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Item Type	Article
Authors	Donohue, J.G.
Citation	Journal of Animal Ecology
Publisher	John Wiley & Sons Ltd
Download date	2026-03-06 08:15:53
Item License	https://creativecommons.org/licenses/by-nc-sa/4.0/
Link to Item	https://doi.org/10.34961/researchrepository-ul.27108769

RESEARCH ARTICLE

Predicted short-term mesoscavenger release gives way to apex-scavenger dominance

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Funding information

Science Foundation Ireland, Grant/Award Number: SFI/13/IA/1923

Handling Editor: Pol Capdevila

Abstract

1. Vultures play a crucial role in scavenging communities as apex scavengers. Scavenging communities in turn are a key component of terrestrial ecosystems, ensuring that dead biomass is removed quickly and efficiently. Anthropogenic disturbances, particularly mass poisonings, have caused crashes in vulture populations in Africa and Asia.
2. We ask if vultures can re-establish themselves in a scavenging community from a point of near extirpation. To allow for maximum knowledge transfer across ecosystems, we focus on an ecosystem that is otherwise considered pristine.
3. We chose Kruger National Park (KNP), a well-documented African scavenging community, as our focal ecosystem and parameterised a mathematical model of scavenging-community dynamics using field data from the park. We predicted the upper limit of vulture population size in an ecosystem like KNP. We then analysed vultures' path to recovery, using this empirically parameterised scavenging-community model. We used perturbation methods to determine how parameter values that may be specific to KNP influence our predictions.
4. Comparisons of predicted vulture carrying capacity with recent population estimates suggest that the cumulative effect of human activities on vulture abundance is larger than previously believed. Our analysis shows that vulture populations can reach their carrying capacity approximately five decades after a poisoning event that would almost extirpate the population. Over shorter time scales, we predict a decade of enhanced mammal abundance (i.e. mesoscavenger release) before the mammals are excluded from the scavenging community. In our study system, jackals and hyenas are the mammalian groups predicted to benefit from the absence of vultures. However, neither group removes biomass as efficiently as vultures and animal carcasses are predicted to accumulate in the ecosystem while the vulture population recovers.
5. In our framework, the carrying capacity for vulture populations is determined by carcass availability. As evidence for an alternative regulating factor is lacking, we conclude that present-day vulture population densities are orders of magnitude below their upper limits. Our results therefore suggest that with a recovery plan

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in place, the long-term prospects for vulture species and the associated ecosystems are positive.

KEYWORDS

competition, conservation, dynamical model, scavengers, transient, vultures

1 | INTRODUCTION

Today, due to anthropogenic pressures on wildlife, scavenging communities in a variety of locations have been pushed far from their equilibrium. Poisoning, habitat destruction and poaching are some of the key drivers of these disruptions (Ogada et al., 2016). Recent empirical and theoretical research (O'Bryan et al., 2019) has suggested that the generic response to such changes is *mesoscavenger release*, whereby less efficient scavengers increase in numbers due to reduced competition for carcasses. This was seen in India in the wake of diclofenac whereby feral dogs replaced functionally extinct vultures (Prakash et al., 2003) and in Spain where red fox populations flourish in regions lacking vultures (Morales-Reyes et al., 2017). That, among the scavenging community, vultures have suffered particularly devastating losses, speaks to their ecological specialisation.

Indeed, among terrestrial scavenging communities, vultures are the apex scavengers (Jones et al., 2015). Mammalian scavengers are unable to match vultures' carcass-detection abilities, something that is generally attributed to flight (in particular, soaring flight) which allows the birds to sweep far larger areas at low energetic cost (Ruxton & Houston, 2004). Vultures alone are obligate scavengers (Ruxton & Houston, 2004), though carrion comprises a significant proportion of mammalian carnivore diets in certain environments (Jones et al., 2015). For instance, hyenas have adaptations to cover large expanses with their characteristic 'rocking-horse' gait which supports a scavenging lifestyle (Jones et al., 2015).

The expansion of mesoscavenger populations in response to apex scavenger declines may have indirect implications for the larger food web (Moleón et al., 2014). For example, mammalian scavengers act as predators and therefore connect predatory and scavenging communities. As their numbers rise, they could exact more top-down control on herbivores through predation (Moleón et al., 2014). Moreover, reduced efficiency in carcass removal can slow rates of decay and accelerate the spread of diseases (Cunningham et al., 2018; Ogada et al., 2012).

International plans have recently been implemented to protect vultures from humans' activities (e.g. Botha et al., 2017). One may therefore expect vulture populations to eventually recover, reducing the influence of their mammalian competitors. However, because vultures are long-lived species, it seems likely that the communities will remain out of equilibrium for years or even decades (Prakash et al., 2019). Although a theoretical framework for the mechanism of mesoscavenger release has been proposed (O'Bryan et al., 2019), the transient dynamics of these ecosystems have yet to be examined, to the best of our knowledge. It therefore remains unclear how recent

disturbances and their knock-on effects will be resolved and how long the recovery process will take.

In this study, we aim to provide an empirically-grounded description of the quantitative changes in carcass-removal rates and scavenging community structure in the years and decades following a reduction in vulture numbers. To do so, we use data from Kruger National Park (KNP) to parameterise a mathematical model of mesoscavenger release. KNP represents a relatively pristine habitat, containing a wide range of carnivores and herbivorous megafauna. It therefore functions as a useful exemplar system for 'typical' responses to vulture declines in natural systems, and a counter-point to case studies in altered agricultural (DeVault et al., 2011) and urban (Butler & Du Toit, 2002; Markandya et al., 2008) ecosystems. Having parameterised the mesoscavenger-release model, we comprehensively analyse both its equilibrium and transient dynamics. In particular, we use a combination of numerical (i.e. sensitivity analysis) (Augusiak et al., 2014) and analytical techniques (i.e. perturbation methods) (Fowler, 1997; Hinch, 1991) to understand the mechanisms driving the observed community dynamics.

2 | KRUGER NATIONAL PARK SCAVENGING-COMMUNITY MODEL

2.1 | KNP scavengers

Ethical approval was not needed in this study. We begin by compiling a list of the dominant members of the KNP vertebrate scavenging community. Apex scavengers have been defined as 'functionally dominant at scavenging' (O'Bryan et al., 2019). We choose African white-backed vultures (*Gyps africanus*) as the operational apex scavenger. This choice was informed by comparison to mammalian and other avian scavengers. The search capacity of soaring vultures results in a carrion encounter rate that far exceeds mammals and sets the birds apart as obligate scavengers (Ruxton & Houston, 2004). White-backed vultures outnumber other vulture species by an order of magnitude in KNP (Murn et al., 2013). This numerical dominance confers a competitive advantage at carcasses even over larger vultures (Kendall, 2013). Finally, their larger population size must translate to a higher rate of carrion consumption in comparison to the other vulture species.

To determine the most important mesoscavengers, we compare a list of African carnivores that have been observed scavenging (Jones et al., 2015) with KNP's official biodiversity statistics. We diverge slightly from O'Bryan et al. (2019) (who define mesoscavengers as

mid-sized scavengers that are less efficient than apex scavengers) in that we do not impose any upper limit on the mesoscavenger body size. Potential mesoscavengers (relative to vultures) that are present in significant numbers in KNP then are black-backed jackals (*Canis mesomelas*), side-striped jackals (*Canis adustus*), spotted hyenas (*Crocuta crocuta*) and lions (*Panthera leo*). We combine the two jackal species on the basis that they have a similar ecology (i.e. body size and diet as outlined by Loveridge and Macdonald (2003)). We assume that the density of invertebrate scavengers is unaffected by carrion availability, due to a lack of detailed information on their behaviour (Shahid et al., 2003). The model therefore consists of five ordinary differential equations that describe the temporal variation of vultures, jackals, hyenas, lions and carrion. In Table 1, we present estimates of the density of the four scavenger groups in Kruger National Park, with 'jackal density' the sum of estimated densities of black-backed and side-striped jackals.

2.2 | Modelling assumptions

O'Bryan et al. (2019) proposed a model of scavenger community dynamics containing an obligate scavenger species, a mesoscavenger species and carrion. In order to accurately assess the status of white-backed vultures in Kruger National Park, we include three distinct mesoscavenger groups (i.e. jackals, hyenas and lions). To use the O'Bryan model to predict the scavenging community dynamics of an ecosystem like KNP without making any further modifications, the following three conditions must be satisfied:

1. Interactions between the four modelled groups are limited to exploitative competition for carcasses. This means that we do not consider antagonistic encounters (e.g. intra-guild predation or interference competition) or indirect but beneficial interactions such as pre-processing of thick-skinned carcasses (Houston, 1974). Consequently, functional responses for each modelled group are classified as 'resource-dependent' (Stouffer & Novak, 2021).

2. We assume that all four groups in our model are food-limited. The assumption that the three mammal groups are regulated by food availability may produce pessimistic predictions for white-backed vultures' food supply (and optimistic predictions for carcass removal rates). Specifically, this assumption allows mammals to produce a

numerical response to carrion availability. In its absence, consumption rates of carrion by mammals would be constrained.

We note that Ferreira and Funston (2016) predict that density of spotted hyenas in KNP is regulated by the availability of prey biomass. However, for lions and jackals, regulation of population density may be slightly more complicated. In the Serengeti, equilibrium lion population density appears to increase abruptly in response to sufficiently large increases in food availability (Packer et al., 2005). As a smaller predator, the jackal group may be subject to top-down control by lions and/or hyenas (Jones et al., 2015). For vultures, we note that a proposed alternative to food limitation is nest-site limitation (Murn & Botha, 2018). However, the latter has generally been observed for cliff-nesting raptors rather than tree-nesting species such as white-backed vultures (Murn & Botha, 2018) and, in any case, Kendall et al. (2018) found that the number of available nesting trees in a similar ecosystem was orders of magnitude greater than the number of breeding pairs.

3. We assume that the effect (on the mammal groups) of these mammals' consumption of prey can be considered independently of scavenging interactions and can be captured phenomenologically by prescribing a nominal carrying capacity for each mammal group. Mammal densities in excess of the nominal carrying-capacity value can only be sustained by scavenging with the group's predation rate assumed to be constant at these densities. This choice is made here, as is commonly the case (e.g. Courchamp et al., 1999; O'Bryan et al., 2019), for convenience as it circumvents the need to identify a large number of interactions in the larger food web and quantify the corresponding prey population dynamics.

2.3 | Mathematical model

We measure carrion density C in kg/km^2 and the densities of vultures V , jackals J , hyenas H and lions L in adult individuals/ km^2 . The differential equation for carrion contains a positive flux generated by animal deaths and five loss rates, corresponding to removal by invertebrates and by four vertebrate scavenging groups, i.e.

$$\frac{dC}{dt} = C_{\text{in}} - \mu_c C - V \frac{e_V C}{1 + h_V e_V C} - J \frac{e_J C}{1 + h_J e_J C} - H \frac{e_H C}{1 + h_H e_H C} - L \frac{e_L C}{1 + h_L e_L C} \quad (1)$$

TABLE 1 Observed/estimated values of scavenger groups in Kruger National Park.

Group	Density (adults/ km^2)	Number (adults)	Source
White-backed vultures	0.09	1808	Murn et al. (2013)
Jackals	0.35	6820	Rowe-Rowe (1982); Kingdon (2014)
Spotted hyenas	0.19	3667	Ferreira and Funston (2016)
Lions	0.05	940	Funston et al. (2003); Ferreira and Funston (2010)

Note: For vultures, hyenas and lions, the 'Number' value is taken from Kruger National Park field counts and used to produce a 'Density' value. However, for jackals, the density value is taken from a habitat similar to KNP and used to produce a numerical count. Note that this 'Jackals' group is a combination of two species, side-striped and black-backed. More details are provided in Section S1.1 of the Supplement.

where C_{in} is the carrion supply rate, and μ_C is the rate at which carrion is lost to invertebrate scavengers. Consistent with Assumption 1 above, the functional responses of vertebrate scavengers are prescribed to be Holling Type II, a commonly used resource-dependent functional response (Skalski & Gilliam, 2001). This means that the rate of carrion consumption by the four scavengers is governed by discovery rates e_j , e_H , e_L and e_V and handling times h_j , h_H , h_L and h_V .

The equations for mesoscavenger population dynamics are characterised by a sum of a net-growth rate sustained by predation and a nonnegative growth rate sustained by scavenging (due to Assumptions 2 and 3 above), that is,

$$\begin{aligned}\frac{dJ}{dt} &= r_J J \left(1 - \frac{J}{K_J}\right) + y_J J \frac{e_J C}{1 + h_J e_J C}, \\ \frac{dH}{dt} &= r_H H \left(1 - \frac{H}{K_H}\right) + y_H H \frac{e_H C}{1 + h_H e_H C}, \\ \frac{dL}{dt} &= r_L L \left(1 - \frac{L}{K_L}\right) + y_L L \frac{e_L C}{1 + h_L e_L C}.\end{aligned}\quad (2)$$

In the absence of carrion, the dynamics of the three relevant mammalian carnivores (henceforth 'mesoscavengers') are modelled using logistic equations (due to Assumption 3 above). The growth-rate parameters of jackals, hyenas and lions are denoted r_j , r_H and r_L , respectively, and nominal carrying capacities given by K_j , K_H and K_L . Carrion consumption rates are converted into a production rate of new adult individuals using efficiency parameters. The conversion efficiency of jackals, hyenas and lions are denoted y_j , y_H and y_L , respectively.

Finally, the equation for vultures has just two terms on its right-hand side, a mortality rate and a nonnegative growth rate. Food limitation is imposed (as outlined in Assumption 2 above) by setting this growth rate to be proportional to carrion consumption yielding

$$\frac{dV}{dt} = -\mu_V V + y_V V \frac{e_V C}{1 + h_V e_V C}.\quad (3)$$

The conversion efficiency of vultures is denoted y_V . We let the constant mortality rate parameter μ_V measure losses occurring due to senescence (i.e. old age) rather than starvation on the assumption that carcasses are generally abundant in KNP and similar ecosystems.

While carrion density is described by a single variable in this model, resource partitioning may play an important role in structuring scavenging communities like that of KNP. In particular, it has been suggested that the foraging of mammalian scavengers at night (when vultures are inactive) gives the mammals preferential access to a proportion of the overall carrion supply (Cozzi et al., 2012). A first-approximation model of this temporal segregation of carrion is described in Section S5 of the Supplement and its behaviour is summarised in Section 3.1.

2.4 | Model parameterisation

In Sections S1.2–S1.6 of the Supplement, we use existing data on KNP and the life history of the four scavenger groups to produce estimates for the 21 system parameters. Their values are given in

Table 2. In this section, we briefly summarise the methodology behind this model parameterisation.

The mortality rate of vultures (μ_V) and the decay rate of ungulate carcasses (μ_C) are taken directly from field studies by Murn and Botha (2018) and Coe (1978), respectively. We produce a novel estimate of the carcass supply rate C_{in} in a spreadsheet in the supplemental material (with a description of its contents given in Section S1.2 of the Supplement). This estimate is built on the assumption that all carcasses are accessible to both vertebrate and invertebrate scavengers, however, and is therefore likely to be a slight overestimate (see Section 2.5). Carrion discovery rates (e_V , e_j , e_H and e_L) are derived using observed foraging velocities and maximum search paths. As detailed in Section S1.6 of the Supplement, the mesoscavenger growth-rate parameters (r_j , r_H and r_L) can be interpreted as the net-growth rate of these populations when negative density dependence is at its weakest (Fagan et al., 2010). Using this idea, we combine the conversion efficiency, handling time and senescence rate of each group to produce an estimate of the population's r parameter. In Sections 2.4.1–2.4.3, we provide further details on the parameterisation of mesoscavenger carrying capacities, carcass handling times and conversion efficiencies, respectively.

2.4.1 | Mesoscavenger carrying capacities

It is important to note that the nominal carrying capacities of the three mesoscavenger populations are taken from the most recent estimates of their population densities in KNP. This is equivalent to assuming that the KNP populations currently rely entirely on prey, rather than carrion. Estimates of the percentage of carnivore diets that are obtained from scavenging are subject to significant uncertainty, however. Jones et al. (2015) report percentages ranging from 0 to 20 for the two jackal species, 5 to 99 for spotted hyenas and 5 to 50 for lions, depending on the location and timing of the study. We therefore opt to use the values in Table 1 as estimates of K_j , K_H and K_L with the understanding that these numbers may overestimate the densities sustainable by predation alone (see Section 2.5).

2.4.2 | Carcass handling times

Our model framework represents scavenger abundance in terms of the number of reproductive adults. However, the overall feeding rate of a given scavenger group depends on the total number of individuals, not just the number of adults. Thus, while the carcass discovery rate for a particular group is assumed to be proportional to the number of adults, the handling time must nevertheless be adjusted to account for the presence of dependent conspecifics, be they newborns, juveniles or sub-adults. In particular, we decrease each adult's digestive pause, a key component of handling time, to allow for food apportioned to their dependents. In Section S1.5 of the supplemental material, we use this approach and life-history data for the four scavenger groups to estimate h_V , h_j , h_H and h_L .

TABLE 2 Parameter values used in solving scavenging community model.

Parameter	Value	Unit	Description	Source
C_{in}	2.26	kg/km ² /day	Carcass supply rate	- Computed ^a
μ_C	0.07	Per day	Carcass decay rate	Coe (1978)
e_V	157.50	km ² /day	Vultures' carcass discovery rate	Cortés-Avizanda et al. (2014); Spiegel et al. (2013)
e_J	4.00	km ² /day	Jackals' carcass discovery rate	Lamprecht (1978); Ferguson et al. (1988)
e_H	27.28	km ² /day	Hyenas' carcass discovery rate	Mills (1989); Kolowski et al. (2007)
e_L	4.00	km ² /day	Lions' carcass discovery rate	Fryxell et al. (2007)
h_V	0.85	Days/kg	Vultures' carcass handling time	- Computed ^b
h_J	0.32	Days/kg	Jackals' carcass handling time	- Computed ^b
h_H	0.21	Days/kg	Hyenas' carcass handling time	- Computed ^b
h_L	0.08	Days/kg	Lions' carcass handling time	- Computed ^b
γ_V	9.35×10^{-4}	Adults/kg	Vultures' conversion efficiency	- Computed ^c
γ_J	2.33×10^{-3}	Adults/kg	Jackals' conversion efficiency	- Computed ^c
γ_H	8.40×10^{-5}	Adults/kg	Hyenas' conversion efficiency	- Computed ^c
γ_L	1.08×10^{-4}	Adults/kg	Lions' conversion efficiency	- Computed ^c
K_J	0.35	Adults/km ²	Jackal carrying capacity	Table 1 ^d
K_H	0.19	Adults/km ²	Hyena carrying capacity	Table 1 ^d
K_L	0.05	Adults/km ²	Lion carrying capacity	Table 1 ^d
μ_V	2.11×10^{-4}	Per day	Vulture mortality rate	Murn and Botha (2018)
r_J	6.37×10^{-3}	Per day	Jackal population growth rate	- Computed ^e
r_H	2.23×10^{-4}	Per day	Hyena population growth rate	- Computed ^e
r_L	1.10×10^{-3}	Per day	Lion population growth rate	- Computed ^e

^aCalculation given in Supplementary spreadsheet file.

^bFormula in Section S1.5 of the supplement adjusts adult handling time to allow for non-reproductive life stages.

^cFormula in Section S1.4 of the Supplement links food intake of a breeding pair with recruitment success.

^dWith assumption that present-day KNP populations do not exploit significant quantities of carrion.

^eFormula in Section S1.6 of the Supplement subtracts senescence rate from the (estimated) maximal recruitment rate.

2.4.3 | Conversion efficiencies

While functional responses and their associated parameters are readily discerned from foraging studies, the quantification of conversion efficiencies (γ_V , γ_J , γ_H and γ_L) is less straightforward. There appears to be little empirical data on the rates at which resource mass is converted into consumer mass (Dell et al., 2014). Our measurement of consumer abundance in numbers of adult individuals adds another layer of complication, as it requires knowledge of how food intake is apportioned to the processes of maintenance, growth and reproduction. Therefore, we opt to use documented life-history information for all modelled groups (e.g. yearly breeding output, longevity, mortality rates and causes) and allometric-scaling arguments to compute estimates of conversion efficiencies. On a per-kilogram basis, we predict that jackals are the most efficient at converting meat into new adults, followed by vultures, lions and hyenas, in that order (see Table 2).

Carbone and Gittleman (2002) compared observed carnivore densities with the biomass of their prey and found that 1 kg of the appropriate prey was associated with higher numbers of small mammals (e.g. red fox, coyote) than lions. In turn, 1 kg of prey was associated with higher numbers of lions than hyenas, despite the

lower body mass of hyenas. The qualitative match between our theoretical predictions (rate of conversion of resource mass into adult individuals: jackals > lions > hyenas) and the pattern found by Carbone and Gittleman (2002) gives us confidence in our ability to accurately capture the numerical-response parameters of these carnivores.

2.5 | Model solution and sensitivity analysis

Using the parameter estimates given in Table 2, we numerically detect all ecologically feasible equilibrium points of Equations (1)–(3). We next solve Equations (1)–(3) numerically to understand transient behaviour of the model. We then perform a numerical sensitivity analysis to assess if the model output is robust to our choice of parameter values. In particular, we note that there are determinants of carrion availability that are not included in our supply-rate calculation but would affect it in reality (Barton et al., 2019). For example, significant spatial variability in ungulate mortality events (e.g. if the animal dies in an inaccessible location) would mean that our estimate of the carcass supply rate is inflated, artificially increasing the growth potential of all modelled scavengers. Similarly, we

do not have dietary information associated with our field estimates of mesoscavenger population densities which means that we may have overestimated the carrying capacities of these groups (see Section 2.4.1).

Direct computation of stable equilibrium points of Equations (1)–(3) is achieved using Maple®. In particular, equilibrium points are located, the system's Jacobian matrix is evaluated at each point and the eigenvalues of the matrix computed. Numerical solutions of the model (and the accompanying sensitivity analyses) are obtained using the in-built MATLAB® solver ode45. In both cases, the associated code is archived at Donohue et al. (2024). Equivalent Maple® and MATLAB® codes for the temporal segregation model (see Section 2.3) are also archived at Donohue et al. (2024).

3 | RESULTS

3.1 | Long-term behaviour

A linear-stability analysis of all ecologically feasible equilibria is presented in Section S2 of Appendix S1. We find just one locally stable equilibrium state, which is given by

$$V = 9.9725, \quad J = 0.3509, \quad H = 0.1934, \quad L = 0.0500, \quad C = 0.0017. \quad (4)$$

This represents the unique configuration towards which the scavenging community is predicted to evolve after a sufficiently long time interval has elapsed. We note that the three mesoscavenger densities are effectively fixed at the prescribed carrying capacity values, indicating that they receive little to no benefit from the auxiliary food source. The standing stock of carrion is so low (1 kg/588 km²) as to be undetectable. This is due to remarkably efficient removal by a dominant vulture population. However, it is important to note that our equilibrium estimate of 9.97 vultures/km² is 110 times larger than the recent estimate for the population, 0.09 adults/km² (see Table 1). While this appears to be a much larger figure than has been reported in any previous KNP census of *Gyps africanus*, it is comparable with the observed density of another Old World vulture, *Aegypius monachus* (Stephens et al., 2019) and well below observed *Necrosyrtes monachus* densities of >100/km² (Henriques et al., 2018). In addition to these population comparisons, we note, as discussed above, that white-backed vulture populations are believed to be food-limited. As mentioned in Section 2.3, temporal segregation of carrion may reduce the effective food supply to the vulture population (as well as allowing equilibrium mesoscavenger densities to exceed the prescribed carrying capacity values). However, we observe in Section S5 of the Supplement that such a resource partition, acting in isolation, would require approximately 90% of added carrion to be reserved for mesoscavengers in order to reduce vulture carrying capacity by a factor of 10. Therefore, we proceed on the assumption that the KNP vulture population has significant potential

for expansion and its growth has been suppressed by mortality rates (e.g. due to repeated poisonings) well exceeding that of the natural senescence rate. The scavenging community, as a whole, is therefore far from equilibrium and steady-state solutions are of limited use in predicting behaviour.

3.2 | Transient behaviour

In order to predict the future behaviour of the KNP scavenging community, we take the density values reported in Table 1 as initial conditions for our model (which is given by Equations (1)–(3)). As data are lacking, it is not immediately obvious what initial value to assign for initial carrion mass. We assign $C = 0.0017$, which is the equilibrium value of carrion in a situation where the modelled vultures are at their maximum value (see Equation (4)). This is intended to represent the community configuration moments after a major vulture-poisoning event (i.e. before enough time has elapsed for the loss of vultures to have had an effect on the larger ecosystem). We then solve our model numerically over a time interval of 50 years, assuming that there are no further disturbances. We observe that vultures steadily increase towards their stable equilibrium value (Figure 1a). Jackal and hyena populations experience significant growth for approximately 1 and 10 years, respectively, whereas lions do not gain any significant boost (Figure 1b). Jackals numerically respond to the reduced competition for carrion quicker than the other mesoscavenger groups. This peak in abundance is sharp due to intensified competition with hyenas (which have slower reproductive rates).

A logarithmic transformation highlights that carrion decreases over the course of the 50 years, after an initial spike in availability due to the absence of vultures (Figure 1c). We plot the carrion removal rates attributed to each group as functions of time in Figure 1d. We note that very little carrion is lost to invertebrate scavengers which, by design, are fixed at their initial densities. Similarly, the lion population is unable to outcompete its vertebrate competitors at any point over the 50 years. The population with the highest carrion-removal rate switches from jackals to hyenas and then finally to vultures as equilibrium is approached. The early advantage (i.e. over the first 2 years) of jackals arises due to their high initial density and fast numerical response. For the following 5 years, hyenas become the most successful scavenger in terms of kilograms removed per day. This can be explained by their high carcass-discovery rates. The jackal population no longer has sufficient food to support its increased density and quickly (i.e. over approximately 7 years) returns to its original (prey-only) carrying capacity.

For the first 5 years, the daily rate of carrion removal by the depleted vulture population is less than a third of that of the (combined) mesoscavenger populations. After this point, the vulture population has expanded sufficiently to begin monopolising carcasses again. The hyena population no longer finds enough meat to maintain its higher density and, like the jackal population before it, returns to its original density. Due to differing mortality rates of hyenas and jackals, the reduction occurs relatively slowly in this case. Hyenas

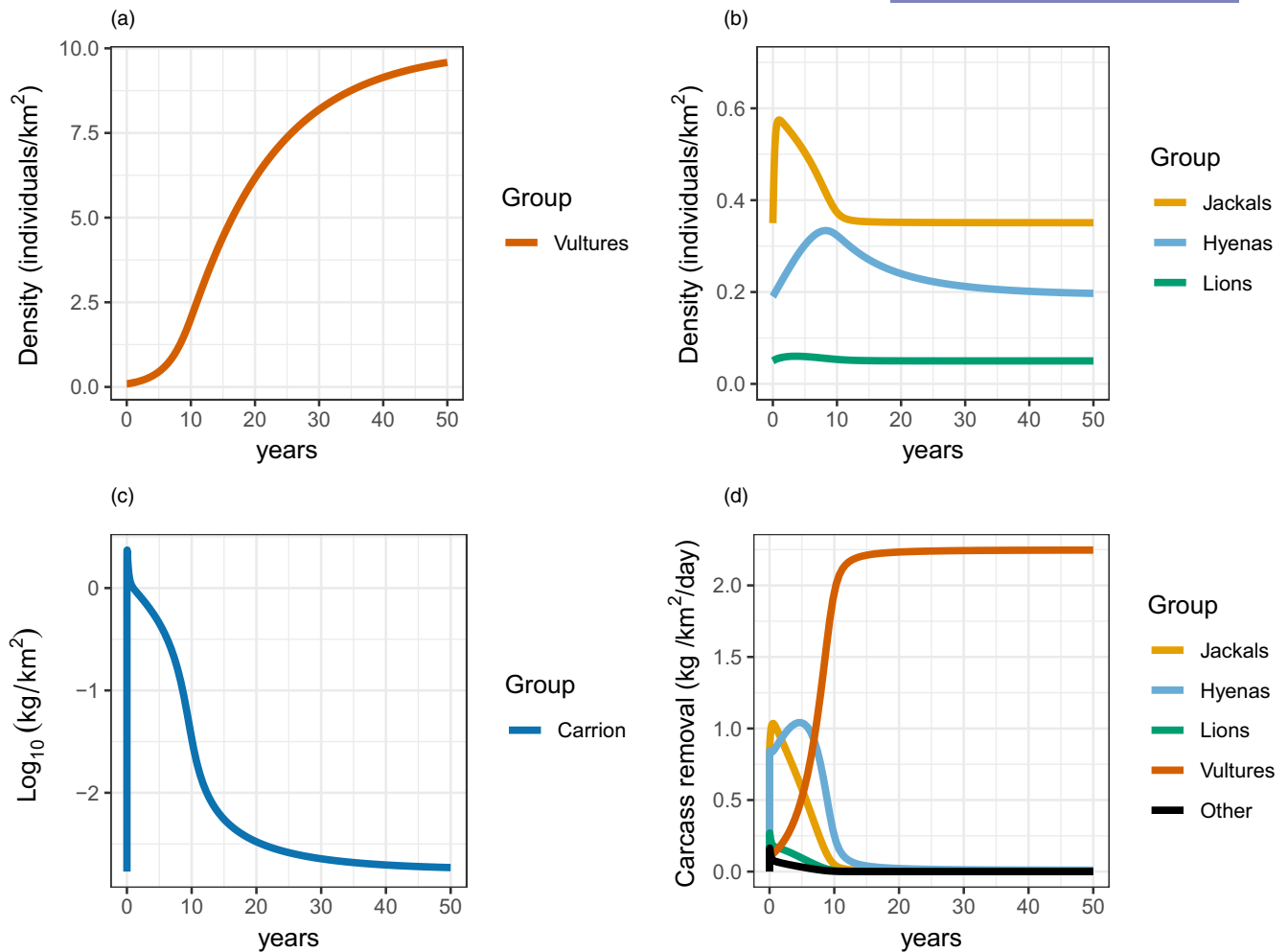


FIGURE 1 (a) Predicted population dynamics of apex scavenger (vultures) over 50-year period. (b) Predicted population dynamics of meso-scavengers over a 50-year period. (c) Predicted dynamics of carrion mass over a 50-year period. (d) Removal rates of carrion attributable to the four modelled vertebrate groups and to invertebrates (denoted here as 'Other').

continue to exploit carrion as a food source (with reduced success rates) until approximately 20 years have elapsed. Hyena numbers remain high for another decade after this point as individuals die of old age without being replaced by new adults.

3.3 | Drivers of transient dynamics

The details of our two numerical sensitivity analyses (outlined in Section 2.5) are presented in Section S3 of the Supplementary Material and we summarise the significant findings here. First, the observed sequence of events is essentially identical across scenarios. In each case, the dynamics involve a transient peak in jackal abundance, followed by a transient peak in hyena abundance and then a permanent peak in vulture abundance. Second, the duration of meso-scavenger release (i.e. the length of time over which there is a surplus of carrion that can be detected by meso-scavengers or invertebrates) did not change when we reduced the meso-scavenger carrying capacities but decreased when we reduced the carcass supply rate.

We use an analytical approach to reconcile these findings with our core predictions (i.e. Section 3.2). While characterisation of the transient dynamics of competition models can often only be accomplished using numerical methods (Caswell, 1982; Hastings, 2001), the vast discrepancy between the carrion-removal abilities of vultures and those of meso-scavengers allows some analytical progress to be made. In Section S4 of the Supplementary Material, we use scaling and perturbation methods to relate the times at which shifts in community structure occur to the model parameters. In particular, a separation of time scales confirms that hyenas, lions and vultures convert carrion into new individuals over a single 'slow' time scale whereas the jackal population reaches its carrion-enhanced peak density more quickly, over a time scale of $\frac{h_j}{y_j}$, which is equal to 137 days. This separation of time scales, combined with the study of equilibrium points in Section 3.1, explains the robustness of the temporal sequence we observed in our numerical sensitivity analysis. Despite their inferiority with respect to finding carrion, jackals are effectively guaranteed to numerically respond to any surplus of carcasses resulting from the removal of vultures. In contrast, hyenas require the vulture recovery to be relatively slow in order to profit from the extra carrion in the ecosystem.

In order for mesoscavenger densities to exceed their carrying capacities, as we have observed, these populations must gain access to carcasses for a period of time. We refer to this period as the duration of mesoscavenger release (d_{release}). In Section S4.2 of the Supplementary Material, we relate this quantity to the abundance and life-history information of the vulture population, via the following formula:

$$d_{\text{release}} = \max\left(\left(\frac{h_V}{\gamma_V - \mu_V h_V}\right) \ln\left(\frac{C_{\text{in}} h_V}{V_{\text{initial}}}\right), 0\right), \quad (5)$$

which corresponds to 3441 days or 9.43 years for the KNP community, in agreement with Figure 1d. The formula for d_{release} in Equation (5) also captures two important features of the model behaviour, consistent with our numerical sensitivity analysis. Firstly, the duration of mesoscavenger release does not depend on the mesoscavenger carrying capacities, as we observed when we numerically reduced these parameters. Secondly, the duration of release is an increasing function of the rate at which carcasses are supplied, consistent with our numerical reduction of C_{in} .

Finally, we note that after the vulture population has excluded its competitors from the scavenging community, the model dynamics are predicted to be relatively simple. In each numerical solution, the gap between the density at which vultures exclude their competitors and the vulture carrying capacity is closed in approximately 40 years. In Section S4.3 of the Supplemental Material, we derive a formula to estimate the time taken for the vulture population to reach its carrying capacity. This analysis validates our numerical finding that the vulture population's equilibration time does not depend on the mesoscavenger carrying capacities or the carcass supply rate.

4 | DISCUSSION

4.1 | Summary

Our results show that a once-extirpated apex scavenger population can recover to its original state and exceed this level to the point of monopolising carrion in a system like KNP. This supports the view that apex scavengers are qualitatively superior to mesoscavengers in searching for carrion and suggests that resource partitioning or a yet-to-be-discovered regulating factor for vultures is necessary for mammals to persistently scavenge in an ecosystem like KNP. In terms of the mesoscavenger response, our model showed a spike in jackal numbers when vulture numbers were at their lowest. Hyenas experience a similar though, not as drastic, increase in population density reflecting their slower life history. However, their capacity for carcass removal quickly surpasses that of the jackal population. We now consider the different elements of model construction and behaviour in turn.

4.2 | Apex-scavenger response

Our predicted vulture densities far exceed those seen in KNP today but are not out of line with vulture densities elsewhere (e.g. cinereous

vultures *Aegypius monachus* occurring at 16.6 birds/km² (Stephens et al., 2019) and hooded vulture *Necrosyrtes monachus* densities of >100/km² (Henriques et al., 2018) though the former measurements apply to a species that is occasionally colonial (Fitter, 1980) and the latter measurements were taken in urban areas containing abattoirs). Moreover, nest-density estimates for *Gyps africanus* of 1.43 nests/km² in the Masai Mara imply that adult densities much higher than 0.09/km² occur in that ecosystem (Virani et al., 2010).

We stress that our model assumes an environment free of poisoning or similar anthropogenic barriers to vulture population increases. Given the many threats felt by African vulture populations today, we argue that current densities are far below carrying capacity. At KNP alone, hundreds of vultures have been killed by poisoning over the past decade—an unsustainable attrition rate (Murn & Botha, 2018). Previous work on griffon vultures and cinereous vultures in Spain suggests that intra-specific interference competition at carcasses and general agonistic interactions act as density-dependent effects curbing population growth (Fernandez et al., 1998; Fernández-Bellon et al., 2016). In African ecosystems, such as KNP, the megafauna population affords a natural supply of large carcasses rarely seen in other regions. Thus, we argue that similar density-dependent effects would be slow to take hold on the vulture population here. Indeed, recent work in the region has assumed carrion rates at KNP are sufficient to support the vulture population at its present density (Murn & Botha, 2018). However, such self-limitation could be incorporated in our functional response for vultures with the effect of some carcasses being left uneaten by vultures and the vultures' carrying capacity value being reduced (Stouffer & Novak, 2021). In reality, conservationists can establish supplementary feeding sites to aid the recovery of vulture populations (Brink et al., 2020). These interventions are not without issue (Yarnell et al., 2015) but can be remarkably successful (Marinković et al., 2020).

Fortunately, it is relatively straightforward to deduce how an inaccuracy in our estimation of the vultures' carrying capacity would influence our predictions. Analysis of our community model indicated that vulture density must fall below a certain value in order for scavenging by mammals to occur. For the parameter values in Table 2, this critical value corresponds to 1.92 adults/km² (see Section S4.2 of the Supplement). If an alternative regulating factor (e.g. nesting-site availability) sets the vulture carrying capacity below this value, carrion is expected to be split between vultures and the resident mammal species in the long run, even in the absence of temporal segregation of carrion.

4.3 | Mesoscavenger response

It has been suggested that, because jackals are competitively subordinate to hyenas and lions, they cannot rely on carrion as much as their larger competitors (Jones et al., 2015). However, we show that a sudden spike in carrion would cause an immediate numerical response in jackals whose life-history traits stand to their benefit. This would echo the response of feral dog populations in India to the near extirpation of vultures. Our findings that hyenas

excel at carcass removal are in line with empirical reports (Moleón et al., 2015). Their large body mass means per capita they are more efficient at consuming carrion than vultures. This supports the consensus that, in African scavenging communities, hyenas stand to gain from a sustained loss of vultures (Jones et al., 2015). Lions fare worst in our modelled scenario which we attribute to their relatively poor search ability. Previous studies show that lions may meet less of their energetic requirements than hyenas through scavenging (Jones et al., 2015, and references therein). Interestingly, recent work found that, for their population size, lions were just as good at finding medium and large carcasses as hyenas (Amorós et al., 2020). The authors state that this may be due to diurnal lions cueing to vulture foraging activity more so than the crepuscular/nocturnal hyenas (Amorós et al., 2020). We expect that this interaction would play a minor role during the early years of vulture recovery but may become more significant after this period. Overall, the relative responses of the three mesoscavengers in our model comports well with published field studies. Further, this is a pattern that emerged naturally without us imposing a hierarchy between the groups. KNP has recently witnessed an increase in herbivore numbers due to a change in management practices (Ferreira & Funston, 2020). Ferreira and Funston (2020) suggest this is responsible for the increase in lion and hyena populations in the park. As vulture populations continue to be poisoned our findings indicate both mesoscavengers will see further population increases. Although the apex scavenger is predicted to recover and eventually depress the mesoscavenger populations, the transient dynamics imply a period of mammalian dominance. The knock-on effects from this mesoscavenger release are likely to be significant, as we discuss in Section 4.6.

4.4 | Carrion response

Carrion density jumps significantly at the beginning of our model run in the absence of vultures. It steadily declines thereafter as the vulture population recovers. This transient glut of carrion with increased decay rates has been reported in numerous systems where apex scavengers are lost (Cunningham et al., 2018; Ogada et al., 2012). In our model run, carrion density remains above 0.1 kg/km² for the first 10 years. This is due to so-called 'scavenger swamping' (Smallwood, 2007) with vultures satiated and unable to process any more meat without a significant increase in numbers. While the consumption rate of scavengers is hypothesised to be constrained by their ability to find food (Ruxton & Houston, 2004), our results suggest that the present-day vulture populations of KNP and similar ecosystems are instead limited by their ability to process a superabundant food supply.

Aside from the mesoscavenger response, there may also be a numerical response from the invertebrate scavenging community. The latter are typically outcompeted by vertebrate scavengers in sub-Saharan Africa (Forbes & Carter, 2015, p. 19), but a system knocked out of equilibrium may afford invertebrate communities additional opportunities to colonise carcasses (Braack, 1987; DeVault

et al., 2003). Moreover, increases in average temperature and potential human encroachment into these ecosystems may make invertebrate scavengers more competitive in the coming decades (Bartel et al., 2024).

4.5 | Model

From a modelling perspective, one of the reasons for our focus on KNP was data availability. In particular, we could draw on a wealth of parameters to estimate conversion efficiencies for converting resources into consumers. Our hope is that this approach could also be applied to other systems with an obvious apex scavenger. This would be relatively easy for Europe, east Africa or the Asian sub-continent where there are many similarities among the scavenging communities. However, applying the model to a system where the apex scavenger is not a vulture would be fascinating to see if a similar recovery time is possible for an initially small population. One example is in Tasmania where the Tasmanian devil (*Sarcophilus harrisii*) acts as an apex scavenger whose decline has 'released' forest ravens (*Corvus tasmanicus*) who are among the mesoscavengers (Cunningham et al., 2018).

It is important to note that we have assumed historic conditions at KNP will persist in our future projections of scavenger densities. Though sustained changes in resource availability are perhaps more common in human-dominated habitats (e.g. in the European Union after the introduction of Bovine Spongiform Encephalopathy regulations (Almaraz et al., 2022)), our formulae for vulture carrying capacity, equilibration time and the duration of mesoscavenger release (see Section 3.3) nonetheless allow us to predict how a scavenging community would track such changes.

As discussed previously, we have also assumed an environment free of catastrophic stochasticity on the basis that conservation initiatives are underway. However, this does not rule out roles for environmental and demographic stochasticity. Environmental stochasticity generally acts to slow down population growth (Sandal et al., 2022). Because of their relatively long life histories, hyenas, lions and vultures should be less affected by this reduction in growth rate, compared to jackals (Benton et al., 1995; Koons et al., 2009). Due to the cumulative effect of historic poisonings, vulture densities are at low levels and therefore would be expected to be significantly affected by demographic stochasticity (Lande, 1993). Murn and Botha (2018) suggest that an effective extinction threshold for white-backed vultures is 20 adults (0.001/km²). Demographic stochasticity may not be strong enough to move the vulture population density below this threshold but could nevertheless slow population growth while density is low. It is therefore possible that we have overestimated the growth rate of both vultures and jackals during the early years of vulture recovery. The former would suggest a longer period of mesoscavenger release than predicted and the latter would suggest more invertebrate activity (or the accumulation of carrion) before jackals and hyenas respond numerically.

The scavenging model that we have used focuses on exploitation competition. Such models represent a minimal-resolution description of energy flow from resource to consumer (Skalski & Gilliam, 2001). More complex behaviours (e.g. interference competition, facilitation and specialisation on a particular type or size of carcass) have been observed in ungulate carcasses (Kane et al., 2017; Moleón et al., 2015; Naves-Alegre et al., 2024). We expect that the inclusion of these behaviours should achieve a similar effect to temporal segregation (i.e. preventing outright exclusion of mammals from the scavenging community while preserving vulture dominance at the aggregate level). Even with a potential redistribution of carrion discoveries among the scavenger groups, the groups themselves will remain subject to the physiological constraints of their digestion rates and maximum reproductive rates.

We recognise some other limitations of our approach. For one, prey species could be modelled explicitly rather than through the logistic growth of the associated predator population. We also employ some crude scaling relationships to estimate population densities for some groups where data was unavailable, for example, for jackals in KNP. However, we have explicitly described the formulae used to compute unknown parameter values and we have represented scavenger dynamics using a mechanistic model. It is therefore reasonably clear what will need to be modified to better match the peculiarities of a specific ecosystem if there is significant disagreement between model predictions and future observations (Geritz & Kisdi, 2012).

Finally, we recognise that the predicted recovery of vultures in our model occurred without invoking social foraging behaviour. This behaviour has traditionally been seen as a key facet of vulture search efficiency (Jackson et al., 2008). Moreover, inter-specific social foraging among mesoscavengers has been reported for the species we focus on, with hyenas and lions known to respond to vulture aggregations (Amorós et al., 2020, and references therein). Yet, in our model, it is the area searched by the birds that is responsible for their growth relative to the mesoscavengers. In the mammalian case, relative differences in search efficiency when coupled with variation in life history traits are likely to overshadow these aspects.

4.6 | Broader ecological impacts

We predict an increasing vulture population to have a strong dampening effect on predation rates and disease transmission around carcasses, as well as the perception of these risks among other species, by flattening 'hills' on landscapes of fear and disgust (Moleón & Sánchez-Zapata, 2021). Areas around carcasses are subject to increased predator activity which results in higher predation rates (e.g. on ground-nesting birds (Cortés-Avizanda et al., 2009)). Given such a risk, herbivores perceive carcasses as scary and avoid them. We would also expect the increased contact between mammals implied by a decade or more of mesoscavenger release to facilitate the spread of disease, particularly rabies and canine distemper virus (Ogada et al., 2012). The persistence of carrion could also punch

holes in the realised habitat of grazers who perceive the sites as likely centres of infection (Moleón & Sánchez-Zapata, 2021). In the long run, the heightened decomposition rate enabled by vultures may aid wildlife conservation in general by limiting the prevalence of disease-carrying bacteria (Hill et al., 2018, but see Blanco, 2018). However, the transient period of mammalian dominance could pose some challenging questions for wildlife managers. The predicted increase in hyena density followed by a reduction in their ability to locate carrion would suggest a transient but potentially acute pressure on prey species. A management solution is not immediately obvious, as culls of hyenas (or lions) may be unpopular and prey-protection measures are often difficult to implement (Kelly & Durant, 2000). Another important, non-trophic impact of vulture recovery, is reduced terrestrial eutrophication (Buechley & Şekercioğlu, 2016) as carcasses and their constituent nutrients spend less time in situ and instead become spread over the wider habitat (Bartel et al., 2024).

Taken together, vulture recovery could act as a positive driver of ecosystem stability given the multiple trophic and non-trophic interactions that their efficient consumption of carrion controls. Such a scenario is worth comparing to ecosystems that have seen the re-introduction or recovery of apex predators (Jiménez et al., 2019). Indeed, this wider effect of apex scavenger recovery could serve to steer more support for vulture conservation.

5 | CONCLUSIONS

The long-term behaviour of our model may not be qualitatively surprising given the known scavenging capabilities of vulture species. However, the time spent at each stage in the route to recovery is dependent on the history of the ecosystem as well as the reproductive rates of the extant vertebrate scavengers. With an assumption that there are no further vulture poisonings, we have produced falsifiable quantitative predictions (Houlahan et al., 2017) of carrion removal rates and scavenger population dynamics in an African ecosystem. These findings offer a hopeful view for the recovery of apex scavengers. We show that, if left unmolested, their numbers could recover, and far exceed the densities of animals we know today, thereby increasing carcass decomposition rates and suppressing mesoscavenger densities. The question remains whether we can afford apex scavengers the opportunity to do so.

AUTHOR CONTRIBUTIONS

J. G. Donohue: Conceptualisation, Data curation, Formal analysis, Methodology, Writing—original draft, Writing—review and editing. P. T. Piironen: Conceptualisation, Methodology, Writing—review and editing. A. Kane: Conceptualisation, Data curation, Methodology, Writing—original draft, Writing—review and editing.

ACKNOWLEDGEMENTS

This publication has emanated from research conducted with the financial support of Science Foundation Ireland under grant number SFI/13/IA/1923. Open access funding provided by IReL.

CONFLICT OF INTEREST STATEMENT

The authors have no competing interests to declare.

DATA AVAILABILITY STATEMENT

The codes used to solve the scavenging model and plot the solutions are permanently archived on Zenodo at <https://doi.org/10.5281/zenodo.13326528> (Donohue et al., 2024). Following Kane and Amin (2023), all versions, updates and additional material are/ will be stored transparently on GitHub <https://github.com/kanead/meso-scavenger>.

ETHICS STATEMENT

Ethical approval was not needed in this study.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Parameter estimation and sensitivity analysis.

Appendix S2: Carrion density estimation.

How to cite this article: Donohue, J. G., Piironen, P. T., & Kane, A. (2024). Predicted short-term mesoscavenger release gives way to apex-scavenger dominance. *Journal of Animal Ecology*, 00, 1–13. <https://doi.org/10.1111/1365-2656.14180>