*).

The negative impact that rehabilitated birds have on long-term population trends is a significant finding of this study. In this case, the tipping point between a declining population and a growing one occurs when the proportion of rehabilitated birds is approximately 50%. This results in a vital rate of survival of between 80 and 85% (the mean survival values for wild and rehabilitated birds were 91.3 and 74.8%, respectively). By coupling this data with accurate surveys on the size of the population, it will become clearer if and when such a tipping point is likely to manifest. It can be seen in Fig. 2 that a population of rehabilitated adults would drive the population below 70 females in 40 years (the estimated maximum life expectancy recorded in captivity) and ultimately to extinction in 100 years. Of course, this is better than not rehabilitating the birds at all, which would simply remove any potential breeders from the population and accelerate the time to extinction. Of further importance is the realization that the survival rate of the adult stage has the greatest effect on the population growth rate as revealed by the sensitivity and elasticity analyses (Table 4; Sæther & Bakke, 2000; Oro *et al.*, 2008).

Our survival estimates for the Cape vulture can be compared with two previous studies. The first estimates used ring recoveries (e.g. Piper, Mundy & Ledger, 1981) and have subsequently been shown to be seriously flawed (Anderson, Burnham & White, 1985). The second study was based on the resightings of color-ringed birds in an isolated (Potberg) population in southern South Africa, and reported high survival rates in subadults (Piper *et al.*, 1999). The survival rate of wild-caught birds in our study was 91.3%, which compares well with the survival of second year birds from the Potberg at 88.8% Piper *et al.* (1999). However, the best

model in our study did not include age as a parameter, whereas the best model in Piper *et al.* (1999) was one which separated birds into four age classes: first year, second year, third year and fourth year or older birds. At Potberg, first year Cape vultures had lower survival rates than second and third year birds, whereas the estimates for older birds was biased by ring loss (Piper *et al.*, 1999), which has been reported in other recent southern African studies involving patagial tags on vultures (Monadjem *et al.*, 2012a) and storks (Monadjem *et al.*, 2012b).

In our study, the best model for estimating survival of Cape vultures did not vary with age class (although the third best model did so). This is surprising (but see Oro *et al.*, 2008) since, in the wild, naïve and inexperienced juvenile birds typically have lower survival rates than adults (Sæther, 1989), something that has been established for several species of vultures (Sarrazin *et al.*, 1994; Monadjem *et al.*, 2012a), including the Cape vulture (Piper *et al.*, 1999). However, it has been shown that food supplementation may significantly increase the survival of birds including juvenile Cape vultures (Piper *et al.*, 1999; Oro *et al.*, 2008; Chauvenet *et al.*, 2012). The birds studied here breed at one of three colonies in the Magaliesberg mountain range, all within 43 km of VulPro where most of the captures and resightings pertaining to our study were made (Wolter *et al.*, 2007). This is easily within daily foraging distances of Cape vultures (Bamford *et al.*, 2007). These birds have received supplementary food at various vulture restaurants in the region for the past decade or more. In fact, telemetry studies of Cape vultures have shown that the Magaliesberg birds have significantly smaller foraging ranges than elsewhere in their range (Naidoo *et al.*, submitted). Furthermore, in contrast to a previous study (Bamford *et al.*, 2007); juvenile and adult foraging ranges were not significantly different in the Magaliesberg (Naidoo *et al.*, submitted). This suggests that vulture food is abundant and easily available to the birds in this region, and which may explain the very high survival rates of juveniles estimated in our study (see Piper *et al.*, 1999 for a similar result).

We were unable to factor the impact of type of injury (poisoning, electrocution, etc.) into the survival models because the injury of most (more than 80%) of the birds that were brought in for rehabilitation were unknown. However, the type of injury is likely to have a significant influence on how quickly the bird recovers and whether it suffers long-term effects. Future research is urgently needed to determine the impact of injury type on survival of rehabilitated vultures. Although we can conjecture that poisoning is the factor most responsible as has been reported in many other instances for other vulture species (for a detailed review see Ogada *et al.*, 2012).

In conclusion, we have shown that rehabilitated Cape vultures have significantly lower survival rates than wild (non-rehabilitated) birds. We have also shown that once the mix between rehabilitated and non-rehabilitated birds in a colony reaches 50:50, the colony will go into decline. Managers can use this to predict at which stage a particular colony is likely to go into decline.

Acknowledgments

VulPro would like to thank the following for ongoing support toward this project, namely, Rand Merchant Bank, Computer Facilities, Lomas Wildlife Protection Trust, Natural Encounters Inc., Cheyenne Mountain Zoo, Bioweb, Mazda Wildlife Fund and the Tusk Trust. Also special thanks go to the organizations and individuals who have assisted us in donating carcasses, in particular to Hugo Meyers from Beluite Investments. The Birds of Prey Programme of the EWT supplied us with vulture tags, sponsored by Sasol Limited. Finally, thanks to numerous volunteers, staff and members of the public who provided important resightings of tagged vultures.

References

- Altwegg, R., Crawford, R.J.M., Underhill, L.G. & Williams, A.J. (2008). Long-term survival of de-oiled Cape gannets *Morus capensis* after the Castillo de Bellver oil spill of 1983. *Biol. Conserv.* **141**, 1924–1929.
- 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.
- Anderson, D.W., Gress, F. & Fry, D.M. (1996). Survival and dispersal of oiled brown pelicans after rehabilitation and release. *Mar. Pollut. Bull.* **32**, 711–718.
- Anderson, M.D. (2000). Cape vulture. In *The Eskom red data book of birds of South Africa, Lesotho and Swaziland*: 73–75. Barnes, K.N. (Ed.). Johannesburg: BirdLife South Africa.
- Bamford, A.J., Diekmann, M., Monadjem, A. & Mendelsohn, J. (2007). Ranging behaviour of Cape vultures *Gyps coprotheres* from an endangered population in Namibia. *Bird Conserv. Int.* **17**, 331–339.
- 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. Wildl. Res.* **39**, 202–208.
- Bamford, A.J., Monadjem, A. & Hardy, I. (2009a). The effect of vegetation density on carcass exploitation by vultures in an African savanna. *Ostrich* **80**, 135–137.
- Beissinger, S.R., Walters, J.R., Catanzaro, D.G., Smith, K.G., Dunning, J.B., Jr, Haig, S.M., Noon, B.R. & Stith, B.M. (2006). *Modeling approaches in avian conservation and the role of field biologists*. Ornithological Monographs.
- Benson, P. (2004). The status of the Kransberg and Manutsa Cape Vulture colonies *Gyps coprotheres* in (2003): causes of mortality, reasons for concern, research needs and recommendations. In *The vultures of Southern Africa – Quo Vadis? Proceedings of a workshop on vulture research and conservation in southern Africa*: 109–118. Monadjem, A., Anderson, M.D., Piper, S.E. & Boshoff, A.F. (Eds). Birds of Prey Working Group: Johannesburg.

- Borkhataria, R.R., Frederick, P.C., Hylton, R., Bryan, A.L., Jr & Rodgers, J.A. (2008). A preliminary model of Wood Stork population dynamics in the southeastern United States. *Waterbirds* **31**, 42–49.
- Boshoff, A.F., Piper, S.E. & Michael, M.D. (2009). On the distribution and breeding status of the Cape Vulture *Gyps coprotheres* in the Eastern Cape Province, South Africa. *Ostrich* **80**, 85–92.
- Botha, A. (2007). A review of colour-marking techniques used on vultures in southern Africa. *Vulture News* **56**, 52–63.
- Burnham, K.P. (1993). A theory for combined analysis of ring recovery and recapture data. In *Marked individuals in the study of bird population*: 199–213. Lebreton, J.-D. & North, P.M. (Eds). Basel: Birkhäuser-Verlag.
- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference. A practical information-theoretic approach*. 2nd edn. New York: Springer-Verlag.
- Butchart, S.H.M., Collar, N.J., Stattersfield, A.J. & Bennun, A. (2010). Conservation of the World's birds: the view from (2010). In *Handbook of the birds of the world. Vol. 15. Weavers to new world warblers*: 13–68. del Hoyo, J., Elliot, A. & Christie, D.A. (Eds). Barcelona: Lynx Edicions.
- Carey, J. & Judge, D. (2000). *Longevity records: life spans of mammals, birds, reptiles, amphibians and fish*. Odense Monographs on Population Aging. University Press of Southern Denmark.
- Caswell, H. (2001). *Matrix population models*. Sunderland: Sinauer Associates.
- Chauvenet, A.L.M., Ewen, J.G., Armstrong, D.P., Coulson, T., Blackburn, T.M., Adams, L., Walker, L.K. & Pettoerli, N. (2012). Does supplemental feeding affect the viability of translocated populations? The example of the hihi. *Anim. Conserv.* **15**, 337–350.
- 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. *Vulture News* **51**, 34–45.
- Fajardo, I., Babiloni, G. & Miranda, Y. (2000). Rehabilitated and wild barn owls (*Tyto alba*): dispersal, life expectancy and mortality in Spain. *Biol. Conserv.* **94**, 287–295.
- Finkelstein, M.E., Doak, D.F., George, D., Burnett, J., Brandt, J., Church, M., Grantham, J. & Smith, D.R. (2012). Lead poisoning and the deceptive recovery of the critically endangered California condor. *Proc. Natl. Acad. Sci. USA* **109**, 11449–11454.
- Goldsworthy, S.D., Giese, M., Gales, R.P., Brothers, N. & Hamill, J. (2000). Effects of the Iron Baron oil spill on little penguins (*Eudyptula minor*). II. Post-release survival of rehabilitated oiled birds. *Wildl. Res.* **27**, 573–582.
- Golightly, R.T., Newman, S.H., Craig, E.N., Carter, H.R. & Mazet, J.A.K. (2002). Survival and behavior of western gulls following exposure to oil and rehabilitation. *Wildl. Soc. Bull.* **30**, 539–546.
- 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.
- Hamilton, L.L., Zwank, P.J. & Olsen, G.H. (1988). Movements and survival of released, rehabilitated hawks. *J. Raptor Res.* **22**, 22–26.
- IUCN. (2012). IUCN Red List of Threatened Species. Version 2012.1. Available from: <http://www.iucnredlist.org>. Downloaded on 25 June 2012.
- Lebreton, J.-D., Morgan, B.J.T., Pradel, R. & Freeman, S.N. (1995). A simultaneous survival rate analysis of dead recovery and live recapture data. *Biometrics* **51**, 1418–1428.
- Monadjem, A., Botha, A. & Murn, C. (2012a). Survival of the African white-backed vulture *Gyps africanus* in north-eastern South Africa. *Afr. J. Ecol.* **51**, 87–93.
- Monadjem, A., Kane, A., Botha, A., Dalton, D. & Kotze, A. (2012b). Survival and population dynamics of the marabou stork in an isolated population, Swaziland. *PLoS ONE* **7**, e46434.
- Mundy, P.J., Butchart, D., Ledger, J.A. & Piper, S.E. (1992). *The vultures of Africa*. Randburg: Acorn books and Russel Friedman books.
- Naidoo, V., Wolter, K., Espie, I. & Kotze, A. (2011). Vulture rescue and rehabilitation in South Africa: an urban perspective. *J. S. Afr. Vet. Assoc.* **82**, 24–31.
- Nicoll, M.A.C., Jones, C.G. & Norris, K. (2004). Comparison of survival rates of captive-reared and wild-bred Mauritius kestrels (*Falco punctatus*) in a re-introduced population. *Biol. Conserv.* **118**, 539–548.
- Ogada, D.L., Keesing, F. & Virani, M.Z. (2012). Dropping dead: causes and consequences of vulture population declines worldwide. *Ann. N. Y. Acad. Sci.* **1249**, 57–71.
- Oro, D., Margalida, A., Carrete, M., Heredia, R. & Donazar, J.A. (2008). Testing the goodness of supplementary feeding to enhance population viability in an endangered vulture. *PLoS ONE* **3**, e4084.
- 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. (2008). The race to prevent the extinction of South Asian vultures. *Bird Conserv. Int.* **18**, S30–S48.
- Piper, S.E. (1994). *Mathematical demography of the Cape vulture*. Cape Town: University of Cape Town.
- Piper, S.E. (2005). Cape Vulture. In *Roberts birds of southern Africa*: 489–491. 7th edn. Hockey, P.A.R., Dean, W.R.J. & Ryan, P.G. (Eds). Cape Town: Trustees of the John Voelcker Bird Book Fund.

- Piper, S.E. (2007). *The Sasol guide to vulture restaurants in Southern Africa*. Johannesburg: Endangered Wildlife Trust.
- 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 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.
- Piper, S.E., Mundy, P.J. & Vernon, C.J. (1989). An ageing guide for the Cape Vulture. *Madoqua* **16**, 105–110.
- Robertson, A., Jarvis, A.M., Brown, C.J. & Simmons, R.E. (1998). Avian diversity and endemism in Namibia: patterns from the Southern African Bird Atlas Project. *Biodivers. Conserv.* **7**, 495–511.
- Sarrazin, F., Bagnolini, C., Pinna, J.L., Danchin, E. & Clobert, J. (1994). High survival estimates of griffon vultures (*Gyps fulvus fulvus*) in a reintroduced population. *Auk* **111**, 853–862.
- Sæther, B.-E. (1989). Survival rates in relation to body weight in European birds. *Ornis Scand.* **20**, 13–21.
- Sæther, B.-E. & Bakke, O. (2000). Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* **81**, 642–653.
- Sharp, B.E. (1996). Post-release survival of oiled, cleaned seabirds in North America. *Ibis* **138**, 222–228.
- Stubben, C., Milligan, B. & Nantel, P. (2012). Construction and analysis of matrix population models. <http://cran.r-project.org/web/packages/popbio/popbio.pdf>.
- Swarup, D., Patra, R.C., Prakash, V., Cuthbert, R., Das, D., Avari, R., Pain, D.J., Green, R.E., Sharma, A.K., Saini, M., Das, D. & Taggart, M. (2007). Safety of meloxicam to critically endangered *Gyps* vultures and other scavenging birds in India. *Anim. Conserv.* **10**, 192–198.
- Sweeney, S.J., Redig, P.T. & Tordoff, H.B. (1997). Morbidity, survival and productivity of rehabilitated peregrine falcons in the upper Midwestern U.S. *J. Raptor Res.* **31**, 347–352.
- Tarboton, W.R. & Allan, D. (1984). *The status and conservation of birds of prey in the Transvaal*. Pretoria: Transvaal Museum.
- Thiollay, J.M. (2007). Raptor population decline in West Africa. *Ostrich* **78**, 405–413.
- Underhill, L.G., Bartlett, P.A., Baumann, L., Crawford, R.J.M., Dyer, B.M., Gildenhuys, A., Nel, D.C., Oatley, T.B., Thornton, M., Upfold, L., Williams, A.J., Whittington, P.A. & Wolfaardt, A.C. (1999). Mortality and survival of African Penguins *Spheniscus demersus* involved in the Apollo Sea oil spill: an evaluation of rehabilitation efforts. *Ibis* **141**, 29–37.
- 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.
- 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**, 120–139.
- Whittington, P.A. (1999). The contribution made by cleaning oiled African penguins *Spheniscus demersus* to population dynamics and conservation of the species. *Mar. Ornithol.* **27**, 177–180.
- Wolter, K., Whittington-Jones, C. & West, S. (2007). Status of cape vultures (*Gyps coprotheres*) in the Magaliesberg, South Africa. *Vulture News* **57**, 24–31.

The Ecology of Obligate Scavengers from Individual Behaviour to Population Dynamics

Adam Kane

Studies on vultures are on the rise, and just as well given the sharp declines in many of the 23 species. Indeed it seems these population crashes are responsible for this research boost. However, there remain obvious gaps in our knowledge when it comes to the world's only terrestrial example of vertebrate obligate scavengers. It has been suggested that a human aversion to carrion is one of the reasons scavengers are reviled by the public and understudied by science. Broadly, the following body of work is an attempt to fill in some of these gaps. To achieve this I use a variety of methods and look at a range of species. I start by giving a description of the impressive ranging abilities of one species, the Cape Vulture, in Southern Africa, and identify causes of variation in these home ranges. I then move to Kenya where I identify a producer-scrounger game occurring between the *Gyps* vultures and scavenging eagles of the area. I use a suite of empirical data and modelling approaches to show vultures use eagles in identifying the location of carcasses. The results of which underscore the importance of ecosystem-level management. Then in chapter 3, I collect data on the food required by the avian scavenging guild of Swaziland and use a novel method, namely population dynamics P systems, to ascertain if the wild fauna of the country can meet this need. Although sufficient for the time being carrion will soon become limiting and I advocate the creation of supplementary feeding sites in the country to counter this. Finally, I visit the Cretaceous Period where I use my understanding of modern day carrion ecology to explore a putative scavenger in *Tyrannosaurus rex*, the infamous carnivorous dinosaur. A proposed hypothesis that *T.rex* took on more carrion in its diet across ontogeny is shown to be false owing to the huge cost of movement as the animal grew