

MATHEMATICAL MODELING OF SCAVENGERS AND ZEBRAS ON THE  
AFRICAN SAVANNA WITH DISEASE DYNAMICS

by

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To God, my parents Donald and Linda,

And my sister Angela

Without whom none of my success would be possible.

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## ABSTRACT

# MATHEMATICAL MODELING OF SCAVENGERS AND ZEBRAS ON THE AFRICAN SAVANNA WITH DISEASE DYNAMICS

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The purpose of this dissertation is to use mathematical models to see how anthrax in the zebra population in Etosha National Park interacts with scavenger populations and disease dynamics. First, we study if scavengers can save zebras from anthrax. Then we introduce a disease in the jackal population to see if anthrax in zebras can help propagate rabies in jackals. Finally, the last two models we develop describe the interaction between competing scavengers: jackals and vultures, with exploitative and interference competition.

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 ENP, allowing for scavengers such as jackals or vultures to feed off these carcasses. The first model, uses a system of nonlinear differential equations to describe the population dynamics of how disease affects the populations of zebras, zebra carcasses, and scavengers. 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 reducing spread by orders of magnitude by eliminating potential infection zones for the zebras. 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.

The zebra carcasses provide a location of conspecific interaction between jackals and may be a means of disease transmission among the jackals. We study how a disease in the zebra population may help to propagate a different disease (rabies) in the jackal population since the carcasses are providing a location of interaction between the jackals. We aim to answer the following research question: how do anthrax and rabies affect each other ability to spread? Using standard qualitative analysis, we found that rabies helps anthrax, and a little anthrax helps rabies invade, but a high level of anthrax prevents rabies by reducing the jackal population through its food source.

There are multiple species of scavengers in ENP, and zebra carcasses provide a food source for facultative and obligate scavengers such as jackals and vultures, respectively. Since the jackals and vultures are competing for these carcasses we study the research question: how does the presence of jackals affect the presence of vultures, in the exploitative model. Analysis verified that classical exploitative competition allows vultures to survive only when they are better competitors than jackals. In addition, we found conditions when the vultures are hurt by the presence of anthrax, and a condition under which the competitive interference caused by vultures' aerial quick access to carrion allows them to persist even when jackals are better competitors. In fact, this extended survival can also allow anthrax to persist when it shouldn't.

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## CHAPTER 1

### Introduction

The majority of recently emerging human diseases, including those with environmental reservoirs, originate in animal populations, and it is estimated that 70% come from wildlife alone [1]. Anthrax is caused by *Bacillus anthracis* (BA) that essentially infects ungulates, whereas other mammals, like humans, tend to be incidental hosts [2]. Inside of Namibia's Etosha National Park (ENP) there are tourist camps that attracted over one million visitors in 2011 [3]. Every year rabid animals, mostly jackals are destroyed inside of the ENP tourist camps. Jackals not only feed on insects, fruit, carrion, but also on human food waste [4]. In addition, anthrax infected carcasses are found near the Okaukuejo tourist camp in ENP [4], so the transmission of rabies and anthrax animal deaths are occurring close to human campsites.

Anthrax is endemic in ENP and there are over two decades worth of data regarding anthrax outbreaks in bovids, elephants, zebras, and other mammals [2]. Between the years 1975 to 1990, there were 811 anthrax confirmed wildlife deaths in ENP, and there were an additional 704 suspected anthrax deaths [5]. In non-human animals, BA is transmitted orally, through the air, or through a cut in the skin [6]. Zebras largely contract anthrax by grazing near the location of a current or previous (no longer present) infected zebra carcasses [6].

ENP is home to several different types of scavengers including the black-backed jackal and lappet-faced vulture. Jackals are facultative scavengers meaning they eat other food sources besides carrion, like fruit and insects [4]. However, vultures are obligate scavengers meaning they only eat carrion.

We use mathematical models to see how anthrax in the zebra population in ENP interacts with scavengers and incorporate disease dynamics. These models consist of a system of nonlinear ordinary differential equations. In this dissertation, key analysis techniques such as equilibria stability analysis, bifurcation and qualitative analysis, and quantitative analysis are used to study each model.

Saad et al. [7], described anthrax transmission in animal populations using a system of ordinary differential equations. They looked at how anthrax transmits in a population of herbivorous livestock in one case, and then how anthrax transmits in a population of carnivores in another case. The authors reported that a vaccination policy or an animal carcass removal policy can be used to eradicate anthrax in the livestock herbivore model. However, a vaccination program for wildlife animals is nearly impossible and we study how scavengers can affect anthrax transmission, and vice versa.

Borchering et al. [8] developed a spatially explicit mathematical model to study how resource availability influences the rate of encounters among consumers. They specifically considered the zebra-anthrax and jackal dynamics in ENP. They found that when the number of zebra carcasses is low then the addition of more carcasses increases the jackal-jackal interactions. Whereas, when there is an abundance of zebra carcasses there is a decrease in jackal-jackal interactions thus the conspecific encounter rate has a maximum at an intermediate carcass density. Since these zebra carcasses are a shared resource for jackals this means the carcasses could be a possible location for a consumer disease like rabies in jackals to be transmitted. There are consumer-resource models [9, 10] that have studied conspecific encounter rates for consumers, and how the resources may indirectly facilitate infectious disease transmission in consumers. Therefore, we aim to study how rabies can be transmitted within the jackal population when the jackals interact at zebra carcasses in ENP.

A special type of consumer-resource model is predator-prey systems. There are several articles that describe predator-prey relationships, where either the predator has a disease [11, 12, 13, 14], or the prey has a disease [15, 16, 17, 18, 19]. In addition, there are some papers that model the same disease in both predator and prey species [20, 21], but there are no papers that have different diseases in both predator and prey, which we present in Chapter 3.

In this dissertation, we create models describing the interaction between zebras, jackals, and vultures. In Chapter 2, we develop a deterministic model to describe how disease affects the population of zebras, zebra carcasses, and scavengers. In Chapter 3, we design a model that considers the jackal-to-jackal interactions at the zebra carcasses and how rabies can spread depending on the number of zebra carcasses. In Chapter 4, we look at two different types of competition between an obligate and a facultative scavenger. In each chapter, standard quantitative analysis techniques for nonlinear differential equations determine outcomes using basic and demographic reproductive numbers.



## CHAPTER 2

### Can scavengers save zebras from anthrax? A modeling study

#### 2.1 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 km<sup>2</sup> and has a single wet and dry season each year with rain between November and April [4]. 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 and account for the most deaths [22]. Carnivores are less likely than herbivores to contract anthrax. Since 1975 to 2012, one jackal, three lions, nine cheetahs have died from anthrax [4]. 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 [22]. Today, ENP remains one of the most continuous sources of documented anthrax dynamics in any natural system [2]. 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 [23].

Anthrax is a zoonosis caused by *Bacillus anthracis* (BA) and mainly infects ungulates such as zebras, springbok and wildebeest [2]. 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 [24]. The bacteria can enter an animal through a skin abrasion, inhalation, or digestion, and leads to death in wildlife [25].

A study by Turner et al. [6] 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 it was found that carcass sites are more likely to be important sources of host-pathogen contacts than water sources [6]. Furthermore, although BA concentration at carcass sites in soil and on grasses decay 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 [6]. Previous studies [23, 26] suggest scavengers could help eliminate these pathogens from the environment that affect ungulates and be a major factor in determining the speed the disease can spread.

Houston et al. [27] 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 [27]. Other studies also support the survival of BA spores in the digestive tract of scavengers [22, 24]. 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.

Saad-Roy et al. [7] 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, and 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 natural means of anthrax removal to eradicate anthrax.

This leads us to our question and exploration of how scavengers help eliminate wildlife diseases. 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 anthrax-causing agent BA by feeding on zebras. 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 ‘eating’ anthrax.

This chapter is organized as follows: in Section 2.2 the model is developed and the existence conditions are found for each of the four equilibria. In addition, the basic reproductive numbers are calculated. In Section 2.3 the local stability conditions are determined. In Section 2.4, we look at reduced systems of our model and determine the global stability of those two systems. Finally, we end with a discussion of results and conclusion.

## 2.2 Model Development

The deterministic mathematical model in this paper uses a system of ordinary differential equations to describe the epidemic of anthrax among a population of zebras and scavengers.

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 has a logistic growth term and is removed by natural death  $(\mu z)$  or by disease-induced death  $(acz)$  from grazing near an anthrax infected carcass site [6]. The carcasses are either naturally decomposing at a rate  $\rho$  or are being eaten by scavengers at a rate of  $\alpha$ . 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  $d$ .

$$z' = rz \left(1 - \frac{z}{K}\right) - \mu z - acz \quad (2.1)$$

$$u' = \mu z - \rho u - \alpha ju \quad (2.2)$$

$$c' = acz - \rho c - \alpha jc \quad (2.3)$$

$$j' = bj(u + c) - dj \quad (2.4)$$

Scavengers eating anthrax laden carcasses are less likely than herbivores to contract the disease [4]. Therefore, we assume that scavengers will not die from anthrax. Moreover, we assume that scavengers do not attack living zebras; their only food source are zebra carcasses and they can not distinguish between a healthy or infected carcass. To simplify the food web for analysis, we assume zebras are representative of all scavenger food sources.

Symbol	Definition
$K$	carrying capacity ( <i>zebras</i> )
$r$	intrinsic growth rate of zebras
$\mu$	natural zebra death rate
$a$	rate zebras come into contact with infected carcasses ( <i>time · zebras</i> ) <sup>-1</sup>
$\rho$	natural decomposition rate of carcasses
$\alpha$	rate scavengers come into contact w/ carcasses to eat ( <i>time · scavengers</i> ) <sup>-1</sup>
$b$	birth rate of scavengers ( <i>time · zebras</i> ) <sup>-1</sup>
$d$	death rate of scavengers

Table 2.1: Parameter table. Units in  $\frac{1}{time}$  except as noted.

### 2.2.1 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 in this section are in Appendix A.1. We can see that  $E_0(0, 0, 0, 0)$  is an equilibrium because equations (2.1)-(2.4) are satisfied when  $(z^* = 0, u^* = 0, c^* = 0, j^* = 0)$ , which represents the extinction equilibrium. Considering  $z^* \neq 0$ , we have

$$z^* \left( r \left( 1 - \frac{z^*}{K} \right) - (\mu + ac^*) \right) = 0 \implies z^* = K \left[ 1 - \frac{1}{r} (\mu + ac^*) \right]. \quad (2.5)$$

Plugging (2.5) into (2.3) and setting (2.3) equal to zero we get a quadratic function in terms of  $c$ . When we solve for  $c$ , we get the following values:

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

Replacing  $c^*$  with  $c_+^*$  in (3.1) we have

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

Likewise, replacing  $c^*$  with  $c_-^*$  in (2.5) gives

$$z_-^* = \frac{\rho + \alpha j^*}{a}. \quad (2.6)$$

Setting (2.2) equal to zero gives

$$u^* = \frac{\mu z^*}{\rho + \alpha j^*}; \quad (2.7)$$

with (2.4) equal to zero, we have  $j^* = 0$  or

$$u^* + c^* = \frac{d}{b}. \quad (2.8)$$

Substituting  $c_+^*$  into (2.8) gives

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

Consider when  $c_+^* = 0$ , so that  $z_+^* = K \left[ 1 - \frac{\mu}{r} \right]$ . Let  $j^* = 0$ , and substitute into (2.7) to get

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

Therefore, we have the equilibrium

$$E_1(z^*, u^*, c^*, j^*) = E_1 \left( K \left[ 1 - \frac{\mu}{r} \right], \frac{\mu}{\rho} K \left[ 1 - \frac{\mu}{r} \right], 0, 0 \right), \quad (2.9)$$

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

Finally, plugging  $z_+^*$  and  $u_+^*$  into (2.7) we find

$$j_+^* = \frac{1}{\alpha} \left[ \frac{b\mu}{d} z_+^* - \rho \right].$$

Therefore, we have the equilibrium

$$E_2(z^*, u^*, c^*, j^*) = E_2\left(K\left[1 - \frac{\mu}{r}\right], \frac{d}{b}, 0, \frac{1}{\alpha}\left[\frac{b\mu}{d}z_+^* - \rho\right]\right), \quad (2.10)$$

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. Now, working with the negative subscript equilibria, we consider (2.6) and

$$c_-^* = \frac{r}{a}\left[1 - \frac{\mu}{r} - \frac{\rho + \alpha j_-^*}{aK}\right] = \frac{r}{aK}\left[K\left(1 - \frac{\mu}{r}\right) - \frac{\rho + \alpha j_-^*}{a}\right] \quad (2.11)$$

to find  $u_-^*$  and  $j_-^*$ . First, we let  $j_-^* = 0$ . Then (2.6) becomes

$$z_-^* = \frac{\rho}{a},$$

(2.7) becomes

$$u_-^* = \frac{\mu}{a},$$

and (2.11) becomes

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

Thus we have the equilibrium

$$E_3(z^*, u^*, c^*, j^*) = E_3\left(\frac{\rho}{a}, \frac{\mu}{a}, \frac{r}{aK}\left[K\left(1 - \frac{\mu}{r}\right) - \frac{\rho}{a}\right], 0\right), \quad (2.12)$$

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 (2.6) and (2.11), (2.8) becomes

$$u_-^* = \frac{d}{b} - \frac{r}{a}\left[1 - \frac{\mu}{r} - \frac{\rho + \alpha j_-^*}{aK}\right]. \quad (2.13)$$

Substituting (2.6) and (2.13) into (2.2) and setting it equal to zero gives:

$$0 = \frac{\alpha^2 r}{a^2 K} j_-^{2*} + \alpha \left[\frac{d}{b} - \frac{r}{a}\left(1 - \frac{2\rho}{aK}\right)\right] j_-^* + \frac{\rho r}{a} \left[\frac{ad}{br} + \frac{\rho}{aK} - 1\right] \quad (2.14)$$

It is shown in Appendix A.1 that there is only one positive root for (2.14), which is

$$j^* = \frac{a}{\alpha} K \left[ 1 - \frac{ad}{br} \right] - \frac{\rho}{\alpha} \quad (2.15)$$

Substituting (A.4) into (2.6) we get the expression for  $z^*$  in  $E_4$  which is

$$z^* = K \left[ 1 - \frac{ad}{br} \right]. \quad (2.16)$$

The equilibrium  $E_4$  is

$$E_4(z^*, u^*, c^*, j^*) = E_4 \left( K \left[ 1 - \frac{ad}{br} \right], \frac{\mu}{a}, \frac{d}{b} - \frac{\mu}{a}, \frac{a}{\alpha} K \left[ 1 - \frac{ad}{br} \right] - \frac{\rho}{\alpha} \right) \quad (2.17)$$

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.

## 2.2.2 Basic Reproductive Numbers

The basic reproductive number (BRN) is defined as the average number of secondary infections that is generated by one infected individual in a population of susceptible individuals, which can be calculated using the next generation operator method as in [28]. When the BRN is less than one, the disease free equilibrium is stable and 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 basic reproductive number of anthrax in the absence of scavengers is  $R_Z = \frac{aK(1-m)}{\rho}$ , where the average infection rate is  $aK(1-m)$  and the average duration of infection is  $\frac{1}{\rho}$ . The basic reproductive number of anthrax in the presence of scavengers is  $R_J = \frac{ad}{b\mu}$ . Here  $\frac{ad}{b}$  is the average infection rate and the average length of infection is  $\frac{1}{\mu}$ .



### 2.3 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 the  $4 \times 4$  Jacobian matrix can be reduced to a  $3 \times 3$  matrix since the second column in the  $4 \times 4$  has zeros except on the diagonal, resulting in the same eigenvalues.

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  $\lambda_1$  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

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

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

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

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  $\det(\hat{J}(E_2)) > 0$  [28]. The trace and determinant of  $\hat{J}(E_2)$  are

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

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  $\lambda_1 = -\rho$  and  $\lambda_2 = \frac{b\mu}{a} + \frac{br}{aK} \left[K\left(1 - \frac{\mu}{r}\right) - \frac{\rho}{a}\right] - d$ . Notice  $\lambda_1$  is always negative, and  $\lambda_2$  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 two dimensional Routh–Hurwitz

criterion to determine the sign of the remaining eigenvalues of  $\hat{J}(E_3)$ . The trace and determinant are

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

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

$$\begin{aligned} \det(J(E_3)) &= \rho \left[ r \left( 1 - \frac{\rho}{aK} \right) - \mu \right] > 0 \\ &\iff 1 - \frac{\rho}{aK} - \frac{\mu}{r} > 0 \\ &\iff \frac{\rho}{aK} - \frac{\mu}{r} < 1 \\ &\iff \frac{\rho}{a} < K \left[ 1 - \frac{\mu}{r} \right]. \end{aligned} \tag{2.18}$$

Recall (2.18) is the existence condition for  $E_3$ . Hence  $E_3$  is LAS if and only if

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

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

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

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

$$\begin{aligned} p(\lambda) &= \lambda^4 + (az^* - A)\lambda^3 + \left[ bj^* \alpha \frac{\mu ad}{a b\mu} - az^* \left( A + \mu \left(1 - \frac{ad}{b\mu}\right) \right) \right] \lambda^2 \\ &+ \left[ -bj^* \alpha \frac{\mu ad}{a b\mu} A + \mu \left(\frac{ad}{b\mu} - 1\right) z^* (\alpha bj^* + a^2 z^*) \right] \lambda \\ &+ \left[ -Abj^* \alpha \mu z^* \left(\frac{ad}{b\mu} - 1\right) \right] = 0. \end{aligned} \quad (2.19)$$

Now,

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

We use the four dimensional 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 A.2); therefore,  $E_4$  is locally asymptotically stable whenever it exists.

A visual representation of the stability analysis is shown in Figures 2.1 and 2.2. The existence and stability conditions for each equilibrium are summarized in Table 2.2 and can be rewritten in terms of  $R_Z$ ,  $R_J$ , and  $m$  as in Table 2.3.

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

Table 2.2: Summary of equilibria and local stability in terms of the parameters.

Equilibrium	Existence	LAS
$E_0(0, 0, 0)$	always	$m > 1$
$E_1\left(K[1-m], \frac{\mu}{\rho}K[1-m], 0, 0\right)$	$m < 1$	$R_Z < 1$ & $D(E_1) < 1$ ( $R_Z < R_J$ )
$E_2\left(K[1-m], \frac{d}{b}, 0, \frac{b\mu}{\alpha d}K[1-m] - \frac{\rho}{\alpha}\right)$	$m < 1$ & $D(E_1) > 1$ ( $R_Z > R_J$ )	$R_J < 1$
$E_3\left(\frac{\rho}{a}, \frac{\mu}{a}, \frac{\mu}{aK}\left[K(1-m) - \frac{\rho}{a}\right], 0\right)$	$m < 1$ & $R_Z > 1$	$D(E_3) < 1$ & $\left(mR_J + \frac{1-m}{R_Z} > 1\right)$
$E_4\left(K[1-mR_J], \frac{\mu}{a}, \frac{d}{b} - \frac{\mu}{a}, \frac{\mu}{\alpha}K[1-mR_J] - \frac{\rho}{\alpha}\right)$	$m < 1$ & $R_J > 1$ & $D(E_3) > 1$ ( $mR_J + \frac{1-m}{R_Z} < 1$ )	whenever it exists

Table 2.3: 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  $D(E_3) = \frac{br}{ad}\left(1 - \frac{\rho}{aK}\right)$ .

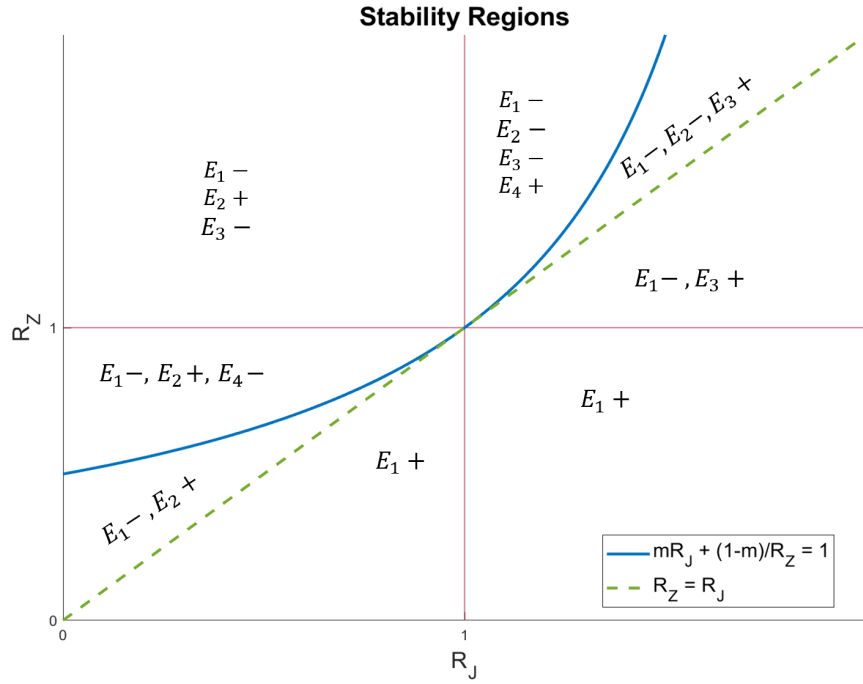


Figure 2.1: Stability Regions. The regions of stability are given by the threshold conditions  $R_Z = 1$ ,  $R_J = 1$ ,  $R_Z = R_J$ , and  $mR_J + \frac{1-m}{R_Z} = 1$ , where  $m=0.5$  in this plot. If  $E_i$  for  $i = 1, 2, 3, 4$  is seen then it means that equilibrium  $E_i$  exists in that region. The  $-$  after the  $E_i$  means that it is not LAS in that region, whereas  $+$  means that equilibrium  $E_i$  is LAS.



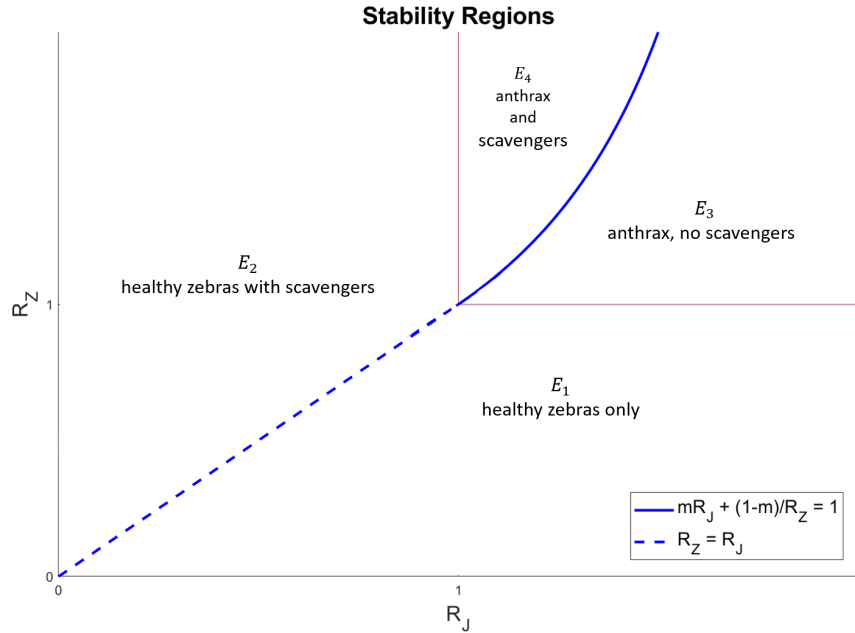


Figure 2.2: Stability Regions with descriptions. Only the regions where there is a change in which equilibrium is stable is distinguished. In addition, a short description of the equilibrium is given.

## 2.4 Global Stability Analysis

A partial global stability analysis is completed for the full four-dimensional system. We first consider the reduced systems. Global behavior is easiest to examine through subsystems involving anthrax but no scavengers. We look at global stability in the ZC and ZUC system, 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.

### 2.4.1 ZC System Global Stability Analysis

The ZC system is the following:

$$z' = rz \left(1 - \frac{z}{K}\right) - \mu z - acz \quad (2.20)$$

$$c' = acz - \rho c \quad (2.21)$$

This system has three equilibria

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

To determine global stability of the equilibria we use the Poincaré–Bendixson Theorem.

First we show that there are no limit cycles by Dulac's Criterion.

**Theorem 2.4.1.** *Dulac's Criterion* If  $\beta(x, y) \in C^1$  in a region  $D \subseteq \mathbb{R}^2$  (simply connected) and  $\frac{\partial}{\partial x}(\beta F) + \frac{\partial}{\partial y}(\beta G) \neq 0$  in  $D$ , then  $x' = F$  and  $y' = G$  has no periodic orbits contained in  $D$ .

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

$$z + c = K\left(1 - \frac{\mu}{r}\right)\left[1 + \frac{r}{4\rho}\left(1 - \frac{\mu}{r}\right)\right] \quad (2.22)$$

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 (2.22), 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 (2.22). Hence solutions are bounded and 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  $K \left( 1 - \frac{\mu}{r} \right) > \frac{\rho}{a}$

#### 2.4.2 ZUC System Global Stability Analysis

The ZUC system is

$$z' = rz \left( 1 - \frac{z}{K} \right) - \mu z - acz \quad (2.23)$$

$$u' = \mu z - \rho u \quad (2.24)$$

$$c' = acz - \rho c. \quad (2.25)$$

This system has three equilibria

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

Notice that (2.23) and (2.25) decouple from (2.24), and we study those first. We already studied the ZC system as in section 2.4.1 and we know all solutions at any initial conditions tends toward some equilibrium, regardless of the parameter values. We use a result by Thieme [29, 30], to say that the solutions of the ZUC system are asymptotic to the solutions of (2.24), where  $z = z^*$  and  $c = c^*$ :

$$u(t) = \frac{\mu z^*}{\rho} + k e^{-\rho t}, \quad (2.26)$$

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.

### 2.4.3 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 (2.1)  $z' \leq rz \left(1 - \frac{z}{K}\right) - \mu z$ . Note that for  $\mu < r$   $z' = rz \left(1 - \frac{z}{K}\right) - \mu z$  has a globally stable equilibrium value of  $z^* = K \left(1 - \frac{\mu}{r}\right)$ . Then  $\limsup z \leq K \left(1 - \frac{\mu}{r}\right)$ . Consider (2.2) 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 (2.3) without jackals, we have  $c' \leq (az - \rho)c$ . Substituting in  $z^*$  we have  $\limsup c' \leq \left(a \frac{\mu}{\rho} K \left(1 - \frac{\mu}{r}\right) - \rho\right) c$ . If  $a \frac{\mu}{\rho} K \left(1 - \frac{\mu}{r}\right) - \rho < 0$ , which is equivalent to  $R_Z < 1$ , then  $c$  goes to zero. In the case where  $c = 0$ , (2.4) is  $j' \leq (bu - d)j$ . Since  $u$  is bounded above, we have  $\limsup j' \leq j \left(b \frac{\mu}{\rho} K \left(1 - \frac{\mu}{r}\right) - d\right)$ . If  $b \frac{\mu}{\rho} K \left(1 - \frac{\mu}{r}\right) - d < 0$ , which is equivalent to  $D(E_1) < 1$ , then  $j$  goes to zero. If  $R_Z < 1$  and  $D(E_1) < 1$  then  $j$  goes to zero and we reduce to the ZU system, which tends towards an unique equilibrium.

## 2.5 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, that is, 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 [28], the demographic reproduction number for scavengers in the absence of anthrax is calculated. That is,

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

Notice that

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

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

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

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:

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

$$= \frac{br}{ad} \left(1 - \frac{\rho}{aK}\right).$$

Notice that

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

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

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

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

To see if 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 2.5.1.** *Let  $m = \frac{\mu}{r}$ . Then  $j_4^* > j_2^*$  if and only if  $\phi = \frac{ad}{br}$  is between  $m$  and  $1 - m$ .*

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

$$\begin{aligned} j_4^* > j_2^* &\iff \frac{aK}{\alpha} \left(1 - \frac{ad}{br}\right) - \frac{\rho}{\alpha} > \frac{b\mu}{\alpha d} K (1 - m) \\ &\iff a \left(1 - \frac{ad}{br}\right) > \frac{b\mu}{d} (1 - m) \\ &\iff \frac{ad}{br} \left(1 - \frac{ad}{br}\right) > \frac{\mu}{r} (1 - m) \\ &\iff \phi(1 - \phi) > m(1 - m) \\ &\iff \phi^2 - m^2 + m - \phi < 0 \end{aligned}$$

$$\iff (\phi - m)(\phi + m) - (\phi - m) < 0$$

$$\iff (\phi - m)(\phi + m - 1) < 0.$$

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

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

**Theorem 2.5.2.**  $D(E_3) > D(E_1)$  if and only if  $p(1 - p) > m(1 - m)$ , where  $p = \frac{\rho}{aK}$  and  $m = \frac{\mu}{r}$ .

*Proof.* Then

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

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

$$\begin{aligned} \iff p(1 - p) &> m(1 - m) \\ \iff p^2 - m^2 + m - p &< 0 \\ \iff (p - m)(p + m) - (p - m) &< 0 \\ \iff (p - m)(p + m - 1) &< 0. \end{aligned}$$

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

The values  $m$ ,  $\phi$ , 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  $\phi = \frac{ad}{br}$  is some measure of natural scavenger death rate to birth rate. The values for  $D(E_1)$  and  $D(E_3)$  tell us if the scavengers will persist whereas,  $j_4^*$  and  $j_2^*$  give the number of scavengers that will persist. From theorems 2.5.1 and 2.5.2, 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  $\phi$  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  $R_Z$  (hurting anthrax). Therefore, scavenger presence hurts 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 (do not need anthrax created carcasses) then their presence hurts anthrax.

## 2.6 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  $R_V$ .

### 2.6.1 Parameter Estimation

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



Symbol	Description	Value	Source
$K$	zebra carrying capacity ( <i>zebras</i> )	13000 – 15000	[25]
$r$	intrinsic growth rate of zebras	$3.06849 \times 10^{-3}$	This study
$\mu$	natural zebra death rate	$7.67123 \times 10^{-4}$	This study
$a$	rate zebras come into contact with infected carcasses ( $week \cdot zebras$ ) <sup>-1</sup>	$1.1433 \times 10^{-5}$	This study
$\rho$	natural decomposition rate of zebra carcasses	0.12727	[31]
$\alpha_j$	rate jackals come into contact with carcasses to eat ( $week \cdot jackals$ ) <sup>-1</sup>	0.03608	This study
$b_j$	birth rate of jackals ( $week \cdot zebras$ ) <sup>-1</sup>	0.051811	This study
$d_j$	death rate of jackals	$4.808 \times 10^{-3}$	[32]
$\alpha_v$	rate vultures come into contact with carcasses to eat ( $week \cdot vultures$ ) <sup>-1</sup>	0.01927	[27]
$b_v$	birth rate of vultures ( $time \cdot zebras$ ) <sup>-1</sup>	0.00959	This study
$d_v$	death rate of vultures	$9.615 \times 10^{-4}$	[33]

Table 2.4: Parameter table with values. Units in  $\frac{1}{week}$  except as noted. The three parameters for scavengers are  $b$ ,  $d$ , and  $\alpha$ . A subscript of  $j$  is the parameter value for jackals and a subscript of  $v$  is for vultures.

The life expectancy of zebras is 15 years according to [34] or 30 years according to [35]. We picked 25 years as the life expectancy. After converting years to weeks we get  $\mu = \frac{1}{1300} weeks^{-1}$ . 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 years old [36] and have one baby every 2 years because they will spend up to a year nursing [35]. We will say a zebra from 21-25 years is too old to reproduce and therefore a female zebra will have 16 years to bear a foal. Therefore,

a 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 [25] and figure out the exposure area that one zebra covers in a single day, which is distance multiplied by 6 meters (the spore dispersal radius around an infected carcass is 3 meters in the environment [23]). 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 [31], 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 [32]. Converting 4 years to weeks we get the natural death rate of jackals to be

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

Now, we calculate  $b_j$ . Coyotes eat 2.5 pounds per day [37]. The average weight of an adult male coyote is 10.3–16 kilograms (22.71–35.27 pounds), whereas it is 8–14.2 kilograms (17.64–31.31 pounds) for an adult female coyote [38]. A black-backed jackal weighs 5–15 kilograms (11–33 pounds) [39]. 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 kilograms of usable meat [40]. We will choose the average and work with 125 kilograms (275 pounds). We can find how many days it would take for a jackal to eat a zebra carcass (only consider usable 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 [32].

Thus during the 194 days one jackal is eating one zebra carcass and produces

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

Now,

$$b_j = \frac{1.4359 \text{ jackals}}{\text{zebra}} \cdot \frac{1}{27.714 \text{ jackal} \cdot \text{week}} = 0.051811 \frac{1}{\text{zebra} \cdot \text{week}}.$$

Vultures have a life expectancy of 20 years [33]. 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 1,200 grams (2.65 pounds) of food [27]. 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  $\alpha_v = 1/51.90 \text{ vulture} \cdot \text{week}$ . Vultures produce one offspring every year per every two vultures [41]:

$$\frac{1 \text{ baby vulture}}{2 \text{ vultures} \cdot \text{year}} = \frac{0.5 \text{ baby vultures}}{\text{vultures} \cdot \text{year}}.$$

Thus during the 363.28 days one vulture is eating one zebra carcass and produces

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

Now,

$$b_v = \frac{0.4976 \text{ baby vultures}}{\text{zebra}} \cdot \frac{0.01927}{\text{vulture} \cdot \text{week}} = 0.00959 \frac{1}{\text{zebra} \cdot \text{week}}.$$

## 2.6.2 Threshold quantities

We let all the parameter values be those that are set in table 2.4 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,  $a = 1.71495 \times 10^{-5} (\text{zebras} \cdot \text{week})^{-1}$  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  $1600 \text{ km}^2$  vs  $2400 \text{ km}^2$ . Moreover, we could also view an

increase in the parameter  $a$  to represent 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 fight the anthrax. Therefore, the zebras benefit from the presence of scavengers.

## 2.7 Results and Discussion

Previous modeling studies [7, 42] of anthrax transmission in animal populations have focused on a control strategy such as vaccination or carcass removal (in [7]) 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 figure 2.2, 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 hurting 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,  $D(E_1) > 1$  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 ( $R_Z > R_J \iff D(E_1) >$

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,  $\phi = \frac{ad}{br}$ , 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  $p = \frac{\rho}{aK}$  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 ( $\phi$ ). Anthrax fosters scavenger survival if  $p$  is less extreme than  $m$ , and increases scavenger population size if  $\phi$  is less extreme than  $m$ .

Notice that all the threshold quantities are independent of the parameter  $\alpha$ , which describes the rate the scavengers feed from the zebra carcasses. Anthrax persistence with and without scavengers, and the scavengers' ability to survive does not depend on the rate at which scavengers eat from zebra carcasses, but on the rate at which scavengers convert that feeding into reproduction.

When we consider the various calculations of BRNs in section 2.6.2 we see that between jackals and vultures neither outperforms the other 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 [43]. 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 [27]. 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.

## CHAPTER 3

### Modeling anthrax-rabies interactions in zebra-jackal cycles

#### 3.1 Introduction

ENP located in Namibia, contains dry savanna habitat [8], where many different species live such as zebras, springbok, wildebeest, jackals, and lions [8, 4]. Anthrax (caused by *Bacillus anthracis*) is endemic in ENP and mainly infects ungulates such as zebras [2], producing more carrion in the park that scavengers like black-backed jackals (*Canis mesomelas*) can feed on. The anthrax outbreaks in plains ungulates occur at the end of the rainy season in March [22]. The zebra carcasses are a resource for the jackals to congregate and interact with one another, which gives the potential for a different disease to spread within the jackal population, such as the rabies virus. The rabies virus is a highly fatal communicable disease that attacks the cerebral and nervous tissues resulting in aggressive behavior like biting or attacking other animals throughout their 5 to 7 day-long infectious period [8, 32]. It is documented [4] that rabies not only persists in jackal populations for a short period of time, but it can persist in jackal populations in northern South Africa independent of spillover from domestic dogs. Black-backed jackals play an important epidemiological role in ENP because of their long dispersal distances, high density, and widespread geographic range [4]. This allows for jackals to interact with others outside of their territory; spreading disease to another group of jackals while interacting at the carcasses.

Consumer-resource interactions occur everywhere in nature and describe the consumer coming into contact with a resource. An example of a consumer-resource relationship is house finches and bird feeders. The consumers are the house finches



and the resource is the bird feeder [9]. Likewise, in this paper, the consumers are the jackals and the resources are the zebra carcasses. The encounter rate describes the interactions between members of the same species, that is, the conspecific encounter rate.

There are several models of predator-prey systems, where only the predator is infected by a disease [11, 12, 13, 14], or only the prey is infected by a disease [15, 16, 17, 18, 19]. In [44], a mathematical model was developed to describe a predator-prey system, where both species are affected by the same disease. A predator-prey system can be generalized into a consumer-resource system. In [45], a consumer-plant resource model was developed where the plant resources are exposed to a disease. The authors calculated the basic reproduction number ( $R_0$ ) and the consumption number ( $C_0$ ), which is understood to be a combination of parameters ensuring the consumer receives enough resources required for survival [46]. While  $R_0 < 1$ , they found that when increasing the consumption number the disease was eradicated faster from the system, which in turn increased the strength of coexistence between the consumer and the resources resulting in faster disease elimination. When  $R_0 > 1$ , their model showed that the disease can be eradicated when the consumption number is large enough. Therefore, their research suggests that the eradication of certain disease from a system and strengthening the coexistence between consumers and resources are associated with each other.

Borchering et al. [8], developed a spatially explicit mathematical model for resource visitation behavior in order to see how changes in resource availability can influence the rate of encounters among consumers. They identified and characterized two qualitatively distinct parameter regimes: a low-resource regime and a high-resource regime. They found that in a low-resource regime, the addition of more resources results in more consumer-consumer encounters, whereas in a high-resource

regime, the addition of more resources led to fewer consumer-consumer encounters. They conducted a specific case study using location data of jackals and the carcasses they scavenged on in ENP. The zebras would become infected by anthrax, which generated more carcasses and the jackals would congregate around the carcasses increasing the risk of spreading rabies.

There are some models [9, 10] that study the relationship between resource availability and conspecific encounter rates for consumers, where these resources may indirectly mediate infectious disease transmission. In [9], the authors studied a host-pathogen system with house finches and their bacterial pathogen *Mycoplasma gallisepticum*, which causes severe conjunctivitis, to determine if the same behaviors enhance both receiving and the transmission of pathogens. They discovered that the time a finch spends at a bird-feeder was the best at determining the risk the finch would become infected. Likewise, the more time an infected finch spent at a bird-feeder, increased the likelihood of transmitting the bacteria. In [10], a spatially explicit individual-based model was developed to study the situation when consumers of the same species meet at a single shared-resource during periods of low resource availability, such as a watering hole during the dry season. They considered a generic fecal transmittable disease in a single-host system. From their study the authors saw that as the lean season increased, the resource sharing increased and this increased the prevalence of the infectious disease. They concluded that seasonal sharing of resources helps to spread an infectious disease through a spatially structured population.

In this paper, we developed a model to describe the relationship between zebra-jackal population dynamics on the one hand, and the transmission dynamics of anthrax and rabies on the other. We are interested in answering the following research question: how do anthrax and rabies affect each other's ability to spread? We further break this question down to two questions. That is, does rabies help or hurt

anthrax and does anthrax help or hurt rabies? In our previous work [47], we explored how scavengers can help eliminate wildlife disease. We focused our attention on the scavengers jackals and vultures and anthrax as the wildlife disease. We concluded that scavengers were able to persist better in the presence of anthrax when the death to birth rate ratio for anthrax is less than the death to birth rate ratio for zebras. Hence anthrax helps scavengers.

This paper is organized as follows: section 3.2 is the model description, including the derivation of the encounter rate function, section 3.3 identifies the equilibria in the model, section 3.4 calculates the basic and invasion reproductive numbers of both anthrax and rabies and section 3.5 is the local stability of each equilibria. Section 3.6 is broken down into three subsections. First, we look at four different scenarios with limit cycles and interpret what is happening biologically in each limit cycle. Then we find which equilibrium is stable when we plug in parameter values obtain from literature. Finally, we answer the questions: does anthrax amplify rabies and does rabies amplify anthrax?

## 3.2 Model

In this paper the deterministic mathematical model uses a system of ordinary differential equations to describe how population is affected by disease. The populations considered in this model are the living zebras, the zebra carcasses from natural death, the zebra carcasses due to anthrax induced death, jackals, and rabid jackals, ( $z, u, c, j, i$ , respectively). The zebra population has a logistic growth term and is removed by natural death ( $\mu z$ ) or by disease-induced death ( $acz$ ) from grazing near an anthrax infected carcass site [6]. The carcasses (healthy or infected) are either naturally decomposing at a rate  $\rho$  or are being eaten by healthy and rabid jackals at a rate of  $\alpha$ . The jackal birth depends on how many carcasses are present in the

environment, and they die at a natural death rate of  $d$ . Healthy jackals become rabid when interacting with rabid jackals at zebra carcasses, which is described by an encounter rate  $\beta$  dependent on the number of carcasses. Finally, rabid jackals die from an additional death rate due to rabies  $\delta$ . Jackals do not attack living zebras; they only scavenge on the zebra carcasses, which is assumed representative of the jackals' food sources. Therefore, we assume that jackals depend solely on zebra carcasses for food regardless of the carcass infection status. A summary of the parameters in equations (3.1)-(3.5) can be found in table 3.1.

$$z' = rz \left(1 - \frac{z}{K}\right) - \mu z - acz \quad (3.1)$$

$$u' = \mu z - \rho u - \alpha (j + i) u \quad (3.2)$$

$$c' = acz - \rho c - \alpha (j + i) c \quad (3.3)$$

$$j' = bj (u + c) - dj - \beta ji \quad (3.4)$$

$$i' = \beta ji - (d + \delta) i \quad (3.5)$$

Symbol	Definition
$K$	carrying capacity for zebra population ( <i>zebras</i> )
$r$	intrinsic growth rate of zebras
$\mu$	natural zebra death rate
$a$	rate zebras come into contact with anthrax infected carcasses ( $time \cdot zebras$ ) <sup>-1</sup>
$\rho$	natural decomposition rate of carcasses
$\alpha$	rate jackals come into contact w/ carcasses to eat ( $time \cdot jackals$ ) <sup>-1</sup>
$b$	birth rate of jackals ( $time \cdot zebras$ ) <sup>-1</sup>
$d$	natural death rate of jackals
$\beta$	function describing interaction between healthy and infected jackals ( $time \cdot jackals$ ) <sup>-1</sup>
$\delta$	additional death rate of jackals from rabies

Table 3.1: Parameter table for system (3.1)-(3.5). Units in  $\frac{1}{time}$  except as noted.

### 3.2.1 Encounter function, $\beta$

Borcherling et al. developed a model to describe the number of conspecific encounters a typical consumer will have when resources are temporarily available. The  $\beta$  in our model is a function that captures the encounter rate between jackals at the same resources, and we use Borcherling's work to derive our  $\beta$  function.

Borcherling et al. considered the encounter rate initially to be a function of three quantities,  $\tilde{\rho}$  (same as Borcherling's  $\rho$ ),  $\kappa$ , and  $\ell$ . Here  $\kappa$  is the resource intensity parameter from a Poisson spatial process and means that for any region of area  $A$  contained in a spatial region  $\mathcal{O}$ , the number of resources in that region is Poisson distributed with mean  $\kappa A$ . Similarly,  $\tilde{\rho}$  is the consumer intensity parameter. These intensity parameters correspond to the expected population density produced by the model for the consumers and resources. The parameter  $\ell$  is the maximum

detection distance a consumer can detect a resource. Therefore, all resources within a circle around the consumer with a radius  $\ell$  are detected by the consumer. However, Borchering et al. rewrote the encounter rate as a function of only two quantities by rescaling: they showed that for every triplet  $(\hat{\rho}, \kappa, R)$  there exists an associated triplet  $\left(1, \frac{\kappa}{\hat{\rho}}, \ell\sqrt{\hat{\rho}}\right)$  that has the same encounter rate. This rescale allows the values inside the logarithmic functions to be dimensionless [8]. Their model revealed that when supplemental resources are scarce, conspecific encounter rates at the resource sites are rare because the consumer isn't close enough to detect a resource. In addition, intermediate levels of the supplemental resource availability produced the highest encounter rates. Finally, when there is an ample amount of resources available, conspecific encounters are rare because each consumer has its own resource.

Borchering et al. described the relationship between encounter rate and the number of zebra carcasses on a log-log scale. We want to construct a function that behaves similarly to the output of Borchering's encounter rate model: when carcasses are scarce, the jackal-to-jackal encounter rate is low, when intermediate levels of carcasses are available, the encounter rate is high, and when carcasses are abundant the encounter rate is low. We will use a hyperbola to estimate the encounter rate function.

The general form of a hyperbola is given by

$$\frac{(y - k)^2}{a^2} - \frac{(w - h)^2}{b^2} = 1$$

with center  $(h, k)$ , vertex  $(h, k - a)$ , and asymptotes  $y = k + \frac{a}{b}(w - h)$  and  $y = k - \frac{a}{b}(w - h)$ . Note that here  $y = \log(\beta)$  and  $w = \log(u^* + c^*)$ .

From Borchering's work we know the center of the hyperbola is

$$(h, k) = \left( \log\left(\frac{1}{\pi R^2}\right), \log(\hat{\rho}\pi R^2) \right)$$

which is given in [8] by the intersection of the small and large resource regimes. In addition, we approximate the vertex using information from [8]. The vertex is

$$(h, k - a) = \left( \log\left(\frac{1}{\pi R^2}\right), \log(1.48\hat{\rho}R^2) \right). \quad (3.6)$$

This vertex is an estimate and will result in the maximum encounter rate occurring at a slightly lower number of available carcasses than the number which truly maximizes the encounter rate. However, this is an acceptable simplification because not all the carcasses are detectable by the jackals [8].

To find the asymptotes, we consider two cases. One case is when resources (carcasses) are scarce and another is when resources are abundant. When resources are scarce, an approximation of the expected number of encounters for a focal consumer is  $(u^* + c^*)\hat{\rho}(\pi R^2)^2$  [8]. Then

$$\begin{aligned} y &= \log(\beta) = \log\left(\hat{\rho}(\pi R^2)^2\right) + \log(u^* + c^*) \\ \implies y &= \log\left(\hat{\rho}(\pi R^2)^2\right) + w. \end{aligned} \quad (3.7)$$

The approximation of the expected number of encounters for a focal consumer when resources are abundant is  $\frac{\rho}{u^* + c^*}$  [8]. Then

$$\begin{aligned} y &= \log(\beta) = \log(\hat{\rho}) - \log(u^* + c^*) \\ \implies y &= \log(\hat{\rho}) - w. \end{aligned} \quad (3.8)$$

Now, we want to find the relationship between  $a$  and  $b$  using the asymptotes. Start with the general form and substitute for  $k$  and  $h$  using (3.6). That is, for the low-resource asymptote,

$$y = k + \frac{a}{b}(w - h)$$

$$= \log(\hat{\rho}\pi R^2) + \frac{a}{b}w + \frac{a}{b}\log(\pi R^2)$$

Then we set the general form above equal to (3.7) to get

$$\log(\hat{\rho}\pi R^2) + \frac{a}{b}w + \frac{a}{b}\log(\pi R^2) = w + \log(\hat{\rho}(\pi R^2)^2)$$

so

$$\frac{a}{b} = 1 \implies a = b.$$

We can find  $a$  and  $b$  using the vertex, that is,

$$\begin{aligned} \log(1.48\hat{\rho}R^2) &= k - a \\ \implies \log(1.48\hat{\rho}R^2) &= \log(\hat{\rho}\pi R^2) - a \\ \implies a &= \log(\hat{\rho}\pi R^2) - \log(1.48\hat{\rho}R^2) \\ \implies a &= \log\left(\frac{\pi\hat{\rho}R^2}{1.48\hat{\rho}R^2}\right) \\ \implies a = b &= \log\left(\frac{\pi}{1.48}\right). \end{aligned}$$

Therefore, the asymptotes are

$$y_1 = w + \log(\hat{\rho}(\pi R^2)^2) \text{ and } y_2 = -w + \log(\hat{\rho}).$$

Let  $q = a = b$ . Then solving for  $y$  in the general form of the hyperbola we get

$$y = k \pm \sqrt{(w - h)^2 + q^2}.$$

We will work with

$$y = k - \sqrt{(w - h)^2 + q^2}$$

because we are interested in the bottom part of the hyperbola only. Then we have that



$$\begin{aligned}
y &= k - \sqrt{(w - h)^2 + q^2} \\
\log(\beta(u^* + c^*)) &= k - \sqrt{[\log(u^* + c^*) - \log(\pi R^2)]^2 + q^2} \\
\beta(u^* + c^*) &= e^{k - \sqrt{(\log(u^* + c^*) + \log(\pi R^2))^2 + q^2}}.
\end{aligned}$$

Let  $x = u^* + c^*$ ; then our encounter rate function is given by

$$\beta(x) = \beta_0 e^{-\sqrt{(\log(x) + \log(\pi R^2))^2 + q^2}}, \quad (3.9)$$

where  $\beta_0 = \hat{\rho}\pi R^2$  and  $q = \log\left(\frac{\pi}{1.48}\right)$ . Following Borchering et. al. parameter ranges for  $R$  and  $\hat{\rho}$ , we set  $R = 7km$  and  $\hat{\rho} = 0.2km^{-1}$ . Figure 3.1 shows what the function  $\beta$  looks like, which is not a hyperbola because Borchering's encounter-rate model was analyzed on a log-log scale. Therefore, we take the exponential to get the function  $\beta$ . Notice when the zebra carcasses are scarce the encounter rate is low, when intermediate values of the carcasses are available then encounter rate reaches a maximum, and when the carcasses are abundant the encounter rate is low again.

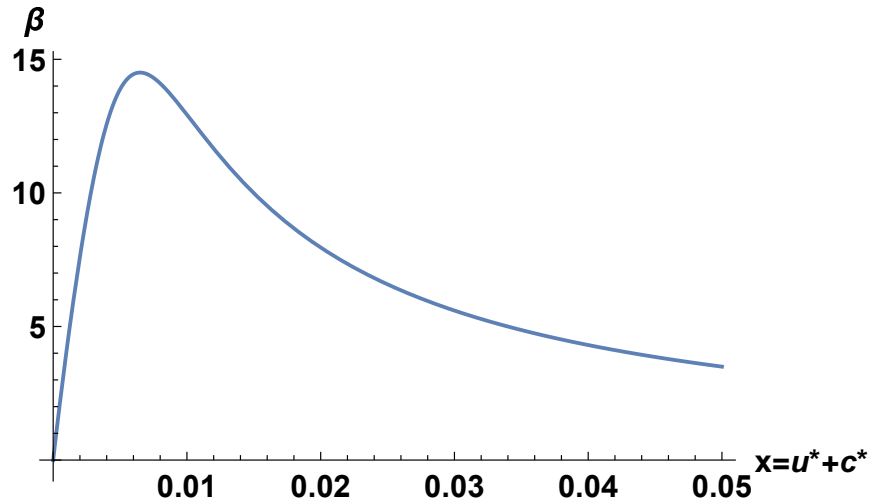


Figure 3.1: Graph of  $\beta(u^* + c^*)$ .

### 3.3 Existence of Equilibria

In this section, we identify seven equilibria in our model and provide the existence conditions for each one. The same five equilibria in [47] are present in this model, that is,  $E_0, E_1, E_2, E_3, E_4$  as in table 3.3.

We have two additional equilibria to investigate:  $E_5$  and  $E_6$ . The equilibrium  $E_5$  represents a state where only rabies is present: no anthrax in the zebra population. The equilibrium  $E_6$  represents a state where both anthrax in the zebra population and rabies in the jackal population are present. Table 3.2 gives a summary of the equilibrium conditions that arise from the system's equations ((3.1) through (3.5)).

(1a) $z^* = 0$	(1b) $z^* = K \left[ 1 - \frac{\mu + ac^*}{r} \right]$
(2) $u^* = \frac{\mu z^*}{\rho + \alpha(j^* + i^*)}$	
(3a) $c^* = 0$	(3b) $z^* = \frac{\rho + \alpha(j^* + i^*)}{a}$
(4a) $j^* = 0$	(4b) $u^* + c^* = \frac{d + \beta(x)i^*}{b}$
(5a) $i^* = 0$	(5b) $j^* = \frac{d + \delta}{\beta(x)}$

Table 3.2: Summary of equilibrium components for system (3.1)-(3.5)

#### 3.3.1 Rabies but no anthrax

We look at the equilibrium  $E_5$  where there is rabies but no anthrax.

$$\begin{aligned}
 z^* &= K \left( 1 - \frac{\mu}{r} \right) \quad (\text{from 1b}) \\
 u^* &= \frac{\mu z^*}{\rho + \alpha(j^* + i^*)} \quad (\text{from 2}) \\
 c^* &= 0 \quad (\text{from 3a}) \\
 u^* &= \frac{d + \beta(x)i^*}{b} \quad (\text{from 4b})
 \end{aligned} \tag{3.10}$$

$$j^* = \frac{d + \delta}{\beta(x)} \text{ (from 5b)}$$

3.3.1.1 Derive  $j^* + i^*$  equation

$$\beta(x)(j^* + i^*) = \delta + b(u^* + c^*) \text{ (from (4b) and (5b))} \quad (3.11)$$

$$(\mu + ac^*)z^* = rz^* \left(1 - \frac{z^*}{K}\right) \text{ (from (2.1))} \quad (3.12)$$

$$(\mu + ac^*)z^* = [\rho + \alpha(j^* + i^*)](u^* + c^*) \text{ (from (2.2) and (2.3))} \quad (3.13)$$

Now, setting (3.12) and (3.13) equal to each other, we get

$$rz^* \left(1 - \frac{z^*}{K}\right) = [\rho + \alpha(j^* + i^*)](u^* + c^*) \quad (3.14)$$

From (3.11) we can solve for  $j^* + i^*$ :

$$j^* + i^* = \frac{\delta + b(u^* + c^*)}{\beta(x)} \quad (3.15)$$

3.3.1.2 Existence

Now,  $z^* > 0$  when  $\mu < r$  and  $j^* > 0$ . Since  $c^* = 0$ , we have  $x = u^* + c^* = u^*$ .

Then

$$g(x) = \frac{\mu}{a} \left(1 - \frac{\mu}{r}\right) \frac{1}{x} - \frac{\rho}{aK} - \frac{\alpha}{aK} \frac{\delta + bx}{\beta(x)} = 0, \quad (3.16)$$

which comes from solving for  $j^* + i^*$  in (3.10) and setting it equal to  $j^* + i^* = \frac{\delta + bx}{\beta(x)}$ .

Then

$$j^* + i^* = \frac{\delta + bx}{\beta(x)} > 0 \text{ with } j^* = \frac{d + \delta}{\beta(x)}$$

$$\text{So we need } i^* = \frac{bu^* - d}{\beta(x)} \geq 0$$

$$\iff bu^* - d \geq 0$$

$$\iff u^* \geq \frac{d}{b}$$

Thus  $i^* \geq 0$  when  $u^* \geq \frac{d}{b}$ .

Notice that  $\frac{\mu}{a} \left(1 - \frac{\mu}{r}\right) \frac{1}{x} - \frac{\rho}{aK}$  in (3.16) is monotone decreasing in  $x$  for  $x > 0$ .

We find that

$$g'(x) = \frac{-\mu}{a} \left(1 - \frac{\mu}{r}\right) \frac{1}{x^2} - \frac{\alpha}{aK} \left[ \frac{\beta(x)b - (\delta + bx) \beta'(x)}{[\beta(x)]^2} \right].$$

Then

$$\begin{aligned} g'(x) = 0 &\iff 0 = -\frac{\mu}{a} \left(1 - \frac{\mu}{r}\right) \frac{1}{x^2} - \frac{\alpha b}{aK} \frac{1}{\beta(x)} + \frac{\alpha}{aK} \frac{\delta + bx}{x\beta(x)} \frac{\log(x) + \log(\pi R^2)}{\sqrt{[\log(x) + \log(\pi R^2)]^2 + q^2}} \\ &\implies \text{has no roots unless } \log(x) + \log(\pi R^2) < 0 \\ &\implies x < \frac{1}{\pi R^2} \end{aligned}$$

For  $x \geq \frac{1}{\pi R^2}$ ,  $g'(x) < 0$  and  $\lim_{x \rightarrow \infty} g(x) \rightarrow -\infty$ . Therefore, we need

$$\begin{aligned} g\left(\frac{d}{b}\right) &= \frac{\mu}{a} \left(1 - \frac{\mu}{r}\right) \frac{b}{d} - \frac{\rho}{aK} - \frac{\alpha}{aK} \frac{\delta + d}{\beta\left(\frac{d}{b}\right)} > 0 \\ &\iff \frac{\beta\left(\frac{d}{b}\right)}{\delta + d} \cdot \frac{a}{\alpha} \left[ \frac{b\mu}{ad} K \left(1 - \frac{\mu}{r}\right) - \frac{\rho}{a} \right] > 1 \\ &\iff \frac{\beta\left(\frac{d}{b}\right)}{\delta + d} \cdot \frac{a}{\alpha} \left[ \frac{1}{R_J} K \left(1 - \frac{\mu}{r}\right) - \frac{\rho}{a} \right] > 1 \end{aligned}$$

for  $E_5 \left( K \left(1 - \frac{\mu}{r}\right), u_5^*, 0, \frac{d+\delta}{\beta(u_5^*)}, \frac{bu_5^* - d}{\beta(u_5^*)} \right)$  to exist. In terms of reproduction numbers defined in section 3.4, we can rewrite this condition as  $R_R > 1$  (see section 3.4.2).

### 3.3.2 Anthrax and rabies present

Now, we look at the equilibrium  $E_6$  where both rabies and anthrax persist.

$$z^* = K \left(1 - \frac{\mu + ac^*}{r}\right) \quad (\text{from 1b}) \quad (3.17)$$

$$u^* = \frac{\mu z^*}{\rho + \alpha(j^* + i^*)} \quad (\text{from 2}) \quad (3.18)$$

$$z^* = \frac{\rho + \alpha(j^* + i^*)}{a} \quad (\text{from 3b}) \quad (3.19)$$

$$u^* + c^* = \frac{d + \beta(x)i^*}{b} \quad (\text{from 4b}) \quad (3.20)$$

$$j^* = \frac{d + \delta}{\beta(x)} \quad (\text{from 5b}) \quad (3.21)$$

Take (1b) and (3b) to get  $c^*$ . Then

$$\begin{aligned} K \left[ 1 - \frac{\mu + ac^*}{r} \right] &= \frac{\rho + \alpha(j^* + i^*)}{a} \\ \frac{\mu + ac^*}{r} &= 1 - \frac{\rho + \alpha(j^* + i^*)}{aK} \\ c^* &= \frac{1}{a} \left[ r \left[ 1 - \frac{\rho + \alpha(j^* + i^*)}{aK} \right] - \mu \right] \\ c^* &= \frac{r}{aK} \left[ K \left[ 1 - \frac{\mu}{r} \right] - \frac{\rho + \alpha(j^* + i^*)}{a} \right] \end{aligned} \quad (3.22)$$

We can see that  $c^* \geq 0$  when  $K \left[ 1 - \frac{\mu}{r} \right] \geq \frac{\rho + \alpha(j^* + i^*)}{a}$ .

Then plug (3b) into (3.18) to get

$$u^* = \frac{\mu}{a}. \quad (3.23)$$

For all the expressions that have  $j^* + i^*$  we can substitute (3.15) into them so that all the components of the equilibrium are in terms of  $u^* + c^*$ , as we do below.

Therefore,

$$\begin{aligned} rz^* \left( 1 - \frac{z^*}{K} \right) &= [\rho + \alpha(j^* + i^*)] (u^* + c^*) \\ \frac{r}{a} [\rho + \alpha(j^* + i^*)] \left( 1 - \frac{[\rho + \alpha(j^* + i^*)]}{aK} \right) &= [\rho + \alpha(j^* + i^*)] (u^* + c^*) \\ \frac{r}{a} \left( 1 - \frac{[\rho + \alpha(j^* + i^*)]}{aK} \right) &= u^* + c^* \\ 1 - \frac{\rho}{aK} - \frac{\alpha}{aK} \left( \frac{\delta + b(u^* + c^*)}{\beta(x)} \right) - \frac{a}{r} (u^* + c^*) &= 0. \end{aligned}$$

With  $x = u^* + c^*$ , we can rewrite this condition as

$$f(x) = 1 - \frac{\rho}{aK} - \frac{\alpha}{aK} \left( \frac{\delta + bx}{\beta(x)} \right) - \frac{a}{r}x = 0.$$

Hence the equilibrium is  $E_6 \left( \frac{\rho}{a} + \frac{\alpha}{a} \left( \frac{\delta + bx}{\beta(x)} \right), \frac{\mu}{a}, x - \frac{\mu}{a}, \frac{d + \delta}{\beta(x)}, \frac{bx - d}{\beta(x)} \right)$ .

Now, we find existence conditions of  $E_6$ . From (4b) and (3.23) we require that

$$x = u^* + c^* \geq \frac{d}{b} \text{ and } x \geq \frac{\mu}{a}.$$

Let

$$\beta_1(x) = \frac{[\log(x) + \log(\pi R^2)]}{x\sqrt{[\log(x) + \log(\pi R^2)]^2 + q^2}} = -\frac{\beta'(x)}{\beta(x)}.$$

Furthermore,  $\lim_{x \rightarrow 0^+} f(x) \rightarrow \infty$  and  $\lim_{x \rightarrow \infty} f(x) \rightarrow -\infty$ . We find that

$$\begin{aligned} f'(x) = 0 &\iff 0 = -\frac{a}{r} - \frac{\alpha}{aK} \left[ \frac{\beta(x)b - (\delta + bx)\beta'(x)}{[\beta(x)]^2} \right] \\ &\iff 0 = -\frac{a}{r} - \frac{\alpha}{aK} \left[ \frac{\beta(x)b + (\delta + bx)\beta(x)\beta_1(x)}{[\beta(x)]^2} \right] \\ &\iff 0 = \frac{a}{r} + \frac{\alpha b}{aK\beta(x)} \left[ 1 + \left( \frac{\delta}{b} + x \right) \frac{1}{x} \frac{\log(x) + \log(\pi R^2)}{\sqrt{[\log(x) + \log(\pi R^2)]^2 + q^2}} \right] \\ &\iff 0 = \frac{a^2 K}{\alpha b r} \beta(x) + \left[ 1 + \left( \frac{\delta}{b} + x \right) \frac{1}{x} \frac{\log(x) + \log(\pi R^2)}{\sqrt{[\log(x) + \log(\pi R^2)]^2 + q^2}} \right] \\ &\implies \text{has no roots unless } \log(x) + \log(\pi R^2) < 0 \\ &\implies x < \frac{1}{\pi R^2} \end{aligned}$$

For all  $x > \frac{1}{\pi R^2}$ ,  $f'(x) < 0$ . As long as  $\frac{d}{b}$  and  $\frac{\mu}{a}$  exceed  $\frac{1}{\pi R^2}$ , we can replace the conditions  $x > \frac{d}{b}$  and  $x > \frac{\mu}{a}$  with  $f\left(\frac{d}{b}\right) > 0$  and  $f\left(\frac{\mu}{a}\right) > 0$ .

Also,

$$f\left(\frac{d}{b}\right) = 1 - \frac{\rho}{aK} - \frac{\alpha}{aK} \left[ \frac{\delta + d}{\beta\left(\frac{d}{b}\right)} \right] - \frac{ad}{br} > 0 \iff \widetilde{R}_R = \left[ \frac{aK}{\alpha} \left( 1 - \frac{ad}{br} \right) - \frac{\rho}{a} \right] \frac{\beta\left(\frac{d}{b}\right)}{d + \delta} > 1$$

Therefore, we need

$$\begin{aligned}
f\left(\frac{\mu}{a}\right) &= 1 - \frac{\mu}{r} - \frac{\rho}{aK} - \frac{\alpha}{aK} \left( \frac{\delta + \frac{b\mu}{a}}{\beta\left(\frac{\mu}{a}\right)} \right) > 0 \\
&\iff Q_A = \frac{aK\left(1 - \frac{\mu}{r}\right)}{\rho + \alpha \left( \frac{\delta + \frac{b\mu}{a}}{\beta\left(\frac{\mu}{a}\right)} \right)} > 1
\end{aligned} \tag{3.24}$$

for  $E_6$  to exist. As will be seen in section 3.4.4,  $Q_A$  is almost identical to anthrax's invasion reproductive number  $\widetilde{R}_A$ , but where  $Q_A$  has  $\frac{\mu}{a}$ ,  $\widetilde{R}_A$  has  $\frac{d}{b}$ . We want to know the relationship between  $\frac{\mu}{a}$  and  $\frac{d}{b}$ . Notice that  $E_5$  has

$$\frac{\mu K(1-m)}{u_5^*} = \rho + \alpha \left( \frac{\delta + bu_5^*}{\beta(u_5^*)} \right),$$

from (3.2) and (3.15). Let

$$\mathcal{L}(x) = \frac{\mu K(1-m)}{x} \text{ and } \mathcal{R}(x) = \rho + \alpha \left( \frac{\delta + bx}{\beta(x)} \right).$$

Then  $\mathcal{L}(x)$  is monotone decreasing in  $x$  for  $x > 0$  and  $\mathcal{R}(x)$  is monotone increasing in  $x$  for  $x \geq \frac{1}{\pi R^2}$  (even a bit sooner), so  $\mathcal{L}(u_5^*) = \mathcal{R}(u_5^*)$ . Then

- $\mathcal{L}(x) > \mathcal{R}(x)$  for  $x < u_5^*$  and
- $\mathcal{L}(x) < \mathcal{R}(x)$  for  $x > u_5^*$  (assuming  $x \geq \frac{1}{\pi R^2}$ ).

But now (3.24) becomes:

$$\begin{aligned}
aK(1-m) > \rho + \alpha \left( \frac{\delta + \frac{b\mu}{a}}{\beta\left(\frac{\mu}{a}\right)} \right) &\iff \frac{\mu K(1-m)}{\mu/a} > \rho + \alpha \left( \frac{\delta + \frac{b\mu}{a}}{\beta\left(\frac{\mu}{a}\right)} \right) \\
&\iff \mathcal{L}\left(\frac{\mu}{a}\right) > \mathcal{R}\left(\frac{\mu}{a}\right) \\
&\iff \frac{\mu}{a} < u_5^*
\end{aligned} \tag{3.25}$$

Also notice that (from section 3.4.4)

$$\widetilde{R}_A = \frac{aK(1-m)}{\rho + \alpha \left( \frac{\delta + bu_5^*}{\beta(u_5^*)} \right)} = \frac{\mathcal{L}\left(\frac{\mu}{a}\right)}{\mathcal{R}(u_5^*)} < 1$$

$$\begin{aligned}
&\iff \mathcal{L}\left(\frac{\mu}{a}\right) < \mathcal{R}(u_5^*) \\
&\iff \mathcal{L}\left(\frac{\mu}{a}\right) < \mathcal{L}(u_5^*) \quad (\text{since } \mathcal{L}(u_5^*) = \mathcal{R}(u_5^*)) \\
&\iff u_5^* < \frac{\mu}{a}
\end{aligned} \tag{3.26}$$

By (3.25) and (3.26), we have that  $u_5^* = \frac{\mu}{a}$ .

**Theorem 3.3.1.**  $\widetilde{R}_A > 1 \iff Q_A > 1$ .

*Proof.* Now,

$$\begin{aligned}
Q_A = \frac{aK\left(1 - \frac{\mu}{r}\right)}{\rho + \alpha\left(\frac{\delta + b\frac{\mu}{a}}{\beta\left(\frac{\mu}{a}\right)}\right)} > 1 &\iff aK\left(1 - \frac{\mu}{r}\right) > \rho + \alpha\left(\frac{\delta + b\frac{\mu}{a}}{\beta\left(\frac{\mu}{a}\right)}\right) \\
&\iff \frac{\mu K\left(1 - \frac{\mu}{r}\right)}{\frac{\mu}{a}} > \rho + \alpha\left(\frac{\delta + b\frac{\mu}{a}}{\beta\left(\frac{\mu}{a}\right)}\right) \\
&\iff \mathcal{L}\left(\frac{\mu}{a}\right) > \mathcal{R}\left(\frac{\mu}{a}\right) \\
&\iff \frac{\mu}{a} < u_5^* \\
&\iff \mathcal{L}\left(\frac{\mu}{a}\right) > \mathcal{L}(u_5^*) \\
&\iff \mathcal{L}\left(\frac{\mu}{a}\right) > \mathcal{R}(u_5^*) \\
&\iff \frac{\mu K\left(1 - \frac{\mu}{r}\right)}{\frac{\mu}{a}} > \rho + \alpha\left(\frac{\delta + bu_5^*}{\beta(u_5^*)}\right) \\
&\iff ak\left(1 - \frac{\mu}{r}\right) > \rho + \alpha\left(\frac{\delta + bu_5^*}{\beta(u_5^*)}\right) \\
&\iff \frac{aK\left(1 - \frac{\mu}{r}\right)}{\rho + \alpha\left(\frac{\delta + bu_5^*}{\beta(u_5^*)}\right)} > 1 \\
&\iff \widetilde{R}_A > 1.
\end{aligned}$$

Therefore,  $\widetilde{R}_A > 1 \iff Q_A > 1$ . Similarly, we can show  $\widetilde{R}_A < 1 \iff Q_A < 1$ .  $\square$

Therefore,  $E_6\left(\frac{\rho}{a} + \frac{\alpha}{a}\left(\frac{\delta + bx}{\beta(x)}\right), \frac{\mu}{a}, x - \frac{\mu}{a}, \frac{d + \delta}{\beta(x)}, \frac{bx - d}{\beta(x)}\right)$  exists when  $\widetilde{R}_R > 1$  and  $\widetilde{R}_A > 1$ .



Note that if  $x \leq \frac{d}{b}$  then no rabies can persist and we go back to  $E_4$ . Also note that if  $x \leq \frac{\mu}{a}$  then there is no anthrax and we go back to  $E_5$ .

### 3.4 Reproductive Numbers

We use the next generation operator method to find the reproductive numbers in this section.

#### 3.4.1 Basic Reproductive Numbers for Anthrax

We use the basic reproductive numbers from [47] and rename them here. The basic reproductive number for anthrax in the absence of jackals is denoted  $R_{AO} = \frac{aK(1-m)}{\rho}$ . The basic reproductive number for anthrax in the presence of jackals is denoted  $R_{AJ} = \frac{ad}{b\mu}$ .

#### 3.4.2 Basic Reproductive Number for Rabies in the absence of Anthrax

To find the basic reproductive number for rabies in the absence of anthrax we consider the  $I$  class as the only infected class. The  $E_2$  equilibrium is the disease free equilibrium with jackals present.

$$\mathcal{X} = \{Z, U, C, J\} \quad \mathcal{Z} = \{I\}$$

$$\begin{aligned} A &= \frac{\partial}{\partial I} \left( \frac{dI}{dt} \right) \Big|_{E_2} = \beta(x)j - (d + \delta) \Big|_{E_2} \\ &= \beta \left( \frac{d}{b} \right) \left[ \frac{1}{\alpha} \left[ \frac{b\mu}{d} z^* - \rho \right] \right] - (d + \delta) \end{aligned}$$

$$\begin{aligned} R_R &= \frac{a}{\alpha} \left[ \frac{b\mu}{ad} K \left( 1 - \frac{\mu}{r} \right) - \frac{\rho}{a} \right] \frac{\beta \left( \frac{d}{b} \right)}{d + \delta} \\ &= \frac{a}{\alpha} \left[ \frac{1}{R_{AJ}} K (1 - m) - \frac{\rho}{a} \right] \frac{\beta \left( \frac{d}{b} \right)}{d + \delta} \end{aligned}$$

$$= \frac{aK}{\alpha} \left[ \frac{1-m}{R_{AJ}} - \frac{\rho}{aK} \right] \frac{\beta \left( \frac{d}{b} \right)}{d+\delta}$$

### 3.4.3 Invasion Reproductive Number for Rabies in the presence of Anthrax

The invasion reproductive number (IRN) for rabies in the presence of anthrax,  $\widetilde{R}_R$  is the average number of secondary infections (of rabies) caused by introducing one rabid jackal into an environment ( $E_4$ ) where anthrax persists in the zebra population with jackals present.

$$\mathcal{X} = \{Z, U, C, J\} \quad \mathcal{Z} = \{I\}$$

$$\begin{aligned} A &= \frac{\partial}{\partial I} \left( \frac{dI}{dt} \right) \Big|_{E_4} = \beta(x)j - (d+\delta) \Big|_{E_4} \\ &= \beta \left( \frac{d}{b} \right) \left[ \frac{aK}{\alpha} \left( 1 - \frac{ad}{br} \right) - \frac{\rho}{\alpha} \right] - (d+\delta) \end{aligned}$$

$$\begin{aligned} \widetilde{R}_R &= \beta \left( \frac{d}{b} \right) \left[ \frac{aK}{\alpha} \left( 1 - \frac{ad}{br} \right) - \frac{\rho}{\alpha} \right] \frac{1}{d+\delta} \\ &= \left[ \frac{aK}{\alpha} \left( 1 - \frac{ad}{br} \right) - \frac{\rho}{\alpha} \right] \frac{\beta \left( \frac{d}{b} \right)}{d+\delta} \\ &= \frac{aK}{\alpha} \left[ (1 - mR_{AJ}) - \frac{\rho}{aK} \right] \frac{\beta \left( \frac{d}{b} \right)}{d+\delta} \end{aligned}$$

### 3.4.4 Invasion Reproductive Number for Anthrax in the presence of Rabies

The IRN for anthrax in the presence of rabies,  $\widetilde{R}_A$ , presupposes that there are jackals so there can be rabies.  $\widetilde{R}_A$  represents the average number of secondary anthrax infections caused by introducing one anthrax infect zebra carcass into an environment, where rabies already persists in the jackal population. The only anthrax class that is considered infected is  $C$  and the  $E_5$  equilibrium is where rabies is present but anthrax is absent.

$$\mathcal{X} = \{Z, U, J, I\} \quad \mathcal{Z} = \{C\}$$

$$\begin{aligned} A &= \frac{\partial}{\partial C} \left( \frac{dC}{dt} \right) \Big|_{E_5} = \frac{\partial}{\partial C} (acz - \rho c - \alpha(j+i)c) \Big|_{E_5} \\ &= az - \rho - \alpha(j+i) \Big|_{E_5} \\ &= aK \left[ 1 - \frac{\mu}{r} \right] - \rho - \alpha \left( \frac{\delta + bu_5^*}{\beta(u_5^*)} \right) \end{aligned}$$

Let  $M = aK \left[ 1 - \frac{\mu}{r} \right]$  and  $D = \rho + \alpha \left( \frac{\delta + bu_5^*}{\beta(u_5^*)} \right)$ . Then

$$\widetilde{R}_A = MD^{-1} = \frac{aK \left[ 1 - \frac{\mu}{r} \right]}{\rho + \alpha \left( \frac{\delta + bu_5^*}{\beta(u_5^*)} \right)}$$

The basic and invasion reproduction numbers are summarized in table 3.4 for both anthrax and rabies.

### 3.5 Stability Analysis

Stability analysis was carried out for equilibria  $E_0$  through  $E_5$  using the Jacobian matrix and standard methods; details are given in appendix B.1.

The extinction equilibrium,  $E_0$  is locally asymptotically stable if the zebra birth rate is less than the zebra death rate, i.e.  $r < \mu$ .

The equilibrium where only zebras and healthy zebra carcasses are present is  $E_1$ , and it exists when  $\mu < r$ .  $E_1$  is locally asymptotically stable if and only if  $z^* < \frac{\rho}{a}$  and  $b\mu z^* < \rho d$ .

The equilibrium  $E_2$  exists when  $\mu < r$  and  $b\mu z^* > \rho d$ . This equilibrium describes when zebras, uninfected carcasses, and jackals are present.  $E_2$  is locally asymptotically stable if and only if  $\beta \left( \frac{d}{b} \right) \left( \frac{b\mu}{d} z^* - \rho \right) < \alpha (d + \delta)$  (the same as  $R_R < 1$ ) and  $\frac{ad}{b\mu} < 1$ .

The equilibrium  $E_3$  exists when  $\mu < r$  and  $K \left( 1 - \frac{\mu}{r} \right) > \frac{\rho}{a}$ .  $E_3$  describes when zebras and anthrax are present. We find that  $E_3$  is locally asymptotically stable if and only if  $u^* + c^* = \frac{\mu}{a} + \frac{r}{aK} \left[ K \left( 1 - \frac{\mu}{r} \right) - \frac{\rho}{a} \right] < \frac{d}{b}$ .

The equilibrium  $E_4$  exists when  $\frac{\rho}{a} < K \left[1 - \frac{ad}{br}\right]$  &  $\frac{ad}{b\mu} > 1$ . This equilibrium is where zebras, anthrax and jackals are present. We find that  $E_4$  is locally asymptotically stable whenever  $\beta \left(\frac{d}{b}\right) j_4^* < d + \delta$ , i.e.,  $\widetilde{R}_R < 1$ .

The equilibrium  $E_5$  is where zebras, jackals, and rabies are present and it exists when  $u^* > \frac{d}{b}$  or equivalently when  $R_R > 1$ . We discover that  $E_5$  is locally asymptotically stable if and only if  $\widetilde{R}_A < 1$  and  $\frac{d}{b} < u_5^* < \frac{d + \sqrt{d^2 + 4b\mu K(1-m)}}{2b}$ .

Through numerical exploration, we found a limit cycle that occurred when  $u_5^* > \frac{d + \sqrt{d^2 + 4b\mu K(1-m)}}{2b}$ . This was verified by selecting points outside and inside of the limit cycle to see it spiral inward and outward, respectively.

Table 3.3 summarizes the existence and stability conditions of each of the seven equilibria.

Equilibrium	Existence	LAS
$E_0(0, 0, 0, 0, 0)$	always	$\mu > r$
$E_1\left(K\left[1 - \frac{\mu}{r}\right], \frac{\mu}{\rho}K\left[1 - \frac{\mu}{r}\right], 0, 0, 0\right)$	$\mu < r$	$R_{AO} < 1$ & $R_{AO} < R_{AJ}$
$E_2\left(K\left[1 - \frac{\mu}{r}\right], \frac{d}{b}, 0, \frac{1}{\alpha}\left[\frac{b\mu}{d}z^* - \rho\right], 0\right)$	$\mu < r$ & $R_{AO} > R_{AJ}$	$R_{AJ} < 1$ & $R_R < 1$
$E_3\left(\frac{\rho}{a}, \frac{\mu}{a}, \frac{r}{aK}\left[K\left(1 - \frac{\mu}{r}\right) - \frac{\rho}{a}\right], 0, 0\right)$	$\mu < r$ & $R_{AO} > 1$	$mR_{AJ} + \frac{1-m}{R_{AO}} > 1$
$E_4\left(K\left[1 - \frac{ad}{br}\right], \frac{\mu}{a}, \frac{d}{b} - \frac{\mu}{a}, \frac{a}{\alpha}K\left[1 - \frac{ad}{br}\right] - \frac{\rho}{\alpha}, 0\right)$	$R_{AJ} > 1$ & $mR_{AJ} + \frac{1-m}{R_{AO}} < 1$	$\widetilde{R}_R < 1$
$E_5\left(K\left(1 - \frac{\mu}{r}\right), u_5^*, 0, \frac{d+\delta}{\beta(u_5^*)}, \frac{bu_5^*-d}{\beta(u_5^*)}\right)$	$\mu < r$ & $R_R > 1$	$\widetilde{R}_A < 1$ & $\frac{d}{b} < u_5^* < \frac{d+\sqrt{d^2+4b\mu K(1-m)}}{2b}$
$E_6\left(\frac{\rho+\alpha(j^*+i^*)}{a}, \frac{\mu}{a}, \frac{r}{aK}\left[K\left[1 - \frac{\mu}{r}\right] - \frac{\rho+\alpha(j^*+i^*)}{a}\right], \frac{d+\delta}{\beta(x)}, \frac{b(u^*+c^*)-d}{\beta(x)}\right)$	$\widetilde{R}_R > 1$ & $\widetilde{R}_A > 1$	$\beta_0 < H(a)$

Table 3.3: Summary of the existence and local stability for the seven equilibria.

RN	Anthrax	Rabies
<b>BRN</b>	$R_{A0} = \frac{K(1-m)}{\rho/a}$ ; $R_{AJ} = \frac{ad}{b\mu}$	$R_R = \frac{aK}{\alpha} \left[ \frac{1-m}{R_{AJ}} - \frac{\rho}{aK} \right] \frac{\beta \left( \frac{d}{b} \right)}{d + \delta}$
<b>IRN</b>	$\widetilde{R}_A = \frac{aK \left[ 1 - \frac{\mu}{r} \right]}{\rho + \alpha \left( \frac{\delta + bu_5^*}{\beta(u_5^*)} \right)}$	$\widetilde{R}_R = \frac{aK}{\alpha} \left[ (1 - mR_{AJ}) - \frac{\rho}{aK} \right] \frac{\beta \left( \frac{d}{b} \right)}{d + \delta}$

Table 3.4: Summary of reproductive numbers (RNs). Basic Reproductive numbers (BRNs) are listed for anthrax and rabies as well as the invasion reproductive numbers (IRNs) for anthrax and rabies. Note  $m = \frac{\mu}{r}$ .

To find the stability of  $E_6$ , we took an ad hoc approach. Numerical exploration for  $E_6$  revealed a Hopf bifurcation beyond which a limit cycle is stable. In order to identify numerically where in the parameter space the Hopf bifurcation occurs, we consider a two-dimensional cross-section in  $\beta_0$  and  $a$  as proxies for rabies and anthrax transmission, respectively. The Hopf bifurcation curve begins as the  $u_5^* = \frac{d + \sqrt{d^2 + 4b\mu K(1-m)}}{2b}$  line (indicating a Hopf bifurcation of  $E_5$ ), and where it crosses the  $\widetilde{R}_A = 1$  curve, it instead begins to denote a Hopf bifurcation of  $E_6$  ( $H(a)$  is the highest value of  $\beta_0$  for which  $E_6$  is stable for a particular value of  $a$ ). The resulting graph is presented in figure 3.2 along with  $R_{AJ} = 1$ ,  $R_R = 1$ ,  $\widetilde{R}_R = 1$ , and  $\widetilde{R}_A = 1$ , and  $u_5^* = \frac{d + \sqrt{d^2 + 4b\mu K(1-m)}}{2b}$ . Recall that  $\beta_0$  denotes the constant coefficient as defined in section 3.2.1, which is the horizontal axis.

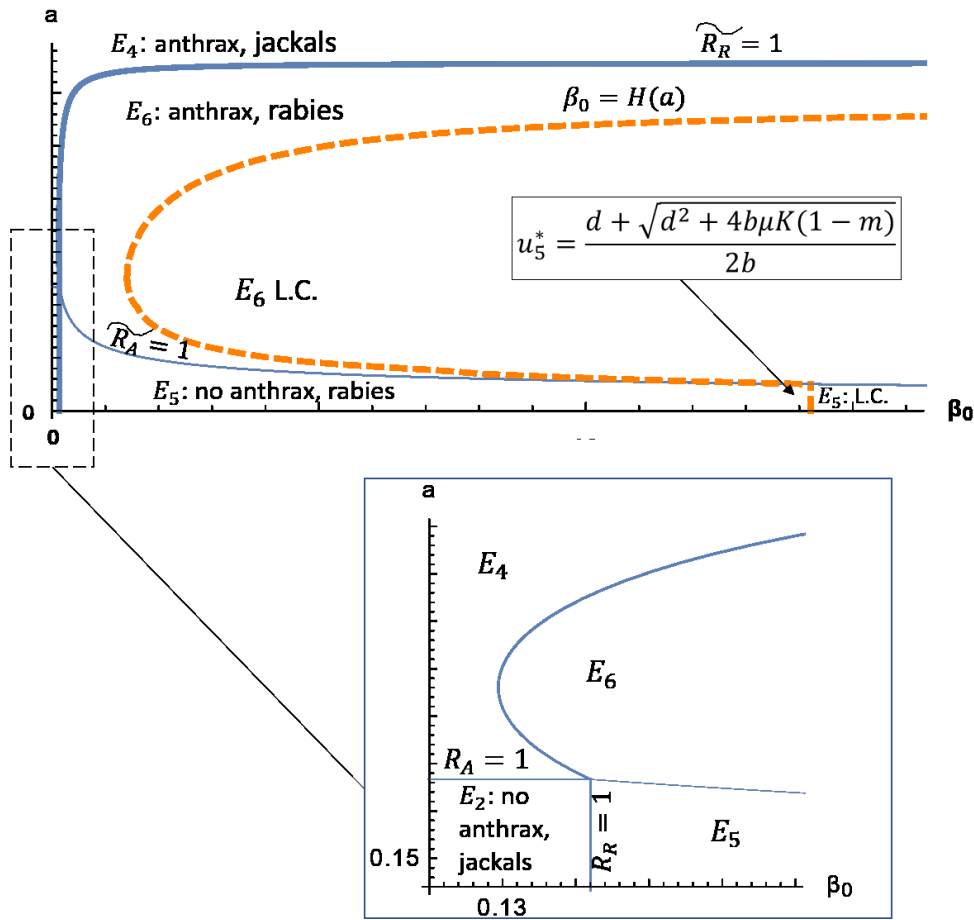


Figure 3.2: Bifurcation Graph. The vertical axis is  $a$  and the horizontal axis is  $\beta_0$ . The regions are generated by plotting  $R_A = 1$ ,  $R_R = 1$ ,  $\widetilde{R}_A = 1$ ,  $\widetilde{R}_R = 1$ ,  $u_5^* = \frac{d + \sqrt{d^2 + 4b\mu K(1-m)}}{2b}$ , and  $\beta_0 = H(a)$ . The regions are labeled with the equilibrium that is LAS followed by a brief description of that equilibrium. The abbreviation ‘L.C.’ is short for limit cycle. The region that is in a rectangular box is blown up as a sub-figure to see how all the curves come together. Note the curve coming in from the top of the sub-figure is  $\widetilde{R}_R = 1$ , and the curve coming in from the right is  $\widetilde{R}_A = 1$  as labeled in the large plot. In addition, the sub-figure displays how the  $\widetilde{R}_R = 1$  curve goes to the right and then to the left, which shows how many  $a$  values there are associated with one  $\beta_0$  value.

The equilibria that have regions of stability in figure 3.2 are  $E_2$ ,  $E_4$ ,  $E_5$ , and  $E_6$ . The equilibrium  $E_2$  is where rabies and anthrax are absent and  $E_4$  is where rabies is absent and anthrax is present. The  $E_2$  and  $E_4$  equilibria share an opposite stability



boundary condition, that is, if  $R_A < 1$  then  $E_2$  is stable but if  $R_A > 1$  then  $E_4$  is stable. The bold solid line ( $\widetilde{R}_R = 1$  and  $R_R = 1$ ) is the threshold for when rabies can persist with or without anthrax. Rabies is present in the equilibria  $E_5$  and  $E_6$ . The equilibrium  $E_5$  is where anthrax is absent and  $E_6$  is where anthrax are present. The  $E_5$  and  $E_6$  equilibria share an opposite stability boundary condition, that is, if  $\widetilde{R}_A < 1$  then  $E_5$  is stable and if  $\widetilde{R}_A > 1$  then  $E_6$  is stable. The thin solid line ( $R_A = 1$  and  $\widetilde{R}_A = 1$ ) is the threshold for anthrax to persist in the presence and absence of rabies. The dashed line ( $u_5^* = \frac{d + \sqrt{d^2 + 4b\mu K(1-m)}}{2b}$  and  $\beta_0 = H(a)$ ) is the threshold for when the solutions oscillate leading to a limit cycle. A limit cycle occurs when rabies is present and anthrax is absent ( $E_5$  limit cycle) and when both anthrax and rabies persist ( $E_6$  limit cycle). In figure 3.2, the jackal population persists in order for rabies to exist. Therefore, equilibria  $E_1$  and  $E_3$  are not seen in figure 3.2 because jackals are not present in those equilibria.

To understand why the curve  $\widetilde{R}_R = 1$  veers off to the right and approaches some asymptote we investigate what is happening with the parameter  $a$ . We do this by writing  $\widetilde{R}_R = 1$  as a quadratic function in terms of  $a$ . Then using the quadratic equation we can find the values between which  $a$  must be bounded.

Consider when  $\widetilde{R}_R = 1$  then

$$\begin{aligned}
\widetilde{R}_R &= \left[ \frac{K}{\alpha}a - \frac{dK}{br\alpha}a^2 - \frac{\rho}{\alpha} \right] \frac{\beta \left( \frac{d}{b} \right)}{d + \delta} = 1 \\
\implies \frac{K}{\alpha}a - \frac{dK}{br\alpha}a^2 - \frac{\rho}{\alpha} &= \frac{d + \delta}{\beta \left( \frac{d}{b} \right)} \\
\implies \frac{dK}{br\alpha}a^2 - \frac{K}{\alpha}a + \frac{\rho}{\alpha} + \frac{d + \delta}{\beta \left( \frac{d}{b} \right)} &= 0 \\
\implies a^2 - \frac{br}{d}a + \frac{br}{dK} \left[ \rho + \frac{\alpha(d + \delta)}{\beta \left( \frac{d}{b} \right)} \right] &= 0
\end{aligned}$$

Using the quadratic formula, we define

$$a_{\pm} = \frac{1}{2} \left( \frac{br}{d} \pm \sqrt{\left(\frac{br}{d}\right)^2 - 4\frac{br}{dK} \left(\rho + \frac{\alpha(d+\delta)}{\beta\left(\frac{d}{b}\right)}\right)} \right). \quad (3.27)$$

Therefore,  $0 < a_{\pm} < \frac{br}{d}$  and exists if and only if  $\frac{br}{d} > \frac{4}{K} \left[ \rho + \frac{\alpha(d+\delta)}{\beta\left(\frac{d}{b}\right)} \right]$ . Hence  $\widetilde{R}_R > 1$  if and only if  $a^2 - \frac{br}{d}a + \frac{br}{dK} \left[ \rho + \frac{\alpha(d+\delta)}{\beta\left(\frac{d}{b}\right)} \right] < 0$ .

Note that

$$\begin{aligned} \beta\left(\frac{d}{b}\right) &= e^{k - \sqrt{(\log(d/b) + \log(\pi R^2))^2 + q^2}} \\ &= \beta_0 e^{-\sqrt{(\log(d/b) + \log(\pi R^2))^2 + q^2}}. \end{aligned}$$

Notice that as  $\beta_0 \rightarrow \infty$  in (3.27), the fraction  $\frac{\alpha(d+\delta)}{\beta\left(\frac{d}{b}\right)} \rightarrow 0$ . Therefore, the asymptote occurs at  $\lim_{\beta_0 \rightarrow \infty} a_{+} = \frac{1}{2} \left( \frac{br}{d} + \sqrt{\left(\frac{br}{d}\right)^2 - 4\frac{\rho br}{dK}} \right)$ . We can rewrite the condition  $\frac{br}{d} > \frac{4}{K} \left[ \rho + \frac{\alpha(d+\delta)}{\beta\left(\frac{d}{b}\right)} \right]$ , which is independent of  $a$  as below.

$$\frac{br}{d} > \frac{4}{K} \left[ \rho + \frac{\alpha(d+\delta)}{\beta\left(\frac{d}{b}\right)} \right] \implies \beta_0 > \frac{\alpha(d+\delta)}{\left( e^{-\sqrt{(\log(d/b) + \log(\pi R^2))^2 + q^2}} \left( \frac{brK}{4d} - \rho \right) \right)}.$$

Let  $\mathcal{A} = \frac{\alpha(d+\delta)}{e^{-\sqrt{(\log(d/b) + \log(\pi R^2))^2 + q^2}}}$ . When

- $\beta_0 < \frac{\mathcal{A}}{\left(\frac{brK}{4d} - \rho\right)}$  then there is no  $a$  value where  $\widetilde{R}_R = 1$ ,
- $\beta_0 = \frac{\mathcal{A}}{\left(\frac{brK}{4d} - \rho\right)}$  then there is 1  $a$  value where  $\widetilde{R}_R = 1$ ,
- $\frac{\mathcal{A}}{\left(\frac{brK}{4d} - \rho\right)} < \beta_0 < \frac{\mathcal{A}}{\rho(D(E_1)-1)}$  then there are 2  $a$  values where  $\widetilde{R}_R = 1$ , where  $D(E_1) = \frac{b\mu}{\rho d} K(1-m)$ , [47] and
- $\beta_0 > \frac{\mathcal{A}}{\rho(D(E_1)-1)}$  there is 1  $a$  value where  $\widetilde{R}_R = 1$ .

$D(E_1)$  is the scavenger demographic reproductive number, which describes the ability for jackals to persist in the absence of anthrax [47]. These regions can be seen from left to right in figure 3.2 by observing the graph of  $H(a)$ .

### 3.6 Discussion

Section 3.6 is broken down into three subsections. First, we present and biologically interpret what is happening in four different scenarios with limit cycles. Then we find which equilibrium is stable when we plug in parameter values obtain from literature, and finally, we answer the questions: does anthrax amplify rabies and does rabies amplify anthrax?

#### 3.6.1 Limit Cycle

In this section, four different scenarios are presented with limit cycles and we interpret biologically what is happening in each limit cycle. We verified numerically that there is an unstable equilibrium in the middle of the limit cycle:  $E_6$  has two eigenvalues (complex conjugates) with a positive real part, while the other three eigenvalues have negative real parts.

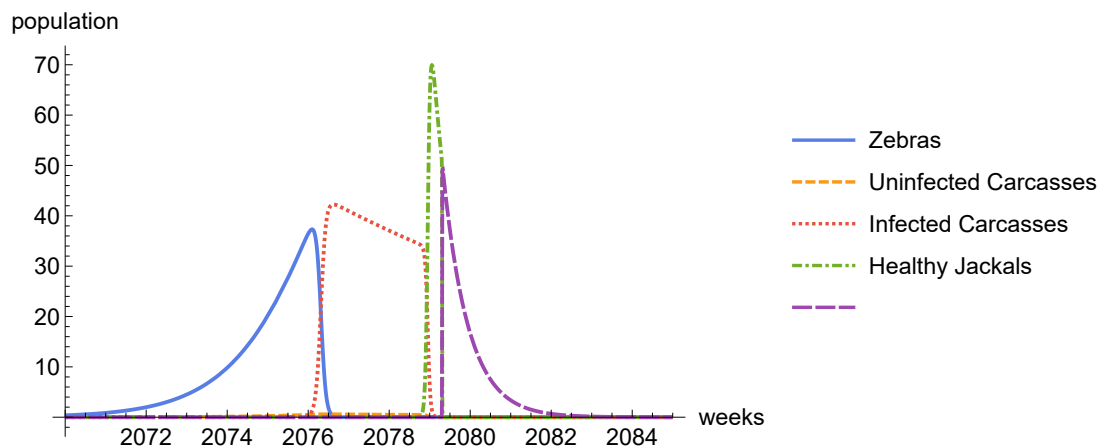


Figure 3.3: Limit Cycle.  $R = 7$

In figure 3.3, the zebra population starts to increase because there is plenty of food available and they are not near their carrying capacity. Once the zebras reach a critical mass they start to get infected quickly. That is, zebras are tripping over

infected carcasses, which is increasing the contact rate between zebras and infected carcasses. Therefore, all the zebras get infected and die. Then the zebra carcasses are decaying for a time period until the jackals discover the carcasses and eat them all. Then the jackals die out because they depleted their food source and since carcasses are scarce they are interacting more so they all get rabies and die.

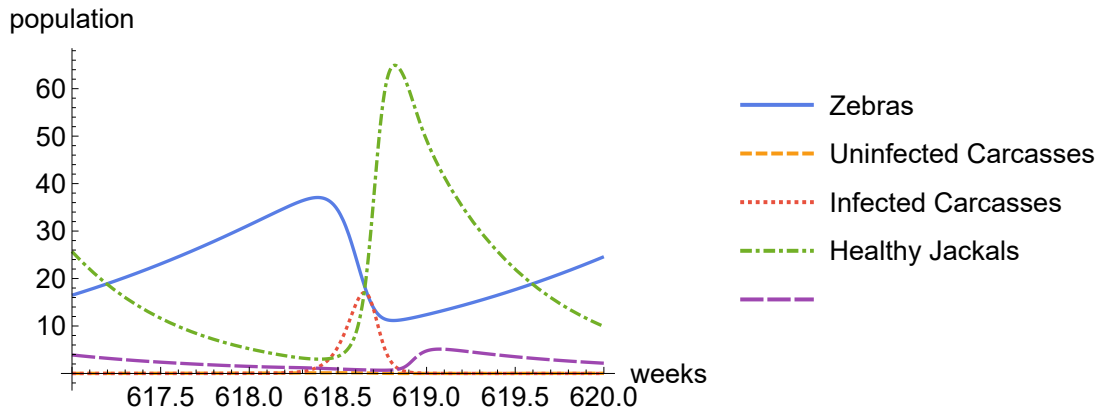


Figure 3.4: Limit Cycle.  $R = 1$

In figure 3.4, the maximum detection radius for jackals is decreased to  $R = 1$ . Here the zebras are increasing in size and as some get infected the infected carcasses start to increase as the zebras start to decrease. Then as the infected carcasses start to increase the jackal population starts to increase because they have food. Once the number of carcasses decrease, this drives more jackals to the same carcasses, hence increasing the contact rate between healthy and rabid jackals. Therefore, the rabid jackals increase but since the carcasses are gone the jackals run out of food until the next anthrax outbreak in zebras occur.

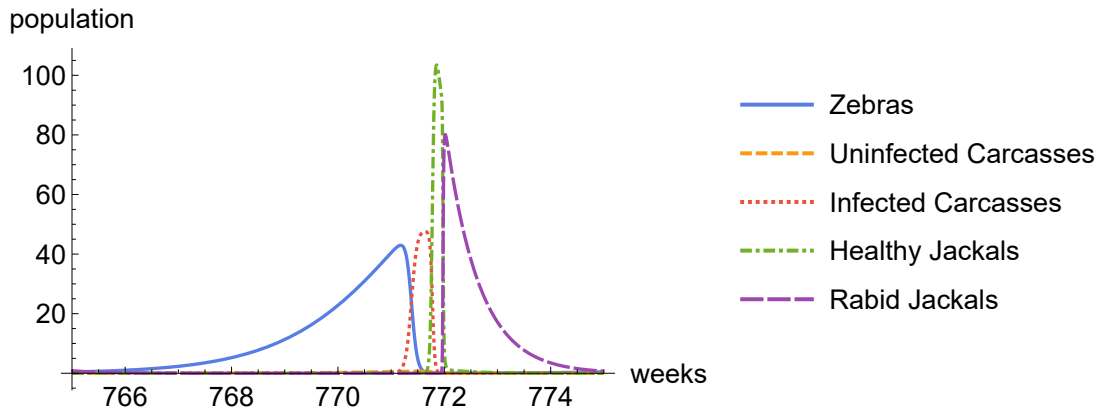


Figure 3.5: Limit Cycle.  $R = 3$

In figure 3.5, the maximum detection radius for jackals was changed from seven to three. This means that the jackals are not able to detect carcasses that are as far away from them. There is still a similar story as described above for figure 3.3; however, there are small changes. Once the zebras are all dead and the land is saturated with carcasses, the jackals find the carcasses and eat them quickly. Then as the jackals are dying, they get rabies and die.

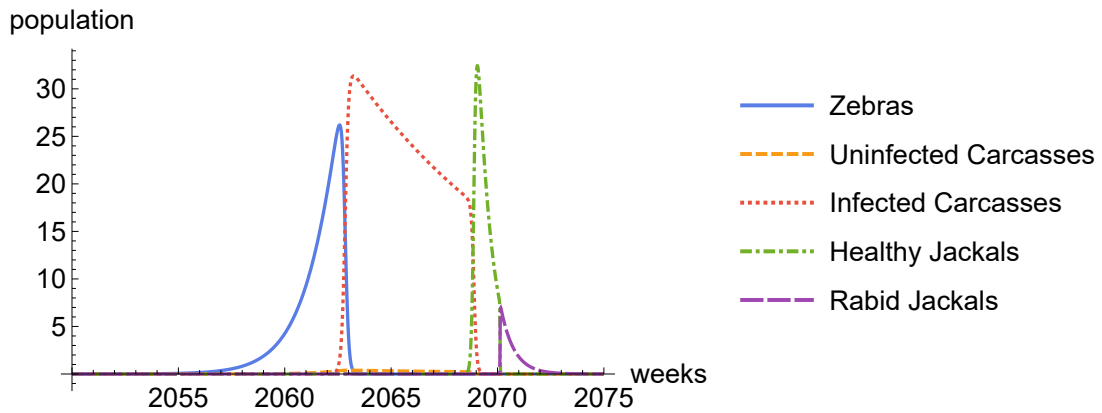


Figure 3.6: Limit Cycle.  $R = 12$

Figure 3.6 is the same story except because the detection distance is farther ( $R = 12$ ) this allows the jackals to find their own carcass so they do not have to share once the carcasses become less abundant. Hence rabies is not the main cause of death when the jackals can detect resources further away.

### 3.6.2 Numerical Analysis

Some of the parameter values were obtained from previously published papers as listed in table 3.5, while the others were estimated in the previous chapter.

Symbol	Description	Value	Source
$K$	zebra carrying capacity ( <i>zebras</i> )	13000 – 15000	[25]
$r$	intrinsic growth rate of zebras	$3.06849 \times 10^{-3}$	[47]
$\mu$	natural zebra death rate	$7.67123 \times 10^{-4}$	[47]
$a$	rate zebras come into contact with infected carcasses ( <i>week · zebras</i> ) <sup>-1</sup>	$1.1433 \times 10^{-5}$	[47]
$\rho$	natural decomposition rate of zebra carcasses	0.12727	[31]
$\alpha$	rate jackals come into contact with carcasses to eat ( <i>week · jackals</i> ) <sup>-1</sup>	0.03608	[47]
$b$	birth rate of jackals ( <i>week · zebras</i> ) <sup>-1</sup>	0.051811	[47]
$d$	death rate of jackals	$4.808 \times 10^{-3}$	[32]
$\delta$	additional death rate of jackals from rabies	1.4	[32]

Table 3.5: Parameter table with values. Units in  $\frac{1}{week}$  except as noted.

When the parameter values in table 3.5 and the  $\hat{\rho}$  and  $R$  values from the end of section 3.2.1 are plugged in, the equilibrium that is stable is  $E_5$ , which describes when rabies is present and anthrax is absent. To figure out where we are on the  $\beta$  curve, we find  $u^*$  by finding the root of the  $g$  function. The root occurs when  $u^* = 4.71$  carcasses (recall  $c^* = 0$ ), which is on the down slope of the  $\beta$  function. Hence the jackal-to-jackal encounter rate is high enough for the rabies to persist. For these parameter values the condition  $x > \frac{1}{\pi R^2}$ , which is assumed in section 3.3 for the existence for  $E_5$  and  $E_6$  is certainly satisfied. When we increase  $a$  by a factor of 15, that is,  $a = 1.715 \times 10^{-4}$  then we just make it in the region where  $E_6$  is stable: rabies is still present, but now anthrax persists. An increase in the parameter  $a$  describes the zebra coming into contact with anthrax more, which may be due to an increase distance of the spore spreading around an infected zebra carcass. However, this large of an increase seems unlikely to happen. In addition, we changed the parameter  $\beta_0$  by a factor of  $3.2 \times 10^{-4}$  to just get into the region where  $E_2$  is stable. This also is unlikely to happen. After changing other parameters,  $E_5$  was still the stable equilibrium. Through numerical exploration, we conclude that we are well inside the region of stability for  $E_5$ .

### 3.6.3 Does anthrax amplify rabies? Does rabies amplify anthrax?

We want to answer the question: does anthrax amplify rabies? Recall  $R_R$  and  $\widetilde{R}_R$  and notice that the only difference is  $\frac{1-m}{R_{AJ}}$  in  $R_R$  and  $1 - mR_{AJ}$  in  $\widetilde{R}_R$ .

**Theorem 3.6.1.** *Anthrax amplifies rabies:  $R_R < \widetilde{R}_R$  when  $R_{AJ}$  is between 1 and  $\frac{1-m}{m}$ .*

*Proof.*

$$R_R < \widetilde{R}_R \iff \frac{1-m}{R_{AJ}} < 1 - mR_{AJ}$$

$$\begin{aligned} &\iff 1 - m < R_{AJ} - mR_{AJ}^2 \\ &\iff mR_{AJ}^2 - R_{AJ} + (1 - m) < 0 \end{aligned}$$

Solve for  $R_{AJ}$  using the quadratic formula. Then  $R_{AJ}$  must be between  $\frac{1 \pm |1-2m|}{2m}$ .

Therefore, when

- $m < \frac{1}{2} \implies 1 < R_{AJ} < \frac{1-m}{m}$  or
- $m > \frac{1}{2} \implies \frac{1-m}{m} < R_{AJ} < 1$

is satisfied then anthrax amplifies rabies.  $\square$

From the ZUCJ system in [47], we know jackal presence interferes with anthrax; therefore, we would guess that the presence of rabies interferes with the jackals. Looking at figure 3.2 we can see that when rabies is present ( $\widetilde{R}_R > 1$  and  $R_R > 1$ ), it is easier to cross the threshold for anthrax persistence (the decrease in the  $\widetilde{R}_A = 1$  curve). Therefore, the rabies amplifies anthrax.

### 3.7 Conclusion

To understand how the prevalence of zebra carcasses affects rabies we look at the  $\beta$  plot in figure 3.1. When  $u^* + c^*$  is small (left side of maximum) the encounter rate is low because there are not enough zebra carcasses for the jackals to find. When  $u^* + c^*$  is large the encounter rate is low because each jackal has its own carcasses to feed from. When  $u^* + c^*$  is in the middle, the right amount of zebra carcasses are available to force the jackals to interact often, which causes high encounter rates as well as the maximum encounter being achieved. When we use the parameter estimates in section 3.6.2, equilibrium  $E_5$  is stable. Equilibrium  $E_5$  describes where anthrax is absent and rabies is present; therefore, there are jackal to jackal interactions. Since



jackals are present and hence interacting we want to know the number of zebra carcasses available to understand the conspecific encounter rate. We can find  $u^*$  by finding the root of the  $g$  function and we get that  $u^* = 4.71$  carcasses (recall  $c^* = 0$ ), which is on the down slope of the  $\beta$  function. Since  $E_5$  is stable, the encounter rate is high enough for the rabies to persist in the jackal population.

One question of interest is does anthrax help or hurt rabies? When anthrax persists at a low level, anthrax makes it easier for rabies to persist. This occurs precisely when  $R_{AJ}$  is between 1 and  $\frac{1-m}{m}$  regardless if  $m$  is less than or greater than  $\frac{1}{2}$ . The sub-figure in figure 3.2, shows how  $\widetilde{R}_R = 1$  curve goes to the left and then to the right. This means that when anthrax barely persists, it helps the rabies a little bit, but if there is a lot of anthrax it hurts rabies and eventually to the point where rabies can't persist (figure 3.2). This invoked the question, why is it that if anthrax is bad enough, the rabies can't persist? The  $a$  value where rabies is no longer able to persist is exactly where the horizontal asymptote occurs, which is at  $a = \frac{1}{2} \left( \frac{br}{d} + \sqrt{\left(\frac{br}{d}\right)^2 - 4\frac{\rho br}{dK}} \right)$ . We were also able to find the  $\beta_0$  value that is associated to the left most point on the  $\widetilde{R}_R = 1$  curve:  $\beta_0 = \frac{\mathcal{A}}{\left(\frac{brK}{4d} - \rho\right)}$ .

The reason why rabies cannot persist if there is too much anthrax is because the rabies is driven by the jackal population. The ability for rabies to persist is dependent on the jackal population at that moment when rabies starts to break out, which is  $E_4$  when anthrax is already present. At that point, the jackal population is driven by food generation, so that anthrax actually increases the food supply but at the same time it decreases the long term food supply visible in  $z_4^* = K \left(1 - \frac{ad}{br}\right)$ , so  $a$  negatively impacts the number of long term zebras and the jackal population also depends on  $a$  to generate short term food. Therefore,  $a$  is depended upon twice in a nonlinear way: once in the generation of food for the jackals and once in the impact of reducing the long term zebra population. It is a negative quadratic dependence

(cf. section 3.5) because of the way it reduces the zebra population. Hence if the anthrax is transmitted too well it reduces the jackal population to the point where rabies cannot spread.

Another question we answer is does rabies help or hurt anthrax? From figure 3.2 we can see that when rabies is present, it is easier to cross the threshold for anthrax persistence (the decrease in the  $\widetilde{R}_A = 1$  curve). This is because the jackals help to get rid of the anthrax by eating infected carcasses, which is how the anthrax stays in the environment. Therefore, if there are fewer jackals present then anthrax is not getting eaten and the anthrax is left unhindered to spread. Therefore, rabies is helping anthrax and the more rabies present means the less anthrax there needs to be for it to persist.

In addition, when  $\beta_0$  is high enough or when rabies is contagious enough (figure 3.2), this leads to a destabilizing effect which causes a limit cycle because the jackals are able to come into contact with each other frequently. However, if the anthrax spreads well then the rabies will get suppressed and then there will not be a limit cycle. The limit cycles only exist when rabies persists.

One limitation of the model that we have seen in [47] is that the zebra carcasses are representative of all the food that jackals consume. Another limitation is that the encounter rate between jackals would be higher because we only consider the interactions between jackals at carcasses. However, jackals are social animals, living in groups [4]. Therefore, there would be more interaction between them than what our  $\beta$  function captures specifically when the number of carcasses is zero.

For future work, the jackals can be modeled as facultative scavengers meaning they have an alternative food source to survive since the carcasses are not required for jackal survival. In addition, we can add an obligate scavenger, like the vulture, to the system to see how jackals and vultures compete for carcasses. According to the study

[48], the authors discovered the absence of vultures at carcasses was associated with longer carcass decomposition times, more individual mammals at carcasses, mammals spending more time at carcasses, and mammals coming into contact with one another more frequently. In our case, we could see if the presence of vultures lowers the jackal-to-jackal encounter rate leading to a decrease in the ability of rabies to spread.

## CHAPTER 4

### Competition between Obligate and Facultative Scavengers

#### 4.1 Introduction

Every year there is an anthrax (caused by *Bacillus anthracis*) outbreak among the zebra population in Etosha National Park. When zebras die from anthrax a localized infection zone (LIZ) is established. This is the zone in which the anthrax is residing in the soil in a three meter radius around the carcass [23]. The bacteria can survive in the soil for up to four years, which infects zebras that graze near the previous carcass sites by pawing at the soil, and hence kicking up the bacteria onto the grasses they eat [6]. Zebra carcasses provide a place for scavengers like jackals and vultures to come into contact with each other. Jackals are facultative scavengers meaning they do not rely only on carrion for food: they eat insects, small animals, and fruit as well [4]. Vultures are the only obligate scavengers and are able to rapidly consume large carcasses [27]. Avian scavengers are able to locate carrion easier than terrestrial scavengers because they fly and have keen eyesight, which give them a competitive advantage over terrestrial scavengers [27, 49]. However, mammalian scavengers have a competitive advantage over avian scavengers because they have a larger body size and greater strength [50]. In [50], the authors observed that mammalian scavengers are diurnal and therefore, mammalian and avian scavengers are actively searching for food at the same time. They further noted that avian scavengers will arrive at the carcasses first, but a mammalian scavenger can displace them. Likewise, the authors in [51] reported that the time of the day the jackals, hyaenas, lions, or vultures arrived at the kill sites did not have any significant variation.

There are two different types of competition: exploitative and interference. Exploitative competition occurs when species compete for the same limited resource, and interference competition is when one species depletes another species' resources by interference such as fighting. In [52], Jensen provides models of pure exploitative and pure interference competition, finds the equilibria of each model, and then tests the models against real data. Jensen notes that many different model forms are possible to describe these two different forms of competition. The Lotka-Volterra model is a basic example of interference, while a similar model can be used to describe exploitative competition with the difference that each species impacts the carrying capacity of the other species. The equilibria in both models are the same. Next, the two models are compared with real data and the models both fit the data well with subtle differences. Jensen argues that this is important because the nature of competition requires the study of interactions and cannot be observed with data only.

In this paper, we develop two models: one describing exploitative competition and another describing interference competition. We discuss the exploitative model development in Section 4.2. In Section 4.3, we identify equilibria and when each equilibrium exists for the exploitative model. In Section 4.4, we find the basic reproductive numbers of anthrax and the demographic numbers of vultures. In Section 4.5, we find stability conditions for each equilibrium. In Section 4.6, parameter estimates are given and finally results for the exploitative model are in Section 4.7. Then we switch and discuss the model development of the interference model in Section 4.8. Next, we find the existence and stability conditions of the equilibria in Sections 4.9 and 4.11, respectively. Finally, we end with results for the interference model and tie together the two models.

## 4.2 Model Development: Exploitative Competition

In this paper the deterministic mathematical model uses a system of ordinary differential equations to describe exploitative competition between jackals and vultures for zebra carcasses. The populations considered in this model are the living zebras, the zebra carcasses from natural death, the zebra carcasses due to anthrax induced death, jackals, and vultures, ( $z$ ,  $u$ ,  $c$ ,  $j$ ,  $v$ , respectively). The zebra population has a logistic growth term and is removed by natural death ( $\mu z$ ) or by disease-induced death ( $acz$ ) from grazing near an anthrax infected carcass site [6]. The carcasses (healthy or infected) are either naturally decomposing at a rate  $\rho$  or are being eaten by jackals or vultures at a rate of  $\alpha$ . The jackals birth rate  $b_j$  depends on how many carcasses that are present in the environment and they die at a natural death rate of  $d_j$ . In addition, since jackals are facultative scavengers, the  $S$  term captures an alternative food source for the them. Finally, the vultures birth rate  $b_v$  strictly depends on the number of zebra carcasses available and the vultures die at a natural death rate of  $d_v$ . Jackals do not attack living zebras; they only scavenge on the zebra carcasses or eat other food sources such as insects, fruit, small mammals, and scavenge on lion and spotted hyena kills [4]. We assume that vultures only scavenge on zebra carcasses, which is representative of the vultures' food sources. Therefore, we assume that vultures depend solely on the zebra carcasses for food regardless of the carcass infection status. A summary of the parameters in equations (4.1)-(4.5) can be found in Table 4.1.

$$z' = rz \left(1 - \frac{z}{K}\right) - \mu z - acz \quad (4.1)$$

$$u' = \mu z - \rho u - \alpha_j j u - \alpha_v v u \quad (4.2)$$

$$c' = acz - \rho c - \alpha_j j c - \alpha_v v c \quad (4.3)$$

$$j' = b_j j (u + c) - d_j j + S \quad (4.4)$$

$$v' = b_v v (u + c) - d_v v \quad (4.5)$$

Symbol	Definition
$K$	carrying capacity for zebra population ( <i>zebras</i> )
$r$	intrinsic growth rate of zebras
$\mu$	natural zebra death rate
$a$	rate zebras come into contact with anthrax infected carcasses ( $time \cdot zebras$ ) <sup>-1</sup>
$\rho$	natural decomposition rate of carcasses
$\alpha_j$	rate jackals come into contact w/ carcasses to eat ( $time \cdot jackals$ ) <sup>-1</sup>
$b_j$	birth rate of jackals ( $time \cdot zebras$ ) <sup>-1</sup>
$d_j$	natural death rate of jackals
$\alpha_v$	rate vultures come into contact w/ carcasses to eat ( $time \cdot vultures$ ) <sup>-1</sup>
$b_v$	birth rate of vultures ( $time \cdot zebras$ ) <sup>-1</sup>
$d_v$	natural death rate of vultures
$S$	alternative food source for jackals ( $jackal/time$ )

Table 4.1: Parameter table for the equations (4.1)–(4.5). Units in  $\frac{1}{time}$  except as noted.

### 4.3 Existence of Equilibria: Exploitative Model

In this section, we identify five equilibria in our model.

Since the jackals' ability to survive does not depend only on carcasses they will never become extinct. Therefore, we do not have an extinction equilibrium. We have the jackal-only equilibrium  $E_0 \left( 0, 0, 0, \frac{S}{d_j}, 0 \right)$ , which always exists. The equilibrium

$$E_1 \left( K \left( 1 - \frac{\mu}{r} \right), \frac{\mu K \left( 1 - \frac{\mu}{r} \right)}{\rho + \alpha_j j_1^*}, 0, j_1^*, 0 \right)$$

describes when there is no disease or vultures present, which exists when  $\mu < r$  (see Appendix C.1 for the expression of  $j_1^*$ ).

The equilibrium

$$E_2 \left( \frac{\rho + \alpha_j j_2^*}{a}, \frac{\mu}{a}, \frac{r}{aK} \left( K \left( 1 - \frac{\mu}{r} \right) - \frac{\rho + \alpha_j j_2^*}{a} \right), j_2^*, 0 \right),$$

which exists when  $\frac{\rho + \alpha_j j_2^*}{a} < K \left( 1 - \frac{\mu}{r} \right)$  describes when anthrax is present and vultures are absent (see Appendix C.1 for the expression of  $j_2^*$ .)

The equilibrium where only anthrax is absent is

$$E_3 \left( K \left( 1 - \frac{\mu}{r} \right), \frac{d_v}{b_v}, 0, \frac{S}{d_j - b_j \left( \frac{d_v}{b_v} \right)}, \frac{1}{\alpha_v} \left( \frac{\mu b_v}{d_v} K \left( 1 - \frac{\mu}{r} \right) - (\rho + \alpha_j j_3^*) \right) \right),$$

which exists when  $\frac{d_v}{b_v} < \frac{d_j}{b_j}$ , and  $\frac{\mu b_v}{d_v} K \left( 1 - \frac{\mu}{r} \right) > \rho + \alpha_j j_3^*$ .

The equilibrium where all components are present is

$$E_4 \left( K \left( 1 - \frac{ad_v}{rb_v} \right), \frac{\mu}{a}, \frac{d_v}{b_v} - \frac{\mu}{a}, \frac{S}{d_j - b_j \left( \frac{d_v}{b_v} \right)}, \frac{1}{\alpha_v} \left( aK \left( 1 - \frac{ad_v}{rb_v} \right) - (\rho + \alpha_j j_4^*) \right) \right),$$

which exists when  $\frac{d_v}{b_v} < \frac{d_j}{b_j}$ ,  $\frac{ad_v}{rb_v} < 1$ ,  $\frac{ad_v}{\mu b_v} > 1$ , and  $aK \left( 1 - \frac{ad_v}{rb_v} \right) > \rho + \alpha_j j_4^*$ .

In the next section we will show that for both  $E_3$  and  $E_4$  the competition condition  $\frac{d_v}{b_v} < \frac{d_j}{b_j}$  is implied by the last condition ( $\frac{\mu b_v}{d_v} K \left( 1 - \frac{\mu}{r} \right) > \rho + \alpha_j j_3^*$  and  $aK \left( 1 - \frac{ad_v}{rb_v} \right) > \rho + \alpha_j j_4^*$ , respectively) and can thus be discarded.

#### 4.4 Reproductive Numbers

The basic reproductive number (BRN) is defined as the average number of secondary infections that is generated by one infected individual in a population of susceptible individuals, which can be calculated using the next generation operator method as in [28]. When the BRN is less than one, the disease free equilibrium is stable and when the BRN is greater than one, the endemic equilibrium is stable. The



demographic reproductive number (DRN) is the birth rate divided by death rate of the scavengers or the birth rate multiplied by how long they reproduce (scavengers reproduce their entire lives, so it is the reciprocal of the death rate). Similarly to the BRN, when the DRN is less than one, the scavenger will die out, and when the DRN is greater than one, the scavenger persists.

In the single-scavenger model of [47], there are two disease free equilibria: one without scavengers ( $E_1$ [47]) and one with scavengers ( $E_2$ [47]). The basic reproductive number of anthrax in the absence of scavengers is  $R_Z = \frac{aK(1-m)}{\rho}$ , (note:  $m = \frac{\mu}{r}$ ) where the average infection rate is  $aK(1-m)$  and the average duration of infection is  $\frac{1}{\rho}$ . The basic reproductive number of anthrax in the presence of scavengers is  $R_J = \frac{ad}{b\mu}$ . Here  $\frac{ad}{b}$  is the average infection rate and the average length of infection is  $\frac{1}{\mu}$ .

We use the next generation operator method as described in [28]. The disease free equilibrium without vultures is  $E_1$ . First, we find the BRN of anthrax in the absence of vultures. That is,

$$\begin{aligned} \mathcal{X} &= \{Z, U, J, V\} & \mathcal{Z} &= \{C\} \\ A &= \frac{\partial}{\partial C} \left( \frac{dC}{dt} \right) \Big|_{E_1} = aK \left( 1 - \frac{\mu}{r} \right) - (\rho + \alpha_j j_1^*) \\ R_{AO} &= \frac{aK \left( 1 - \frac{\mu}{r} \right)}{\rho + \alpha_j j_1^*} \end{aligned} \tag{4.6}$$

Next, we find the BRN of anthrax in the presence of vultures. The disease free equilibrium in the presence of vultures is  $E_3$ .

$$\begin{aligned} \mathcal{X} &= \{Z, U, J, V\} & \mathcal{Z} &= \{C\} \\ A &= \frac{\partial}{\partial C} \left( \frac{dC}{dt} \right) \Big|_{E_3} = aK \left( 1 - \frac{\mu}{r} \right) - \frac{\mu b_v}{d_v} K \left( 1 - \frac{\mu}{r} \right) \\ R_{AV} &= aK \left( 1 - \frac{\mu}{r} \right) \frac{d_v}{\mu b_v} \frac{1}{K \left( 1 - \frac{\mu}{r} \right)} = \frac{ad_v}{\mu b_v} \end{aligned}$$

The DRN of vultures in the absence of anthrax is

$$D_V(E_1) = \frac{b_v(u^* + c^*)}{d_v} \Big|_{E_1} = \frac{b_v}{d_v} \frac{\mu K \left(1 - \frac{\mu}{r}\right)}{\rho + \alpha_j j_1^*} \quad (4.7)$$

The DRN of vultures in the presence of anthrax is

$$\begin{aligned} D_V(E_2) &= \frac{b_v(u^* + c^*)}{d_v} \Big|_{E_2} \\ &= \frac{b_v}{d_v} \left( \frac{\mu}{a} + \frac{r}{aK} \left( K \left(1 - \frac{\mu}{r}\right) - \frac{\rho + \alpha_j j_2^*}{a} \right) \right) \\ &= \frac{b_v}{d_v} \left( \frac{r}{a} \left(1 - \frac{z_2^*}{K}\right) \right) \\ &= \frac{r b_v}{a d_v} \left(1 - \frac{\rho + \alpha_j j_2^*}{aK}\right) \end{aligned}$$

We see how one of the existence conditions for  $E_3$  is  $\frac{d_v}{b_v} < \frac{d_j}{b_j}$ , which insures  $j_3^* > 0$ , but we will show that  $D_V(E_1) > 1$  implies  $\frac{d_v}{b_v} < \frac{d_j}{b_j}$ .

**Theorem 4.4.1.** *Let  $x = \frac{d_j}{b_j}$ ,  $y = \frac{d_v}{b_v}$ , and  $m = \frac{\mu}{r}$ . Then  $D_V(E_1) > 1$  implies  $y < x$ .*

*Proof.* Note that we can rewrite  $\frac{d_v}{b_v} < \frac{d_j}{b_j}$  as  $y < x$ , and we can rewrite  $D_V(E_1) > 1$  as  $y < \frac{\mu K(1-m)}{\rho + \alpha_j j_1^*}$ . The inequality (4.8),

$$F < \frac{1}{2} \left[ (F + H) + \sqrt{(F + H)^2 + GH} \right], \quad (4.8)$$

with  $G, H > 0$ , trivially holds. Note that  $F = \frac{\mu z_1^*}{\alpha_j x} - \frac{\rho}{\alpha_j}$ ,  $G = \frac{4\rho}{\alpha_j}$ , and  $H = \frac{S}{d_j}$ . Now,

$$\begin{aligned} F &< \frac{1}{2} \left[ (F + H) + \sqrt{(F + H)^2 + GH} \right] \\ \iff \frac{\mu z_1^*}{\alpha_j x} - \frac{\rho}{\alpha_j} &< \frac{1}{2} \left[ \frac{\mu z_1^*}{\alpha_j x} - \frac{\rho}{\alpha_j} + \frac{S}{d_j} + \sqrt{\left( \frac{\mu z_1^*}{\alpha_j x} - \frac{\rho}{\alpha_j} + \frac{S}{d_j} \right)^2 + 4 \frac{\rho S}{\alpha_j d_j}} \right] \\ \iff \frac{\mu z_1^*}{\alpha_j x} - \frac{\rho}{\alpha_j} &< j_1^* \\ \iff \mu K(1 - m) - x\rho &< \alpha_j x j_1^* \\ \iff \frac{\mu K(1 - m)}{\rho + \alpha_j j_1^*} &< x \end{aligned}$$

Therefore, we have just shown that  $\frac{\mu K(1-m)}{\rho + \alpha_j j_1^*} < x$ . Therefore,

$$y < \frac{\mu K(1-m)}{\rho + \alpha_j j_1^*} < x$$

shows that  $y < \frac{\mu K(1-m)}{\rho + \alpha_j j_1^*}$  implies  $y < x$ . Hence we only need to write  $D_V(E_1) > 1$  as an existence condition for  $E_3$ .  $\square$

Next, we do a similar proof with the existence conditions for  $E_4$ .

**Theorem 4.4.2.** *Let  $x = \frac{d_j}{b_j}$ ,  $y = \frac{d_v}{b_v}$ , and  $m = \frac{\mu}{r}$ . Then  $D_V(E_2) > 1$  implies  $y < x$ .*

*Proof.* Note that we can rewrite  $\frac{d_v}{b_v} < \frac{d_j}{b_j}$  as  $y < x$ , and we can rewrite  $D_V(E_2) > 1$  as  $y < \frac{r}{a} \left(1 - \frac{\rho + \alpha_j j_2^*}{aK}\right)$ . The inequality (4.9),

$$F < \frac{1}{2} \left[ F + \sqrt{F^2 + G} \right], \quad (4.9)$$

with  $G > 0$ , trivially holds. Let  $F = \frac{1}{\alpha_j} \left( aK \left(1 - \frac{a}{r}x\right) - \rho \right)$ , and  $G = \frac{4a^2KS}{\alpha_j b_j r}$ . Now,

$$\begin{aligned} F &< \frac{1}{2} \left[ F + \sqrt{F^2 + G} \right] \\ \iff &\left[ \frac{1}{\alpha_j} \left( aK \left(1 - \frac{a}{r}x\right) - \rho \right) + \sqrt{\left( -\frac{1}{\alpha_j} \left( aK \left(1 - \frac{a}{r}x\right) - \rho \right) \right)^2 + 4 \frac{a^2KS}{\alpha_j b_j r}} \right] \\ &> \frac{2}{\alpha_j} \left[ aK \left(1 - \frac{a}{r}x\right) - \rho \right] \\ \iff &\alpha_j j_2^* > aK \left(1 - \frac{a}{r}x\right) - \rho \\ \frac{r}{a} \left(1 - \frac{\rho + \alpha_j j_2^*}{aK}\right) &< x \end{aligned}$$

Therefore,  $\frac{r}{a} \left(1 - \frac{\rho + \alpha_j j_2^*}{aK}\right) < x$ . Therefore,

$$y < \frac{r}{a} \left(1 - \frac{\rho + \alpha_j j_2^*}{aK}\right) < x$$

shows that  $y < \frac{r}{a} \left(1 - \frac{\rho + \alpha_j j_2^*}{aK}\right)$  implies  $y < x$ . Hence we can exclude  $y < x$  as an existence condition for  $E_4$ .  $\square$

## 4.5 Stability Analysis

All calculations for this section are shown in Appendix C.2.

The equilibrium  $E_0 \left( 0, 0, 0, \frac{S}{d_j}, 0 \right)$  always exists, and is locally asymptotically stable (LAS) when the zebra birth rate is less than the zebra death rate, i.e.  $r < \mu$ .

The equilibrium

$$E_1 \left( K \left( 1 - \frac{\mu}{r} \right), \frac{\mu K \left( 1 - \frac{\mu}{r} \right)}{\rho + \alpha_j j_1^*}, 0, j_1^*, 0 \right)$$

exists when  $\mu < r$  and is LAS when  $R_{AO} = \frac{aK \left( 1 - \frac{\mu}{r} \right)}{\rho + \alpha_j j_1^*} < 1$  and  $D_V(E_1) = \frac{\frac{\mu b_v}{d_v} K \left( 1 - \frac{\mu}{r} \right)}{\rho + \alpha_j j_1^*} < 1$ .

The equilibrium

$$E_2 \left( \frac{\rho + \alpha_j j_2^*}{a}, \frac{\mu}{a}, \frac{r}{aK} \left( K \left( 1 - \frac{\mu}{r} \right) - \frac{\rho + \alpha_j j_2^*}{a} \right), j_2^*, 0 \right)$$

exists when  $\frac{aK \left( 1 - \frac{\mu}{r} \right)}{\rho + \alpha_j j_2^*} > 1$ , and is LAS when  $\frac{aK \left( 1 - \frac{ad_v}{rb_v} \right)}{\rho + \alpha_j j_2^*} < 1$ . We relate this latter stability condition of  $E_2$  to  $D_V(E_2) < 1$  below in Theorem 4.5.1.

**Theorem 4.5.1.**  $\frac{rb_v}{ad_v} \left( 1 - \frac{\rho + \alpha_j j_2^*}{aK} \right) < 1$  if and only if  $\frac{aK \left( 1 - \frac{ad_v}{rb_v} \right)}{\rho + \alpha_j j_2^*} < 1$ .

$$\begin{aligned} \frac{rb_v}{ad_v} \left( 1 - \frac{\rho + \alpha_j j_2^*}{aK} \right) < 1 &\iff -\frac{\rho + \alpha_j j_2^*}{aK} < \frac{ad_v}{rb_v} - 1 \\ &\iff \rho + \alpha_j j_2^* > aK \left( 1 - \frac{ad_v}{rb_v} \right) \\ &\iff \frac{aK \left( 1 - \frac{ad_v}{rb_v} \right)}{\rho + \alpha_j j_2^*} < 1 \end{aligned}$$

Therefore, by Theorem 4.5.1 that means  $D_V(E_2) < 1$  can replace  $\frac{aK \left( 1 - \frac{ad_v}{rb_v} \right)}{\rho + \alpha_j j_2^*} < 1$  when we talk about stability conditions for  $E_2$ . Hence we have proven that the above conditions are required for  $E_2$  to be LAS, and numerical analysis indicates it is the only condition.

The equilibrium

$$E_3 \left( K \left( 1 - \frac{\mu}{r} \right), \frac{d_v}{b_v}, 0, \frac{S}{d_j - b_j \left( \frac{d_v}{b_v} \right)}, \frac{1}{\alpha_v} \left( \frac{\mu b_v}{d_v} K \left( 1 - \frac{\mu}{r} \right) - (\rho + \alpha_j j_3^*) \right) \right),$$

exists when  $\frac{d_v}{b_v} < \frac{d_j}{b_j}$ , and  $\frac{\frac{\mu b_v}{d_v} K \left( 1 - \frac{\mu}{r} \right)}{\rho + \alpha_j j_3^*} > 1$ , and is LAS when  $R_{AV} = \frac{ad_v}{\mu d_v} < 1$ .

The equilibrium where all components are present is

$$E_4 \left( K \left( 1 - \frac{ad_v}{rb_v} \right), \frac{\mu}{a}, \frac{d_v}{b_v} - \frac{\mu}{a}, \frac{S}{d_j - b_j \left( \frac{d_v}{b_v} \right)}, \frac{1}{\alpha_v} \left( aK \left( 1 - \frac{ad_v}{rb_v} \right) - (\rho + \alpha_j j_4^*) \right) \right),$$

which exists when  $\frac{d_v}{b_v} < \frac{d_j}{b_j}$ ,  $R_{AV} = \frac{ad_v}{\mu b_v} > 1$ , and  $\frac{aK \left( 1 - \frac{ad_v}{rb_v} \right)}{\rho + \alpha_j j_4^*} > 1$ . The stability for  $E_4$  was determined through numerical exploration. We found that whenever  $E_4$  existed it is always LAS.

Furthermore, notice that the stability condition for  $E_1$  is similar to the existence condition of  $E_2$ . Numerically, we checked to see if  $j_1^* = j_2^*$  when  $R_{AO} = 1$  and the two  $j$ -values were equal. We also did this to see if  $j_1^* = j_3^*$  when  $D_V(E_1) = 1$  and for  $j_2^* = j_4^*$  when  $D_V(E_2) = 1$ , which both also held.

Numerical explorations indicate that all LAS equilibria are in fact globally asymptotically stable. Existence and stability conditions are summarized in Table 4.3 and Table 4.6 has the conditions written using the BRNs and DRNs.

Equilibrium	Existence	LAS
$E_0(0, 0, 0, \frac{S}{d_j}, 0)$	always	$r < \mu$
$E_1\left(K\left(1 - \frac{\mu}{r}\right), \frac{\mu K\left(1 - \frac{\mu}{r}\right)}{\rho + \alpha_j j_1^*}, 0, j_1^*, 0\right)$	$\mu < r$	$\frac{aK\left(1 - \frac{\mu}{r}\right)}{\rho + \alpha_j j_1^*} < 1$ & $\frac{\mu b_v}{d_v} K\left(1 - \frac{\mu}{r}\right) < \rho + \alpha_j j_1^*$
$E_2\left(\frac{\rho}{a} + \frac{\alpha_j}{a} j_2^*, \frac{\mu}{a}, \frac{r}{aK} \left[ K\left(1 - \frac{\mu}{r}\right) - \frac{\rho + \alpha_j j_2^*}{a} \right], j_2^*, 0\right)$	$\frac{aK\left(1 - \frac{\mu}{r}\right)}{\rho + \alpha_j j_2^*} > 1$	$aK\left(1 - \frac{ad_v}{rb_v}\right) < \rho + \alpha_j j_2^*$
$E_3\left(K\left(1 - \frac{\mu}{r}\right), \frac{d_v}{b_v}, 0, \frac{S}{d_j - b_j \left(\frac{d_v}{b_v}\right)}, \frac{1}{\alpha_v} \left(\frac{\mu b_v}{d_v} K\left(1 - \frac{\mu}{r}\right) - \rho - \alpha_j j_3^*\right)\right)$	$\frac{b_v \mu}{d_v} K\left(1 - \frac{\mu}{r}\right) > \rho + \alpha_j j_1^*$	$\frac{ad_v}{\mu b_v} < 1$
$E_4\left(K\left(1 - \frac{ad_v}{rb_v}\right), \frac{\mu}{a}, \frac{d_v}{b_v} - \frac{\mu}{a}, \frac{S}{d_j - b_j \left(\frac{d_v}{b_v}\right)}, \frac{aK}{\alpha_v} \left(1 - \frac{ad_v}{rb_v}\right) - \frac{1}{\alpha_v} (\rho + \alpha_j j_4^*)\right)$	$\frac{ad_v}{\mu b_v} > 1, \frac{ad_v}{rb_v} < 1, \&$ $aK\left(1 - \frac{ad_v}{rb_v}\right) > \rho + \alpha_j j_2^*$	whenever it exists

Table 4.2: Summary of the existence and local stability for the five equilibria for the exploitative competition model (4.1)–(4.5).

Equilibrium	Existence	LAS
$E_0(0, 0, 0, \frac{S}{d_j}, 0)$	always	$r < \mu$
$E_1\left(K\left(1 - \frac{\mu}{r}\right), \frac{\mu K\left(1 - \frac{\mu}{r}\right)}{\rho + \alpha_j j_1^*}, 0, j_1^*, 0\right)$	$\mu < r$	$R_{AO} < 1$ & $D_V(E_1) < 1$
$E_2\left(\frac{\rho}{a} + \frac{\alpha_j}{a} j_2^*, \frac{\mu}{a}, \frac{\tau}{aK} \left[ K\left(1 - \frac{\mu}{r}\right) - \frac{\rho + \alpha_j j_2^*}{a} \right], j_2^*, 0\right)$	$R_{AO} > 1$	$D_V(E_2) < 1$
$E_3\left(K\left(1 - \frac{\mu}{r}\right), \frac{d_v}{b_v}, 0, \frac{S}{d_j - b_j \left(\frac{d_v}{b_v}\right)}, \frac{1}{\alpha_v} \left(\frac{\mu b_v}{d_v} K\left(1 - \frac{\mu}{r}\right) - \rho - \alpha_j j_3^*\right)\right)$	$D_V(E_1) > 1$	$R_{AV} < 1$
$E_4\left(K\left(1 - \frac{ad_v}{rb_v}\right), \frac{\mu}{a}, \frac{d_v}{b_v} - \frac{\mu}{a}, \frac{S}{d_j - b_j \left(\frac{d_v}{b_v}\right)}, \frac{aK}{\alpha_v} \left(1 - \frac{ad_v}{rb_v}\right) - \frac{1}{\alpha_v} (\rho + \alpha_j j_4^*)\right)$	$1 < R_{AV} < \frac{1}{m}$ , & $D_V(E_2) > 1$	whenever it exists

Table 4.3: Summary of the existence and local stability for the five equilibria for the exploitative competition model (4.1)–(4.5).

## 4.6 Parameter Estimates

Some of the parameter values were obtained from previously published papers as listed in Table 4.4, while the others were previously estimated in [47]. Since jackals are facultative scavengers and can find food from other sources besides carrion, we need to estimate  $b_j$ ,  $\alpha_j$ , and  $S$ . In [47], it was assumed that zebras were representative of all the jackals' food. However, we make this distinction of jackals being facultative scavengers now. In [53], the diet of a golden jackal was studied and the authors obtained data of the stomach contents. They report that 55% of the weight of the stomach content was from carrion and viscera. This means 45% is from some other food source.

From [47], we use that jackals eat 1.42 pounds of food per day. Since 55% of the stomach food content is carrion [53], we say 55% of the 1.42 pounds of food per day is the amount of food from carrion, which is 0.781 pounds per day. Now, we find how many days it takes a jackal to eat a zebra carcass:

$$\frac{275 \text{ lbs}}{\text{zebra}} \cdot \frac{\text{day}}{0.781 \text{ lbs}} \approx \frac{352.1126 \text{ days}}{\text{zebra}} \approx \frac{50.3018 \text{ weeks}}{\text{zebra}}.$$

Therefore,  $\alpha_j = 1/50.3018 \text{ jackal} \cdot \text{week}$ . On average, 5.4 pups are born per year per jackal pair [32]. Therefore, during the 352.1126 days one jackal eating a zebra carcass produces

$$\frac{1 \text{ year}}{365 \text{ days}} \cdot \frac{352.1126 \text{ days}}{\text{zebra}} \cdot \frac{2.7 \text{ baby jackals}}{\text{year}} = \frac{2.604 \text{ baby jackals}}{\text{zebra}}.$$

Now,

$$b_j = \frac{2.604 \text{ jackals}}{\text{zebra}} \cdot \frac{1}{50.3018 \text{ jackal} \cdot \text{week}} = \frac{0.0517808}{\text{zebra} \cdot \text{week}}.$$



Symbol	Description	Value	Source
$K$	zebra carrying capacity ( <i>zebras</i> )	13000 – 15000	[25]
$r$	intrinsic growth rate of zebras	$3.06849 \times 10^{-3}$	[47]
$\mu$	natural zebra death rate	$7.67123 \times 10^{-4}$	[47]
$a$	rate zebras come into contact with infected carcasses ( <i>week · zebras</i> ) <sup>-1</sup>	$1.1433 \times 10^{-5}$	[47]
$\rho$	natural decomposition rate of zebra carcasses	0.12727	[31]
$\alpha_j$	rate jackals come into contact with carcasses to eat ( <i>week · jackals</i> ) <sup>-1</sup>	0.01988	This study
$b_j$	birth rate of jackals ( <i>week · zebras</i> ) <sup>-1</sup>	0.0517808	This study
$d_j$	death rate of jackals	$4.808 \times 10^{-3}$	[32]
$\alpha_v$	rate vultures come into contact with carcasses to eat ( <i>week · vultures</i> ) <sup>-1</sup>	0.01927	[27]
$b_v$	birth rate of vultures ( <i>week · zebras</i> ) <sup>-1</sup>	0.00959	[47]
$d_v$	natural death rate of vultures	$9.615 \times 10^{-4}$	[33]
$S$	alternative food source for jackals ( <i>jackal/week</i> )	$6.144 \times 10^{-4}$	This study

Table 4.4: Parameter table with values. Units in  $\frac{1}{week}$  except as noted.

Next we find  $S$ , which is the alternative food source and makes up 45% of the weight of the stomach content of a jackal [53]. From  $E_0$ , we know that  $j_0^* = \frac{S}{d_j}$  and we know the value for  $d_j$ . Therefore, we can estimate  $j_0^*$  to be the observed jackal density multiplied by the 45% of food from non-scavenged sources. We use the jackal density given in [8], which is  $0.2 \text{ km}^{-2}$ . The area of Etosha National Park is  $22,915 \text{ km}^2$  [4].

Hence

$$j_0^* = \frac{0.2 \text{ jackal}}{\text{km}^2} \times 22,915 \text{ km}^2 \times 0.45 \times 1.42 \text{ lbs} = 0.1278 \text{ jackal} \cdot \text{lbs}.$$

Then  $S$  is

$$S = 0.1278 \text{ jackal} \cdot \text{lbs} \times \frac{4.808 \times 10^{-3}}{\text{week}} = \frac{6.144 \times 10^{-4} \text{ jackal} \cdot \text{lbs}}{\text{week}}.$$

When the parameter values from Table 4.4 are plugged into the system we get that the  $E_1$  equilibrium is LAS. This equilibrium represents the disease free equilibrium without vultures. If we increase  $\frac{b_v}{d_v}$  by a factor of 1.09, which is the same as increasing  $b_v$  by a factor of 1.09, we get that  $E_3$  is LAS.  $E_3$  is where anthrax is absent but vultures are present.

If we increase the parameter  $a$  by a factor of 723, then  $E_2$  is LAS, which is where anthrax is present, and vultures are absent. This is a significantly large increase, which seems unlikely to happen in real life. Biologically, if  $a$  is increased then that means the zebras are coming into contact more often with anthrax laden carcasses.

#### 4.7 Results: Exploitative Model

We set out to answer the question how does the presence of jackals affect the presence of vultures? Using the previous work in [47] for scavengers (we specifically work with vultures here and add subscript  $v$ 's), the demographic reproduction number for vultures in the absence of anthrax and jackals is

$$D(E_1[47]) = \frac{b_v \mu}{\rho d_v} K \left( 1 - \frac{\mu}{r} \right),$$

and the DRN of vultures in the absence of anthrax but in the presence of jackals is

$$D_V(E_1) = \frac{b_v \mu}{(\rho + \alpha_j j_1^*) d_v} K \left( 1 - \frac{\mu}{r} \right).$$

Notice that the only difference is in the denominator of  $D(E_1[47])$  and  $D_V(E_1)$ . Since  $\alpha_j j_1^* > 0$ , we can see that  $D(E_1[47]) > D_V(E_1)$ . This means that in the absence of anthrax, the vultures are able to persist better in the absence of jackals because in  $D_V(E_1)$ , we can see how jackals are eating the carcasses, which in turns lowers the birth rate for the vultures because there are fewer carcasses available to eat.

From [47], the DRN of vultures in the presence of anthrax, absence of jackals is

$$D(E_3[47]) = \frac{rb_v}{ad_v} \left(1 - \frac{\rho}{aK}\right),$$

and the DRN of vultures in the presence of anthrax and jackals is

$$D_V(E_2) = \frac{rb_v}{ad_v} \left(1 - \frac{\rho + \alpha_j j_2^*}{aK}\right).$$

Here the difference is in the numerator and  $\alpha_j j_2^* > 0$ . Therefore,  $D(E_3[47]) > D_V(E_2)$ .

In the presence of anthrax, the vultures persist better without jackals present because again we can see how jackals are helping to get rid of the carcasses, which decreases the food source for vultures, lowering vulture birth rate.

In setting out to answer the question if anthrax affects vultures, we compare  $v_3^*$  and  $v_4^*$  to each other. Recall that

$$v_3^* = \frac{1}{\alpha_v} \left( \frac{\mu b_v}{d_v} K \left(1 - \frac{\mu}{r}\right) - (\rho + \alpha_j j_3^*) \right)$$

and we can rewrite  $v_4^*$  as

$$v_4^* = \frac{1}{\alpha_v} \left( \frac{\mu b_v}{d_v} R_{AV} K \left(1 - R_{AV} \frac{\mu}{r}\right) - (\rho + \alpha_j j_3^*) \right), \quad (4.10)$$

and notice that  $j_3^* = j_4^*$ . Furthermore, (4.10) is quadratic in  $R_{AV}$ , where the linear term has a positive coefficient and the quadratic term has a negative coefficient, so it is an upside down parabola. Consider

$$f(R_{AV}) = \mu K R_{AV} - \frac{\mu^2 K}{r} (R_{AV})^2. \quad (4.11)$$

The vertex of this parabola occurs at  $\left(\frac{r}{2\mu}, \frac{Kr}{4}\right)$ . The roots of (4.11) occur at  $x = 0$  and  $x = \frac{r}{\mu}$ . We know that  $\frac{r}{\mu} > 1$  since  $\frac{\mu}{r} < 1$  and therefore, we know  $1 \in \left(0, \frac{r}{\mu}\right)$ . We have two cases for when  $v_3^* > v_4^*$ . That is,

- if  $\frac{r}{2\mu} < 1$ , then 1 lies to the right of the vertex and that means the  $f(1) < \frac{Kr}{4}$ .

Therefore, the function value gets lower as you move to the right, thus  $v_4^* < v_3^*$

regardless of what the parameter values are as long as the existence criteria hold.

- If  $\frac{r}{2\mu} > 1$ , then 1 lies to the left of the vertex. The function value is initially higher than  $f(1)$  as you move to the right then after  $\frac{Kr}{4}$  is reached the function values start to decrease again. Because of symmetry of a parabola  $f(1) = f\left(\frac{\mu}{r} - 1\right)$ . All values after  $R_{AV} = \frac{\mu}{r} - 1$  is when  $v_4^* < v_3^*$ .

In summary, if  $\frac{\mu}{r} > \frac{1}{2}$  or  $R_{AV} > \frac{r}{\mu} - 1$  then the vultures are hurt by the presence of anthrax.

In order for the vultures to survive we need  $\frac{d_v}{b_v} < \frac{d_j}{b_j}$  to hold. This means that the vultures have to beat the jackals in the competition. The vultures beating the jackals does not affect the jackal survival, but it does affect the vulture survival.

#### 4.8 Model Development: Incorporate Interference Competition

All parameter values are the exact same as previously along with equations (4.12) and (4.16). The difference is that this model incorporates the effect vultures have on jackals when competing for zebra carcasses through the parameter  $\kappa$ . We assume that vultures will be at the carcasses first since they can see carcasses from long distances, and then the jackals will come and displace due to their size. Since jackals are facultative scavengers and do not require carcasses for survival, the jackals will not be at risk of becoming extinct. When  $k = 0$  this means that there is no competition between the jackals and vultures for carcasses. When  $k$  approaches infinity, the jackals do not get to eat any of the zebra carcasses. When this happens, the jackals decouple:  $j' = S - d_j j$ , existing independently from any other class. A summary of the parameters in equations (4.12)-(4.16) can be found in Table 4.5.

$$z' = rz \left(1 - \frac{z}{K}\right) - \mu z - acz \quad (4.12)$$

$$u' = \mu z - \rho u - \frac{\alpha_j j u}{1 + kv} - \alpha_v v u \quad (4.13)$$

$$c' = acz - \rho c - \frac{\alpha_j j c}{1 + kv} - \alpha_v v c \quad (4.14)$$

$$j' = \frac{b_j j (u + c)}{1 + kv} - d_j j + S \quad (4.15)$$

$$v' = b_v v (u + c) - d_v v \quad (4.16)$$

Symbol	Definition	Units
$K$	carrying capacity for zebra population	(zebras)
$r$	intrinsic growth rate of zebras	
$\mu$	natural zebra death rate	
$a$	rate zebras come into contact with anthrax infected carcasses	(time · zebras) <sup>-1</sup>
$\rho$	natural decomposition rate of carcasses	
$\alpha_j$	rate jackals come into contact w/ carcasses to eat	(time · jackals) <sup>-1</sup>
$b_j$	birth rate of jackals	(time · zebras) <sup>-1</sup>
$d_j$	natural death rate of jackals	
$\alpha_v$	rate vultures come into contact w/ carcasses to eat	(time · vultures) <sup>-1</sup>
$b_v$	birth rate of vultures	(time · zebras) <sup>-1</sup>
$d_v$	natural death rate of vultures	
$S$	alternative food source for jackals	(jackal/time)
$k$	extent vultures interfere with jackals	(vultures) <sup>-1</sup>

Table 4.5: Parameter table. Units in  $\frac{1}{time}$  except as noted.

#### 4.9 Equilibria: Interference Competition

For this model we identified five equilibria. The equilibria  $E_0$ ,  $E_1$ ,  $E_2$  are exactly the same as in the exploitative model (equations (4.1)-(4.5)) and therefore,

the existence conditions remain the same. In the interference model we get two  $E_3$  and  $E_4$  equilibria. We notate the two  $E_3$  equilibria as  $E_{3+}$  and  $E_{3-}$ . Similarly for  $E_4$ , we write  $E_{4+}$  and  $E_{4-}$ . More detailed calculations on how  $E_3$  and  $E_4$  are found are in Appendix C.3.

The two different  $E_3$  equilibria are

$$E_{3+} \left( K \left( 1 - \frac{\mu}{r} \right), \frac{d_v}{b_v}, 0, \frac{S}{d_j - b_j \left( \frac{d_v}{b_v(1+kv_{3+}^*)} \right)}, v_{3+}^* \right),$$

which exists when  $\frac{d_v}{b_v} < \frac{d_j}{b_j}(1 + kv_{3+}^*)$ , or  $D_V(E_1) > 1$ , and

$$E_{3-} \left( K \left( 1 - \frac{\mu}{r} \right), \frac{d_v}{b_v}, 0, \frac{S}{d_j - b_j \left( \frac{d_v}{b_v(1+kv_{3-}^*)} \right)}, v_{3-}^* \right),$$

which exists when  $\frac{d_v}{b_v} < \frac{d_j}{b_j}(1 + kv_{3-}^*)$ , and  $D_V(E_1) < 1$ .

In addition, the two  $E_4$  equilibria are

$$E_{4+} \left( K \left( 1 - \frac{ad_v}{rb_v} \right), \frac{\mu}{a}, \frac{d_v}{b_v} - \frac{\mu}{a}, \frac{S}{d_j - b_j \left( \frac{d_v}{b_v(1+kv_{4+}^*)} \right)}, v_{4+}^* \right),$$

which exists when  $1 < R_{AV} < \frac{1}{m}$ , and either  $\frac{d_v}{b_v} < \frac{d_j}{b_j}(1 + kv_{4+}^*)$ , or  $D_V(E_2) > 1$ , and

$$E_{4-} \left( K \left( 1 - \frac{ad_v}{rb_v} \right), \frac{\mu}{a}, \frac{d_v}{b_v} - \frac{\mu}{a}, \frac{S}{d_j - b_j \left( \frac{d_v}{b_v(1+kv_{4-}^*)} \right)}, v_{4-}^* \right),$$

which exists when  $1 < R_{AV} < \frac{1}{m}$ ,  $\frac{d_v}{b_v} < \frac{d_j}{b_j}(1 + kv_{4-}^*)$ , and  $D_V(E_2) < 1$ . The existence conditions that take the form  $\frac{d_v}{b_v} < \frac{d_j}{b_j}(1 + kv_{3/4}^*)$  for  $E_3$  and  $E_4$  can be written in a different way and the next section goes into detail with how we can replace those two conditions.

### 4.9.1 Existence

Next, we determine the left most boundary of the interference model where there are two  $E_3$  equilibria.

$$B^2 - 4AC = 0 \iff x = \frac{\alpha_v r y}{\alpha_v r \pm 2r \sqrt{\alpha_v k \nabla + aKkr - rk\rho - a^2Kky}} \quad (4.17)$$

Let  $F = \frac{y}{x} - 1$ ,  $G = \frac{k}{\alpha_v} \left( \frac{\mu}{y} z_3^* - \rho \right)$ , and  $H = \frac{\nabla k}{\alpha_v}$ , where  $\nabla = \frac{\alpha_j S}{d_j}$ . Now,

$$\begin{aligned} \frac{y}{x} - 1 &\leq kv_3^* \\ \frac{y}{x} - 1 &\leq -\frac{k}{2} \left( \frac{1}{k} \left( 1 - \frac{y}{x} \right) - \frac{1}{\alpha_v} \left( \frac{\mu}{y} z_3^* - \rho \right) \right) \\ &\pm \frac{k}{2} \sqrt{\left[ \frac{1}{k} \left( 1 - \frac{y}{x} \right) - \frac{1}{\alpha_v} \left( \frac{\mu}{y} z_3^* - \rho \right) \right]^2 - \frac{4}{\alpha_v k} \left( \frac{\mu}{y} z_3^* - \rho \right) \left( \frac{y}{x} - 1 \right) - \frac{4\nabla}{\alpha_v k}} \\ F &\leq \frac{1}{2} \left( F + G \pm \sqrt{\left[ \left( \frac{y}{x} - 1 \right) + \frac{k}{\alpha_v} \left( \frac{\mu}{y} z_3^* - \rho \right) \right]^2 - 4FG - 4H} \right) \\ F &\leq \frac{1}{2} \left( F + G \pm \sqrt{(F + G)^2 - 4FG - 4H} \right) \\ F - G &\leq \pm \sqrt{(F - G)^2 - 4H} \end{aligned} \quad (4.18)$$

In order for the right hand side of (4.18) to be real, we require  $(F - G)^2 > 4H$ , from which

$$|F - G| > 2\sqrt{H}. \quad (4.19)$$

If  $F > G$ , with  $H > 0$  then (4.18) can never hold. Therefore, we require  $F < G$  for (4.18) to be true, and (4.19) becomes

$$F \leq G - 2\sqrt{H}. \quad (4.20)$$

Thus if (4.20), the left hand side of (4.18) is negative and the right hand side of a real number. Trivially, (4.18) holds for the positive sign on the right hand side. Now, for  $v_{3-}^*$ , we multiply (4.18) by negative one to get

$$G - F \geq \sqrt{(G - F)^2 - 4H}, \quad (4.21)$$

and this inequality is true. Therefore, the true boundary curve arises not from the original condition,  $y < x(1 + kv_3)$ , but from (4.20). Furthermore, we show that  $F = G - 2\sqrt{H}$  implies  $x = \frac{\alpha_v y^2}{(\alpha_v - \rho k - 2\sqrt{\alpha_v k \nabla})y + k\mu z_3^*}$ . Now,

$$\begin{aligned}
F &= G - 2\sqrt{H} \\
\iff \frac{y}{x} - 1 &= \frac{k}{\alpha_v} \left( \frac{\mu}{y} z_3^* - \rho \right) - 2\sqrt{\frac{\nabla k}{\alpha_v}} \\
\iff \frac{y}{x} - \frac{k\mu z_3^*}{\alpha_v y} &= 1 - 2\sqrt{\frac{\nabla k}{\alpha_v}} - \frac{k\rho}{\alpha_v} \\
\iff \alpha_v y^2 &= x \left[ \alpha_v y \left( 1 - 2\sqrt{\frac{\nabla k}{\alpha_v}} - \frac{k\rho}{\alpha_v} \right) + k\mu z_3^* \right] \\
\iff x &= \frac{\alpha_v y^2}{\alpha_v y \left( 1 - 2\sqrt{\frac{\nabla k}{\alpha_v}} - \frac{k\rho}{\alpha_v} \right) + k\mu z_3^*} \\
\iff x &= \frac{\alpha_v y^2}{(\alpha_v - \rho k - 2\sqrt{\nabla k \alpha_v})y + k\mu z_3^*} \tag{4.22}
\end{aligned}$$

Similarly, we determine the left most boundary of the interference model where there are two  $E_4$  equilibria.

$$B^2 - 4AC = 0 \iff x = \frac{\alpha_v r y}{\alpha_v r \pm 2r\sqrt{\alpha_v k \nabla} + aKkr - rk\rho - a^2Kky} \tag{4.23}$$

Let  $F = \frac{y}{x} - 1$ ,  $G = \frac{k}{\alpha_v} (az_4^* - \rho)$ , and  $H = \frac{\nabla k}{\alpha_v}$ , where  $\nabla = \frac{\alpha_j S}{d_j}$ . Now,

$$\begin{aligned}
2 \left( \frac{y}{x} - 1 \right) &\leq kv_4^* \\
\iff 2 \left( \frac{y}{x} - 1 \right) &\leq \left( \frac{y}{x} - 1 \right) + \frac{k}{\alpha_v} (az_4^* - \rho) \\
&\quad \pm k \sqrt{\left[ -\frac{1}{k} \left( \frac{y}{x} - 1 \right) - \frac{1}{\alpha_v} (az_4^* - \rho) \right]^2 - \frac{4}{\alpha_v k} (az_4^* - \rho) \left( \frac{y}{x} - 1 \right) - \frac{4\nabla k}{\alpha_v}} \\
\iff 2F &\leq F + G \pm \sqrt{\left[ \left( \frac{y}{x} - 1 \right) + \frac{k}{\alpha_v} (az_4^* - \rho) \right]^2 - 4FG - 4H} \\
\iff 2F &\leq F + G \pm \sqrt{(F + G)^2 - 4FG - 4H} \\
\iff F - G &\leq \pm \sqrt{(F - G)^2 - 4H} \tag{4.24}
\end{aligned}$$



For the right hand side to be a real we require  $(F - G)^2 > 4H$  if and only if

$$|F - G| > 2\sqrt{H}. \quad (4.25)$$

If  $F > G$ , with  $H > 0$  then (4.24) can never be true. Therefore, we need  $F < G$  for (4.24) to be true, and (4.25) becomes

$$F \leq G - 2\sqrt{H}. \quad (4.26)$$

Thus if (4.26) holds, then the left hand side of (4.24) is negative and the right hand side of (4.24) is real. Trivially, (4.24) holds for the plus sign on the right hand side.

For  $v_{4-}$ , we multiply through by negative one to get

$$F - G \leq -\sqrt{(F - G)^2 - 4H} \iff G - F \geq \sqrt{(G - F)^2 - 4H}$$

so this inequality is true. Therefore, the true boundary curve arises from the condition

given by (4.25). Now, we show that  $F = G - 2\sqrt{H}$  implies  $x = \frac{\alpha_v r y}{\alpha_v r \pm 2r \sqrt{\alpha_v k \nabla + aKkr - rk\rho - a^2Kky}}$ .

$$\begin{aligned} F &= G - 2\sqrt{H} \\ \iff \frac{y}{x} - 1 &= \frac{k}{\alpha_v} (az_4^* - \rho) - 2\sqrt{\frac{\nabla k}{\alpha_v}} + 1 \\ \iff \frac{1}{x} &= \frac{\left(1 - 2\sqrt{\frac{\nabla k}{\alpha_v}} + \frac{aKk - k\rho}{\alpha_v}\right) \alpha_v r - a^2Kky}{\alpha_v r y} \\ \iff x &= \frac{\alpha_v r y}{\alpha_v r - 2r\sqrt{\alpha_v \nabla k} + aKkr - rk\rho - a^2Kky} \end{aligned}$$

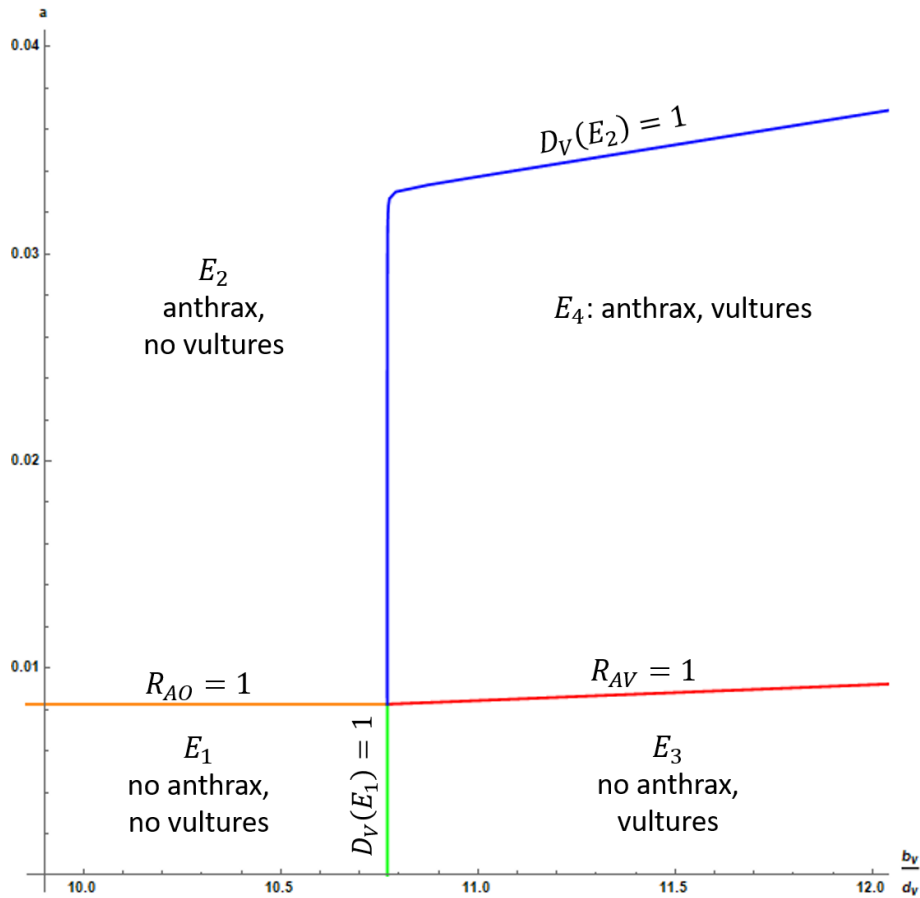


Figure 4.1: Bifurcation Graph for the exploitative competition model (4.1)–(4.5). The vertical axis is  $a$  and the horizontal axis is  $\frac{b_v}{d_v}$ . The regions are created by plotting the basic reproductive and demographic numbers when they are equal to 1. The regions are labeled with the corresponding LAS equilibrium. The parameter values used are in Table 4.4.

Equilibrium	Existence	LAS
$E_0(0, 0, 0, \frac{S}{d_j}, 0)$	always	$r < \mu$
$E_1 \left( K \left( 1 - \frac{\mu}{r} \right), \frac{\mu K \left( 1 - \frac{\mu}{r} \right)}{\rho + \alpha_j j_1^*}, 0, j_1^*, 0 \right)$	$\mu < r$	$R_{AO} < 1$ & $D_V(E_1) < 1$
$E_2 \left( \frac{\rho}{a} + \frac{\alpha_j}{a} j_2^*, \frac{\mu}{a}, \frac{r}{aK} \left[ K \left( 1 - \frac{\mu}{r} \right) - \frac{\rho + \alpha_j j_2^*}{a} \right], j_2^*, 0 \right)$	$R_{AO} > 1$	$D_V(E_2) < 1$
$E_{3+} \left( K \left( 1 - \frac{\mu}{r} \right), \frac{d_v}{b_v}, 0, \frac{S}{d_j - b_j \left( \frac{d_v}{b_v(1 + kv_{3+}^*)} \right)}, v_{3+}^* \right)$	$y < x(1 + kv_{3+})$	$R_{AV} < 1$
$E_{3-} \left( K \left( 1 - \frac{\mu}{r} \right), \frac{d_v}{b_v}, 0, \frac{S}{d_j - b_j \left( \frac{d_v}{b_v(1 + kv_{3-}^*)} \right)}, v_{3-}^* \right)$	$y < x(1 + kv_{3+})$ & $D_V(E_1) < 1$	never
$E_{4+} \left( K \left( 1 - \frac{adv}{rb_v} \right), \frac{\mu}{a}, \frac{d_v}{b_v} - \frac{\mu}{a}, \frac{S}{d_j - b_j \left( \frac{d_v}{b_v(1 + kv_{4+}^*)} \right)}, v_{4+}^* \right)$	$1 < R_{AV} < \frac{1}{m}$ & $y < x(1 + kv_{4+})$	whenever it exists
$E_{4-} \left( K \left( 1 - \frac{adv}{rb_v} \right), \frac{\mu}{a}, \frac{d_v}{b_v} - \frac{\mu}{a}, \frac{S}{d_j - b_j \left( \frac{d_v}{b_v(1 + kv_{4-}^*)} \right)}, v_{4-}^* \right)$	$1 < R_{AV} < \frac{1}{m}$ , $D_V(E_2) < 1$ & $y < x(1 + kv_{4+})$	never

Table 4.6: Summary of the existence and local stability for the five equilibria for the interference competition model (4.12)–(4.16).  $R_{AO} = \frac{aK(1-\frac{\mu}{r})}{\rho+\alpha_j j_1^*}$ ,  $R_{AV} = \frac{adv}{\mu b_v}$ ,  $D_V(E_1) = \frac{b_v \mu K(1-\frac{\mu}{r})}{d_v}$ ,  $\rho + \alpha_j j_1^*$ , and  $D_V(E_2) = \frac{rb_v}{adv} \left( 1 - \frac{\rho + \alpha_j j_2^*}{aK} \right)$ .

#### 4.10 Reproductive Numbers

The reproductive and demographic numbers of the interference model reduce to the same expressions as in the exploitative model.

The basic reproductive number of anthrax in the absence of vultures,  $R_{AO}$  is easy to see how it is the same as equation (4.6). Next, we find the BRN of anthrax in the presence of vultures. The disease free equilibrium in the presence of vultures is  $E_3$ .

$$\mathcal{X} = \{Z, U, J, V\} \quad \mathcal{Z} = \{C\}$$

$$\begin{aligned} A &= \frac{\partial}{\partial C} \left( \frac{dC}{dt} \right) \Big|_{E_3} = az_3^* - \rho - \frac{\alpha_j J_3^*}{1 + kv_3^*} - \alpha_v v_3^* \\ &= ak \left( 1 - \frac{\mu}{r} \right) - \rho - \frac{\alpha_j S}{d_j (1 + kv_3^*) - b_j \frac{d_v}{b_v}} - \alpha_v v_3^* \end{aligned}$$

Then

$$R_{AV2} = \frac{aK \left( 1 - \frac{\mu}{r} \right)}{\rho + \frac{\alpha_j S}{d_j (1 + kv_3^*) - b_j \frac{d_v}{b_v}} + \alpha_v v_3^*}.$$

Now, plugging in  $v_3^*$ , and using Mathematica to simplify the expression we get

$$R_{AV2} = \frac{ad_v}{\mu b_v} \frac{K(r - \mu)}{rK \left( 1 - \frac{\mu}{r} \right)} = \frac{ad_v}{\mu b_v} = R_{AV}.$$

The demographic reproductive number of vultures in the absence of anthrax,  $D_V(E_1)$  and DRN of vultures in the presence of anthrax  $D_V(E_2)$  are both easy to see how they are the same values as in the exploitative model.

#### 4.11 Stability

The stability conditions of  $E_0$ ,  $E_1$ , and  $E_2$  are the same as in the exploitative model. The stability conditions are summarized in Table 4.6. Stability regions are shown in Figure 4.2 for each equilibria. Note that where  $E_3$  and  $E_4$  are LAS (in

Figures 4.2, 4.3b, and 4.3c) it is  $E_{3+}$  and  $E_{4+}$  that are LAS since  $E_{3-}$  and  $E_{4-}$  are not stable whenever they exist. More detail are provided in Appendix C.1 for the stability conditions for  $E_3$  and  $E_4$ .

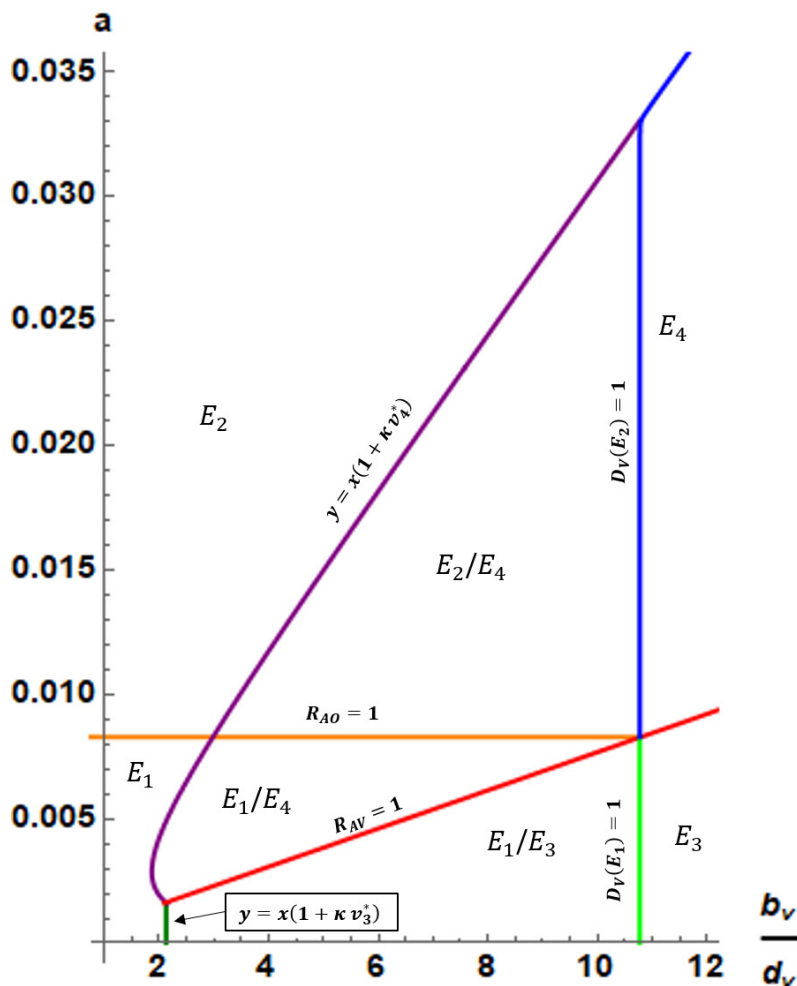


Figure 4.2: Stability regions for the interference model, (4.12)–(4.16) with  $k = 0.005$ . The vertical axis is  $a$  and the horizontal axis is  $\frac{b_v}{d_v}$ . The regions are created by the vulture demographic numbers ( $D_V(E_1) = 1$  and  $D_V(E_2) = 1$ ), the basic reproductive numbers of anthrax ( $R_{AO} = 1$  and  $R_{AV} = 1$ ), and the curves  $y = x(1 + kv_3^*)$  and  $y = x(1 + kv_4^*)$ , which represents vultures survivability with interference competition. The regions are labeled with the equilibria that are LAS. Note that where  $E_3$  and  $E_4$  are LAS it is  $E_{3+}$  and  $E_{4+}$  that are LAS since  $E_{3-}$  and  $E_{4-}$  are not stable whenever they exist.

## 4.12 Results: Interference Competition

In this section we discuss the results for the interference model, which are equations (4.12)–(4.16). We see (in Figures 4.3a and 4.3b or 4.3c ) that interference competition extends the region of vulture survival in parameter space by reversing the direction of the bifurcation at vulture extinction.

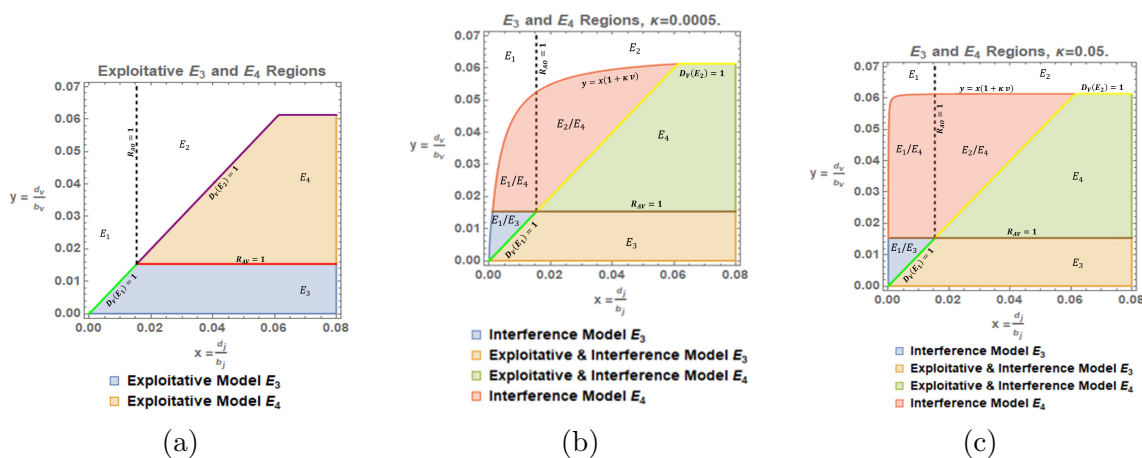


Figure 4.3: The vertical axis is  $\frac{d_v}{b_v}$  and the horizontal axis is  $\frac{d_j}{b_j}$ . The regions are created by the vulture demographic numbers ( $D_V(E_1) = 1$  and  $D_V(E_2) = 1$ ), and the basic reproductive numbers of anthrax ( $R_{AO} = 1$  and  $R_{AV} = 1$ ). (a) Stability regions for the exploitative model, (4.1)–(4.5). (b) Stability regions for the interference model, (4.12)–(4.16) with  $k = 0.0005$ . The left most curve for the ‘Interference Model  $E_3$ ’ is  $y = x(1 + kv_3^*)$ , and for the ‘Interference Model  $E_4$ ’ is  $y = x(1 + kv_4^*)$ . (c) Stability regions for the interference model with  $k = 0.05$ .

Figures 4.3b and 4.3c present the regions of existence and stability for each equilibrium in competition-related parameter space, with all other parameters held constant. The only difference between Figures 4.3b and 4.3c is the  $k$  value. Figure 4.3b has a smaller  $k$  value than Figure 4.3c. A larger  $k$  value means that the vultures interfere more with jackal feeding. We see how the interference regions for both  $E_3$  and  $E_4$  extend closer to  $x = 0$  in Figure 4.3c. When  $R_{AV} < 1$  and  $D_V(E_1) > 1$  hold

then only  $E_{3+}$  is stable (orange region, Figures 4.3b and 4.3c). As  $\frac{d_j}{b_j}$  decreases so that  $D_V(E_1) < 1$  then  $E_{3+}$  and  $E_1$  are both stable and  $E_{3-}$  exists (blue region, Figures 4.3b and 4.3c). If we decrease  $\frac{d_j}{b_j}$  more so that  $y > x(1 + kv_3^*)$  then  $E_{3+}$  and  $E_{3-}$  will annihilate each other and only  $E_1$  is stable (left white region, Figures 4.3b and 4.3c).

When  $R_{AV} > 1$  and  $D_V(E_2) > 1$  then we are in the region where only  $E_{4+}$  exists (green region, Figures 4.3b and 4.3c). As  $\frac{d_j}{b_j}$  decreases so that  $D_V(E_2) < 1$  and  $R_{AO} > 1$  then we go from only  $E_{4+}$  being stable to both  $E_{4+}$  and  $E_2$  being stable and  $E_{4-}$  exists (right red region, Figures 4.3b and 4.3c). If we continue to decrease  $\frac{d_j}{b_j}$  to where  $R_{AO} < 1$ , then the two equilibria that are stable are  $E_{4+}$  and  $E_1$  (left red region, Figures 4.3b and 4.3c). In this region, anthrax can spread with vultures, but not without. If we decrease  $\frac{d_j}{b_j}$  more so that  $y > x(1 + kv_4^*)$  then  $E_{4+}$  and  $E_{4-}$  will annihilate each other and only  $E_1$  is stable (left white region, Figures 4.3b and 4.3c). Suppose we are in the region where  $R_{AV} > 1$  and  $D_V(E_2) > 1$ , but far enough over so that when we increase  $\frac{d_v}{b_v}$  to where  $D_V(E_2) < 1$  then  $E_2$  becomes stable (right white region, Figures 4.3b and 4.3c). This means the vultures cannot survive ( $v_4^* \rightarrow 0$ ) because the vulture demographic number with anthrax is less than one, and so  $E_4$  crosses to  $E_2$  and is stable. If we increase  $\frac{d_v}{b_v}$  while we are in the region  $y < x(1 + kv_4^*)$ ,  $R_{AO} > 1$ , and  $R_{AV} > 1$  (right red region, Figures 4.3b and 4.3c), then the vultures are not able to compete with the jackals and the vultures die out, making  $E_2$  stable. If now  $R_{AO} < 1$  (left red region, Figures 4.3b and 4.3c), and we increase  $\frac{d_v}{b_v}$  so that  $y > x(1 + kv_4^*)$  then  $E_{4-}$  and  $E_{4+}$  annihilate each other and only  $E_1$  is stable (left white region, Figures 4.3b and 4.3c). If we are in the region where  $E_1$  and  $E_{3+}$  are stable (blue region, Figures 4.3b and 4.3c) and we increase  $\frac{d_v}{b_v}$  so that  $R_{AV} > 1$  then anthrax persists and  $E_{4+}$  becomes stable (left red region, Figures 4.3b and 4.3c).

Now, we discuss the three new regions seen in Figures 4.2, 4.3b, and 4.3c due to the interference model. With interference competition we have a region where both  $E_1$  and  $E_{3+}$  are locally asymptotically stable, so now vultures persist where normally (in exploitative model) no vultures were able to persist. When anthrax is present, vultures are able to persist where they normally would not be able to, which is the combined  $E_2$  and  $E_{4+}$  region. Finally, the other region we gain in the interference model is where both  $E_1$  and  $E_{4+}$  are locally asymptotically stable. In this region, we have both vultures and anthrax present, where normally anthrax and vultures did not exist.

When we plug in the parameter values from Table 4.4 into the interference model and look at how  $k$  plays a role in the behavior of the system we see that when  $k$  is  $2.1 \times 10^{-7}$  vultures<sup>-1</sup> or any number greater than that then we are in the region where both  $E_1$  and  $E_{3+}$  are locally asymptotically stable. Therefore, the interference competition helped the vultures to survive, where normally they would be extinct. If  $k$  is  $2.1 \times 10^{-5}$  vultures<sup>-1</sup>, then only  $E_1$  is locally asymptotically stable.

To interpret these results biologically, we return to the question of vulture survival. In the interference model in order for vultures to persist in an environment where zebras contract anthrax, vultures must reproduce efficiently meaning  $D_V(E_2) > 1$ , and be competitive with jackals,  $y < x(1 + kv^*)$ . The competitive edge,  $k$ , granted by interference competition extends vulture survivability into some scenarios where normally they would not be able to co-persist with jackals (i.e.,  $D_V(E_2) < 1$ ).

#### 4.13 Discussion

In this paper, we developed two models describing the interaction between jackals and vultures, that is, exploitative and interference competition. We analyzed systems of nonlinear ordinary equations to describe the dynamics between competing



scavengers and anthrax-zebra interactions. We answer the following research questions: how does the presence of jackals affect the presence of vultures, by considering the demographic reproduction numbers of vultures, and how does the nature of the competition affect the vultures' survivability? When we compared the demographic reproduction numbers of vultures, we saw that in the absence and presence of anthrax, the vultures are able to persist better in the absence of jackals in both instances. This is due to the fact that vultures solely depend on carcasses to reproduce. However, the jackals are eating those carcasses, which results in less food for the vultures and therefore a lower vulture birth rate.

From Figure 4.1, we see that the presence of anthrax and vultures make it harder for each other to persist. That is, the threshold for anthrax to persist increases when vultures are present and the threshold for vultures to persist increases when anthrax is present. We can also see that when anthrax is transmitting well enough, the zebra population (and thus the number of carcasses) becomes too small for vultures to have enough food to eat.

We also want to see if anthrax affects vultures. Therefore, we found conditions for when the number of vultures without anthrax ( $v_3^*$ ), is greater than the number of vultures with anthrax ( $v_4^*$ ). When the death-to-birth rate ratio of zebras is greater than  $\frac{1}{2}$  or when the basic reproductive number of anthrax in the presence of vultures is greater than  $\frac{r}{\mu} - 1$ , then the vultures are hurt by anthrax.

In addition, in order for the vultures to persist, we need the vultures to beat the jackals in the competition for zebra carcasses: the death to birth rate ratio of vultures needs to be less than the death to birth rate ratio of jackals. Vultures are obligate scavengers, relying on carcass availability, whereas the jackals are facultative scavengers and can find other food sources. Therefore, if the vultures get to the carcasses before the jackals, the jackal population will not go extinct.

The difference between the exploitative model ( $k = 0$ ) and the interference model ( $k > 0$ ) model is that in the interference model, vultures interfere with jackal feeding to an extent  $k$ , by arriving at the carrion before jackals. Without interference, vulture survival is determined purely by their demographic reproductive numbers (with or without anthrax present), but interference extends the region of vulture survival in parameter space by reversing the direction of the bifurcation at vulture extinction, analogous to a backward bifurcation in epidemic modeling. In addition, using our best estimate parameter values, exploitative competition alone cannot account for vulture survival.

One limitation of the model, is the assumption that the zebra carcasses are representative of all vulture food. Another limitation is how the interaction between scavengers is modeled. We assume that vultures will arrive at the carcass sites before jackals because of their keen eyesight and advantage of flying long distances. However, jackals are able to see at night and may find a carcass just before sunrise to beat the vultures.

A future study that can be done is to see how the transmission of rabies in jackals is affected with exploitative and interference competition between jackals and vultures. Under the conditions where vultures are out competing the jackals, we would expect less jackal-to-jackal encounters at zebra carcasses and therefore, less rabid jackals. However, if vultures are not able to survive then we would have the same results that we saw in Chapter 3.

## CHAPTER 5

### Conclusion

In this paper, we studied anthrax-zebra and scavenger interactions with disease dynamics using systems of non-linear differential equations. In the literature there are several predator-prey systems that consider only one disease in either one of the species or in both of the species. This dissertation looks at two different diseases in the two different species, which has not been seen yet.

In Chapter 2, we developed a model that consisted of zebras, uninfected carcasses, infected carcasses, and scavengers. We set out to find how scavengers help to eliminate anthrax in the zebra population in ENP. Scavengers (jackals and vultures) did benefit from the presence of anthrax because it created more carcasses (food) for them. However, anthrax was at a disadvantage when the scavengers were present because they would eat the anthrax thus eliminating it from the environment.

In Chapter 3, we modeled anthrax-rabies interactions in zebra-jackals cycles. We wanted to see how anthrax in zebras can help propagate rabies in jackals, since the zebra carcasses provide a location for the jackals to interact with each other. Our results show that depending on the amount of anthrax present, it may help or hurt the ability for rabies to persist. We also see that rabies is helping anthrax because the less jackals there are means anthrax is not being eaten or rid of from the environment.

In Chapter 4, we consider two different types of competition models: exploitative and interference competition. We aim to answer the question how the nature of competition affects the vultures' survivability? Analysis showed that interference competition extends the threshold for where the vultures can survive, meaning

typically where vultures are not able to persist, they can now persist with interference competition. We also found that exploitative competition alone cannot account for vulture survival.

Lastly, we discuss how our conclusions might help inform ENP wildlife management. In Chapter 2, we saw that the scavengers are clearly a helpful force in controlling anthrax infection in zebras and keeping outbreaks in check. In Chapter 3, we looked at how anthrax and rabies affect each other. Ideally, we want to manage the carcass density (away from what maximizes the  $\beta$  function) to limit jackal interactions in order to control rabies, which in turn will prevent wild fluctuations (limit cycles) that could endanger zebras or jackals. In Chapter 4, first, we saw that vultures appear to persist here only because of the competitive (interference) edge their flight lends them. Secondly, competition between scavenger types may amplify anthrax outbreaks because the total scavenging (by both types) may go down under interference competition.

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## APPENDIX A

## A.1 Equilibrium Calculations for Chapter 2

We calculate the equilibria and existence conditions. To get (2.1) we consider  $z^* \neq 0$ , and we have

$$\begin{aligned} z^* \left( r \left( 1 - \frac{z^*}{K} \right) - (\mu + ac^*) \right) &= 0 \\ r \left( 1 - \frac{z^*}{K} \right) &= (\mu + ac^*) \\ 1 - \frac{z^*}{K} &= \frac{1}{r} (\mu + ac^*) \\ \frac{z^*}{K} &= - \left[ \frac{1}{r} (\mu + ac^*) - 1 \right] \\ z^* &= K \left[ 1 - \frac{1}{r} (\mu + ac^*) \right]. \end{aligned}$$

Plugging (2.1) into (2.3) and setting (2.3) equal to zero we have

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

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 (2.1) we have

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

Likewise, replacing  $c^*$  with  $c_-^*$  in (2.1) gives (2.6):

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

$$= \frac{\rho + \alpha j^*}{a}.$$

Setting (2.2) equal to zero gives (2.7):

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

with (2.4) equal to zero, we have  $j^* = 0$  or we get (2.8):

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

Substituting  $c_+^*$  into (2.8) gives

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

Finally, plugging  $z_+^*$  and  $u_+^*$  into (2.7) we find

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

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 (2.6) and get (2.11):

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

to find  $u_-^*$  and  $j_-^*$ . First, we let  $j_-^* = 0$ . Then (2.6) becomes

$$z_-^* = \frac{\rho}{a},$$

(2.11) becomes

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

and (2.7) 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 (2.6) and (2.11), (2.8) becomes

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

Substituting (2.6) and (2.13) into (2.2) and setting it equal to zero gives (2.14):

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

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  $A > 0$ . Hence we get

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

where  $R_J = \frac{ad}{b\mu}$  and is discussed in section 2.2.2.

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

$$C > 0 \implies \frac{\rho}{aK} + \frac{ad}{br} > 1 \tag{A.2}$$



and

$$\begin{aligned}
B < 0 &\implies \frac{ad}{ba} - \frac{rb}{ba} \left(1 - \frac{2\rho}{aK}\right) < 0 \\
&\implies ad - rb \left(1 - \frac{2\rho}{aK}\right) < 0 \\
&\implies 1 - \frac{2\rho}{aK} > \frac{ad}{br} \\
&\implies \frac{2\rho}{aK} + \frac{ad}{br} < 1
\end{aligned} \tag{A.3}$$

However, conditions (A.2) and (A.3) contradict each other; therefore, our quadratic equation must have only one positive root, which occurs with condition (A.1).

From the quadratic equation (2.14), we get

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

Substituting (A.4) into (2.6) we get the expression for  $z^*$  in  $E_4$  which is

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

$$= K \left( 1 - \frac{ad}{br} \right)$$

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.

## A.2 Stability of $E_4$ for Chapter 2

We use the 4D 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 4D 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

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

Now we will show that the conditions needed above hold.

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

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

$$\begin{aligned}
B_1B_2 - B_3 &= (az^* - A)bj^*\alpha\frac{\mu ad}{a b\mu} - az^*\left(A + \mu\left(1 - \frac{ad}{b\mu}\right)\right) \\
&\quad - \left(-bj^*\alpha\frac{\mu ad}{a b\mu}A + \mu\left(\frac{ad}{b\mu} - 1\right)z^*(\alpha bj^* + a^2z^*)\right) \\
&= az^*bj^*\alpha\frac{\mu ad}{a b\mu} - a^2z^{*2}\left[A + \mu\left(1 - \frac{ad}{b\mu}\right)\right] \\
&\quad - Abj^*\alpha\frac{\mu ad}{a b\mu} + Aaz^*\left[A + \mu\left(1 - \frac{ad}{b\mu}\right)\right] \\
&\quad + Abj^*\alpha\frac{\mu ad}{a b\mu} + \mu\left(1 - \frac{ad}{b\mu}\right)az^*\left(az^* + \frac{\alpha}{a}bj^*\right) \\
&= -A(az^*)^2 + A^2(az^*) - A(az^*)\mu\left(\frac{ad}{b\mu} - 1\right) + \mu az^*\frac{\alpha}{a}bj^* \\
&> 0 \text{ since } \frac{ad}{b\mu} > 1 \text{ and } A < 0.
\end{aligned}$$

$$\begin{aligned}
B_3(B_1B_2 - B_3) - B_1^2B_4 &= \left[-bj^*\alpha\frac{\mu ad}{a b\mu}A + \mu\left(\frac{ad}{b\mu} - 1\right)z^*(\alpha bj^* + a^2z^*)\right] \\
&\quad \times \left[-A(az^*)^2 + A^2(az^*) - A(az^*)\mu\left(\frac{ad}{b\mu} - 1\right) + \mu az^*\frac{\alpha}{a}bj^*\right] \\
&\quad - [(az^*)^2 + 2az^*(-A) + A^2]\left[(-A)bj^*\alpha\frac{\mu}{a}(az^*)\left(\frac{ad}{b\mu} - 1\right)\right] \\
&= A^2bj^*\alpha\frac{\mu}{a}(az^*)^2\frac{ad}{b\mu} + (-A)^3bj^*\alpha\frac{\mu}{a}(az^*)\frac{ad}{b\mu} \\
&\quad + A^2bj^*\alpha\frac{\mu}{a}(az^*)\mu\left(\frac{ad}{b\mu} - 1\right)\frac{ad}{b\mu} + (-A)(bj^*)^2\left(\alpha\frac{\mu}{a}\right)^2(az^*)\frac{ad}{b\mu} \\
&\quad + (-A)bj^*\alpha\frac{\mu}{a}(az^*)^3\left(\frac{ad}{b\mu} - 1\right) + A^2bj^*\alpha\frac{\mu}{a}(az^*)^2\left(\frac{ad}{b\mu} - 1\right) \\
&\quad + (-A)bj^*\alpha\frac{\mu}{a}(az^*)^2\mu\left(\frac{ad}{b\mu} - 1\right)^2 + (bj^*)^2\left(\alpha\frac{\mu}{a}\right)^2(az^*)^2\left(\frac{ad}{b\mu} - 1\right) \\
&\quad + (-A)(az^*)^4\mu\left(\frac{ad}{b\mu} - 1\right) + A^2(az^*)^3\mu\left(\frac{ad}{b\mu} - 1\right) \\
&\quad + (-A)(az^*)^3\mu^2\left(\frac{ad}{b\mu} - 1\right)^2 + (bj^*)\left(\alpha\frac{\mu}{a}\right)(az^*)^3\mu\left(\frac{ad}{b\mu} - 1\right) \\
&\quad - (-A)bj^*\alpha\frac{\mu}{a}(az^*)^3\left(\frac{ad}{b\mu} - 1\right) - (-A)^3bj^*\left(\alpha\frac{\mu}{a}\right)(az^*)\left(\frac{ad}{b\mu} - 1\right)
\end{aligned}$$

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

We have shown that  $B_1 > 0$ ,  $B_4 > 0$ ,  $B_1B_2 > B_3$ , and  $B_3(B_1B_2 - B_3) > B_1^2B_4$  without any additional conditions; therefore,  $E_4$  is locally asymptotically stable whenever it exists.

## APPENDIX B

### B.1 Stability Analysis for Chapter 3

The Jacobian matrix for system (3.1)-(3.5) is

$$J = \begin{bmatrix} r - \frac{2r}{K}z - \mu - ac & 0 & -az & 0 & 0 \\ \mu & -\rho - \alpha(j+i) & 0 & -\alpha u & -\alpha u \\ ac & 0 & az - \rho - \alpha(j+i) & -\alpha c & -\alpha c \\ 0 & bj + \beta(x)\beta_1(x)ij & bj + \beta(x)\beta_1(x)ij & b(u+c) - d - \beta(x)i & -\beta(x)j \\ 0 & 0 & 0 & \beta(x)i & \beta(x)j - d - \delta \end{bmatrix}$$

where

$$\beta_1(x) = \frac{[\log(x) + \log(\pi R^2)]}{x\sqrt{[\log(x) + \log(\pi R^2)]^2 + q^2}} = -\frac{\beta'(x)}{\beta(x)}.$$

The Jacobian matrix evaluated at the extinction equilibrium,  $E_0$  is

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

If the zebra birth rate is less than the zebra death rate, i.e.  $r < \mu$ , then the extinction equilibrium is locally asymptotically stable.

The Jacobian matrix for  $E_1 \left( K \left[ 1 - \frac{\mu}{r} \right], \frac{\mu}{\rho} K \left[ 1 - \frac{\mu}{r} \right], 0, 0, 0 \right)$  is

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

$$\begin{aligned}
& \rightarrow \begin{bmatrix} \mu - r & 0 & -aK \left[1 - \frac{\mu}{r}\right] & 0 \\ \mu & -\rho & 0 & -\alpha \frac{\mu}{\rho} K \left[1 - \frac{\mu}{r}\right] \\ 0 & 0 & aK \left[1 - \frac{\mu}{r}\right] - \rho & 0 \\ 0 & 0 & 0 & b \frac{\mu}{\rho} K \left[1 - \frac{\mu}{r}\right] - d \end{bmatrix} \\
& \rightarrow \begin{bmatrix} \mu - r & 0 & 0 \\ \mu & -\rho & -\alpha \frac{\mu}{\rho} K \left[1 - \frac{\mu}{r}\right] \\ 0 & 0 & b \frac{\mu}{\rho} K \left[1 - \frac{\mu}{r}\right] - d \end{bmatrix} \\
& \rightarrow \begin{bmatrix} -\rho & -\alpha \frac{\mu}{\rho} K \left[1 - \frac{\mu}{r}\right] \\ 0 & b \frac{\mu}{\rho} K \left[1 - \frac{\mu}{r}\right] - d \end{bmatrix}.
\end{aligned}$$

The eigenvalues are  $\lambda_1 = -d - \delta$ ,  $\lambda_2 = az^* - \rho$ ,  $\lambda_3 = \frac{b\mu}{\rho}z^* - d$ ,  $\lambda_4 = -\rho$ , and  $\lambda_5 = \mu - r$ . Notice that  $\lambda_1$  and  $\lambda_4$  are always negative. However,  $\lambda_2 < 0$  if and only if  $z^* < \frac{\rho}{a}$ ,  $\lambda_3 < 0$  if and only if  $b\mu z^* < \rho d$ , and  $\lambda_5 < 0$  since  $\mu < r$ . Hence  $E_1$  is locally asymptotically stable if and only if  $z^* < \frac{\rho}{a}$  and  $b\mu z^* < \rho d$ .

The Jacobian matrix for  $E_2 \left( K \left[1 - \frac{\mu}{r}\right], \frac{d}{b}, 0, \frac{1}{\alpha} \left[ \frac{b\mu}{d} z^* - \rho \right], 0 \right)$  is

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

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

After evaluating the Jacobian matrix at  $E_2$ , the eigenvalues are  $\lambda_1 = \frac{1}{\alpha}\beta \left( \frac{d}{b} \right) \left( \frac{b\mu}{d}z^* - \rho \right) - d - \delta$ ,  $\lambda_2 = \left( a - \frac{b\mu}{d} \right) z^*$ , and  $\lambda_3 = \mu - r$ . Note  $\lambda_1 < 0$  if and only if  $\beta \left( \frac{d}{b} \right) \left( \frac{b\mu}{d}z^* - \rho \right) < \alpha(d + \delta)$ ,  $\lambda_2 < 0$  if and only if  $R_{AJ} = \frac{ad}{b\mu} < 1$ , and  $\lambda_3 < 0$  since  $\mu < r$ . We find the trace, determinant and use the 2-dimensional Routh-Hurwitz criterion to determine the sign of the real part of the remaining eigenvalues. The determinant, that is,  $\det(\hat{J}(E_2)) = \frac{b\mu}{d}z^* - \rho d$ , is positive since  $b\mu z^* > \rho d$  (that is,  $R_{AO} > R_{AJ}$ ). The trace:  $\text{tr}(\hat{J}(E_2)) = -\frac{b\mu}{d}z^*$  is always negative. Hence  $E_2$  is locally asymptotically stable if and only if  $\beta \left( \frac{d}{b} \right) \left( \frac{b\mu}{d}z^* - \rho \right) < \alpha(d + \delta)$  (the same as  $R_R < 1$ ) and  $\frac{ad}{b\mu} < 1$ .

The Jacobian matrix for  $E_3 \left( \frac{\rho}{a}, \frac{\mu}{a}, \frac{r}{aK} \left[ K \left( 1 - \frac{\mu}{r} \right) - \frac{\rho}{a} \right], 0, 0 \right)$  is

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



$$\begin{aligned} &\rightarrow \begin{bmatrix} \frac{-\rho r}{aK} & 0 & -\rho \\ \mu & -\rho & 0 \\ \frac{r}{K} \left( K \left( 1 - \frac{\mu}{r} \right) - \frac{\rho}{a} \right) & 0 & 0 \end{bmatrix} \\ &\rightarrow \begin{bmatrix} \frac{-\rho r}{aK} & -\rho \\ \frac{r}{K} \left( K \left( 1 - \frac{\mu}{r} \right) - \frac{\rho}{a} \right) & 0 \end{bmatrix} = \hat{J}(E_3). \end{aligned}$$

The equilibrium  $E_3$  exists when  $\mu < r$  and  $K \left( 1 - \frac{\mu}{r} \right) > \frac{\rho}{a}$ . Three of the eigenvalues of  $J(E_3)$  are  $\lambda_1 = -d - \delta$ ,  $\lambda_2 = b(u^* + c^*) - d$ , and  $\lambda_3 = -\rho$ . Notice that  $\lambda_1 = -d - \delta$  is always negative,  $\lambda_2 = b(u^* + c^*) - d < 0$  if and only if  $u^* + c^* < \frac{d}{b}$ ,  $\lambda_3 = -\rho$  is always negative. The trace and the determinant of  $\hat{J}(E_3)$  are

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

The trace is always negative and the determinant is positive since  $K \left( 1 - \frac{\mu}{r} \right) > \frac{\rho}{a}$ . Therefore,  $E_3$  is locally asymptotically stable if and only if  $u^* + c^* = \frac{\mu}{a} + \frac{r}{aK} \left[ K \left( 1 - \frac{\mu}{r} \right) - \frac{\rho}{a} \right] < \frac{d}{b}$ .

The equilibrium  $E_4$  exists when  $\frac{\rho}{a} < K \left[ 1 - \frac{ad}{br} \right]$  &  $\frac{ad}{b\mu} > 1$ . The Jacobian matrix for  $E_4 \left( K \left[ 1 - \frac{ad}{br} \right], \frac{\mu}{a}, \frac{d}{b} - \frac{\mu}{a}, \frac{a}{\alpha} K \left[ 1 - \frac{ad}{br} \right] - \frac{\rho}{\alpha}, 0 \right)$  is

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

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

The equilibrium  $E_4$  exists when  $\frac{\rho}{a} < K \left[1 - \frac{ad}{br}\right]$  &  $\frac{ad}{b\mu} > 1$ . We note that matrix  $\hat{J}(E_4)$  (cf. B.1) is exactly the Jacobian of  $E_4$  in [47] and found that it was locally asymptotically stable whenever it existed. Now, consider the eigenvalue  $\lambda = \beta \left(\frac{d}{b}\right) j^* - d - \delta < 0$  when  $\beta \left(\frac{d}{b}\right) j^* < d + \delta$ . Therefore,  $E_4$  is locally asymptotically stable whenever  $\beta \left(\frac{d}{b}\right) j_4^* < d + \delta$ , i.e.,  $\widetilde{R}_R < 1$ .

The equilibrium  $E_5$  exists when  $u^* > \frac{d}{b}$  or equivalently when  $R_R > 1$ . The Jacobian matrix for  $E_5 \left(K \left(1 - \frac{\mu}{r}\right), u^*, 0, \frac{d+\delta}{\beta(u^*)}, \frac{bu^*-d}{\beta(u^*)}\right)$  is

$$J(E_5) = \begin{bmatrix} \mu - r & 0 & -az^* & 0 & 0 \\ \mu & -\rho - \alpha \left(\frac{\delta+bu^*}{\beta(u^*)}\right) & 0 & -\alpha u^* & -\alpha u^* \\ 0 & 0 & az^* - \rho - \alpha \left(\frac{\delta+bu^*}{\beta(u^*)}\right) & 0 & 0 \\ 0 & \left(\frac{\delta+bu^*}{\beta(u^*)}\right) [b + \beta_1(u^*) (bu^* - d)] & \left(\frac{\delta+bu^*}{\beta(u^*)}\right) [b + \beta_1(u^*) (bu^* - d)] & 0 & d - bu^* \\ 0 & 0 & 0 & bu^* - d & 0 \end{bmatrix}$$

$$\rightarrow \begin{bmatrix} -\rho - \alpha \left(\frac{\delta+bu^*}{\beta(u^*)}\right) & -\alpha u^* & -\alpha u^* \\ \left(\frac{\delta+bu^*}{\beta(u^*)}\right) [b + \beta_1(u^*) (bu^* - d)] & 0 & d - bu^* \\ 0 & bu^* - d & 0 \end{bmatrix}$$

The eigenvalues are

$$\lambda_1 = az^* - \rho - \alpha \left( \frac{\delta + bu_5^*}{\beta(u_5^*)} \right) < 0 \iff \widetilde{R}_A = \frac{aK \left( 1 - \frac{\mu}{r} \right)}{\rho + \alpha \left[ \frac{\delta + bu_5^*}{\beta(u_5^*)} \right]} < 1$$

and  $\lambda_2 = \mu - r < 0$  since  $\mu < r$ . We find the rest of the characteristic polynomial and then use the Routh-Hurwitz Criterion to determine the stability of  $E_5$ .

Let  $S = b + \beta_1(u^*) (bu^* - d)$ . Then the remaining characteristic polynomial is  $p(\lambda) = 0$ , where

$$\begin{aligned} p(\lambda) &= \lambda^3 - \lambda^2 \left( -\rho - \alpha \frac{\delta + bu^*}{\beta(u^*)} \right) + \lambda \left[ \alpha u^* \frac{\delta + d}{\beta(u^*)} S + (d - bu^*)^2 \right] \\ &\quad + (d - bu^*)^2 \left[ \rho + \alpha \frac{\delta + bu^*}{\beta(u^*)} \right] - \alpha u^* \frac{d + \delta}{\beta(u^*)} (d - bu^*) S \\ &= \lambda^3 + \lambda^2 \left( \rho + \alpha \frac{\delta + bu^*}{\beta(u^*)} \right) + \lambda \left[ \alpha u^* \frac{\delta + d}{\beta(u^*)} S + (d - bu^*)^2 \right] \\ &\quad + (d - bu^*)^2 \left[ \rho + \alpha \frac{\delta + bu^*}{\beta(u^*)} \right] - \alpha u^* \frac{d + \delta}{\beta(u^*)} (d - bu^*) S. \end{aligned}$$

The third order Routh Hurwitz criteria are as follows: Let  $\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0$ . Then  $\text{Re}(\lambda) < 0$  if and only if  $a_1 > 0$ ,  $a_1a_2 > a_3$ , and  $a_3 > 0$ . Clearly, we see that

$$a_1 = \rho + \alpha \frac{\delta + bu^*}{\beta(u^*)} > 0.$$

Now,

$$a_3 = (d - bu^*)^2 \left[ \rho + \alpha \frac{\delta + bu^*}{\beta(u^*)} \right] - \alpha u^* \frac{d + \delta}{\beta(u^*)} (d - bu^*) S > 0 \iff S > 0.$$

**Theorem B.1.1.**  $S = b + \beta_1(x) (bx - d) > 0$ , where  $\beta_1(x) = \frac{[\log(x) + \log(\pi R^2)]}{x\sqrt{[\log(x) + \log(\pi R^2)]^2 + q^2}}$ ,  $q = \log\left(\frac{\pi}{1.48}\right)$ ,  $\hat{\rho} > 0$ , and  $R > 0$ .

*Proof.* We rewrite S as

$$S = b + \frac{\log(x) + \log(\pi R^2)}{x\sqrt{(\log(x) + \log(\pi R^2))^2 + q^2}} (bx - d)$$

$$\begin{aligned}
&= b + \frac{\log(x) + \log(\pi R^2)}{\sqrt{(\log(x) + \log(\pi R^2))^2 + q^2}} \left( b - \frac{d}{x} \right) \\
&= b \left[ 1 + \frac{\log(x) + \log(\pi R^2)}{\sqrt{(\log(x) + \log(\pi R^2))^2 + q^2}} \left( 1 - \frac{d/b}{x} \right) \right] \tag{B.1}
\end{aligned}$$

Note

$$\left| 1 - \frac{d/b}{x} \right| < 1 \text{ and } \left| \frac{\log(x) + \log(\pi R^2)}{\sqrt{(\log(x) + \log(\pi R^2))^2 + q^2}} \right| < 1$$

since  $x > \frac{d}{b}$  and  $[\log(x\pi R^2)]^2 > 0$  always. Then  $\sqrt{(\log(x) + \log(\pi R^2))^2 + q^2} > \log(x\pi R^2)$  regardless of the sign of  $\log(x\pi R^2)$ . Therefore, the product of two terms with magnitude less than one has a magnitude less than one. Hence the expression in hard brackets in (B.1) is always greater than 0. Therefore,  $a_3 > 0$ .

The last part we need to show is that  $a_1 a_2 > a_3$ .

$$\begin{aligned}
a_1 a_2 - a_3 > 0 &\iff (d - bu^*)^2 \left[ \rho + \alpha \frac{\delta + bu^*}{\beta(u^*)} \right] + \alpha u^* \frac{d + \delta}{\beta(u^*)} S \left[ \rho + \alpha \frac{\delta + bu^*}{\beta(u^*)} \right] \\
&\quad - (d - bu^*)^2 \left[ \rho + \alpha \frac{\delta + bu^*}{\beta(u^*)} \right] - \alpha u^* \frac{d + \delta}{\beta(u^*)} S(bu^* - d) > 0
\end{aligned}$$

Therefore we need to show that

$$\rho + \alpha \frac{\delta + bu^*}{\beta(u^*)} > bu^* - d. \tag{B.2}$$

We know that

$$j^* + i^* = \frac{\delta + bu_5^*}{\beta(u_5^*)} \text{ by (3.15) and } \rho + \alpha(j_5^* + i_5^*) = \frac{\mu K(1 - m)}{u_5^*} \text{ by (2.2)}.$$

So the condition becomes

$$\frac{\mu K(1 - m)}{u_5^*} > bu_5^* - d,$$

which can be rewritten as

$$b(u_5^*)^2 - du_5^* - \frac{\mu K(1 - m)}{u_5^*} < 0.$$

Clearly,

$$b \cdot 0^2 - d \cdot 0 - \frac{\mu K(1-m)}{u_5^*} < 0,$$

so the condition is satisfied for some  $u_5^* > 0$ . We need  $u_5^*$  between the roots

$$\frac{d \pm \sqrt{d^2 + 4b\mu K(1-m)}}{2b},$$

but recall that  $u_5^* > \frac{d}{b}$  (satisfied when  $R_R < 1$ ). So the condition is

$$\frac{d}{b} < u_5^* < \frac{d + \sqrt{d^2 + 4b\mu K(1-m)}}{2b}. \quad (\text{B.3})$$

Hence  $E_5$  is locally asymptotically stable if and only if  $\widetilde{R}_A < 1$  and  $\frac{d}{b} < u_5^* < \frac{d + \sqrt{d^2 + 4b\mu K(1-m)}}{2b}$ .  $\square$

## APPENDIX C

## C.1 Equilibria Calculations: Exploitative Model

Table C.1 gives a summary of the equilibrium conditions that arise from the system's equations, (4.1) through (4.5).

(1a) $z^* = 0$	(1b) $z^* = K \left[ 1 - \frac{1}{r} (\mu + ac^*) \right]$
(2) $u^* = \frac{\mu z^*}{\rho + \alpha_j j^* + \alpha_v v^*}$	
(3a) $c^* = 0$	(3b) $c^* = \frac{r}{aK} \left( K \left( 1 - \frac{\mu}{r} \right) - \frac{\rho + \alpha_j j^* + \alpha_v v^*}{a} \right)$
(4) $j^* = \frac{S}{d_j - b_j(u^* + c^*)}$	
(5a) $v^* = 0$	(5b) $u^* + c^* = \frac{d_v}{b_v}$

Table C.1: Summary of equilibrium components for system (4.1)-(4.5)

To find  $E_1$  we consider (1b), (2), (3a), (4), and (5a) in table C.1. Substitute (2) into (4) to get

$$\begin{aligned}
 j_1^* = \frac{S}{d_j - b_j \left( \frac{\mu z_1^*}{\rho + \alpha_j j_1^*} \right)} &\iff \left( d_j - \frac{b_j \mu z_1^*}{\rho + \alpha_j j_1^*} \right) j_1^* = S \\
 &\iff \frac{b_j \mu z_1^*}{\rho + \alpha_j j_1^*} j_1^* = d_j j_1^* - S \\
 &\iff b_j \mu z_1^* j_1^* = (d_j j_1^* - S) (\rho + \alpha_j j_1^*) \\
 &\iff b_j \mu z_1^* j_1^* = d_j \rho j_1^* + \alpha_j d_j (j_1^*)^2 - \rho S - \alpha_j S j_1^* \\
 &\iff \alpha_j d_j (j_1^*)^2 + (d_j \rho - b_j \mu z_1^* - \alpha_j S) j_1^* - \rho S = 0. \quad (\text{C.1})
 \end{aligned}$$

Consider a quadratic equation of the form  $ax^2 + bx + c = 0$ . If  $ac < 0$  then there is only one positive root. In (C.1),  $a > 0$  and  $c < 0$ , thus  $ac < 0$  and there is exactly one positive root, which is

$$j_1^* = \frac{b_j \mu z_1^* + \alpha_j S - d_j \rho + \sqrt{(d_j \rho - b_j \mu z_1^* - \alpha_j S)^2 + 4 \alpha_j d_j \rho S}}{2 \alpha_j d_j} \quad (\text{C.2})$$

In summary,  $E_1 \left( K \left( 1 - \frac{\mu}{r} \right), \frac{\mu K \left( 1 - \frac{\mu}{r} \right)}{\rho + \alpha_j j_1^*}, 0, j_1^*, 0 \right)$  exists when  $\mu < r$ .

To find  $E_2$  we consider (1b), (2), (3b), (4), and (5a) in table C.1. To get  $u_2^* = \frac{\mu}{a}$ , we substitute (3b) into (2). We solve for  $c_2^*$  in (1b) and then substitute (3b) in for  $z_2^*$ , that is,

$$\begin{aligned} \frac{z_2^*}{K} &= 1 - \frac{\mu}{r} - \frac{a}{r} c_2^* \\ \iff c_2^* &= \frac{r}{a} \left( 1 - \frac{\mu}{r} - \frac{z_2^*}{K} \right) \\ \iff c_2^* &= \frac{r}{aK} \left( K \left( 1 - \frac{\mu}{r} \right) - z_2^* \right) \\ \iff c_2^* &= \frac{r}{aK} \left( K \left( 1 - \frac{\mu}{r} \right) - \frac{\rho + \alpha_j j_2^*}{a} \right) \end{aligned} \quad (\text{C.3})$$

Substitute (C.3) into (4), we get

$$\begin{aligned} j_2^* (d_j - b_j (u_2^* + c_2^*)) &= S \\ j_2^* \left( d_j - b_j \left( \frac{\mu}{a} + \frac{r}{aK} \left( K \left( 1 - \frac{\mu}{r} \right) - \frac{\rho + \alpha_j j_2^*}{a} \right) \right) \right) &= S \\ \frac{\alpha_j b_j r}{a^2 K} (j_2^*)^2 + \left( d_j + \frac{b_j \rho r}{a^2 K} - \frac{b_j \mu}{a} - \frac{b_j r}{a} \left( 1 - \frac{\mu}{r} \right) \right) j_2^* - S &= 0 \\ (j_2^*)^2 + \frac{a^2 K}{\alpha_j b_j r} \left( d_j + \frac{b_j \rho r}{a^2 K} - \frac{b_j \mu}{a} - \frac{b_j r}{a} \left( 1 - \frac{\mu}{r} \right) \right) j_2^* - \frac{a^2 K}{\alpha_j b_j r} S &= 0 \\ (j_2^*)^2 + \left( \frac{aK}{\alpha_j} \left( \frac{ad_j}{rb_j} - 1 \right) + \frac{\rho}{\alpha_j} \right) j_2^* - \frac{a^2 K}{\alpha_j b_j r} S &= 0 \end{aligned} \quad (\text{C.4})$$



Note that (C.4) is a quadratic equation where the coefficient on the quadratic term is positive and the constant is negative. This means there is exactly one positive solution which is

$$j_2^* = \frac{1}{2} \left( \frac{aK}{\alpha_j} \left( 1 - \frac{adj}{rb_j} \right) - \frac{\rho}{\alpha_j} + \sqrt{\left( \frac{aK}{\alpha_j} \left( \frac{adj}{rb_j} - 1 \right) + \frac{\rho}{\alpha_j} \right)^2 + 4 \frac{a^2 K}{\alpha_j b_j r} S} \right) \quad (\text{C.5})$$

Therefore, we get that

$$E_2 \left( \frac{\rho + \alpha_j j_2^*}{a}, \frac{\mu}{a}, \frac{r}{aK} \left( K \left( 1 - \frac{\mu}{r} \right) - \frac{\rho + \alpha_j j_2^*}{a} \right), j_2^*, 0 \right),$$

which exists when  $\frac{\rho + \alpha_j j_2^*}{a} < K \left( 1 - \frac{\mu}{r} \right)$ .

To find  $E_3$  we consider (1b), (2), (3a), (4), and (5b) in table C.1. We have that  $c_3^* = 0$ , so we can easily get that  $z_3^* = K \left( 1 - \frac{\mu}{r} \right)$ . We substitute (3a) into (5b) to get  $u_3^* = \frac{d_v}{b_v}$ , and then we easily get that  $j_3^* = \frac{S}{d_j - b_j \left( \frac{d_v}{b_v} \right)}$ . Finally, we solve for  $v^*$  in (2) and then substitute what we got for  $z_3^*$ ,  $u_3^*$ , and  $j_3^*$  to get  $v_3^* = \frac{1}{\alpha_v} \left( \frac{b_v \mu z_3^*}{d_v} - (\rho + \alpha_j j_3^*) \right)$ .

Therefore, we get that

$$E_3 \left( K \left( 1 - \frac{\mu}{r} \right), \frac{d_v}{b_v}, 0, \frac{S}{d_j - b_j \left( \frac{d_v}{b_v} \right)}, \frac{1}{\alpha_v} \left( \frac{\mu b_v}{d_v} K \left( 1 - \frac{\mu}{r} \right) - (\rho + \alpha_j j_3^*) \right) \right),$$

which exists when  $\frac{d_v}{b_v} < \frac{d_j}{b_j}$ , and  $\frac{\mu b_v}{d_v} K \left( 1 - \frac{\mu}{r} \right) > \rho + \alpha_j j_3^*$ .

To find  $E_4$  we consider (1b), (2), (3b), (4), and (5b) in table C.1. We substitute (5b) into (4) to get

$$j_4^* = \frac{S}{d_j - b_j \left( \frac{d_v}{b_v} \right)}. \quad (\text{C.6})$$

We substitute (3b) into (2) to get

$$u_4^* = \frac{\mu}{a} \quad (\text{C.7})$$

Plugging  $u_4^*$  into (5b), we get

$$c_4^* = \frac{d_v}{b_v} - \frac{\mu}{a} \quad (\text{C.8})$$

Then plugging (C.8) into (1b), we get

$$\begin{aligned}
z_4^* &= K \left[ 1 - \frac{1}{r} (\mu + ac_4^*) \right] \\
&= K \left[ 1 - \frac{1}{r} \left( \mu + \frac{a\mu}{a} \left( \frac{ad_v}{\mu b_v} - 1 \right) \right) \right] \\
&= K \left( 1 - \frac{\mu}{r} - \frac{ad_v}{rb_v} + \frac{\mu}{r} \right) \\
&= K \left( 1 - \frac{ad_v}{rb_v} \right)
\end{aligned}$$

We solve for  $v^*$  in (2) and then substitute  $z_4^*$  and  $u_4^*$  to get

$$v_4^* = \frac{1}{\alpha_v} \left( \frac{\mu z_4^*}{u_4^*} - (\rho + \alpha_j j_4^*) \right) = \frac{1}{\alpha_v} \left( aK \left( 1 - \frac{ad_v}{rb_v} \right) - (\rho + \alpha_j j_4^*) \right) \quad (\text{C.9})$$

Therefore, we get that

$$E_4 \left( K \left( 1 - \frac{ad_v}{rb_v} \right), \frac{\mu}{a}, \frac{d_v}{b_v} - \frac{\mu}{a}, \frac{S}{d_j - b_j \left( \frac{d_v}{b_v} \right)}, \frac{1}{\alpha_v} \left( aK \left( 1 - \frac{ad_v}{rb_v} \right) - (\rho + \alpha_j j_4^*) \right) \right),$$

which exists when  $\frac{d_v}{b_v} < \frac{d_j}{b_j}$ ,  $\frac{ad_v}{\mu b_v} > 1$ , and  $aK \left( 1 - \frac{ad_v}{rb_v} \right) > \rho + \alpha_j j_4^*$ .

## C.2 Stability Analysis

The Jacobian matrix for system (4.1)-(4.5) is

$$J = \begin{bmatrix} r - \frac{2r}{K}z - \mu - ac & 0 & -az & 0 & 0 \\ \mu & -\rho - \alpha_j j - \alpha_v v & 0 & -\alpha_j u & -\alpha_v u \\ ac & 0 & az - \rho - \alpha_j j - \alpha_v v & -\alpha_j c & -\alpha_v c \\ 0 & b_j j & b_j j & b_j(u + c) - d_j & 0 \\ 0 & b_v v & b_v v & 0 & b_v(u + c) - d_v \end{bmatrix}.$$

The Jacobian matrix evaluated at the  $E_0$  equilibrium is

$$J(E_0) = \begin{bmatrix} r - \mu & 0 & 0 & 0 & 0 \\ \mu & -\rho - \alpha_j \frac{S}{d_j} & 0 & 0 & 0 \\ 0 & 0 & -\rho - \alpha_j \frac{S}{d_j} & 0 & 0 \\ 0 & \frac{b_j S}{d_j} & \frac{b_j S}{d_j} & -d_j & 0 \\ 0 & 0 & 0 & 0 & -d_v \end{bmatrix}.$$

If the zebra birth rate is less than the zebra death rate, i.e.  $r < \mu$ , then the  $E_0$  equilibrium is locally asymptotically stable.

Recall that  $E_1 \left( K \left( 1 - \frac{\mu}{r} \right), \frac{\mu K \left( 1 - \frac{\mu}{r} \right)}{\rho + \alpha_j j_1^*}, 0, j_1^*, 0 \right)$  exists when  $\mu < r$ . The Jacobian matrix for  $E_1$  is

$$\begin{aligned} J(E_1) &= \begin{bmatrix} \mu - r & 0 & -aK \left[ 1 - \frac{\mu}{r} \right] & 0 & 0 \\ \mu & -\rho - \alpha_j j_1^* & 0 & -\alpha_j u_1^* & -\alpha_v u_1^* \\ 0 & 0 & aK \left[ 1 - \frac{\mu}{r} \right] - \rho - \alpha_j j_1^* & 0 & 0 \\ 0 & b_j j_1^* & b_j j_1^* & b_j u_1^* - d_j & 0 \\ 0 & 0 & 0 & 0 & b_v u_1^* - d_v \end{bmatrix} \\ &\rightarrow \begin{bmatrix} \mu - r & 0 & -aK \left[ 1 - \frac{\mu}{r} \right] & 0 \\ \mu & -\rho - \alpha_j j_1^* & 0 & -\alpha_j u_1^* \\ 0 & 0 & aK \left[ 1 - \frac{\mu}{r} \right] - \rho - \alpha_j j_1^* & 0 \\ 0 & b_j j_1^* & b_j j_1^* & b_j u_1^* - d_j \end{bmatrix} \\ &\rightarrow \begin{bmatrix} \mu - r & 0 & 0 \\ \mu & -\rho - \alpha_j j_1^* & -\alpha_j u_1^* \\ 0 & b_j j_1^* & b_j u_1^* - d_j \end{bmatrix} \\ &\rightarrow \begin{bmatrix} -\rho - \alpha_j j_1^* & -\alpha_j u_1^* \\ b_j j_1^* & b_j u_1^* - d_j \end{bmatrix} = \hat{J}(E_1) \end{aligned}$$

The eigenvalues are  $\lambda_1 = b_v u_1^* - d_v$ ,  $\lambda_2 = aK \left[1 - \frac{\mu}{r}\right] - \rho - \alpha_j j_1^*$ , and  $\lambda_3 = \mu - r$ .

Then

$$\begin{aligned}
\lambda_1 < 0 &\iff u_1^* < \frac{d_v}{b_v} \\
&\iff \frac{\mu K \left(1 - \frac{\mu}{r}\right)}{\rho + \alpha_j j_1^*} < \frac{d_v}{b_v} \\
&\iff \frac{b_v \mu K \left(1 - \frac{\mu}{r}\right)}{d_v \rho + \alpha_j j_1^*} < 1 \\
&\iff D_V(E_1) < 1.
\end{aligned}$$

Also,

$$\begin{aligned}
\lambda_2 = aK \left[1 - \frac{\mu}{r}\right] - \rho - \alpha_j j_1^* &< 0 \\
\iff aK \left[1 - \frac{\mu}{r}\right] &< \rho + \alpha_j j_1^* \\
\iff \frac{aK \left(1 - \frac{\mu}{r}\right)}{\rho + \alpha_j j_1^*} &< 1 \\
\iff R_{AO} &< 1
\end{aligned}$$

and  $\lambda_3 < 0$  since  $\mu < r$ . Using Routh Hurwitz 2-D criterion, we find the trace and determinant of  $\hat{J}(E_1)$  to find other stability conditions. First, we find when the trace of  $\hat{J}(E_1) < 0$ . That is,

$$\begin{aligned}
\text{tr}\left(\hat{J}(E_1)\right) &= -\rho - \alpha_j j_1^* + b_j u_1^* - d_j < 0 \\
&\iff b_j u_1^* - d_j < \rho + \alpha_j j_1^* \\
&\iff u_1^* < \frac{d_j + \rho + \alpha_j j_1^*}{b_j} \tag{C.10}
\end{aligned}$$

Note that for  $j_1^* > 0$  implies that  $u_1^* < \frac{d_j}{b_j}$ ; therefore, the condition (C.10) is always satisfied since  $u_1^* < \frac{d_j}{b_j} < \frac{d_j + \rho + \alpha_j j_1^*}{b_j}$ .

$$\det\left(\hat{J}(E_1)\right) = (-\rho - \alpha_j j_1^*) (b_j u_1^* - d_j) + \alpha_j u_1^* b_j j_1^* > 0$$

$$\begin{aligned}
&\iff \rho d_j - \rho b_j u_1^* + \alpha_j d_j j_1^* > 0 \\
&\iff \rho + \alpha_j j_1^* > \frac{\rho b_j}{d_j} u_1^* \\
&\iff u_1^* < \frac{d_j}{b_j} \left( 1 + \frac{\alpha_j}{\rho} j_1^* \right)
\end{aligned} \tag{C.11}$$

Note that for  $j_1^* > 0$  implies that  $u_1^* < \frac{d_j}{b_j}$ ; therefore, the condition (C.11) is always satisfied since  $u_1^* < \frac{d_j}{b_j} < \frac{d_j}{b_j} \left( 1 + \frac{\alpha_j}{\rho} j_1^* \right)$ . Therefore,  $E_1$  is LAS if and only if  $D_V(E_1) = \frac{b_v}{d_v} \frac{\mu K (1 - \frac{\mu}{r})}{\rho + \alpha_j j_1^*} < 1$  and  $R_{AO} = \frac{aK(1 - \frac{\mu}{r})}{\rho + \alpha_j j_1^*} < 1$ .

The Jacobian matrix for  $E_2$  is

$$\begin{aligned}
J(E_2) &= \begin{bmatrix} -\frac{r}{K} z_2^* & 0 & -a z_2^* & 0 & 0 \\ \mu & -a z_2^* & 0 & -\alpha_j u_2^* & -\alpha_v u_2^* \\ a c_2^* & 0 & 0 & -\alpha_j c_2^* & -\alpha_v c_2^* \\ 0 & b_j j_2^* & b_j j_2^* & b_j (u_2^* + c_2^*) - d_j & 0 \\ 0 & 0 & 0 & 0 & b_v (u_2^* + c_2^*) - d_v \end{bmatrix} \\
&\rightarrow \begin{bmatrix} -\frac{r}{K} z_2^* & 0 & -a z_2^* & 0 \\ \mu & -a z_2^* & 0 & -\alpha_j u_2^* \\ a c_2^* & 0 & 0 & -\alpha_j c_2^* \\ 0 & b_j j_2^* & b_j j_2^* & b_j (u_2^* + c_2^*) - d_j \end{bmatrix} = \hat{J}(E_2)
\end{aligned}$$

One eigenvalue is  $\lambda_1 = b_v (u_2^* + c_2^*) - d_v$ . For  $\lambda_1 < 0$  we have

$$\begin{aligned}
&b_v (u_2^* + c_2^*) - d_v < 0 \\
&\iff u_2^* + c_2^* < \frac{d_v}{b_v} \\
&\iff \frac{\mu}{a} + \frac{r}{aK} \left( K \left( 1 - \frac{\mu}{r} \right) - \frac{\rho + \alpha_j j_2^*}{a} \right) < \frac{d_v}{b_v} \\
&\iff \frac{r}{a} \left( 1 - \frac{\rho + \alpha_j j_2^*}{aK} \right) < \frac{d_v}{b_v}
\end{aligned}$$

$$\begin{aligned}
&\iff \frac{\rho + \alpha_j j_2^*}{aK} > 1 - \frac{ad_v}{rb_v} \\
&\iff \frac{aK \left(1 - \frac{ad_v}{rb_v}\right)}{\rho + \alpha_j j_2^*} < 1 \\
&\iff D_V(E_2) < 1.
\end{aligned}$$

The analysis for using the 4D Routh-Hurwitz criterion was complex; therefore, through numerical exploration, we found that no additional stability conditions exist.

The Jacobian matrix for  $E_3$  is

$$\begin{aligned}
J(E_3) &= \begin{bmatrix} \mu - r & 0 & -az_3^* & 0 & 0 \\ \mu & -\frac{\mu b_v}{d_v} z_3^* & 0 & -\alpha_j u_3^* & -\alpha_v u_3^* \\ 0 & 0 & aK \left(1 - \frac{\mu}{r}\right) \left(1 - \frac{\mu b_v}{ad_v}\right) & 0 & 0 \\ 0 & b_j j_3^* & b_j j_3^* & b_j u_3^* - d_j & 0 \\ 0 & b_v v_3^* & b_v v_3^* & 0 & 0 \end{bmatrix} \\
&\rightarrow \begin{bmatrix} \mu - r & 0 & 0 & 0 \\ \mu & -\frac{\mu b_v}{d_v} z_3^* & -\alpha_j u_3^* & -\alpha_v u_3^* \\ 0 & b_j j_3^* & b_j u_3^* - d_j & 0 \\ 0 & b_v v_3^* & 0 & 0 \end{bmatrix} \\
&\rightarrow \begin{bmatrix} -\frac{\mu b_v}{d_v} z_3^* & -\alpha_j u_3^* & -\alpha_v u_3^* \\ b_j j_3^* & b_j u_3^* - d_j & 0 \\ b_v v_3^* & 0 & 0 \end{bmatrix} = \hat{J}(E_3)
\end{aligned}$$

The eigenvalues are  $\lambda_1 = aK \left(1 - \frac{\mu}{r}\right) \left(1 - \frac{\mu b_v}{ad_v}\right)$  and  $\lambda_2 = r - \mu$ . Notice that  $\lambda_1 < 0$  if and only if  $\frac{ad_v}{\mu b_v} < 1$  and  $\lambda_2 < 0$  since  $\mu < r$  is an existence condition.

We find the rest of the characteristic polynomial and then use the 3-D Routh-Hurwitz Criterion to determine the stability of  $E_3$ .

$$\begin{aligned}
p(\lambda) &= \left( -\frac{\mu b_v}{d_v} z_3^* - \lambda \right) [(b_j u_3^* - d_j)(-\lambda) + \lambda^2] + \frac{\alpha_j d_v}{b_v} (-b_j j_3^* \lambda) + \frac{\alpha_v d_v}{b_v} (b_j u_3^* - d_j - \lambda)(b_j v_3^*) \\
&= \frac{b_v \mu}{d_v} z_3^* (b_j u_3^* - d_j) \lambda - \frac{b_v \mu}{d_v} z_3^* \lambda^2 + (b_j u_3^* - d_j) \lambda^2 - \lambda^3 - \frac{\alpha_j d_v}{b_v} b_j j_3^* \lambda \\
&\quad + \frac{\alpha_v d_v}{b_v} b_j v_3^* (b_j u_3^* - d_j) - \frac{\alpha_v d_v}{b_v} b_j v_3^* \lambda \\
&= -\lambda^3 + \left( b_j u_3^* - d_j - \frac{b_v \mu}{d_v} z_3^* \right) \lambda^2 + \left( \frac{b_v \mu}{d_v} z_3^* (b_j u_3^* - d_j) - \frac{\alpha_j d_v}{b_v} b_j j_3^* - \frac{\alpha_v d_v}{b_v} b_j v_3^* \right) \lambda \\
&\quad + \frac{\alpha_v d_v}{b_v} b_j v_3^* (b_j u_3^* - d_j) \\
&= \lambda^3 + \left( \frac{b_v \mu}{d_v} z_3^* - (b_j u_3^* - d_j) \right) \lambda^2 + \left( \frac{\alpha_j d_v}{b_v} b_j j_3^* - \frac{b_v \mu}{d_v} z_3^* (b_j u_3^* - d_j) + \frac{\alpha_v d_v}{b_v} b_j v_3^* \right) \lambda \\
&\quad + \frac{\alpha_v d_v}{b_v} b_j v_3^* (d_j - b_j u_3^*)
\end{aligned}$$

Let  $p(\lambda) = 0$ . The third order Routh Hurwitz criteria are as follows: Let  $\lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3 = 0$ . Then  $\text{Re}(\lambda) < 0$  if and only if  $a_1 > 0$ ,  $a_1 a_2 > a_3$ , and  $a_3 > 0$ . We see that

$$a_1 = \frac{\mu b_v}{d_v} z_3^* + (d_j - b_j u_3^*) > 0$$

since  $\frac{d_v}{b_v} < \frac{d_j}{b_j}$ . In addition,

$$a_3 = \frac{\alpha_v d_v}{b_v} b_j v_3^* (d_j - b_j u_3^*) > 0$$

since  $\frac{d_v}{b_v} < \frac{d_j}{b_j}$ .

Now,

$$\begin{aligned}
a_1 a_2 - a_3 &= \left[ \frac{\mu b_v}{d_v} z_3^* + (d_j - b_j u_3^*) \right] \left[ \frac{\mu b_v}{d_v} z_3^* (d_j - b_j u_3^*) + \frac{\alpha_j d_v}{b_v} b_j j_3^* + \frac{\alpha_v d_v}{b_v} b_j v_3^* \right] \\
&\quad - \frac{\alpha_v d_v}{b_v} b_j v_3^* (d_j - b_j u_3^*) \\
&= \frac{b_v \mu}{d_v} z_3^* \left[ \frac{\mu b_v}{d_v} z_3^* (d_j - b_j u_3^*) + \frac{\alpha_j d_v}{b_v} b_j j_3^* + \frac{\alpha_v d_v}{b_v} b_j v_3^* \right] \\
&\quad + (d_j - b_j u_3^*) \left[ \frac{\alpha_j d_v}{b_v} b_j j_3^* + \frac{\mu b_v}{d_v} z_3^* (d_j - b_j u_3^*) \right] > 0
\end{aligned}$$

since  $\frac{d_v}{b_v} < \frac{d_j}{b_j}$ . This means there are no additional stability criteria. Therefore,  $E_3$  is LAS if and only if  $\frac{ad_v}{\mu b_v} < 1$ .

The Jacobian matrix for  $E_4$  is

$$J(E_4) = \begin{bmatrix} r \left( \frac{ad_v}{rb_v} - 1 \right) & 0 & -az^* & 0 & 0 \\ \mu & aK \left( \frac{ad_v}{\mu b_v} - 1 \right) & 0 & -\alpha_j u^* & -\alpha_v u^* \\ \mu \left( \frac{ad_v}{\mu b_v} - 1 \right) & 0 & az^* - \frac{\mu K}{r} \left( \frac{ad_v}{\mu b_v} - 1 \right) & -\alpha_j c^* & -\alpha_v c^* \\ 0 & b_j j^* & b_j j^* & b_j \frac{d_v}{b_v} - d_j & 0 \\ 0 & b_v v^* & b_v v^* & 0 & 0 \end{bmatrix}.$$

### C.3 Equilibria Calculations: Interference Model

Table C.2 gives a summary of the equilibrium conditions that arise from the system's equations, (4.12) through (4.16).

(1a) $z^* = 0$	(1b) $z^* = K \left[ 1 - \frac{1}{r} (\mu + ac^*) \right]$
(2) $u^* = \frac{\mu z^*}{\rho + \frac{\alpha_j j^*}{1+kv^*} + \alpha_v v^*}$	
(3a) $c^* = 0$	(3b) $z^* = \frac{1}{a} \left( \rho + \frac{\alpha_j j^*}{1+kv^*} + \alpha_v v^* \right)$
(4) $j^* = \frac{S}{d_j - \frac{b_j(u^* + c^*)}{1+kv^*}}$	
(5a) $v^* = 0$	(5b) $u^* + c^* = \frac{d_v}{b_v}$

Table C.2: Summary of equilibrium components for system (4.12)-(4.16)

Equilibrium  $E_3$  comes from (1b), (2), (3a), (4), and (5b) in table C.2. Since  $c_3^* = 0$  then (1b) simplifies to  $z_3^* = K \left( 1 - \frac{\mu}{r} \right)$ , and (5b) reduces to  $u_3^* = \frac{d_v}{b_v}$ .



Plugging (5b) and (4) into (2) we get

$$\frac{d_v}{b_v} = \frac{\mu z_3^*}{\rho + \frac{\alpha_j S}{(1+kv_3^*)d_j - \frac{b_j d_v}{b_v}} + \alpha_v v_3^*}. \quad (\text{C.12})$$

The rearranging we get a quadratic equation in  $v_3^*$ :

$$\begin{aligned} & -\alpha_v d_j k (v_3^*)^2 + \left( -\alpha_v d_j + d_j k \left( \frac{\mu b_v}{d_v} z_3^* - \rho \right) + \frac{\alpha_v d_v b_j}{b_v} \right) v_3 + \left( \frac{\mu b_v}{d_v} z_3^* - \rho \right) \left( d_j - \frac{b_j d_v}{b_v} \right) \\ & - \alpha_j S = 0 \\ & (v_3^*)^2 + \left( \frac{1}{k} \left( 1 - \frac{d_v b_j}{b_v d_j} \right) - \frac{1}{\alpha_v} \left( \frac{\mu b_v}{d_v} z_3^* - \rho \right) \right) v_3 + \frac{1}{\alpha_v k} \left( \frac{\mu b_v}{d_v} z_3^* - \rho \right) \left( \frac{d_v b_j}{b_v d_j} - 1 \right) \\ & + \frac{\alpha_j S}{\alpha_v d_j k} = 0. \end{aligned} \quad (\text{C.13})$$

Therefore, we have that

$$\begin{aligned} v_{3\pm} &= -\frac{1}{2} \left( \frac{1}{k} \left( 1 - \frac{d_v b_j}{b_v d_j} \right) - \frac{1}{\alpha_v} \left( \frac{\mu b_v}{d_v} z_3^* - \rho \right) \right) \\ & \pm \frac{1}{2} \sqrt{\left[ \frac{1}{k} \left( 1 - \frac{d_v b_j}{b_v d_j} \right) - \frac{1}{\alpha_v} \left( \frac{\mu b_v}{d_v} z_3^* - \rho \right) \right]^2 - 4 \left( \frac{1}{\alpha_v k} \left( \frac{\mu b_v}{d_v} z_3^* - \rho \right) \left( \frac{d_v b_j}{b_v d_j} - 1 \right) + \frac{\alpha_j S}{\alpha_v d_j k} \right)} \end{aligned} \quad (\text{C.14})$$

Next, we show that there is only one positive root. Using the general form  $A(v_3^*)^2 + Bv_3^* + C = 0$ , we note that  $A > 0$ , so we show that  $C < 0$  to ensure there is only one positive root to (C.13).

**Theorem C.3.1.** *If  $D_V(E_1) > 1$  or  $\frac{d_v}{b_v} \in (0, y_{3-}) \cup (y_{3+}, \infty)$  hold, then  $C = \frac{1}{\alpha_v k} \left( \frac{\mu b_v}{d_v} z_3^* - \rho \right) \left( \frac{d_v b_j}{b_v d_j} - 1 \right) + \frac{\alpha_j S}{\alpha_v d_j k} < 0$*

*Proof.*

**Case 1.** *If  $\frac{b_j d_v}{d_j b_v} - 1 < 0$  then*

$$\begin{aligned} \frac{\mu b_v}{d_v} z_3^* - \rho &> \frac{-\alpha_j S}{d_j \left( \frac{b_j d_v}{d_j b_v} - 1 \right)} \\ \iff \frac{\mu b_v}{d_v} z_3^* &> \rho + \frac{\alpha_j S}{d_j \left( 1 - \frac{b_j d_v}{d_j b_v} \right)} \end{aligned}$$

$$\begin{aligned}
&\iff \frac{\frac{\mu b_v}{d_v} z_3^*}{\rho + \frac{\alpha_j S}{d_j \left(1 - \frac{b_j d_v}{d_j b_v}\right)}} > 1 \\
&\iff \frac{\frac{\mu b_v}{d_v} z_3^*}{\rho + \alpha_j j_3^* [1^{st} \text{ model}]} > 1 \\
&\iff D_V(E_1) > 1,
\end{aligned}$$

since  $j_3^* [1^{st} \text{ model}] = \frac{S}{d_j \left(1 - \frac{b_j d_v}{d_j b_v}\right)}$ . Furthermore,  $j_3^* [1^{st} \text{ model}] = j_1^* [2^{nd} \text{ model}] = j_1^* [1^{st} \text{ model}]$ , and we have already seen in section 4.5 that when  $D_V(E_1) = 1$  that  $j_3^* [1^{st} \text{ model}] = j_1^* [1^{st} \text{ model}]$ .

**Case 2.** Let  $x = \frac{d_j}{b_j}$  and  $y = \frac{d_v}{b_v}$ . If  $\frac{b_j d_v}{d_j b_v} - 1 > 0$  then

$$\begin{aligned}
&\left(\frac{\mu b_v}{d_v} z_3^* - \rho\right) \left(\frac{d_v b_j}{b_v d_j} - 1\right) + \frac{\alpha_j S}{d_j} < 0 \\
&\iff -\frac{\rho}{x} y^2 + \left(\frac{\mu}{x} z_3^* + \rho + \frac{\alpha_j S}{d_j}\right) y - \mu z_3^* < 0 \\
&\iff y^2 - \left(\frac{\mu z_3^*}{\rho} + x + \frac{\alpha_j S x}{d_j \rho}\right) y + \frac{\mu x z_3^*}{\rho} > 0,
\end{aligned}$$

so

$$y_{3\pm} = \frac{1}{2} \left( \frac{\mu z_3^*}{\rho} + x + \frac{\alpha_j S x}{d_j \rho} \pm \sqrt{\left(\frac{\mu z_3^*}{\rho} + x + \frac{\alpha_j S x}{d_j \rho}\right)^2 - 4 \frac{\mu z_3^* x}{\rho}} \right). \quad (\text{C.15})$$

Therefore,  $C > 0$  when either  $D_V(E_1) > 1$  or  $\frac{d_v}{b_v} \in (0, y_{3-}) \cup (y_{3+}, \infty)$  is satisfied.

This means there is only one positive value for  $v_3^*$ .  $\square$

Equilibrium  $E_4$  comes from (1b), (2), (3b), (4), and (5b) in table C.2. We find  $u_4^*$  by substituting (3b) into (2) to get

$$u_4^* = \frac{\frac{\mu}{a} \left( \rho + \frac{\alpha_j j_3^*}{1 + k v_4^*} + \alpha_v v_4^* \right)}{\rho + \frac{\alpha_j j_4^*}{1 + k v_4^*} + \alpha_v v_4^*} = \frac{\mu}{a}. \quad (\text{C.16})$$

Now, (5b) becomes  $u_4^* + c_4^* = \frac{d_v}{b_v} \iff c_4^* = \frac{d_v}{b_v} - \frac{\mu}{a}$ . In order for  $c_4^* > 0$ , we need  $\frac{ad_v}{\mu b_v} > 1$ . By substituting the  $c_4^*$  into (1b), we get  $z_4^* = K \left(1 - \frac{ad_v}{rb_v}\right)$ . Next, we plug (4) into (2) and use  $u_4^* = \frac{\mu}{a}$  to get

$$\begin{aligned}
\frac{\mu}{a} &= \frac{\mu K \left(1 - \frac{ad_v}{rb_v}\right)}{\rho + \frac{\alpha_j S}{(1+kv_4^*) \left(d_j - \frac{b_j d_v}{b_v(1+kv_4^*)}\right)} + \alpha_v v_4^*} \\
\iff \frac{\mu}{a} &= \frac{\mu K \left(1 - \frac{ad_v}{rb_v}\right)}{\rho + \frac{\alpha_j S}{d_j(1+kv_4^*) - \frac{b_j d_v}{b_v}} + \alpha_v v_4^*} \\
\iff \frac{\mu}{a} \left(\rho + \frac{\alpha_j S}{d_j(1+kv_4^*) - \frac{b_j d_v}{b_v}} + \alpha_v v_4^*\right) &= \mu K \left(1 - \frac{ad_v}{rb_v}\right) \\
\iff \alpha_j S &= \left(d_j(1+kv_4^*) - \frac{b_j d_v}{b_v}\right) \left(aK \left(1 - \frac{ad_v}{rb_v}\right) - \rho - \alpha_v v_4^*\right) \\
\iff (v_4^*)^2 + \left[\frac{1}{k} \left(1 - \frac{d_v b_j}{b_v d_j}\right) - \frac{1}{\alpha_v} (az_4^* - \rho)\right] v_4^* & \\
&+ \frac{1}{\alpha_v k} \left[(az_4^* - \rho) \left(\frac{d_v b_j}{b_v d_j} - 1\right) + \frac{\alpha_j S}{d_j}\right] = 0 \tag{C.17}
\end{aligned}$$

Therefore,

$$\begin{aligned}
v_4^* &= -\frac{1}{2} \left[ \frac{1}{k} \left(1 - \frac{d_v b_j}{b_v d_j}\right) - \frac{1}{\alpha_v} (az_4^* - \rho) \right] \\
&\pm \frac{1}{2} \sqrt{\left[ \frac{1}{k} \left(1 - \frac{d_v b_j}{b_v d_j}\right) - \frac{1}{\alpha_v} (az_4^* - \rho) \right]^2 - \frac{4}{\alpha_v k} \left[ (az_4^* - \rho) \left(\frac{d_v b_j}{b_v d_j} - 1\right) + \frac{\alpha_j S}{d_j} \right]}.
\end{aligned}$$

Next, we show that there is only one positive root. Using the general form  $A(v_4^*)^2 + Bv_4^* + C = 0$ , we note that  $A > 0$ , so we show that  $C < 0$  to ensure there is only one positive root to (C.17).

**Theorem C.3.2.** *If  $D_V(E_2) > 1$  or  $\frac{d_v}{b_v} \in (0, y_{4-}) \cup (y_{4+}, \infty)$  is true, then  $C = (az_4^* - \rho) \left(\frac{d_v b_j}{b_v d_j} - 1\right) + \frac{\alpha_j S}{d_j} < 0$*

*Proof.*

**Case 3.** If  $\frac{b_j d_v}{d_j b_v} - 1 < 0$  then

$$\begin{aligned}
az_4^* - \rho &> \frac{-\alpha_j S}{d_j \left( \frac{b_j d_v}{d_j b_v} - 1 \right)} \\
\iff az_4^* &> \rho + \frac{\alpha_j S}{d_j \left( 1 - \frac{b_j d_v}{d_j b_v} \right)} \\
\iff az_4^* &> \rho + \alpha_j j_4^* [1^{\text{st}} \text{ model}] \\
\iff \frac{az_4^*}{\rho + \alpha_j j_4^* [1^{\text{st}} \text{ model}]} &> 1 \\
\iff D_V(E_2) &> 1,
\end{aligned}$$

since  $j_4^* [1^{\text{st}} \text{ model}] = \frac{S}{d_j \left( 1 - \frac{b_j d_v}{d_j b_v} \right)}$ . Furthermore,  $j_4^* [1^{\text{st}} \text{ model}] = j_2^* [2^{\text{nd}} \text{ model}] = j_2^* [1^{\text{st}} \text{ model}]$ , and we have already seen in section 4.5 that when  $D_V(E_2) = 1$  that  $j_4^* [1^{\text{st}} \text{ model}] = j_2^* [1^{\text{st}} \text{ model}]$ .

**Case 4.** Let  $x = \frac{d_j}{b_j}$  and  $y = \frac{d_v}{b_v}$ . If  $\frac{b_j d_v}{d_j b_v} - 1 > 0$  then

$$\begin{aligned}
(az_4^* - \rho) \left( \frac{d_v b_j}{b_v d_j} - 1 \right) + \frac{\alpha_j S}{d_j} &< 0 \\
\left( aK \left( 1 - \frac{a}{r} y \right) - \rho \right) \left( \frac{y}{x} - 1 \right) + \frac{\alpha_j S}{d_j} &< 0 \\
\iff \frac{a^2 K}{xr} y^2 + \left[ -\frac{aK}{x} - \frac{a^2 K}{r} + \frac{\rho}{x} \right] y + \left( -\frac{\alpha_j S}{d_j} - \rho + aK \right) &> 0
\end{aligned}$$

so

$$y_{4\pm} = \frac{1}{2} \left( \frac{aK}{x} + \frac{a^2 K}{r} - \frac{\rho}{x} \pm \sqrt{\left( -\frac{aK}{x} - \frac{a^2 K}{r} + \frac{\rho}{x} \right)^2 + 4 \frac{a^2 K}{xr} \left( \frac{\alpha_j S}{d_j} + \rho - aK \right)} \right). \quad (\text{C.18})$$

Therefore,  $C > 0$  when either  $D_V(E_2) > 1$  or  $\frac{d_v}{b_v} \in (0, y_{4-}) \cup (y_{4+}, \infty)$  is satisfied.

This means there is only one positive value for  $v_4^*$ .  $\square$

## BIOGRAPHICAL STATEMENT

Crystal Mackey was born and raised in northeast Ohio. She earned her Bachelor of Science degree in Mathematics with a minor in Chemistry from Youngstown State University in 2016. During her undergraduate career, Crystal participated in two Research Experiences for Undergraduates (REUs), where she was able to discover her love of mathematics, specifically mathematical epidemiology. She continued her education and started the PhD program at the University of Texas at Arlington (UTA) under the supervision of Christopher Kribs. During her graduate studies, Crystal was a co-author on a grant to invite high school students to UTA for a day to celebrate women in math.