



Can scavengers save zebras from anthrax? A modeling study

Crystal Mackey*, Christopher Kribs

Department of Mathematics, University of Texas at Arlington, 411 South Nedderman Drive, Box 19408, Arlington, TX, 76019, USA



ARTICLE INFO

Article history:

Received 27 October 2019

Received in revised form 4 October 2020

Accepted 31 October 2020

Available online 7 November 2020

Handling editor: Dr. J Wu

Keywords:

Disease ecology

Anthrax

Scavengers

Demographic reproductive number

Dynamical system

ABSTRACT

Namibia's Etosha National Park (ENP) is home to many different animals such as lions, jackals, hyenas, zebras, elephants, etc. Each year, grazing animals are infected and die from anthrax caused by the bacteria *Bacillus anthracis*. This increases the number of carcasses in the park, which serve as food for scavengers such as jackals. This study investigates the interplay between anthrax transmission in zebras and the scavenging of zebra carcasses in ENP, using a deterministic mathematical model to describe the population dynamics. We strive to answer the following research questions: Under what conditions can the presence of scavengers control anthrax outbreaks in zebra populations? Does carcass production by anthrax help or hurt scavengers in the long term? Standard qualitative analysis techniques distinguished outcomes (stable equilibria) using reproduction numbers as threshold quantities. We found that, when scavengers feed on anthrax-laden carcasses, the scavengers help the zebras, by eliminating potential infection zones for the zebras. In this way they reduce anthrax's spread by orders of magnitude. We also identify conditions under which the presence of anthrax benefits the scavengers, in terms of death-to-birth ratios for zebras, scavengers and anthrax.

© 2020 The Authors. Production and hosting by Elsevier B.V. on behalf of KeAi Communications Co., Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

In the 1960s, data collection regarding anthrax outbreaks in ungulates and other mammals began in Etosha National Park (ENP), Namibia. The national park is about 23,000 km² and has a single wet and dry season each year, with rain from November to April (Bellan et al., 2012). From 1964 to 1992, about 3000 carcasses were confirmed or suspected cases of anthrax in ENP among 11 different herbivorous species, two of which are zebras, which account for the most deaths (Lindeque & Turnbull, 1994). Carnivores are less likely than herbivores to contract anthrax. From 1975 to 2012, one jackal, three lions and nine cheetahs died from anthrax (Bellan et al., 2012). The seasonal peak of anthrax cases for elephants occurs in November at the end of the dry season, whereas the seasonal peak for plains ungulates occurs at the end of the rainy season in March (Lindeque & Turnbull, 1994). Today, ENP remains one of the most-documented continuous sources of anthrax dynamics in any natural system (Carlson et al., 2018). The carrion that is provided by the anthrax deaths of zebras feed many different scavenger species in ENP, such as black-backed jackals (*Canis mesomelas*), spotted hyenas, white-backed vultures, lappet-faced vultures and others (Bellan et al., 2013).

* Corresponding author.

E-mail address: crystal.mackey@mavs.uta.edu (C. Mackey).

Peer review under responsibility of KeAi Communications Co., Ltd.

Anthrax is a zoonosis caused by *Bacillus anthracis* (BA) and mainly infects ungulates such as zebras, springbok and wildebeest (Carlson et al., 2018). BA exists in two forms. One is a vegetative form, which is not resistant in harsh conditions, such as an acidic environment. BA can also be found in the form of infectious spores, which are resistant to harsh conditions and can survive for long periods of time, waiting to infect a host (Hugh-Jones & De Vos, 2002). The bacteria can enter an animal through a skin abrasion, inhalation or digestion and leads to death in wildlife (Zidon et al., Saltz).

A study by Turner et al. (Turner et al., 2016) gives insight to the different pathogen sources and transmission pathways of infectious agents such as BA in grazing animals. After tracking pathogen concentrations at carcass sites and waterholes for five years, they found that carcass sites are more likely to be important sources of host–pathogen contacts than water sources (Turner et al., 2016). Furthermore, although BA concentration at carcass sites in soil and on grasses decays exponentially, the bacteria can still be detected in the soil four years after death at high enough concentrations for a grazing animal to receive a lethal dose (Turner et al., 2016). Previous studies (Bellan et al., 2013; Carrasco-Garcia et al., 2018) suggest scavengers could help eliminate these pathogens from the environment that affect ungulates and could be a major factor in limiting the speed at which the disease can spread.

Houston et al. (Houston & Cooper, 1975) studied the digestive tract of the whiteback griffon vulture and the role it plays in disease transmission in wild ungulates. In the study, pH values were measured in different organs, and the digestive tract and stomach were found to be highly acidic. The authors found that, while the vegetative form of BA was killed in the digestive tract, the highly resistant spores survived (Houston & Cooper, 1975). Other studies also support the survival of BA spores in the digestive tract of scavengers (Hugh-Jones & De Vos, 2002; Lindeque & Turnbull, 1994). This suggests that if the anthrax-laden carcasses are detected by scavengers before sporulation takes place, scavengers could help eliminate the spread of anthrax in wildlife. In this way, the scavengers generally only benefit zebras, since, of the scavenger species in ENP, only the spotted hyena has been observed to hunt (in packs) a living zebra, and research has found that spotted hyenas avoid hunting zebras in central ENP, and hunt them in eastern ENP only when the zebras are numerous (Trinkel, 2010).

Saad-Roy et al. (Saad-Roy et al., 2017) developed a deterministic mathematical model using a system of differential equations to describe anthrax transmission in animal populations. Their general model contained susceptible animals, infected animals, infected carcasses and BA spores in the environment as the state variables. They considered two special cases of their model. In one case, the animals were herbivorous livestock; in the other case, the animals were carnivores. A result from their herbivore model showed that a vaccination policy or an animal-carcass-removal policy can be used to eradicate anthrax. However, this would largely depend on the associated costs of vaccination programs and carcass removal. It is nearly impossible to vaccinate wildlife animals, so we are interested in determining whether scavengers can be a significant natural means of anthrax removal. In particular, we shall study the extent to which scavengers can interrupt anthrax transmission by removing carcasses (leaving aside for simplicity other sources of BA spores in the zebra habitat).

We develop a deterministic model using ordinary differential equations describing how anthrax affects the population dynamics of zebras, zebra carcasses and scavengers. While scavengers benefit from the presence of anthrax (because it provides them with a food source), anthrax is disadvantaged by the presence of scavengers that help to eliminate the presence of BA by feeding on zebra carcasses. The two scavengers we consider are jackals and vultures. We will compare the basic reproduction number of anthrax in the presence of jackals and in the presence of vultures to see if one scavenger is better at eliminating anthrax.

This paper is organized as follows: In Section 2 the model is developed. In Section 3 the model's equilibria are identified, along with conditions on their existence and stability (local and global). In addition, the basic reproductive numbers for anthrax are derived, and Section 4 derives the demographic numbers for the scavengers. We end with a discussion of results and conclusion.

2. Model development

The populations considered in this model are living zebras, zebra carcasses due to natural death, zebra carcasses due to anthrax, and scavengers (z , u , c , j , respectively). The zebra population grows logistically and is removed by natural death (μz) or by disease-induced death (acz) from grazing near an anthrax-infected carcass site (Turner et al., 2016). The mass-action term used to describe zebras' anthrax deaths (implicitly, their encounters with anthrax-laden carcasses) draws on an assumption of homogeneous mixing, since the zebras in ENP travel in nomadic family groups, and grazing areas include carcass sites. The carcasses are either naturally decomposing at a rate ρ or are being eaten by scavengers at a rate of α . Scavengers do not attack living zebras; they only scavenge on the zebra carcasses. In this model, scavenger survival depends on the number of carcasses available, $bj(u + c)$, and scavengers die naturally at a rate of d .

$$z' = rz\left(1 - \frac{z}{K}\right) - \mu z - acz \quad (1)$$

$$u' = \mu z - \rho u - \alpha j u \quad (2)$$

$$c' = acz - \rho c - \alpha j c \quad (3)$$

$$j' = bj(u + c) - dj \tag{4}$$

Scavengers eating anthrax-laden carcasses are less likely than herbivores to contract the disease (Bellan et al., 2012). Therefore, we assume that scavengers will not die from anthrax. Moreover, as previously noted, we consider that scavengers do not attack living zebras. To simplify the food web for analysis, we take zebra carcasses as representative of scavengers' food source and thus model the scavengers as obligate. We assume that scavengers cannot distinguish between a healthy or infected carcass. We also assume that infected zebra carcasses c are representative of (proxies for) all BA spores in the study region. Model parameters are summarized in Table 1.

3. Equilibrium analysis

3.1. Existence of equilibria

In this section, we identify the equilibria in our model (it turns out there are four) and provide the existence condition for each one. The detailed calculations for this section are in Appendix A.

We can see that $E_0 = (0, 0, 0, 0)$ is an equilibrium because equations (1)–(4) are satisfied when $(z^* = 0, u^* = 0, c^* = 0, j^* = 0)$, which represents the extinction equilibrium. We also have the equilibrium

$$E_1(z^*, u^*, c^*, j^*) = \left(K \left[1 - \frac{\mu}{r} \right], \frac{\mu}{\rho} K \left[1 - \frac{\mu}{r} \right], 0, 0 \right), \tag{5}$$

which exists when $\mu < r$. E_1 is the disease-free equilibrium in the absence of scavengers. The equilibrium

$$E_2(z^*, u^*, c^*, j^*) = \left(K \left[1 - \frac{\mu}{r} \right], \frac{d}{b}, 0, \frac{1}{\alpha} \left[\frac{b\mu}{d} z^* - \rho \right] \right), \tag{6}$$

which exists when $\mu < r$ and $b\mu z^* > \rho d$, is the disease-free equilibrium in the presence of scavengers. The equilibrium

$$E_3(z^*, u^*, c^*, j^*) = \left(\frac{\rho}{a}, \frac{\mu}{a}, \frac{r}{aK} \left[K \left(1 - \frac{\mu}{r} \right) - \frac{\rho}{a} \right], 0 \right), \tag{7}$$

which exists when $\mu < r$ and $K \left(1 - \frac{\mu}{r} \right) > \frac{\rho}{a}$, is endemic for anthrax in the absence of scavengers. Finally, the equilibrium E_4 is

$$E_4(z^*, u^*, c^*, j^*) = \left(K \left[1 - \frac{ad}{br} \right], \frac{\mu}{a}, \frac{d}{b} - \frac{\mu}{a}, \frac{a}{\alpha} K \left[1 - \frac{ad}{br} \right] - \frac{\rho}{\alpha} \right) \tag{8}$$

and exists if and only if $\frac{\rho}{a} < K \left(1 - \frac{ad}{br} \right)$ and $\frac{ad}{b\mu} > 1$. (These conditions mean that scavengers reproduce well in the presence of anthrax and anthrax spreads well in the presence of scavengers, respectively, as will be seen in later sections through the lens of reproductive numbers.) This equilibrium is endemic for anthrax in the presence of scavengers.

3.2. Basic reproductive numbers

The basic reproductive number (BRN) is defined as the average number of secondary infections generated by one infected individual in a population of susceptible individuals, which can be calculated using the next-generation-operator method as in (Brauer & Castillo-Chavez, 2011). When the BRN is less than one, the disease-free equilibrium is stable; when the BRN is greater than one, the endemic equilibrium is stable. In our model, we have two disease-free equilibria: one without scavengers (E_1) and one with scavengers (E_2). The BRN of anthrax in the absence of scavengers is $R_Z = \frac{aK(1-m)}{\rho}$, where the average infection rate is $aK(1 - m)$, $m = \mu/r$, and the average duration of infection is $\frac{1}{\rho}$. The BRN of anthrax in the presence of

Table 1
Parameter definitions. Estimates use time units of weeks (see Table 4).

Symbol	Definition	Units
K	carrying capacity	(zebras)
R	intrinsic growth rate of zebras	1/time
M	natural zebra death rate	1/time
A	rate zebras come into contact with infected carcasses	(time·zebras) ⁻¹
P	natural decomposition rate of carcasses	1/time
A	rate scavengers come into contact carcasses to eat	(time·scavengers) ⁻¹
B	birth rate of scavengers	(time·zebras) ⁻¹
D	death rate of scavengers	1/time

scavengers is $R_j = \frac{ad}{b\mu}$. Here $\frac{ad}{b}$ is the average infection rate and the average length of infection is $\frac{1}{\mu}$. How these two component BRNs fit into an overall measure of anthrax persistence will be deferred until the equilibrium stability analysis is complete.

3.3. Local stability analysis

To determine the local stability conditions for each equilibrium, we calculate the Jacobian matrix of our model and evaluate the Jacobian at each equilibrium point. The equilibrium is stable if and only if the real part of the eigenvalues of the Jacobian matrix are negative. Therefore, we find the conditions that are required to have negative eigenvalues. The Jacobian matrix of our model is

$$J = \begin{bmatrix} r - \frac{2r}{K}z - \mu - ac & 0 & -az & 0 \\ \mu & -\rho - \alpha j & 0 & -\alpha u \\ ac & 0 & az - \rho - \alpha j & -\alpha c \\ 0 & bj & bj & bu + bc - d \end{bmatrix}$$

The Jacobian evaluated at the extinction equilibrium is

$$J(E_0) = \begin{bmatrix} r - \mu & 0 & 0 & 0 \\ \mu & -\rho & 0 & 0 \\ 0 & 0 & -\rho & 0 \\ 0 & 0 & 0 & -d \end{bmatrix}$$

If the death rate is greater than the birth rate, i.e., $\mu > r$, then the extinction equilibrium is locally asymptotically stable. The Jacobian evaluated at E_1 is

$$J(E_1) = \begin{bmatrix} \mu - r & 0 & -aK\left(1 - \frac{\mu}{r}\right) & 0 \\ \mu & -\rho & 0 & \frac{-\alpha\mu}{\rho}K\left(1 - \frac{\mu}{r}\right) \\ 0 & 0 & aK\left(1 - \frac{\mu}{r}\right) - \rho & 0 \\ 0 & 0 & 0 & \frac{b\mu}{\rho}K\left(1 - \frac{\mu}{r}\right) - d \end{bmatrix}$$

$$\rightarrow \begin{bmatrix} \mu - r & -aK\left(1 - \frac{\mu}{r}\right) & 0 \\ 0 & aK\left(1 - \frac{\mu}{r}\right) - \rho & 0 \\ 0 & 0 & \frac{b\mu}{\rho}K\left(1 - \frac{\mu}{r}\right) - d \end{bmatrix} = \hat{J}(E_1)$$

The arrow above represents the property of determinants that, for purposes of determining eigenvalues, the 4×4 Jacobian matrix can be decomposed to the diagonal element (and eigenvalue) $-\rho$ and a 3×3 matrix since the second column in the 4×4 has zeros except on the diagonal.

The eigenvalues are $\lambda_1 = -\rho$, $\lambda_2 = \mu - r$, $\lambda_3 = aK\left(1 - \frac{\mu}{r}\right) - \rho$, and $\lambda_4 = \frac{b\mu}{\rho}K\left(1 - \frac{\mu}{r}\right) - d$. Notice that λ_1 is always less than zero, $\lambda_2 < 0$ if and only if $\mu < r$, $\lambda_3 < 0$ if and only if $z^* < \frac{\rho}{a}$, and $\lambda_4 < 0$ if and only if $b\mu z^* < d\rho$. Therefore, E_1 is locally asymptotically stable if and only if $z^* < \frac{\rho}{a}$ and $b\mu z^* < d\rho$. We rewrite the local stability conditions in terms of R_z and R_j : $R_z < 1$ and $R_z < R_j$.

The Jacobian evaluated at E_2 is

$$\begin{aligned}
 J(E_2) &= \begin{bmatrix} \mu - r & 0 & -aK\left(1 - \frac{\mu}{r}\right) & 0 \\ \mu & \frac{-b\mu z^*}{d} & 0 & \frac{-\alpha d}{b} \\ 0 & 0 & z^*\left(a - \frac{b\mu}{d}\right) & 0 \\ 0 & \frac{b}{\alpha}\left(\frac{b\mu z^*}{d} - \rho\right) & \frac{b}{\alpha}\left(\frac{b\mu z^*}{d} - \rho\right) & 0 \end{bmatrix} \\
 &\rightarrow \begin{bmatrix} \mu - r & 0 & 0 \\ \mu & \frac{-b\mu z^*}{d} & \frac{-\alpha d}{b} \\ 0 & \frac{b}{\alpha}\left(\frac{b\mu z^*}{d} - \rho\right) & 0 \end{bmatrix} \\
 &\rightarrow \begin{bmatrix} \frac{-b\mu z^*}{d} & \frac{-\alpha d}{b} \\ \frac{b}{\alpha}\left(\frac{b\mu z^*}{d} - \rho\right) & 0 \end{bmatrix} = \hat{J}(E_2)
 \end{aligned}$$

Thus, two of the eigenvalues of $J(E_2)$ are $\lambda_1 = z^*\left(a - \frac{b\mu}{d}\right)$ and $\lambda_2 = \mu - r$. Notice that

$$\lambda_1 = z^*\left(a - \frac{b\mu}{d}\right) < 0 \Leftrightarrow a < \frac{b\mu}{d} \Leftrightarrow \frac{ad}{b\mu} < 1$$

and $\lambda_2 = \mu - r < 0$ if and only if $\mu < r$. The two-dimensional Routh–Hurwitz criterion determines if the other two eigenvalues of the Jacobian matrix of E_2 have negative real parts without having to find the eigenvalues. Considering the matrix $\hat{J}(E_2)$, the eigenvalues have negative real parts if $\text{tr}(\hat{J}(E_2)) < 0$ and $\det(\hat{J}(E_2)) > 0$ (Brauer & Castillo-Chavez, 2011). The trace and determinant of $\hat{J}(E_2)$ are

$$\text{tr}(\hat{J}(E_2)) = \frac{-b\mu z^*}{d} \text{ and } \det(\hat{J}(E_2)) = \frac{b\mu z^*}{d} - \rho.$$

Notice that the trace is always negative, and the determinant is negative if and only if $b\mu z^* > \rho d$. Recall $b\mu z^* > \rho d$ is an existence condition for E_2 . Therefore, E_2 is locally asymptotically stable if and only if $\frac{ad}{b\mu} < 1$. Recall that $R_J = \frac{ad}{b\mu}$. When $R_J < 1$, anthrax will diminish in the presence of scavengers, since E_2 is locally asymptotically stable.

The Jacobian evaluated at E_3 is

$$\begin{aligned}
 J(E_3) &= \begin{bmatrix} -\frac{\rho r}{aK} & 0 & -\rho & 0 \\ \mu & -\rho & 0 & -\frac{\alpha u}{a} \\ r\left(1 - \frac{\rho}{aK}\right) - \mu & 0 & 0 & -\frac{\alpha r}{aK} \left[K\left(1 - \frac{\mu}{r}\right) - \frac{\rho}{a}\right] \\ 0 & 0 & 0 & \frac{b\mu}{a} + \frac{br}{aK} \left[K\left(1 - \frac{\mu}{r}\right) - \frac{\rho}{a}\right] - d \end{bmatrix} \\
 &\rightarrow \begin{bmatrix} -\frac{\rho r}{aK} & -\rho & 0 \\ r\left(1 - \frac{\rho}{aK}\right) - \mu & 0 & -\frac{\alpha r}{aK} \left[K\left(1 - \frac{\mu}{r}\right) - \frac{\rho}{a}\right] \\ 0 & 0 & \frac{b\mu}{a} + \frac{br}{aK} \left[K\left(1 - \frac{\mu}{r}\right) - \frac{\rho}{a}\right] - d \end{bmatrix} \\
 &\rightarrow \begin{bmatrix} -\frac{\rho r}{aK} & -\rho \\ r\left(1 - \frac{\rho}{aK}\right) - \mu & 0 \end{bmatrix} = \hat{J}(E_3)
 \end{aligned}$$

Two of the eigenvalues are

$$\lambda_1 = -\rho \text{ and } \lambda_2 = \frac{b\mu}{a} + \frac{br}{aK} \left[K\left(1 - \frac{\mu}{r}\right) - \frac{\rho}{a}\right] - d.$$

Notice λ_1 is always negative, and λ_2 is negative if and only if $d > \frac{b\mu}{a} + \frac{br}{aK} \left[K\left(1 - \frac{\mu}{r}\right) - \frac{\rho}{a}\right]$. We find the trace and determinant and use the second-order Routh–Hurwitz criterion to determine the sign of the remaining eigenvalues of $\hat{J}(E_3)$. The trace and determinant are

$$\text{tr}(J(E_3)) = -\frac{\rho r}{aK} \text{ and } \det(J(E_3)) = \rho \left[r\left(1 - \frac{\rho}{aK}\right) - \mu\right]$$

The trace is always less than zero, and the determinant is

$$\begin{aligned}
 \det(J(E_3)) &= \rho \left[r\left(1 - \frac{\rho}{aK}\right) - \mu\right] > 0 \\
 &\Leftrightarrow \frac{\rho}{a} < K \left[1 - \frac{\mu}{r}\right]
 \end{aligned} \tag{9}$$

Recall (9) is the existence condition for E_3 . Hence E_3 is locally asymptotically stable (LAS) if and only if

$$\begin{aligned}
 \frac{d}{b} &> \frac{\mu}{a} + \frac{r}{aK} \left[K\left(1 - \frac{\mu}{r}\right) - \frac{\rho}{a}\right] \\
 &\Leftrightarrow \frac{\rho}{a} > K \left(1 - \frac{ad}{br}\right)
 \end{aligned}$$

We rewrite the local stability conditions in terms of R_Z and R_J : $mR_J + \frac{1-m}{R_J} > 1$, where $m = \frac{\mu}{r}$.

The Jacobian evaluated at E_4 is

$$J(E_4) = \begin{bmatrix} r\left(1 - \frac{ad}{br} - \frac{2z^*}{K}\right) & 0 & -az^* & 0 \\ \mu & -az^* & 0 & -\frac{\alpha u}{a} \\ \mu\left(\frac{ad}{b\mu} - 1\right) & 0 & 0 & \alpha \frac{\mu}{a} \left(1 - \frac{ad}{b\mu}\right) \\ 0 & bj^* & bj^* & 0 \end{bmatrix}$$

Let $A = r\left(1 - \frac{ad}{br} - \frac{2}{K}z^*\right)$. The characteristic equation is

$$\begin{aligned}
 p(\lambda) = & \lambda^4 + (az^* - A)\lambda^3 + \left[bj^* \alpha \frac{\mu}{a} \frac{ad}{b\mu} - az^* \left(A + \mu \left(1 - \frac{ad}{b\mu} \right) \right) \right] \lambda^2 \\
 & + \left[-bj^* \alpha \frac{\mu}{a} \frac{ad}{b\mu} A + \mu \left(\frac{ad}{b\mu} - 1 \right) z^* (\alpha bj^* + a^2 z^*) \right] \lambda \\
 & + \left[-Abj^* \alpha \mu z^* \left(\frac{ad}{b\mu} - 1 \right) \right] = 0.
 \end{aligned}
 \tag{10}$$

Now,

$$\begin{aligned}
 A &= r\left(1 - \frac{ad}{br} - \frac{2}{K}z^*\right) = r\left(\frac{ad}{br} - 1\right) \\
 &< 0 \text{ since } \frac{ad}{br} < 1.
 \end{aligned}$$

We use the fourth-order Routh–Hurwitz criterion to determine whether the roots of the polynomial have negative real part. The Routh–Hurwitz criterion holds without any additional conditions (as shown in Appendix B); therefore, E_4 is locally asymptotically stable whenever it exists.

A visual representation of the stability analysis is shown in Figs. 1 and 2. The existence and stability conditions for each equilibrium are summarized in Table 2 and can be rewritten in terms of R_Z, R_J and m as in Table 3. As can be seen most clearly in Fig. 2, in order for anthrax to persist, both R_Z and R_J must exceed 1. In that sense, we may say $R_0 = \max(R_Z, R_J)$, although the actual mean number of secondary anthrax infections per infected carcass at the edge of an outbreak is given by whichever of the two is indicated by the presence or absence of scavengers.

3.4. Global stability analysis

A partial global stability analysis is completed for the full four-dimensional system. We first consider the reduced systems. It is easiest to build up to the global behavior of the full model from the subsystems involving anthrax but no scavengers. We look at global stability in the ZC and ZUC systems, respectively. We show that the equilibria in both systems are globally stable, that is, the solutions of the system are tending towards an equilibrium regardless of the initial conditions.

3.4.1. ZC system global stability analysis

The ZC system is the following:

$$z' = rz\left(1 - \frac{Z}{K}\right) - \mu z - acz
 \tag{11}$$

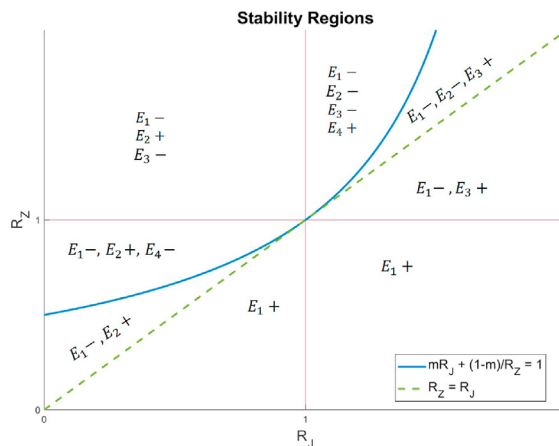


Fig. 1. Stability Regions. The regions of stability are given by the threshold conditions $R_Z = 1, R_J = 1, R_Z = R_J$ and $mR_J + \frac{1-m}{R_Z} = 1$, where $m = 0.5$ in this plot. If E_i ($i = 1, 2, 3, 4$) is present, then it means that equilibrium E_i exists in that region. The $-$ after the E_i means that it is not LAS in that region, whereas $+$ means that equilibrium E_i is LAS.

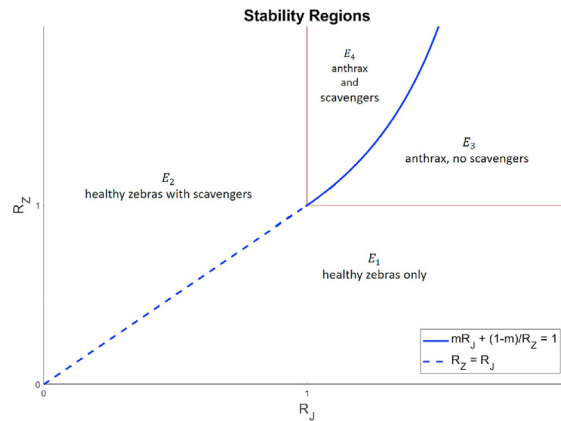


Fig. 2. Stability Regions with descriptions. Only the regions where there is a change in which equilibrium is stable are distinguished. In addition, a short description of the equilibrium is given.

Table 2 Summary of equilibria and local stability in terms of the parameters.

Equilibrium	Interpretation	Existence	Locally Asymptotically Stable
$E_0(0, 0, 0, 0)$	extinction	Always	$\mu > r$
$E_1\left(K\left[1 - \frac{\mu}{r}\right], \frac{\mu}{a}K\left[1 - \frac{\mu}{br}\right], 0, 0\right)$	no anthrax, no scavengers	$\mu < r$	$\frac{z^*}{a} < \frac{\rho}{a}$ & $b\mu z^* < \rho d$
$E_2\left(K\left[1 - \frac{\mu}{r}\right], 0, 0, \frac{\mu}{a}\left[1 - \frac{\mu}{br}\right]\right)$	no anthrax, scavengers	$\mu < r$ & $b\mu z^* > \rho d$	$\frac{z^*}{a} < 1$
$E_3\left(\frac{\rho}{a}, \frac{\mu}{r}, \frac{\mu}{a}, \frac{\mu}{a}\left[1 - \frac{\rho}{ad}\right]\right)$	anthrax, no scavengers	$\frac{\mu}{a} < r$ & $K\left[1 - \frac{\mu}{br}\right] > \frac{\rho}{ad}$	$\frac{b\mu}{a} > K\left[1 - \frac{ad}{br}\right]$
$E_4\left(\frac{\rho}{a}, \frac{\mu}{a}, \frac{\mu}{a}, \frac{\mu}{a}\left[1 - \frac{ad}{br}\right] - \frac{\rho}{a}\right)$	anthrax, scavengers	$\frac{\mu}{a} < K\left[1 - \frac{ad}{br}\right]$ & $\frac{\mu}{b\mu} > 1$	Whenever it exists

Table 3 Summary of equilibria and local stability in terms $m = \frac{\mu}{r}$, $R_z = \frac{aK(1-m)}{\rho}$, $R_j = \frac{ad}{b\mu}$, $D(E_1) = \frac{b\mu}{\rho d}K(1-m)$, and $D(E_3) = \frac{br}{ad}\left(1 - \frac{\rho}{aK}\right)$.

Equilibrium	Existence	Locally Asymptotically Stable
$E_0(0, 0, 0, 0)$	always	$m > 1$
$E_1\left(K[1-m], \frac{\mu}{a}K[1-m], 0, 0\right)$	$m < 1$	$R_z < 1$ & $D(E_1) < 1$ ($R_z < R_j$)
$E_2\left(K[1-m], 0, 0, \frac{\mu}{a}\left[1 - \frac{\rho}{ad}\right]\right)$	$m < 1$ & $D(E_1) > 1$ ($R_z > R_j$)	$R_j < 1$
$E_3\left(\frac{\rho}{a}, \frac{\mu}{r}, \frac{\mu}{a}, \frac{\mu}{a}\left[1 - \frac{\rho}{ad}\right]\right)$	$m < 1$ & $R_z > 1$	$D(E_3) < 1$ ($mR_j + \frac{1-m}{R_z} > 1$)
$E_4\left(\frac{\rho}{a}, \frac{\mu}{a}, \frac{\mu}{a}, \frac{\mu}{a}\left[1 - \frac{ad}{br}\right] - \frac{\rho}{a}\right)$	$m < 1$ & $D(E_3) > 1$ ($mR_j + \frac{1-m}{R_z} < 1$) & $R_j > 1$	whenever it exists

Table 4 Parameter table with values. Units in $\frac{1}{week}$ except as noted. The three parameters for scavengers are b , d , and α . A subscript of j is the parameter value for jackals and a subscript of v is for vultures.

Symbol	Description	Value	Source
K	zebra carrying capacity (zebras)	13000–15000	(Zidon et al., Saltz)
R	intrinsic growth rate of zebras	3.06849×10^{-3}	This study
M	natural zebra death rate	7.67123×10^{-4}	This study
A	rate zebras come into contact with infected carcasses ($week \cdot zebras$) ⁻¹	1.1433×10^{-5}	This study
P	natural decomposition rate of zebra carcasses	0.12727	Jennelle et al. (2009)
α_j	rate jackals come into contact with carcasses to eat ($week \cdot jackals$) ⁻¹	0.03608	This study
b_j	birth rate of jackals ($week \cdot zebras$) ⁻¹	0.051811	This study
d_j	death rate of jackals	4.808×10^{-3}	Rhodes et al. (1998)
α_v	rate vultures come into contact with carcasses to eat ($week \cdot vultures$) ⁻¹	0.01927	Houston and Cooper, (1975)
b_v	birth rate of vultures ($time \cdot zebras$) ⁻¹	0.00959	This study
d_v	death rate of vultures	9.615×10^{-4}	Cardona et al. (2008)

$$c' = acz - \rho c \tag{12}$$

This system has three equilibria

$$E_0(0, 0), E_1\left(K\left[1 - \frac{\mu}{r}\right], 0\right), \text{ and } E_2\left(\frac{\rho}{a}, \frac{r}{aK}\left[K\left[1 - \frac{\mu}{r}\right] - \frac{\rho}{a}\right]\right)$$

To determine global asymptotic stability (GAS) of the equilibria we use the Poincaré–Bendixson Theorem. First we show that there are no limit cycles by Dulac’s Criterion.

Let $\beta(z, c) = \frac{1}{zc} \in C^1$ in $D = \{(z, c) \in \mathbb{R}^2 : z, c > 0\}$. Then

$$\frac{\partial}{\partial z}\left(\frac{1}{zc} \cdot z\left[r\left(1 - \frac{z}{K}\right) - \mu - ac\right]\right) + \frac{\partial}{\partial c}\left(\frac{1}{zc} \cdot c[az - \rho]\right) = \frac{-r}{cK} < 0$$

in D . Therefore, by Dulac’s Criterion there are no limit cycles in D .

To show that the solutions are bounded, a bounding box is found. The solutions are bounded between the c -axis, z -axis and the line

$$z + c = K\left(1 - \frac{\mu}{r}\right)\left[1 + \frac{r}{4\rho}\left(1 - \frac{\mu}{r}\right)\right] \tag{13}$$

when $E_2\left(\frac{\rho}{a}, \frac{r}{aK}\left[K\left(1 - \frac{\mu}{r}\right) - \frac{\rho}{a}\right]\right)$ exists.

To obtain the line in (13), notice that

$$(z + c)' = rz\left(1 - \frac{\mu}{r}\right) - \mu z - \rho c < 0$$

when

$$\frac{1}{\rho}\left[rz\left(1 - \frac{z}{K}\right) - \mu z\right] < c.$$

Let $g(z) = \frac{1}{\rho}\left[rz\left(1 - \frac{z}{K}\right) - \mu z\right]$. Therefore, if $c > g(z)$ then $(z + c)' < 0$. Hence everything above $g(z)$ will decrease. Note that $g(z)$ is a parabola, where $E_0(0, 0)$ and $E_1\left(K\left[1 - \frac{\mu}{r}\right], 0\right)$ are the z -intercepts and the vertex is

$$\left(\frac{K}{2}\left(1 - \frac{\mu}{r}\right), \frac{rK}{4\rho}\left(1 - \frac{\mu}{r}\right)^2\right)$$

We add the z -component of E_1 and the c -component of the vertex to get the line (13). Hence solutions are bounded; by the Poincaré–Bendixson Theorem, all solutions tend toward an equilibrium point, so, for $\mu < r$.

- $E_0(0, 0)$ is unstable
- $E_1\left(K\left[1 - \frac{\mu}{r}\right], 0\right)$ is GAS iff $K\left(1 - \frac{\mu}{r}\right) < \frac{\rho}{a}$
- $E_2\left(\frac{\rho}{a}, \frac{r}{aK}\left[K\left(1 - \frac{\mu}{r}\right) - \frac{\rho}{a}\right]\right)$ is GAS iff $K\left(1 - \frac{\mu}{r}\right) > \frac{\rho}{a}$.

3.4.2. ZUC system global stability analysis

The ZUC system is

$$z' = rz\left(1 - \frac{z}{K}\right) - \mu z - acz \tag{14}$$

$$u' = \mu z - \rho u \tag{15}$$

$$c' = acz - \rho c. \tag{16}$$

This system has three equilibria

$$E_0(0, 0, 0), E_1\left(K\left[1 - \frac{\mu}{r}\right], \frac{\mu}{\rho}K\left[1 - \frac{\mu}{r}\right], 0\right), \text{ and } E_2\left(\frac{\rho}{a}, \frac{\mu}{a}, \frac{r}{aK}\left[K\left[1 - \frac{\mu}{r}\right] - \frac{\rho}{a}\right]\right)$$

Notice that (14) and (16) decouple from (15), so we study those first. We already studied the ZC system in section 3.4.1, and we know all solutions at any initial conditions tend toward some equilibrium, regardless of the parameter values. We use a

result by Thieme (Thiemia; Thiemeb), to say that the solutions of the ZUC system are asymptotic to the solutions of (15), where $z = z^*$ and $c = c^*$:

$$u(t) = \frac{\mu z^*}{\rho} + ke^{-\rho t}, \tag{17}$$

where k is a constant. As $t \rightarrow \infty$ we get the u^* values in E_1 and E_2 with the respective z^* plugged in. Therefore, because ZC decouple from U, the solutions to the ZUC system are tending towards an equilibrium and hence are globally stable.

3.4.3. ZUCJ system global stability analysis

The disease-free equilibrium in the absence of scavengers is globally asymptotically stable if $R_Z < 1$ and $D(E_1) < 1$ holds. Notice that, from (1), $z' \leq rz(1 - \frac{z}{K}) - \mu z$. Note that, for $\mu < r$, $z' = rz(1 - \frac{z}{K}) - \mu z$ has a globally stable equilibrium value of $z^* = K(1 - \frac{\mu}{r})$. Then $\limsup z \leq K(1 - \frac{\mu}{r})$. Consider (2) without jackals; then $u' \leq \mu z - \rho u$, and substituting in z^* , $\limsup u \leq \frac{\mu}{\rho}K(1 - m)$. Thus $\limsup u \leq \frac{\mu}{\rho}K(1 - m)$.

Consider (3) without jackals. We have $c' \leq (az - \rho)c$. Substituting in z^* we have $\limsup c' \leq (a\frac{\mu}{\rho}K(1 - \frac{\mu}{r}) - \rho)c$. If $a\frac{\mu}{\rho}K(1 - \frac{\mu}{r}) - \rho < 0$, which is equivalent to $R_Z < 1$, then c approaches zero. In the case where $c = 0$, (4) is $j' \leq (bu - d)j$. Since u is bounded above, we have $\limsup j' \leq j(b\frac{\mu}{\rho}K(1 - \frac{\mu}{r}) - d)$. If $b\frac{\mu}{\rho}K(1 - \frac{\mu}{r}) - d < 0$, which is equivalent to $D(E_1) < 1$ (see next section), then j goes to zero. If $R_Z < 1$ and $D(E_1) < 1$, then j approaches zero and we reduce to the ZU system, which tends towards a unique equilibrium.

4. Scavenger demographic reproductive numbers

We find the scavenger persistence threshold by calculating the scavenger demographic reproduction numbers. We want to determine if the scavengers help or hurt the anthrax and if the anthrax helps or hurts the scavengers. To answer these questions we look at the scavenger demographic reproductive number (DRN) evaluated through a next-generation-operator-type method. The DRN is the birth rate divided by death rate of the scavengers or the birth rate multiplied by how long the scavengers reproduce (they reproduce for their entire lives, so it is the death rate). We have two scavenger-free equilibria—one without anthrax (E_1) and one with anthrax (E_3)—so we have two different thresholds for when scavengers persist in the absence of anthrax $D(E_1)$ and in the presence of anthrax $D(E_3)$.

Using the next-generation-operator method (Brauer & Castillo-Chavez, 2011), the demographic reproduction number for scavengers in the absence of anthrax is calculated. That is,

$$D(E_1) = \frac{b(u^* + c^*)}{d}_{E_1} = \frac{b\mu}{\rho d}K\left(1 - \frac{\mu}{r}\right)$$

Notice that

$$D(E_1) > 1 \Leftrightarrow \frac{b\mu}{\rho d}K\left(1 - \frac{\mu}{r}\right) > 1 \Leftrightarrow b\mu K\left(1 - \frac{\mu}{r}\right) > \rho d \Leftrightarrow b\mu z^* > \rho d,$$

which is a condition for E_1 to be unstable and for E_2 to exist. In addition,

$$\begin{aligned} R_Z > R_J &\Leftrightarrow \frac{aK\left(1 - \frac{\mu}{r}\right)}{\rho} > \frac{ad}{b\mu} \\ &\Leftrightarrow b\mu K\left(1 - \frac{\mu}{r}\right) > \rho d \\ &\Leftrightarrow b\mu z^* > \rho d \\ &\Leftrightarrow D(E_1) > 1. \end{aligned}$$

Therefore, $D(E_1) > 1$ is equivalent to $R_J < R_Z$. The presence of scavengers hurts anthrax if and only if scavengers can persist without anthrax present.

The DRN of scavengers in the presence of anthrax is given below:

$$\begin{aligned} D(E_3) &= \frac{b(u^* + c^*)}{d} E_3 \\ &= \frac{b}{d} \left(\frac{\mu}{a} + \frac{r}{aK} \left[K \left(1 - \frac{\mu}{r} \right) - \frac{\rho}{a} \right] \right) \\ &= \frac{br}{ad} \left(1 - \frac{\rho}{aK} \right) \end{aligned}$$

Notice that

$$D(E_3) > 1 \Leftrightarrow \frac{br}{ad} \left(1 - \frac{\rho}{aK} \right) > 1 \Leftrightarrow 1 - \frac{\rho}{aK} > \frac{ad}{br} \Leftrightarrow \frac{\rho}{a} < K \left(1 - \frac{ad}{br} \right)$$

Thus $D(E_3) > 1$ is a condition for E_4 to exist and E_3 to be unstable. In addition,

$$\begin{aligned} mR_J + \frac{1-m}{R_Z} < 1 &\Leftrightarrow \frac{\mu}{r} \frac{ad}{b\mu} + \left(1 - \frac{\mu}{r} \right) \frac{\rho}{aK \left(1 - \frac{\mu}{r} \right)} < 1 \\ &\Leftrightarrow 1 < \frac{br}{ad} \left(1 - \frac{\rho}{aK} \right) \\ &\Leftrightarrow D(E_3) > 1 \end{aligned}$$

Thus $D(E_3) > 1$ is equivalent to $mR_J + \frac{1-m}{R_Z} < 1$, which implies $R_J < R_Z$.

To see whether anthrax helps the scavengers, we show that anthrax increases the scavenger population precisely when $\frac{ad}{br}$ is less extreme (closer to 1/2) than m .

Theorem 1. Let $m = \frac{\mu}{r}$. Then $J_4^* > J_2^*$ if and only if $\varphi = \frac{ad}{br}$ is between m and $1 - m$.

Proof. Let $\varphi = \frac{ad}{br}$. Then

$$\begin{aligned} J_4^* > J_2^* &\Leftrightarrow \frac{aK}{\alpha} \left(1 - \frac{ad}{br} \right) - \frac{\rho}{\alpha} > \frac{b\mu}{\alpha d} K \left(1 - m \right) \\ &\Leftrightarrow \frac{ad}{br} \left(1 - \frac{ad}{br} \right) > \frac{\mu}{r} (1 - m) \\ &\Leftrightarrow \varphi(1 - \varphi) > m(1 - m) \\ &\Leftrightarrow (\varphi - m)(\varphi + m - 1) < 0. \end{aligned}$$

If $m > \frac{1}{2}$ then $1 - m < \frac{ad}{br} < m$, and if $m < \frac{1}{2}$ then $m < \frac{ad}{br} < 1 - m$. Hence $\frac{ad}{br}$ is between m and $1 - m$.

Next, we look at when the scavenger DRN with anthrax is higher than the scavenger DRN without anthrax.

Theorem 2. $D(E_3) > D(E_1)$ if and only if $p(1 - p) > m(1 - m)$, where $p = \frac{\rho}{aK}$ and $m = \frac{\mu}{r}$.

Proof. We have

$$\begin{aligned} D(E_3) > D(E_1) &\Leftrightarrow \frac{br}{ad} \left(1 - \frac{\rho}{aK} \right) > \frac{b\mu}{\rho d} K \left(1 - \frac{\mu}{r} \right) \\ &\Leftrightarrow p(1 - p) > m(1 - m) \end{aligned}$$

Therefore, $D(E_3) > D(E_1)$ if and only if $p(1 - p) > m(1 - m)$. Furthermore,

$$p(1 - p) > m(1 - m) \Leftrightarrow (p - m)(p + m - 1) < 0.$$

If $m > \frac{1}{2}$ then $1 - m < p < m$, and if $m < \frac{1}{2}$ then $m < p < 1 - m$. Hence p is between m and $1 - m$.

The values m , φ and p are death-rate-to-birth-rate ratios for zebras, scavengers, and anthrax. The ratio $p = \frac{\rho}{aK}$ describes the natural spore-source decay to spore creation, $m = \frac{\mu}{r}$ is the ratio of natural zebra death to reproduction, and $\varphi = \frac{ad}{br}$ is some measure of natural scavenger death rate to birth rate. The values for $D(E_1)$ and $D(E_3)$ tell us whether the scavengers will persist, whereas J_4^* and J_2^* give the number of scavengers that persist. From [Theorems 1 and 2](#), anthrax helps scavengers persist if and only if p is less extreme (closer to 1/2) than m , and increases the scavenger population if and only if φ is less extreme than m .

If the reproductive number with scavengers (R_j) is less than the reproductive number without scavengers (R_z) then that means scavengers are hurting the reproductive number R_z (reducing anthrax). Therefore, scavenger presence reduces anthrax exactly when scavengers persist without the anthrax present (at E_1 and E_3 there is no anthrax), and if the scavengers do not need the anthrax to persist, then their presence reduces anthrax.

5. Numerical analysis

We find parameter values either from previous literature or by estimation. The basic reproductive numbers for anthrax without scavengers, with jackals, and with vultures are denoted R_z , R_j , and R_v , respectively. We consider two different scenarios of parameter values and interpret the values for R_z , R_j , and R_v .

5.1. Parameter estimation

Some of the parameter values were obtained from previously published papers, while the others were estimated in this study.

The life expectancy of zebras is 15 years according to (Bartlam-Brooks et al., 2011) or 30 years according to (He et al., 2014). We picked 25 years as the life expectancy. After converting years to weeks we get $\mu = \frac{1}{1300} \text{weeks}^{-1}$. The intrinsic growth rate was determined by figuring out how many babies a female zebra will have in her lifetime. Zebras are reproductively mature at the age of 4 (Millar & Zammuto, 1983) and have one baby every two years, because they will spend up to a year nursing (He et al., 2014). We will say a zebra aged 21–25 years is too old to reproduce and therefore a female zebra will have 16 years to bear a foal. Therefore, an average female zebra will have eight babies in her lifetime. Finally, we account for only female zebras giving birth by considering only half of the population. Thus we get

$$r = \frac{1}{2} \cdot \frac{8 \text{ zebra}}{\text{zebra} \cdot 25 \text{ years}} \cdot \frac{1 \text{ year}}{52 \text{ weeks}} = 3.06849 \times 10^{-3} \text{ week}^{-1}.$$

To calculate the parameter a , we find the area within which zebras travel (Zidon et al., Saltz) and figure out the exposure area that one zebra covers in a single day, which is distance multiplied by 6 m (the spore dispersal radius around an infected carcass is 3 m in the environment (Bellan et al., 2013)). Then we divide those two areas and the quotient estimates how many days it takes a zebra to be exposed to the entire zebra habitat. Next, we divide that number by two because on average the zebra has to cover half of the habitat before running into a single carcass. Moreover, this is because any one carcass can be in any one of the days with equal probability, so the average is halfway.

The natural decomposition rate of zebra carcasses was taken from (Jennelle et al., 2009), which gave the decomposition rate of deer carcasses in winter months in Wisconsin. The warmest month in the study was used as a proxy for the natural decomposition rate of zebra carcasses.

Jackals have a life expectancy of 4 years in the wild (Rhodes et al., 1998). Converting 4 years to weeks, we get the natural death rate of jackals as

$$d_j = \frac{1}{4 \text{ years}} \cdot \frac{1 \text{ year}}{52 \text{ weeks}} = 4.80769 \times 10^{-3} \text{ week}^{-1}.$$

Now, we calculate b_j . Coyotes eat 2.5 pounds per day (Bolton, 2017). The average weight of an adult male coyote is 10.3–16 kg (22.71–35.27 pounds), whereas it is 8–14.2 kg (17.64–31.31 pounds) for an adult female coyote (Bekoff & Gese, 2003, p. 224). A black-backed jackal weighs 5–15 kg (11–33 pounds) (James et al., 2017). We suppose that coyotes weigh 30 pounds and jackals weigh 17 pounds for the remaining calculations. Using the previous information, we calculate the amount of food a black-backed jackal needs to eat, that is,

$$\frac{2.5 \text{ pounds}}{\text{day}} \cdot \frac{17 \text{ pounds}}{30 \text{ pounds}} = 1.42 \text{ pounds per day}.$$

One zebra contains 120–130 kg of useable meat (Nel, 2017). We will choose the average and work with 125 kg (275 pounds). We can find how many days it would take for a jackal to eat a zebra carcass (only considering useable meat):

$$\frac{275 \text{ lbs}}{\text{zebra}} \cdot \frac{\text{day}}{1.42 \text{ lbs}} \approx \frac{194 \text{ days}}{\text{zebra}} \approx \frac{27 \text{ weeks}}{\text{zebra}}.$$

Hence $\alpha_j = 1/27 \text{ jackal} \cdot \text{week}$. On average, 5.4 pups are born per year per jackal pair (Rhodes et al., 1998), so a single jackal produces 2.7 pups/year. Thus during the 194 days one jackal is eating one zebra carcass, it produces

$$\frac{1 \text{ year}}{365 \text{ days}} \cdot \frac{194.117 \text{ lbs}}{\text{zebra}} \cdot \frac{2.7 \text{ baby jackals}}{\text{year}} = \frac{1.4359 \text{ baby jackals}}{\text{zebra}}$$

Now,

$$b_j = \frac{1.4359 \text{ baby jackals}}{\text{zebra}} \cdot \frac{1}{27.714 \text{ week}} = 0.0051811 \frac{1}{\text{zebra} \cdot \text{week}}$$

Vultures have a life expectancy of 20 years (Cardona et al., 2008). Converting 20 years to weeks, we get the natural death rate of scavengers to be

$$d_v = \frac{1}{20 \text{ years}} \cdot \frac{1 \text{ year}}{52 \text{ weeks}} = 9.615 \times 10^{-4} \text{ week}^{-1}.$$

Vultures eat every 3–4 days, and their crop holds 1200 g (2.65 pounds) of food (Houston & Cooper, 1975). For calculations, we suppose vultures eat 2.65 pounds of food every 3.5 days.

Therefore, a vulture needs 0.757 pounds of food per day. We calculate how long it would take a vulture to eat a zebra. It would take 363.28 vulture days to eat a zebra carcass:

$$\frac{275 \text{ lbs}}{\text{zebra}} \cdot \frac{\text{day}}{0.757 \text{ lbs}} \approx \frac{363.28 \text{ days}}{\text{zebra}} \approx \frac{51.90 \text{ weeks}}{\text{zebra}}$$

Hence $\alpha_v = 1/51.90$ vulture · week. Since a pair of vultures produces one offspring every year per every two vultures (Johnson, 2018), a single vulture produces 0.5 baby vultures/year. Thus during the 363.28 days one vulture is eating one zebra carcass, it produces

$$\frac{1 \text{ year}}{365 \text{ days}} \cdot \frac{363.28 \text{ days}}{\text{zebra}} \cdot \frac{0.5 \text{ baby vultures}}{\text{year}} = \frac{0.4976 \text{ baby vultures}}{\text{zebra}}$$

Now,

$$b_v = \frac{0.4976 \text{ baby vultures}}{\text{zebra}} \cdot \frac{1}{51.90 \text{ vulture} \cdot \text{week}} = 0.00959 \frac{1}{\text{zebra} \cdot \text{week}}$$

5.2. Threshold quantities

We let all the parameter values be those that are set in Table 4 with $K = 13000$ zebras. We found that

$$R_Z = 0.876, R_J = 0.00138, \text{ and } R_V = 0.00149.$$

Notice that $R_J < R_V < R_Z < 1$. This means that any small outbreak of anthrax will die out in the presence of scavengers since $R_Z < R_J$ ($R_Z < R_V$) and $R_J < 1$ ($R_V < 1$). Furthermore, jackals eradicate anthrax better than vultures when there is a small outbreak since $R_J < R_V$.

If environmental conditions shift to increase zebras' exposure rate—for example, by reducing their grazing territory—then scavengers may become necessary to eliminate the spread of anthrax. With just a 15% increase in the parameter a , R_Z is just greater than one, and when a increases by 50%—that is, $a = 1.71495 \times 10^{-5}$ (zebras · week)⁻¹—we get

$$R_Z = 1.3138, R_J = 0.0020744, \text{ and } R_V = 0.0022414.$$

When a takes on this value, it means that we are looking at a smaller area that the zebras are roaming, which is 1600 km² vs 2400 km². Moreover, we could also view an increase in the parameter a as representing a greater distance that the spores diffuse around an anthrax-laden carcass, which could be spread by the wind or by some other natural means. Since $R_Z > 1$ and $R_J, R_V < 1$, the zebras need the scavengers present in order to control the anthrax. Therefore, the zebras benefit from the presence of scavengers.

6. Results and discussion

Previous modeling studies (Furniss & Hahn, 1981; Saad-Roy et al., 2017) of anthrax transmission in animal populations have focused on control strategies such as vaccination or carcass removal (in (Saad-Roy et al., 2017)) to help eradicate anthrax.

These policies are possible for livestock but not for wild animals. Our model looks at how scavengers affect the dynamics of anthrax in ungulates (zebras) in the wild.

We looked at the persistence of anthrax as measured by threshold quantities with and without scavengers. Anthrax persists whenever the basic reproductive numbers of anthrax with and without scavengers are greater than one. In Fig. 2, we can easily see that if either $R_Z < 1$ or $R_J < 1$, then there is no anthrax present and any small outbreaks will die out. In addition, when $R_J < R_Z$ (existence condition for E_2), this shows that the presence of scavengers is reducing the anthrax. Therefore, when the scavengers feed from the anthrax-laden carcasses (thus eating anthrax), this helps the zebras because the vegetative cells of BA will not sporulate and reside in the grass or on the ground to infect more zebras.

By definition, when the scavenger DRN without anthrax, $D(E_1)$, exceeds 1, then scavengers persist: E_1 is unstable and E_2 exists. When $D(E_3) > 1$, then scavengers persist in the presence of anthrax: E_3 is unstable and E_4 exists and is stable. The scavenger DRNs allow us to determine that the presence of scavengers hurts anthrax if and only if scavengers can persist in the absence of anthrax ($R_Z > R_J \Leftrightarrow D(E_1) > 1$). In addition, we show that the number of scavengers in the presence of anthrax (J_4^*) is higher than the number of scavengers in the absence of anthrax (J_2^*) precisely when the death rate to birth rate ratio of scavengers, $\varphi = \frac{ad}{br}$, is less extreme (closer to 1/2) than m . Furthermore, the scavenger DRN with anthrax is larger than the scavenger DRN without anthrax ($D(E_3) > D(E_1)$), so that the scavengers persist better in the presence of anthrax, precisely when the death to birth rate ratio for anthrax $p = \frac{p}{ak}$ is less extreme (closer to 1/2) than the ratio for zebras m . The DRNs allow us to answer the question: does anthrax help scavengers, in terms of the three death to birth rate ratios, for zebras (m), anthrax (p), and scavengers (φ)? Anthrax fosters scavenger survival if p is less extreme than m , and it increases the scavenger population size if φ is less extreme than m .

Notice that all the threshold quantities are independent of the parameter α , which describes the rate the scavengers feed from the zebra carcasses. Anthrax persistence (with and without scavengers) and the scavengers' ability to survive do not depend on the rate at which scavengers eat from zebra carcasses, but on how well they convert that consumption into reproduction.

When we consider the various calculations of BRNs in Section 5.2, we see that neither jackals nor vultures outperform the others substantially in eradicating anthrax. Note that the BRNs of the scavengers were both of a similar magnitude, but the BRN of anthrax without scavengers was about 650 times larger than the BRNs of the scavengers. Hence scavengers are effective at reducing anthrax risk.

One limitation to our model is the assumption that zebra carcasses are representative of the only food source for scavengers. In fact, scavengers play a more complex role in the food web. In addition, jackals have been observed attacking and killing a young adult springbok (Krofel, 2008). However, given scavengers' estimated efficiency in reducing anthrax risk, they are still helpful even if they are less dependent on zebras. Another limitation of the model is that scavengers will not necessarily eat from a fresh carcass and, therefore, the vegetative cells of the BA may have transformed into resistant spores. In this case, the scavengers can potentially play a role in helping to spread the anthrax rather than eradicating it, since spores have been found to pass through the digestive tract of vultures (Houston & Cooper, 1975). More broadly, there may be other sources of BA spores than [recent] carcasses, so this study addresses only the interplay between scavengers and anthrax transmission from an ongoing outbreak. In addition, the parameter estimates are rough, and some are not based on any direct measure of infection. It would be helpful for future field studies to gather more data on the mechanics of anthrax infection like the rate at which ungulates (zebras) come into contact with BA spores.

Declaration of competing interest

None.

Acknowledgements

The authors thank Dr. Gaik Ambartsoumian for his support on the development of this work.

Appendix A. Equilibrium Calculations

We calculate the equilibria and existence conditions. To get z^* for E_1 and E_2 we consider $z^* \neq 0$, and we have

$$z^* \left(r \left(1 - \frac{z^*}{K} \right) - (\mu + ac^*) \right) = 0,$$

$$\text{from which } z^* = K \left[1 - \frac{1}{r} (\mu + ac^*) \right]$$

Plugging this into (3) and setting (3) equal to zero we have

$$c^* \left(aK \left[1 - \frac{1}{r}(\mu + ac^*) \right] - \rho - \alpha j^* \right) = 0.$$

Then either

$$c_+^* = 0 \text{ or } c_-^* = \frac{r}{a} \left[1 - \frac{\mu}{r} - \frac{\rho - \alpha j^*}{aK} \right] = \frac{r}{aK} \left[K \left(1 - \frac{\mu}{r} \right) - \frac{\rho + \alpha j^*}{a} \right]$$

Replacing c^* with c_+^* in z^* we have

$$z_+^* = K \left[1 - \frac{\mu}{r} \right]$$

Likewise, replacing c^* with c_-^* in z^* gives

$$\begin{aligned} z_-^* &= K \left[1 - \frac{1}{r} \left(\mu + \frac{ar}{a} \left[1 - \frac{\mu}{r} - \frac{\rho + \alpha j^*}{aK} \right] \right) \right] \\ &= K \left[\frac{\rho + \alpha j^*}{aK} \right] \\ &= \frac{\rho + \alpha j^*}{a}. \end{aligned}$$

Setting (2) equal to zero gives u^* :

$$\begin{aligned} \mu z^* - \rho u^* - \alpha j^* u^* &= 0 \\ u^* &= \frac{\mu z^*}{\rho + \alpha j^*}; \end{aligned}$$

with (4) equal to zero, we have either $j^* = 0$ or else

$$\begin{aligned} bj^*(u^* + c^*) - dj^* &= 0 \\ u^* + c^* &= \frac{d}{b}. \end{aligned}$$

Substituting c_+^* into this last equation gives

$$u_+^* = \frac{d}{b}.$$

Finally, plugging z_+^* and u_+^* into $u^* = \frac{\mu z^*}{\rho + \alpha j^*}$ we find

$$\begin{aligned} \frac{d}{b}(\rho + \alpha j_+^*) &= \mu z_+^*, \\ \text{from which } j_+^* &= \frac{1}{\alpha} \left[\frac{b\mu}{d} z_+^* - \rho \right] \end{aligned}$$

Therefore, we have the equilibrium

$$E_2(z_+^*, u_+^*, c_+^*, j_+^*) = E_2 \left(K \left[1 - \frac{\mu}{r} \right], \frac{d}{b}, 0, \frac{1}{\alpha} \left[\frac{b\mu}{d} z_+^* - \rho \right] \right),$$

which exists when $\mu < r$ and $b\mu z_+^* > \rho d$. The equilibrium E_2 is the disease-free equilibrium in the presence of scavengers. Consider when $c_+^* = 0$, so that $z_+^* = K \left[1 - \frac{\mu}{r} \right]$. Letting $j^* = 0$,

$$u^* = \frac{\mu}{\rho} K \left[1 - \frac{\mu}{r} \right]$$

Therefore, we have the equilibrium

$$E_1(z^*, u^*, c^*, j^*) = E_1\left(K\left[1 - \frac{\mu}{r}\right], \frac{\mu}{\rho}K\left[1 - \frac{\mu}{r}\right], 0, 0\right),$$

which exists when $\mu < r$. The equilibrium E_1 is the disease-free equilibrium in the absence of scavengers.

Now, working with the negative subscript equilibria, we consider $z^* = \frac{\rho + \alpha j^*}{a}$ and get

$$c^* = \frac{r}{a} \left[1 - \frac{\mu}{r} - \frac{\rho + \alpha j^*}{aK}\right] = \frac{r}{aK} \left[K\left(1 - \frac{\mu}{r}\right) - \frac{\rho + \alpha j^*}{a}\right] \tag{A.1}$$

to find u^* and j^* . First, we let $j^* = 0$. Then $z^* = (\rho + \alpha j^*)/a$ becomes $z^* = \rho/a$, (A.1) becomes

$$c^* = \frac{r}{aK} \left[K\left(1 - \frac{\mu}{r}\right) - \frac{\rho}{a}\right],$$

and u^* becomes

$$u^* = \frac{\mu\rho}{\rho a} = \frac{\mu}{a}.$$

Thus we have the equilibrium

$$E_3(z^*, u^*, c^*, j^*) = E_3\left(\frac{\rho}{a}, \frac{\mu}{a}, \frac{r}{aK} \left[K\left(1 - \frac{\mu}{r}\right) - \frac{\rho}{a}\right], 0\right),$$

which exists when $\mu < r$ and $K\left(1 - \frac{\mu}{r}\right) > \frac{\rho}{a}$. The equilibrium E_3 is endemic for anthrax in the absence of scavengers.

When $j^* \neq 0$, then using $z^* = (\rho + \alpha j^*)/a$ and (A.1), $u^* + c^* = d/b$ becomes

$$u^* = \frac{d}{b} - \frac{r}{a} \left[1 - \frac{\mu}{r} - \frac{\rho + \alpha j^*}{aK}\right] \tag{A.2}$$

Substituting $z^* = (\rho + \alpha j^*)/a$ and (A.2) into (2) and setting it equal to zero gives:

$$\begin{aligned} 0 &= \frac{\mu(\rho + \alpha j^*)}{a} - \rho \left[\frac{d}{b} - \frac{r}{a} \left(1 - \frac{\mu}{r} - \frac{\rho + \alpha j^*}{aK}\right) \right] - \alpha j^* \left[\frac{d}{b} - \frac{r}{a} \left(1 - \frac{\mu}{r} - \frac{\rho + \alpha j^*}{aK}\right) \right] \\ 0 &= \frac{\alpha^2 r j^{2*}}{a^2 K} + \alpha \left[\frac{d}{b} - \frac{r}{a} \left(1 - \frac{2\rho}{aK}\right) \right] j^* + \frac{\rho r}{a} \left[\frac{ad}{br} + \frac{\rho}{aK} - 1 \right] \end{aligned}$$

Consider the quadratic formula, where the quadratic is represented as $Aj^2 + Bj + C = 0$. If $AC < 0$, then a unique positive root exists. In this problem, that means $C < 0$ since $A > 0$. The condition can be further rewritten:

$$\begin{aligned} C < 0 &\Leftrightarrow \frac{\rho}{aK} + \frac{ad}{br} < 1 \\ &\Leftrightarrow \frac{\rho}{a} < K\left(1 - R_j \frac{\mu}{r}\right), \end{aligned} \tag{A.3}$$

where $R_j = \frac{ad}{b\mu}$ and is discussed in Section 3.2.

The quadratic equation has two positive roots if $C > 0$, $B < 0$ and $B^2 > 4AC$. For our problem, we have

$$C > 0 \Leftrightarrow \frac{\rho}{aK} + \frac{ad}{br} > 1 \tag{A.4}$$

and

$$\begin{aligned} B < 0 &\Leftrightarrow \frac{ad}{ba} - \frac{rb}{ba} \left(1 - \frac{2\rho}{aK}\right) < 0 \\ &\Leftrightarrow \frac{2\rho}{aK} + \frac{ad}{br} < 1. \end{aligned} \tag{A.5}$$

However, conditions (A.4) and (A.5) contradict each other; therefore, our quadratic equation must have only one positive root, which occurs with condition (A.3).

From the quadratic equation for j^* , we get

$$\begin{aligned}
 j^* &= \frac{-\alpha \left[\frac{d}{b} - \frac{r}{a} \left(1 - \frac{2\rho}{aK} \right) \right] + \sqrt{\left[\alpha \left[\frac{d}{b} - \frac{r}{a} \left(1 - \frac{2\rho}{aK} \right) \right] \right]^2 - \frac{4\alpha^2 r}{a^2 K} \frac{\rho r}{a} \left[\frac{ad}{br} + \frac{\rho}{aK} - 1 \right]}}{\frac{2\alpha^2 r}{a^2 K}} \\
 &= \frac{abK r \alpha + a^2 K \left(-d\alpha + b \sqrt{\frac{(ad - br)^2 \alpha^2}{a^2 b^2}} \right) - 2br\alpha\rho}{2br\alpha^2} = \frac{a}{\alpha} \left[K \left(1 - \frac{ad}{br} \right) \right] - \frac{\rho}{\alpha}.
 \end{aligned}
 \tag{A.6}$$

Substituting (A.6) into $z^* = (\rho + \alpha j^*)/a$ we get the expression for z^* in E_4 which is

$$\begin{aligned}
 z^* &= \frac{\rho}{a} + \frac{\alpha j^*}{a} \\
 &= \frac{\rho}{a} + \frac{\alpha}{a} \left[\frac{a}{\alpha} \left[K \left(1 - \frac{ad}{br} \right) \right] - \frac{\rho}{\alpha} \right] \\
 &= K \left(1 - \frac{ad}{br} \right)
 \end{aligned}$$

The equilibrium E_4 is represented as

$$E_4(z^*, u^*, c^*, j^*) = E_4 \left(K \left[1 - \frac{ad}{br} \right], \frac{\mu}{a} \frac{d}{b} - \frac{\mu}{a} \frac{a}{\alpha} K \left[1 - \frac{ad}{br} \right] - \frac{\rho}{\alpha} \right)$$

and exists if and only if $\frac{\rho}{a} < K \left(1 - \frac{ad}{br} \right)$ and $\frac{ad}{b\mu} > 1$. This equilibrium is endemic for anthrax in the presence of scavengers.

Appendix B. Stability of E_4

We use the fourth-order Routh–Hurwitz Criterion to find the stability of E_4 . Consider the characteristic equation $p(\lambda) = \lambda^4 + B_1\lambda^3 + B_2\lambda^2 + B_3\lambda + B_4 = 0$. For the fourth-order Routh–Hurwitz criterion, the conditions are $B_1 > 0$, $B_4 > 0$, $B_1B_2 > B_3$, and $B_3(B_1B_2 - B_3) > B_1^2B_4$ for the roots of $p(\lambda)$ to have negative real part.

Let

$$\begin{aligned}
 B_1 &= (az^* - A) \\
 B_2 &= bj^* \alpha \frac{\mu}{a} \frac{ad}{b\mu} - az^* \left(A + \mu \left(1 - \frac{ad}{b\mu} \right) \right) \\
 B_3 &= -bj^* \alpha \frac{\mu}{a} \frac{ad}{b\mu} A + \mu \left(\frac{ad}{b\mu} - 1 \right) z^* (\alpha bj^* + a^2 z^*) \\
 B_4 &= -Abj^* \alpha \mu z^* \left(\frac{ad}{b\mu} - 1 \right)
 \end{aligned}$$

Now we will show that the conditions needed above hold.

$$B_1 = (az^* - A) > 0 \text{ since } A < 0.$$

$$B_4 = -Abj^* \alpha \mu z^* \left(\frac{ad}{b\mu} - 1 \right) > 0 \text{ (recall } \frac{ad}{b\mu} > 1 \text{ for } E_4 \text{ to exist)}$$

$$\begin{aligned}
 B_1 B_2 - B_3 &= (az^* - A)bj^* \alpha \frac{\mu}{a} \frac{ad}{b\mu} - az^* \left(A + \mu \left(1 - \frac{ad}{b\mu} \right) \right) \\
 &\quad - \left(-bj^* \alpha \frac{\mu}{a} \frac{ad}{b\mu} A + \mu \left(\frac{ad}{b\mu} - 1 \right) z^* (\alpha bj^* + a^2 z^*) \right) \\
 &= -A(az^*)^2 + A^2(az^*) - A(az^*)\mu \left(\frac{ad}{b\mu} - 1 \right) + \mu az^* \alpha \frac{bj^*}{a} \\
 &> 0 \quad \text{since } \frac{ad}{b\mu} > 1 \quad \text{and } A < 0.
 \end{aligned}$$

$$\begin{aligned}
 B_3(B_1 B_2 - B_3) - B_1^2 B_4 &= \left[-bj^* \alpha \frac{\mu}{a} \frac{ad}{b\mu} A + \mu \left(\frac{ad}{b\mu} - 1 \right) z^* (\alpha bj^* + a^2 z^*) \right] \\
 &\quad \times \left[-A(az^*)^2 + A^2(az^*) - A(az^*)\mu \left(\frac{ad}{b\mu} - 1 \right) + \mu az^* \alpha \frac{bj^*}{a} \right] \\
 &\quad - \left[(az^*)^2 + 2az^*(-A) + A^2 \right] \left[(-A)bj^* \alpha \frac{\mu}{a} (az^*) \left(\frac{ad}{b\mu} - 1 \right) \right] \\
 &= A^2 bj^* \alpha \frac{\mu}{a} (az^*)^2 + (-A)^3 bj^* \alpha \frac{\mu}{a} (az^*) + A^2 bj^* \alpha \frac{\mu}{a} (az^*) \mu \left(\frac{ad}{b\mu} - 1 \right) \frac{ad}{b\mu} \\
 &\quad + (-A)(bj^*)^2 \left(\alpha \frac{\mu}{a} \right)^2 (az^*) \frac{ad}{b\mu} + (-A)bj^* \alpha \frac{\mu}{a} (az^*)^2 \mu \left(\frac{ad}{b\mu} - 1 \right)^2 \\
 &\quad + (bj^*)^2 \left(\alpha \frac{\mu}{a} \right)^2 (az^*)^2 \left(\frac{ad}{b\mu} - 1 \right) + (-A)(az^*)^4 \mu \left(\frac{ad}{b\mu} - 1 \right) \\
 &\quad + A^2 (az^*)^3 \mu \left(\frac{ad}{b\mu} - 1 \right) + (-A)(az^*)^3 \mu^2 \left(\frac{ad}{b\mu} - 1 \right)^2 \\
 &\quad + (bj^*) \left(\alpha \frac{\mu}{a} \right) (az^*)^3 \mu \left(\frac{ad}{b\mu} - 1 \right) \\
 &> 0 \quad \text{since } \frac{ad}{b\mu} > 1 \quad \text{and } A < 0.
 \end{aligned}$$

We have shown that $B_1 > 0$, $B_4 > 0$, $B_1 B_2 > B_3$ and $B_3(B_1 B_2 - B_3) > B_1^2 B_4$ without any additional conditions; therefore, E_4 is locally asymptotically stable whenever it exists.

References

Bartlam-Brooks, H., Bonyongo, M., & Harris, S. (2011). Will reconnecting ecosystems allow long-distance mammal migrations to resume? A case study of a zebra *Equus burchelli* migration in Botswana. *Oryx*, 45(2), 210–216.

Bekoff, M., & Gese, E. M. (2003). *Coyote (Canis latrans)*. USDA National Wildlife Research Center-Staff Publications. URL https://digitalcommons.unl.edu/cgi/viewcontent.cgi?article=1218&context=icwdm_usdanwrc.

Bellan, S. E., Cizauskas, C. A., Miyen, J., Ebersohn, K., Küsters, M., Prager, K., Van Vuuren, M., Sabeta, C., & Getz, W. M. (2012). Black-backed jackal exposure to rabies virus, canine distemper virus, and *Bacillus anthracis* in Etosha National Park, Namibia. *Journal of Wildlife Diseases*, 48(2), 371–381.

Bellan, S. E., Turnbull, P. C., Beyer, W., & Getz, W. M. (2013). Effects of experimental exclusion of scavengers from carcasses of anthrax-infected herbivores on *Bacillus anthracis* sporulation, survival, and distribution. *Applied and Environmental Microbiology*, 79(12), 3756–3761.

Bolton, N. (2017). *Hunting the hunter: The coyote hunter's handbook*. CreateSpace Independent Publishing Platform.

Brauer, F., & Castillo-Chavez, C. (2011). *Mathematical models in population biology and epidemiology* (Vol. 40). Springer Science & Business Media.

Cardona, M., Colomer, M. A., Pérez-Jiménez, M. J., Sanuy, D., & Margalida, A. (2008). Modeling ecosystems using p systems: The bearded vulture, a case study. In *International workshop on membrane computing* (pp. 137–156). Springer.

Carlson, C. J., Getz, W. M., Kausrud, K. L., Cizauskas, C. A., Blackburn, J. K., Bustos Carrillo, F. A., Colwell, R., Easterday, W. R., Ganz, H. H., Kamath, P. L., et al. (2018). Spores and soil from six sides: Interdisciplinarity and the environmental biology of anthrax (*Bacillus anthracis*). *Biological Reviews*, 93(4), 1813–1831.

Carrasco-García, R., Barroso, P., Perez-Olivares, J., Montoro, V., & Vicente, J. (2018). Consumption of big game remains by scavengers: A potential risk as regards disease transmission in central Spain. *Frontiers in veterinary science*, 5, 4.

Furniss, P., & Hahn, B. (1981). A mathematical model of an anthrax epizootic in the Kruger National Park. *Applied Mathematical Modelling*, 5(3), 130–136.

He, L., Zhaozheng, W., Jinguo, Z., Zezhong, W., & Yue, W. (2014). Hand rearing common zebra (*Equus quagga*). *Animal Husbandry and Feed Science*, 6(1), 4.

Houston, D. C., & 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(3), 306–313.

Hugh-Jones, M., & De Vos, V. (2002). Anthrax and wildlife. *Revue Scientifique et Technique-Office International des Epizooties*, 21(1), 359–384.

James, R. S., Scott, D., Yarnell, R., & Overall, A. (2017). Food availability and population structure: How do clumped and abundant sources of carrion affect the genetic diversity of the black-backed jackal? *Journal of Zoology*, 301(3), 184–192.

- Jennelle, C. S., Samuel, M. D., Nolden, C. A., & Berkley, E. A. (2009). Deer carcass decomposition and potential scavenger exposure to chronic wasting disease. *Journal of Wildlife Management*, 73(5), 655–662.
- Johnson, T. F. (2018). Exceptional nest attendance and solo breeding attempt by an African White-backed Vulture. *Vulture News*, 74(1), 31–34.
- Krofel, M. (2008). Opportunistic hunting behaviour of black-backed jackals in Namibia. *African Journal of Ecology*, 46(2), 220.
- Lindeque, P., & Turnbull, P. (1994). Ecology and epidemiology of anthrax in the Etosha National Park, Namibia. *Onderstepoort Journal of Veterinary Research*, 61(1), 71–84.
- Millar, J. S., & Zammuto, R. M. (1983). Life histories of mammals: An analysis of life tables. *Ecology*, 64(4), 631–635.
- Nel, S. Expected harvest. URL <https://bowhunterscorner.com/2017/11/expected-harvest/>.
- Rhodes, C., Atkinson, R., Anderson, R., & Macdonald, D. (1998). Rabies in Zimbabwe: Reservoir dogs and the implications for disease control. *Philosophical Transactions of the Royal Society of London - Series B: Biological Sciences*, 353(1371), 999–1010.
- Saad-Roy, C., Van den Driessche, P., & Yakubu, A.-A. (2017). A mathematical model of anthrax transmission in animal populations. *Bulletin of Mathematical Biology*, 79(2), 303–324.
- H. Thieme, Convergence results and a Poincaré-Bendixson trichotomy for asymptotically autonomous differential equations, *Journal of Mathematical Biology* 30.
- H. Thieme, Asymptotically autonomous differential equations in the plane, *Rocky Mountain Journal of Mathematics* 24.
- Trinkel, M. (2010). Prey selection and prey preferences of spotted hyenas *Crocuta crocuta* in the Etosha National Park, Namibia. *Ecological Research*, 25, 413–417.
- Turner, W. C., Kausrud, K. L., Beyer, W., Easterday, W. R., Barandongo, Z. R., Blaschke, E., Cloete, C. C., Lazak, J., Van Ert, M. N., Ganz, H. H., et al. (2016). Lethal exposure: An integrated approach to pathogen transmission via environmental reservoirs. *Scientific Reports*, 6, 27311.
- R. Zidon, S. Garti, W. M. Getz, D. Saltz, Zebra migration strategies and anthrax in Etosha National Park, Namibia, *Ecosphere* 8 (8).