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A MATHEMATICAL MODEL FOR FERAL CAT ECOLOGY
WITH APPLICATION TO DISEASE

by

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A dissertation submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy
in the Department of Mathematics
in the College of Sciences
at the University of Central Florida
Orlando, Florida

Fall Term
2016

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ABSTRACT

We formulate and analyze a mathematical model for feral cats living in an isolated colony. The model contains compartments for kittens, adult females and adult males. Kittens are born at a rate proportional to the population of adult females and mature at equal rates into adult females and adult males. Adults compete with each other in a manner analogous to Lotka-Volterra competition. This competition comes in four forms, classified by gender. Native house cats, and their effects are also considered, including additional competition and abandonment into the feral population. Control measures are also modeled in the form of per-capita removal rates. We compute the net reproduction number (R_0) for the colony and consider its influence. In the absence of abandonment, if $R_0 > 1$, the population always persists at a positive equilibrium and if $R_0 \leq 1$, the population always tends toward local extinction. This work will be referred to as the *core model*.

The model is then expanded to include a set of colonies (*patches*) such as those in the core model (this time neglecting the effect of abandonment). Adult females and kittens remain in their native patch while adult males spend a fixed proportion of their time in each patch. Adult females experience competition from both the adult females living in the same patch as well as the visiting adult males. The proportion of adult males in patch j suffer competition from both adult females resident to that patch as well the proportion of adult

males also in the patch. We formulate a net reproduction number for each patch (a patch reproduction number) R_j . If $R_j > 1$ for at least one patch, then the collective population always persists at some nontrivial (but possibly semitrivial) steady state. We consider the number of possible steady states and their properties. This work will be referred to as the *patch model*.

Finally, the core model is expanded to include the introduction of the *feline leukemia virus*. Since this disease has many modes of transmission, each of which depends on the host's gender and life-stage, we regard this as a model disease. A basic reproduction number R_0 for the disease is defined and analyzed. Vaccination terms are included and their role in disease propagation is analyzed. Necessary and sufficient conditions are given under which the disease-free equilibrium is stable.

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CHAPTER 1

THE CORE MODEL

1.1 Introduction

Unowned, free-roaming cats (or *feral* cats as in [1]) have a well-known presence in cities around the world [2–4]. There is strong evidence in many instances of free-roaming cats causing great ecological damage [5–8]. A meta-analysis of the impacts of invasive mammalian predators considered a total of 738 threatened or extinct species and linked free-roaming cats to the endangered status of 430 different animals and the extinction of 63 [9]. For example, since their introduction in 1810 to the Australian territory of Macquarie Island, cats have been blamed for the extinction of a native species of parakeet (though rabbits and other animals may have also played a role) [10]. Similarly, since their introduction in 1888, free-roaming cats (along with black rats and yellow crazy ants) are believed to have driven into extinction four or five species of mammal on the Australian territory of Christmas Island [11]. Free-roaming cat predation on rodents may also place indirect pressure on other predators (e.g. raptors) [12]. In 2002, their presence was estimated to cost \$17 billion per year in the US alone [13].

In addition to the ecological impacts that feral cats may have, they also pose an epidemiological threat to local wildlife [14, 15], pet animals [1], and humans [1, 3, 16–19]. This issue is only exacerbated if these animals are permitted to live in dense colonies [20]. However, the removal of these animals is logistically difficult, work intensive and requires substantial investments of money. The general consensus among the public that cats are pet-animals complicates matters further, as the techniques which are quickest and cheapest are generally lethal (e.g., hunting, trapping [21], and poisoning [22]) and often regarded by the public as inhumane. Conversely, the techniques which are regarded as humane (e.g., trap-neuter-release or trap-adopt) are slower, more expensive and debate continues on their efficacy [13, 21, 23–26]. Even successful programs for their removal can have unintended side-effects, which further stresses the need to more deeply consider the complexities of this population [27]. A full understanding of the dynamics at work is critical to ensuring that the removal can be minimally invasive while still being effective.

When food and shelter are at extremely high abundance, the behavior of feral cats shifts from the solitary lifestyle of their wild counterparts to a colony-style one with communal litters and social grooming [28]. These colonies are typically matrilineal, being composed primarily of related adult females and their immature offspring [29]. The behavior of adults varies significantly by gender [28]. Adult females provide the entirety of the parental care. Interactions between females can be so mild that they will eat from the same source “nose-to-nose” and social grooming is not uncommon [28–30]. Litters birthed in close proximity may even become “communal,” with kittens nursing on any lactating female [29]. In these

types of colonies, adult females display very little in the way of territoriality with regard to other adult females (in particular related adult females), whereas their behavior towards adult males is more varied and even potentially hostile. Adult males provide no parental aid and their interactions with unreceptive females and kittens is minimal. On the other hand, their behavior towards each other typically ranges between neutral and hostile [28,29,31,32].

A complicating factor is free-roaming cats with owners (or *house cats*). This is a population of cats permitted outside, but which has access to shelter, food and veterinary care. This population may provide competition with the feral population and can potentially provide mates for receptive females if no others are present. These animals may also be abandoned by their caretakers and thereby enter the feral population [1, 28, 33].

Previous modeling efforts for feral cats are generally secondary to the modeling of the diseases affecting them [34–38]. In most of these works, the underlying ecology model is logistic in nature, with the exception of [36] in which exponential growth is considered. In general, there is no distinction between gender or life-stage, although in [39], cats are divided as social or asocial. A notable exception to this lack of population structure is the incredibly detailed model by McCarthy, who presents a 28 variable stochastic dynamical system to address the effectiveness of two methods of prophylaxis. The model presented there places cats into categories divided by gender and life-stage [40].

In this work, we consider a gender-based model to analyze real populations that are clumped and with high resource abundance [28], such as those described in [32, 41–44]. In Section 1.2 we state the assumptions of the model and the differential equations they imply

as well as state our main results, with particular focus on the existence, uniqueness and stability of equilibria. Section 1.3 interprets selected composite parameters and theorem biologically. Section 1.4 details several intermediate results. Section 1.5 describes the proofs of selected theorems and finally Section 1.6 summaries weaknesses of the model and potential directions for future work.

1.2 Mathematical model

1.2.1 Description

Consider a population of feral cats consisting of kittens ($i = 1$), adult females ($i = 2$), and adult males ($i = 3$). Let $x_i(t)$ be the density of feral cats of type $i = 1, 2, 3$ (or i -cats) at time $t \geq 0$. Assume the following:

- (A1) Feral adult females produce feral kittens at rate $b > 0$.
- (A2) The intrinsic death rate for feral i -cats is $d_i > 0$.
- (A3) Feral kittens mature into feral adults of each sex at per-capita rate $m > 0$.
- (A4) Feral i -cats are removed from the population at per-capita rate $s_i \geq 0$.
- (A5) The competitive effect of feral adult j -cats on feral adult i -cats is $c_{ij} \geq 0$ ($i, j = 2, 3$).
- (A6) The interaction coefficient $c_{ij} > 0$ when $i = j$ ($i, j = 2, 3$).

Assumption (A4) represents a combination of practical animal control measures such as impounding, adoption, and euthanasia. Assumptions (A5) and (A6) together imply that all adults interact negatively with members of their own sex (e.g., by competing for limited resources) and possibly with those of the opposite sex. The feral population also interacts with a constant population of house cats (i.e., cats that live with people and also spend some time outdoors). Assume

(A7) The density of house cats of type $i = 1, 2, 3$ (or house i -cats) is $n_i > 0$.

(A8) House i -cats are abandoned (and become instantly feral) at rate $\alpha_i \geq 0$.

(A9) The competitive effect of adult house j -cats on feral adult i -cats is $e_{ij} \geq 0$ ($i, j = 2, 3$).

In the Discussion section, we address some aspects concerning the biological realism of the assumptions above. Assumptions (A1) to (A9) produce an initial value problem

$$\begin{aligned}
 \dot{x}_1 &= bx_2 + \alpha_1 n_1 - x_1(d_1 + s_1 + 2m), & x_1(0) &\geq 0 \\
 \dot{x}_2 &= mx_1 + \alpha_2 n_2 - x_2(d_2 + s_2 + c_{22}x_2 + c_{23}x_3 + e_{22}n_2 + e_{23}n_3), & x_2(0) &\geq 0 \\
 \dot{x}_3 &= mx_1 + \alpha_3 n_3 - x_3(d_3 + s_3 + c_{32}x_2 + c_{33}x_3 + e_{32}n_2 + e_{33}n_3), & x_3(0) &\geq 0
 \end{aligned} \tag{A}$$

It is convenient to introduce notation representing the corporate abandonment rate and effective death rate for each category

$$a_i = \alpha_i n_i, \quad \delta_1 = d_1 + s_1, \quad \delta_2 = d_2 + s_2 + e_{22}n_2 + e_{23}n_3, \quad \text{and} \quad \delta_3 = d_3 + s_3 + e_{32}n_2 + e_{33}n_3 \tag{B}$$

Core model box-diagram

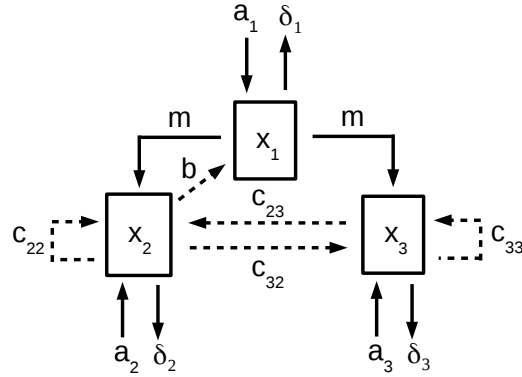


Figure 1.1: A box-diagram visualization of system (1.2.1).

(observe that $a_i \geq 0$ and $\delta_i > 0$ for $i = 1, 2, 3$). We then obtain a more concise initial value problem

$$\begin{aligned}
 \dot{x}_1 &= bx_2 + a_1 - x_1(\delta_1 + 2m), & x_1(0) &\geq 0 \\
 \dot{x}_2 &= mx_1 + a_2 - x_2(\delta_2 + c_{22}x_2 + c_{23}x_3), & x_2(0) &\geq 0 \\
 \dot{x}_3 &= mx_1 + a_3 - x_3(\delta_3 + c_{32}x_2 + c_{33}x_3), & x_3(0) &\geq 0
 \end{aligned}
 \tag{1.2.1}$$

See Table 1.1 for a description of all variables and parameters (and see Figure 1.1). Numerical simulations suggest that if house cats of type 1 and 2 cannot be abandoned ($a_1 = 0$ and $a_2 = 0$), then their feral counterparts can both become eradicated. See Figure 1.2 (a). As we will see, the outcome in this case is partly determined by the corporate rate at which house cats of type 3 are abandoned (a_3). However, if house cats of type 1 or 2 can be abandoned ($a_1 > 0$ or $a_2 > 0$), then both of their feral counterparts will always persist. See Figure 1.2 (b).

Table 1.1: Quantities associated with models (A) and (1.2.1)

Quantity	Description (type)	Units	Equation
t	time	time	(A)
x_i	density of feral cats (i)	cat	(A)
n_i	density of house cats (i)	cat	(A)
b	kitten birth rate	kitten \cdot adult ⁻¹ \cdot time ⁻¹	(A)
m	kitten maturation rate	adult \cdot kitten ⁻¹ \cdot time ⁻¹	(A)
d_i	intrinsic death rate (i)	time ⁻¹	(A)
s_i	control rate (i)	time ⁻¹	(A)
α_i	abandonment rate (i)	time ⁻¹	(A)
c_{ij}	competitive effect of ferals (j) on ferals (i)	adult ⁻¹ \cdot time ⁻¹	(A)
e_{ij}	competitive effect of house cats (j) on ferals (i)	adult ⁻¹ \cdot time ⁻¹	(A)
a_i	corporate abandonment rate (i)	cat \cdot time ⁻¹	(B)
δ_i	effective death rate (i)	time ⁻¹	(B)
\bar{x}_i	equilibrium density (i)	cat	(1.2.2)
\bar{z}_3	equilibrium density of adult males	cat	(1.2.3)
R_0	net reproduction number for adult females	none	(1.2.4)
k^*	threshold equilibrium density of adult males	cat	(1.2.5)
c_{32}^*	threshold competition coefficient	adult ⁻¹ \cdot time ⁻¹	(1.2.5)
a_3^*	threshold corporate male abandonment rate	cat \cdot time ⁻¹	(1.2.5)
ξ^*	threshold equilibrium density of adult males	cat	(1.2.6)
a_3^{**}	threshold corporate male abandonment rate	cat \cdot time ⁻¹	(1.2.6)

Numerical simulations of system (1.2.1)

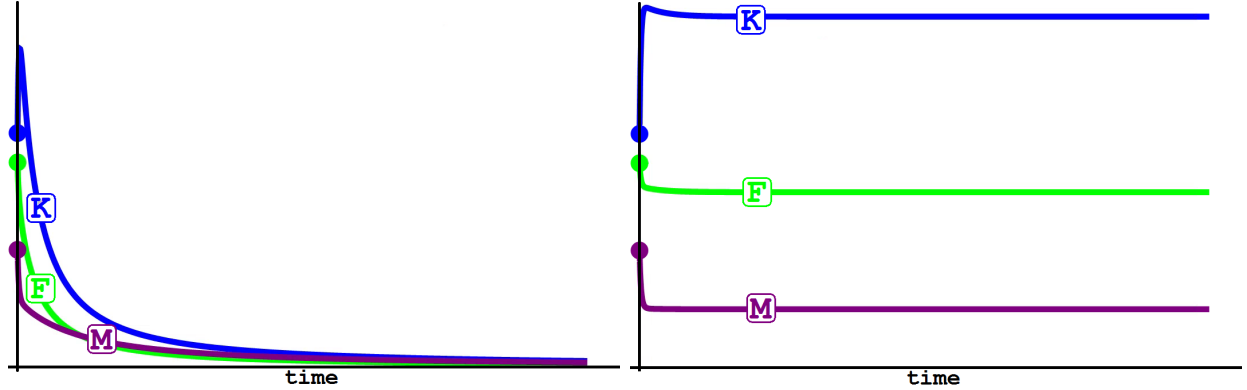


Figure 1.2: If house cats of type 1 and 2 cannot be abandoned ($a_1 = 0$ and $a_2 = 0$), then their feral counterparts can both become eradicated (left). However, if house cats of type 1 or 2 can be abandoned ($a_1 > 0$ or $a_2 > 0$), then both of their feral counterparts will always persist (right). The parameter values used here are: $m = 1$, $\delta_1 = 10$, $\delta_2 = 1$, $\delta_3 = 1$, $c_{22} = 0.25$, $c_{23} = 0.5$, $c_{32} = 0.9$, $c_{33} = 1.2$, $a_3 = 6.8$

1.2.2 Statement of main results

In this section we state the main properties of system (1.2.1). Biological interpretations of selected results can be found in Section 1.3 and the proofs of selected theorems can be found in Section 1.5. Let $\mathbb{R}^3 = \{(u_1, u_2, u_3) : u_1, u_2, u_3 \text{ are real numbers}\}$, $\mathbb{R}_+^3 = \{(u_1, u_2, u_3) : u_1 \geq 0, u_2 \geq 0, \text{ and } u_3 \geq 0\}$ (*the non-negative cone*), $\text{Int}(\mathbb{R}_+^3) = \{(u_1, u_2, u_3) : u_1 > 0, u_2 > 0, \text{ and } u_3 > 0\}$ (*the positive cone*), and $\partial\mathbb{R}_+^3 = \mathbb{R}_+^3 - \text{Int}(\mathbb{R}_+^3)$ (*the boundary*). Let $\mathbf{0} = (0, 0, 0)$. If a vector \mathbf{u} is in \mathbb{R}_+^3 then \mathbf{u} is *non-negative* and we write $\mathbf{u} \geq \mathbf{0}$. If a vector \mathbf{u} is in $\text{Int}(\mathbb{R}_+^3)$ then \mathbf{u} is *positive* and we write $\mathbf{u} \gg \mathbf{0}$. Also, for $\mathbf{u}, \mathbf{v} \in \mathbb{R}^3$ define $\mathbf{u} \leq \mathbf{v}$ when $\mathbf{v} - \mathbf{u} \in \mathbb{R}_+^3$, $\mathbf{u} < \mathbf{v}$ when $\mathbf{v} - \mathbf{u} \in \mathbb{R}_+^3 - \{\mathbf{0}\}$, and $\mathbf{u} \ll \mathbf{v}$ when $\mathbf{v} - \mathbf{u} \in \text{Int}(\mathbb{R}_+^3)$. Let $\mathbf{x}(t) = (x_1(t), x_2(t), x_3(t))$

denote a solution of (1.2.1). The system is *strongly persistent* if every solution $\mathbf{x}(t)$ satisfies $\liminf\{x_i(t) : t \geq 0\} > 0$ for $i = 1, 2, 3$. The first result concerns the situation in which $a_1 = 0$ and $a_2 = 0$.

Theorem 1.2.1. *Let $a_1 = 0$ and $a_2 = 0$.*

- (a) *A solution $\mathbf{x}(t)$ exists for all time. Moreover, it is unique, non-negative, and bounded.*
- (b) *The non-negative x_3 -axis is a forward invariant set.*
- (c) *If $\mathbf{x}(0)$ is on the boundary but not the x_3 -axis then $\mathbf{x}(t)$ immediately enters the positive cone.*
- (d) *If $\mathbf{x}(0)$ is positive then $\mathbf{x}(t)$ is positive for all time.*

The next result is analogous but concerns the situation in which $a_1 > 0$ or $a_2 > 0$.

Theorem 1.2.2. *Let $a_1 > 0$ or $a_2 > 0$.*

- (a) *A solution $\mathbf{x}(t)$ exists for all time. Moreover, it is unique, non-negative, and bounded.*
- (b) *If $\mathbf{x}(0)$ is on the boundary, then $\mathbf{x}(t)$ immediately enters the positive cone.*
- (c) *If $\mathbf{x}(0)$ is positive, then $\mathbf{x}(t)$ is positive for all time.*
- (d) *The system is strongly persistent.*

An *equilibrium* is a constant vector $\bar{\mathbf{x}} = (\bar{x}_1, \bar{x}_2, \bar{x}_3)$ in \mathbb{R}_+^3 that is a solution of (1.2.1).

It satisfies

$$\begin{aligned} b\bar{x}_2 + a_1 &= \bar{x}_1(\delta_1 + 2m) \\ m\bar{x}_1 + a_2 &= \bar{x}_2(\delta_2 + c_{22}\bar{x}_2 + c_{23}\bar{x}_3) \\ m\bar{x}_1 + a_3 &= \bar{x}_3(\delta_3 + c_{32}\bar{x}_2 + c_{33}\bar{x}_3) \end{aligned} \tag{1.2.2}$$

Let $\bar{\mathbf{z}} = (0, 0, \bar{z}_3)$ where \bar{z}_3 is the unique non-negative number such that

$$a_3 = \bar{z}_3(\delta_3 + c_{33}\bar{z}_3) \tag{1.2.3}$$

Notice that if $a_3 = 0$, then $\bar{\mathbf{z}} = \mathbf{0}$ and if $a_3 > 0$, then $\bar{\mathbf{z}} > \mathbf{0}$. Also, define

$$R_0 = \frac{bm}{(\delta_1 + 2m)\delta_2} \tag{1.2.4}$$

Theorem 1.2.3. *Let $a_1 = 0$ and $a_2 = 0$.*

- (a) $\bar{\mathbf{z}}$ is the unique boundary equilibrium.
- (b) If $R_0 \leq 1$, then $\bar{\mathbf{z}}$ is the only equilibrium.
- (c) If $R_0 > 1$ and $c_{23} = 0$, then there is one positive equilibrium $\bar{\mathbf{x}}$.

The next two results are extensions of Theorem 1.2.3 to the situation in which $R_0 > 1$ and $c_{23} > 0$ (see Figure 1.3). The first such result involves the composite parameters

$$k^* = \frac{(R_0 - 1)\delta_2}{c_{23}}, \quad c_{32}^* = \frac{2c_{22}c_{33}}{c_{23}} + \frac{c_{22}\delta_3 + c_{23}R_0\delta_2}{(R_0 - 1)\delta_2}, \quad \text{and} \quad a_3^* = k^*(\delta_3 + c_{33}k^*) \tag{1.2.5}$$

all of which are positive when $R_0 > 1$ and $c_{23} > 0$.

Theorem 1.2.4. *Let $a_1 = 0$, $a_2 = 0$, $R_0 > 1$, $c_{23} > 0$, and $c_{32} \leq c_{32}^*$.*

System (1.2) bifurcation diagram: $c_{32} - a_3$

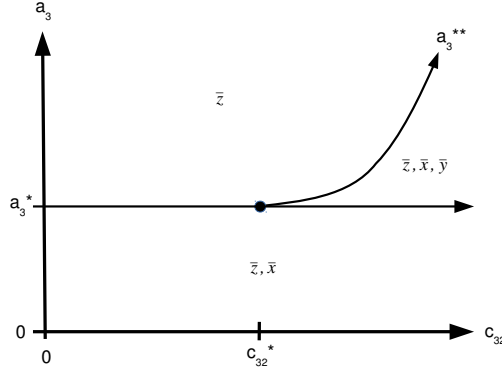


Figure 1.3: The equilibrium points that exist in the $c_{32} a_3$ -plane when $a_1 = a_2 = 0$, $R_0 > 1$, and $c_{23} > 0$.

- (a) If $a_3 < a_3^*$, then there is one positive equilibrium $\bar{\mathbf{x}} = (\bar{x}_1, \bar{x}_2, \bar{x}_3)$ and $\bar{x}_3 < k^*$.
- (b) If $a_3 \geq a_3^*$, then there is no positive equilibrium.

The next result complements the previous two and involves two additional composite parameters

$$\begin{aligned} \xi^* &= \frac{c_{22}\delta_3 + c_{23}R_0\delta_2 + c_{32}(R_0 - 1)\delta_2}{2(c_{23}c_{32} - c_{22}c_{33})} \\ a_3^{**} &= \frac{[c_{22}\delta_3 + c_{23}R_0\delta_2 + c_{32}(R_0 - 1)\delta_2]^2}{4c_{22}(c_{23}c_{32} - c_{22}c_{33})} - \frac{R_0\delta_2(R_0 - 1)\delta_2}{c_{22}} \end{aligned} \quad (1.2.6)$$

Theorem 1.2.5. Let $a_1 = 0$, $a_2 = 0$, $R_0 > 1$, $c_{23} > 0$, and $c_{32} > c_{32}^*$. Then $0 < \xi^* < k^*$ and $a_3^{**} > a_3^*$. Also:

- (a) If $a_3 \leq a_3^*$, then there is one positive equilibrium $\bar{\mathbf{x}} = (\bar{x}_1, \bar{x}_2, \bar{x}_3)$ and $\bar{x}_3 < \xi^*$.
- (b) If $a_3^* < a_3 < a_3^{**}$, then there are two positive equilibrium points $\bar{\mathbf{x}}$ and $\bar{\mathbf{y}}$ and they satisfy

(i) $\bar{\mathbf{x}} = (\bar{x}_1, \bar{x}_2, \bar{x}_3)$ and $\bar{\mathbf{y}} = (\bar{y}_1, \bar{y}_2, \bar{y}_3)$

(ii) $\bar{x}_3 < \xi^* < \bar{y}_3 < k^*$

(iii) $\frac{1}{2}(\bar{x}_3 + \bar{y}_3) = \xi^*$.

(c) If $a_3 = a_3^{**}$, then there is one positive equilibrium $\bar{\mathbf{x}} = (\bar{x}_1, \bar{x}_2, \bar{x}_3)$ and $\bar{x}_3 = \xi^*$.

(d) If $a_3 > a_3^{**}$, then there is no positive equilibrium.

The previous three theorems together imply that if $a_1 = 0$ and $a_2 = 0$, then there can be at most two positive equilibrium points. See Figure 1.4 (a). Next, we show that if $a_1 > 0$ or $a_2 > 0$, then there can be more than two positive equilibrium points. See Figure 1.4 (b).

Core model bifurcation diagram

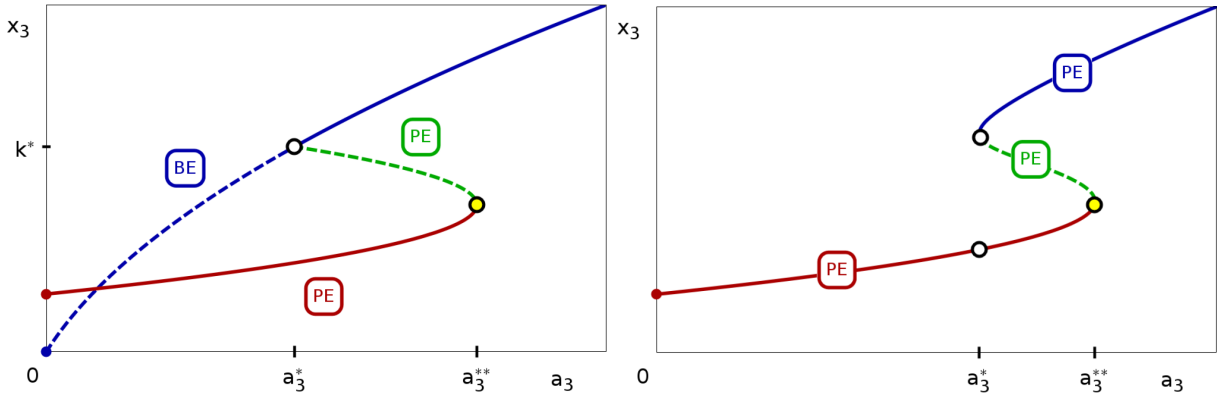


Figure 1.4: If $a_1 = 0$ and $a_2 = 0$, then there can be two positive equilibrium points (left). If $a_1 > 0$ or $a_2 > 0$, then there can be more than two positive equilibrium points (right). The parameter values used on the left are: $b = 20$, $m = 2$, $\delta_1 = 10$, $\delta_2 = 1$, $\delta_3 = 1$, $c_{22} = 1$, $c_{23} = 2$, $c_{32} = 10$, $c_{33} = 1$, $a_1 = 0$, and $a_2 = 0$. The same parameter values are used on the right but with $a_1 = 0.05$ and $a_2 = 0.002$.

Theorem 1.2.6. *Let $a_1 > 0$ or $a_2 > 0$.*

- (a) *There are no boundary equilibrium points.*
- (b) *A positive equilibrium \bar{x} exists.*
- (c) *If $c_{23} = 0$, then there is one positive equilibrium \bar{x} .*
- (d) *If $c_{23} > 0$, then there can be at most four positive equilibrium points.*

An equilibrium is *locally asymptotically stable* (LAS) if every solution that starts near it remains near it and also is attracted to it. When $a_1 = 0$ and $a_2 = 0$, then the boundary equilibrium is stable when there are an even number of positive equilibrium points and it is unstable otherwise.

Theorem 1.2.7. *Let $a_1 = 0$ and $a_2 = 0$.*

- (a) *If $R_0 < 1$, then \bar{z} is LAS.*
- (b) *If $R_0 > 1$ and $c_{23} = 0$, then \bar{z} is unstable.*
- (c) *If $R_0 > 1$, $c_{23} > 0$, and $a_3 < a_3^*$, then \bar{z} is unstable.*
- (d) *If $R_0 > 1$, $c_{23} > 0$, and $a_3 > a_3^*$, then \bar{z} is LAS.*

When $a_1 = 0$ and $a_2 = 0$, then a positive equilibrium is stable when it is unique. In cases where there are two positive equilibrium points, then only the one with a smaller \bar{x}_3 is stable.

Theorem 1.2.8. *Let $a_1 = 0$ and $a_2 = 0$.*

- (a) *If $R_0 > 1$ and $c_{23} = 0$, then \bar{x} is LAS.*

- (b) If $R_0 > 1$, $c_{23} > 0$, $c_{32} \leq c_{32}^*$, and $a_3 < a_3^*$, then $\bar{\mathbf{x}}$ is LAS.
- (c) If $R_0 > 1$, $c_{23} > 0$, $c_{32} > c_{32}^*$, and $a_3 \leq a_3^*$, then $\bar{\mathbf{x}}$ is LAS.
- (d) If $R_0 > 1$, $c_{23} > 0$, $c_{32} > c_{32}^*$, and $a_3^* < a_3 < a_3^{**}$, then $\bar{\mathbf{x}}$ is LAS and $\bar{\mathbf{y}}$ is unstable.

The next result is a partial analogue to Theorems 1.2.7 and 1.2.8 but concerns the situation in which $a_1 > 0$ or $a_2 > 0$. It involves the composite parameter

$$c_{32}^{**} = \frac{2c_{22}c_{33}}{c_{23}} \quad (1.2.7)$$

Theorem 1.2.9. *Let $a_1 > 0$ or $a_2 > 0$.*

- (a) If $c_{23} = 0$, then $\bar{\mathbf{x}}$ is LAS.
- (b) If $c_{23} > 0$ and $c_{32} \leq c_{32}^{**}$, then $\bar{\mathbf{x}}$ is LAS.
- (c) If $c_{23} > 0$, $c_{32} > c_{32}^{**}$, and $a_3 = 0$ (or a_3 is sufficiently small), then $\bar{\mathbf{x}}$ is LAS.

System (1.2.1) is *point dissipative* if there exists a bounded set in \mathbb{R}_+^3 which every solution must eventually enter and remain inside thereafter. An equilibrium is *globally attracting* (GA) if it attracts all solutions. If a global attractor is LAS then it is *globally asymptotically stable* (GAS). Define the composite parameter

$$a_3^\circ = (R_0 - 1)\delta_2 \left[\frac{1}{c_{23}} \left\{ \delta_3 + \frac{c_{33}(R_0 - 1)\delta_2}{c_{23}} \right\} - \frac{R_0\delta_2}{c_{22}} \right] \quad (1.2.8)$$

Notice that when $R_0 > 1$, then a_3° can be of any sign.

Theorem 1.2.10. *Let $a_1 = 0$ and $a_2 = 0$.*

- (a) *The system is point dissipative.*
- (b) *The basin of attraction for $\bar{\mathbf{z}}$ includes the non-negative x_3 -axis.*
- (c) *If $R_0 \leq 1$, then $\bar{\mathbf{z}}$ is GA (if $R_0 < 1$, then $\bar{\mathbf{z}}$ is GAS).*
- (d) *If $R_0 > 1$ and $c_{23} = 0$, then $\bar{\mathbf{x}}$ is GAS relative to \mathbb{R}_+^3 minus the non-negative x_3 -axis.*
- (e) *If $R_0 > 1$, $c_{23} > 0$, $c_{32} \leq \frac{1}{2}c_{32}^{**}$, and $a_3 < a_3^\circ$, then $\bar{\mathbf{x}}$ is GAS relative to \mathbb{R}_+^3 minus the x_3 -axis.*

Theorem 1.2.10 does not address all parameter combinations in which $R_0 > 1$, $c_{23} > 0$, and $c_{32} \geq 0$. The final result concerns the situation in which $a_1 > 0$ and $a_2 > 0$.

Theorem 1.2.11. *Let $a_1 > 0$ or $a_2 > 0$.*

- (a) *The system is point dissipative.*
- (b) *If $c_{23} = 0$, then $\bar{\mathbf{x}}$ is GAS.*

Let $\mathbf{m} = (0, 1, 1)$ and consider the Jacobian matrix

$$J(\mathbf{x}) = \begin{bmatrix} -\delta_1 - 2m & b & 0 \\ m & -\delta_2 - 2c_{22}\bar{x}_2 - c_{23}\bar{x}_3 & -c_{23}\bar{x}_2 \\ m & -c_{32}\bar{x}_3 & -\delta_3 - c_{32}\bar{x}_2 - 2c_{33}\bar{x}_3 \end{bmatrix}$$

If we multiply the entries (i, j) of $J(\mathbf{x})$ by $(-1)^{m_i+m_j}$, then we obtain a non-positive matrix. It follows then that system (1.2.1) is competitive with respect to the cone $K = \{(u_1, u_2, u_3) : u_1 \geq 0, u_2 \leq 0, u_3 \leq 0\}$ [45]. For $\mathbf{u}, \mathbf{v} \in \mathbb{R}^3$ define $\mathbf{u} \leq_K \mathbf{v}$ when $\mathbf{v} - \mathbf{u} \in K$ and $\mathbf{u} \ll_K \mathbf{v}$ when $\mathbf{v} - \mathbf{u} \in \text{Int}(K)$. Next, let $A = \text{diag}(1, -1, -1)$. Then A is an order isomorphism: $\mathbf{u} \leq_K \mathbf{v}$ if

and only if $A\mathbf{u} \leq A\mathbf{v}$. Furthermore, if we write system (1.2.1) as $\dot{\mathbf{x}} = f(\mathbf{x})$ and let $\mathbf{y} = A\mathbf{x}$, then $\dot{\mathbf{y}} = A\dot{\mathbf{x}} = Af(\mathbf{x}) = Af(A\mathbf{y}) = g(\mathbf{y})$. The result above implies that the system $\dot{\mathbf{y}} = g(\mathbf{y})$ is competitive with respect to the positive cone. Some additional consequences include (i) a (compact) limit set cannot contain two points ordered by \ll_K and (ii) a (compact) limit set that does not contain $\bar{\mathbf{x}}$ is a periodic orbit (see Theorems 3.2 and Theorem 4.1 in Chapter 3 of [45]).

1.3 Biological interpretation of results

Here we interpret the results of the previous section biologically.

1.3.1 Net reproduction number

A feral population that includes some abandonment always persists. In view of the previous results, we say that a feral population is *sustained by abandonment* if it cannot persist without some abandonment ($R_0 \leq 1$). On the other hand, if the population can persist even without abandonment ($R_0 > 1$), then the feral population is *self-sustaining*. Let us now approximate the net reproduction number (or replacement rate) for feral adult females in a closed population (i.e., one in which feral cats interact with house cats but there is no actual abandonment). Define R'_0 to be the maximum number of first generation adult female offspring that an adult female can have in her lifetime. Consider now a population consisting

of only a small number of adult females whose population density at time t is $U(t)$. We will assume that, since the number of feral cats is small, competitive effects between feral cats are negligible. The initial population of females will produce kittens whose density at time t is $V(t)$. These kittens mature into adult females, whose cumulative density at time t is $W(t)$. We will show that $W(t) \rightarrow \overline{W}$ as $t \rightarrow \infty$ with $\overline{W} > 0$. Then, the replacement rate will be $R'_0 = \overline{W} \div U(0)$ [46, 47].

The initial value problem that interests us is

$$\begin{aligned}\dot{U} &= -\delta_2 U, & U(0) &= \epsilon \\ \dot{V} &= bU - (\delta_1 + 2m)V, & V(0) &= 0 \\ \dot{W} &= mV, & W(0) &= 0\end{aligned}$$

The system of differential equations is linear and triangular, and so it can be solved in a forward manner:

$$\begin{aligned}U(t) = \epsilon e^{-\delta_2 t} &\implies V(t) = \frac{b\epsilon}{\delta_1 + 2m - \delta_2} [e^{-\delta_2 t} - e^{-(\delta_1 + 2m)t}] \\ &\implies W(t) = \frac{bm\epsilon}{\delta_1 + 2m - \delta_2} \left[\frac{e^{-(\delta_1 + 2m)t}}{\delta_1 + 2m} - \frac{e^{-\delta_2 t}}{\delta_2} - \frac{1}{\delta_1 + 2m} + \frac{1}{\delta_2} \right]\end{aligned}$$

Hence

$$\lim_{t \rightarrow \infty} W(t) = \frac{bm\epsilon}{\delta_1 + 2m - \delta_2} \left[-\frac{1}{\delta_1 + 2m} + \frac{1}{\delta_2} \right] = \frac{bm\epsilon}{\delta_1 + 2m - \delta_2} \left[\frac{\delta_1 + 2m - \delta_2}{(\delta_1 + 2m)\delta_2} \right] = \frac{bm\epsilon}{(\delta_1 + 2m)\delta_2} = \overline{W}$$

We obtain, then, that

$$R'_0 = \frac{\overline{W}}{\epsilon} = \frac{bm}{(\delta_1 + 2m)\delta_2} = R_0$$

Written in terms of the primary parameters of the model, we have

$$R'_0 = R_0 = \frac{bm}{(d_1 + s_1 + 2m)(d_2 + s_2 + e_{22}n_2 + e_{23}n_3)}$$

The manner in which each model parameter influences the ability of a feral population to sustain itself is now clear. An increase in the kitten birth rate (b) or maturation rate (m) can transform a feral population that is sustained by abandonment to one that is self-sustaining itself. However, an increase in the kitten death rate (d_2), the kitten control rate (s_1), the adult female death rate (d_2), the adult female control rate (s_2), the density of adult house cats (n_2 and n_3), or the competitive effect of adult house cats on adult females (e_{22} and e_{23}) can transform a feral population from one that can sustain itself to one that can be sustained only by abandonment.

1.3.2 The expressions \bar{z}_3 and \bar{z}

The composite parameter \bar{z}_3 in (1.2.3) represents the density of feral adult males at the equilibrium (\bar{z}) where there are neither adult females nor kittens present. This density is zero when there is no abandonment ($a_1 = a_2 = a_3 = 0$) and positive when only adult males can be being abandoned ($a_1 = a_2 = 0, a_3 > 0$).

1.3.3 The expressions \bar{x} , \bar{y} and ξ^*

When an equilibrium exists such that all sub-populations are present, the equilibrium is denoted \bar{x} . If two such equilibria exists simultaneously, they are denoted as \bar{x} and \bar{y} . In

the case where two such equilibria exist, the average of the third component of each (which represents the density of adult males present) is ξ^* .

1.3.4 The composite parameter k^*

The composite parameter k^* represents a threshold value of the density of adult males. If the density of adult males is at or above this threshold, the competitive effect on adult females imposed by adult males is sufficient to prevent both adult females and kittens from coexisting. This can generally only be achieved if the abandonment adult males experience (a_3) is large and only in the absence of abandonment of adult females and kittens ($a_1 = a_2 = 0$).

1.3.5 Theorems 1.2.1 and 1.2.2

Theorems 1.2.1 and 1.2.2 confirm that no model population can become negative, or can experience an unending population explosion. Also, if the initial population is composed of only adult males, then the population will remain this way provided that there is no abandonment for adult females or kittens ($a_1 = a_2 = 0$). Finally, if there is abandonment of either adult females or kittens ($a_1 > 0$ or $a_2 > 0$), the population will always persist. This holds regardless of control efforts and so if a population is to be controlled, it is essential that house cats not be abandoned.

1.3.6 Theorem 1.2.3

Theorem 1.2.3 discusses types of possible equilibria when neither adult females nor kittens are being abandoned ($a_1 = a_2 = 0$). First, there is always a single boundary equilibrium ($\bar{\mathbf{z}}$), for which the densities of adult females and kittens are zero. This equilibrium, which is independent of the net reproduction number R_0 , has adult males when they experience abandonment ($a_3 > 0$) and no adult males otherwise ($a_3 = 0$). If the net reproduction number is small ($R_0 \leq 1$), then this is the only equilibrium. If the net reproduction number is large ($R_0 > 1$) and adult females do not experience competition from adult males ($c_{23} = 0$) then there is also a single positive equilibrium ($\bar{\mathbf{x}}$).

1.3.7 Theorems 1.2.4 and 1.2.5 and the composite parameters c_{32}^* , a_3^* , and a_3^{**}

Theorems 1.2.4 and 1.2.5 detail the influence of the composite parameters c_{32}^* , a_3^* , and a_3^{**} on the number and type of possible *positive equilibria*, that is, equilibria for which subpopulations are present. These theorems specifically address the case where neither adult females nor kittens are being abandoned ($a_1 = a_2 = 0$), the net reproduction number is large ($R_0 > 1$), and when adult females experience competition from adult males ($c_{23} > 0$).

When the competition adult males experience from adult females is small ($c_{32} \leq c_{32}^*$), then a positive equilibrium ($\bar{\mathbf{x}}$) exists when the competition adult males experience from adult females is small ($a_3 > a_3^*$) and none exist otherwise ($a_3 \leq a_3^*$). If instead the competition adult

males experience from adult females is large ($c_{32} > c_{23}^*$), then a positive equilibrium ($\bar{\mathbf{x}}$) exists if the abandonment adult males experience is small $a_3 \leq a_3^*$, none exists if it is too large and two equilibria ($\bar{\mathbf{x}}$ and $\bar{\mathbf{y}}$) exist if it takes on an intermediate value ($a_3^* < a_3 < a_3^{**}$).

1.3.8 Theorem 1.2.6

Theorem 1.2.6 states that when adult females or kittens are being abandoned ($a_1 > 0$ or $a_2 > 0$) the full feral cat population always persists. If females suffer no competition from males ($c_{23} = 0$) then there is always a single positive equilibrium ($\bar{\mathbf{x}}$). Otherwise there may be up to four possible positive equilibria.

1.3.9 Theorems 1.2.7 and the composite parameter a^{**}

Theorem 1.2.7 details stability of boundary equilibrium ($\bar{\mathbf{z}}$), which is the equilibria for which there are neither adult females nor kittens in the case where neither adult females and kittens can be abandoned ($a_1 = a_2 = 0$). The boundary equilibrium is always stable if the net reproduction number is too small ($R_0 \leq 1$). It is also stable if adult females experience competition from males ($c_{23} > 0$) and the abandonment of males is too large ($a_3 > a_3^*$). If the net reproduction number is large enough ($R_0 > 1$), then the boundary equilibrium will be unstable if either adult females experience no competition from adult males ($c_{23} = 0$) or

they do experience such competition ($c_{23} > 0$) but the abandonment of adult males is not too severe ($a_3 < a_3^*$).

1.3.10 Theorems 1.2.8

Theorem 1.2.8 details the stability of equilibria for which all population densities are positive in the case where neither adult females nor kittens are being abandoned ($a_1 = a_2 = 0$). The description of in Section 1.3.7 details the number and type of equilibria exist. This theorem states that a positive equilibrium ($\bar{\mathbf{x}}$) will always be stable so long as it is the only positive equilibrium. In the case that there are multiple positive equilibria ($\bar{\mathbf{x}}$ and $\bar{\mathbf{y}}$), the equilibrium with fewer males will be stable while the other will be unstable.

1.3.11 Theorem 1.2.9 and the composite parameter c_{32}^{**}

Theorem 1.2.9 discusses the stability of the equilibria ($\bar{\mathbf{x}}$) for which all sub-populations are present in the cases where either adult females or kittens are being abandoned ($a_1 > 0$ or $a_2 > 0$). When adult females do not experience competition from adult males ($c_{23} = 0$), the equilibrium ($\bar{\mathbf{x}}$) is always stable. If adult females do experience competition from adult males ($c_{23} > 0$) then this equilibrium will still be stable if the competition adult males experience from adult females is not too large ($c_{32} \leq c_{32}^{**}$) or it is large ($c_{32} > c_{32}^{**}$) but the abandonment of adult males (a_3) is sufficiently small (see the proof of Theorem 1.2.9 for details).

1.3.12 Theorem 1.2.10 and the composite parameter a°

Theorem 1.2.10 details the asymptotic behavior of populations, that is how populations behave as time is allowed to grow very large. These results hold when neither adult females nor kittens are not being abandoned ($a_1 = a_2 = 0$). The theorem states that there is a number such that, eventually, all population densities will be less than this number. This theorem also states that if a population has no adult females and no kittens (who might mature into adult females), then the population will remain this way for all time. Moreover, this population will tend toward the equilibrium (\bar{z}) described in Section 1.3.6. Theorem 1.2.10 also states that any population (no matter the initial population) will tend toward this equilibrium (\bar{z}) if the net reproduction number is not large enough ($R_0 \leq 1$). When initial populations contain either adult females or kittens, the following can be said. If the net reproduction number is large enough ($R_0 > 1$) and adult females experience no competition from adult males ($c_{23} = 0$), then the population will tend toward the equilibrium (\bar{x}) described in Section 1.3.6. If instead adult females do experience competition from adult males but the competition adult males experience from adult females is not too great ($c_{32} < c_{32}^{**}$) and the rate of abandonment of adult males is not too large ($a_3 < a_3^\circ$), then populations will still tend toward this equilibrium (\bar{x}). An immediate biological result of this theorem is that if control rates for adult females (s_2) and kittens (s_1) can be raised so that the net reproduction number is small enough ($R_0 \leq 1$) then the population will tend toward extinction, so long as abandonment can be prevented.

1.3.13 Theorem 1.2.11

Theorem 1.2.11 details the asymptotic behavior of populations, that is how populations behave as time is allowed to grow very large. These results hold when neither adult females either kittens are being abandoned ($a_1 > 0$ or $a_2 > 0$). This theorem states that there exists a number such that, eventually, all populations densities will be less than this number. Moreover, it states that whenever adult females do not experience competition from adult males ($c_{23} = 0$) that the population will always tend toward the equilibrium ($\bar{\mathbf{x}}$) described in Section 1.3.8.

1.4 Intermediate results

The theorems are proved using results that we will state in the form of lemmas. Let $\mathbb{R}_+ = \{U : U \geq 0\}$.

Lemma 1.4.1. *Let $A \geq 0$, $B > 0$, and $C > 0$. Let*

$$\dot{U} = A - F(U), \quad U(T) \geq 0$$

with $F(U) = BU$ or $F(U) = U(B + CU)$. Let U^ be the non-negative solution of $A = F(U)$.*

- (a) *The solution $U(t)$ is unique, non-negative, bounded, and exists for $t \geq T$.*
- (b) *If $U(T) > 0$, then $U(t) > 0$ for $t \geq T$.*
- (c) *If $A = 0$, then $U^* = 0$ and if $A > 0$, then $U^* > 0$.*

(d) U^* is LAS and its basin of attraction includes \mathbb{R}_+ .

(e) If $-F(V) \leq \dot{V} \leq A - F(V)$ with $V(T) \geq 0$ and \dot{V} is a continuous function of V and t ,
then

(i) $V(t)$ exists for $t \geq T$

(ii) $0 \leq \liminf_{t \rightarrow \infty} V(t) \leq \limsup_{t \rightarrow \infty} V(t) \leq U^*$.

(f) If $\dot{V} \leq -F(V)$ with $V(T) \geq 0$ and $V(t)$ exists for $t \geq T$, then $\limsup_{t \rightarrow \infty} V(t) \leq 0$.

(g) If $\dot{V} \geq A - F(V)$ with $V(T) \geq 0$ and $V(t)$ exists for $t \geq T$, then $\liminf_{t \rightarrow \infty} V(t) \geq U^*$.

Proof. Parts (a) to (d) follow immediately from the graph of $G(U) = A - F(U)$ as a function of U . Observe that $G(U)$ describes either a line with negative slope or a concave downward parabola. In either case, if $A = 0$, then $F(0) = 0$ and $F(U) < 0$ for $U > 0$ and if $A > 0$, then there exists $U^* > 0$ such that $F(U) > 0$ for $0 \leq U < U^*$, $F(U^*) = 0$, and $F(U) < 0$ for $U > U^*$. We now prove part (e). Let $-F(V) \leq \dot{V} \leq A - F(V)$ with $V(T) \geq 0$ and consider the comparison equations $\dot{U} = -F(U)$ with $U(T) = V(T)$ and $\dot{W} = A - F(W)$ with $W(T) = V(T)$. Then $U(t) \leq V(t) \leq W(t)$ so long as all three functions exist. The assumption that \dot{V} is a continuous function of V and t implies that $V(t)$ exists as long as it remains bounded. Recall from parts (c) and (d) that $U(t) \rightarrow 0$ as $t \rightarrow \infty$ and $W(t) \rightarrow U^*$ as $t \rightarrow \infty$ where $U^* \geq 0$. Therefore, $U(t)$ and $W(t)$ are bounded. It follows that $V(t)$ is also bounded, it exists for $t \geq T$, and that $0 \leq \liminf_{t \rightarrow \infty} V(t) \leq \limsup_{t \rightarrow \infty} V(t) \leq U^*$. Parts (f) and (g) are proved in a similar manner. □

Let $\mathbb{R}^2 = \{(U, V) : U, V \text{ are real numbers}\}$, $\mathbb{R}_+^2 = \{(U, V) : U \geq 0 \text{ and } V \geq 0\}$, $\text{Int}(\mathbb{R}_+^2) = \{(U, V) : U > 0 \text{ and } V > 0\}$, and $\partial\mathbb{R}_+^2 = \mathbb{R}_+^2 - \text{Int}(\mathbb{R}_+^2)$. Let $\mathbf{0} = (0, 0)$. If a vector \mathbf{u} is in \mathbb{R}_+^2 , then \mathbf{u} is *non-negative* and we write $\mathbf{u} \geq \mathbf{0}$. If a vector \mathbf{u} is in $\text{Int}(\mathbb{R}_+^2)$, then \mathbf{u} is *positive* and we write $\mathbf{u} \gg \mathbf{0}$. Also, for $\mathbf{u}, \mathbf{v} \in \mathbb{R}^2$ define $\mathbf{u} \leq \mathbf{v}$ when $\mathbf{v} - \mathbf{u} \in \mathbb{R}_+^2$, $\mathbf{u} < \mathbf{v}$ when $\mathbf{v} - \mathbf{u} \in \mathbb{R}_+^2 - \{\mathbf{0}\}$, and $\mathbf{u} \ll \mathbf{v}$ when $\mathbf{v} - \mathbf{u} \in \text{Int}(\mathbb{R}_+^2)$.

Lemma 1.4.2. *Let*

$$\dot{U} = -U(\delta_1 + 2m), \quad U(0) \geq 0$$

$$\dot{V} = -V(\delta_2 + c_{22}V), \quad V(0) \geq 0$$

- (a) *The solution $(U(t), V(t))$ is unique, non-negative, bounded, and exists for all time.*
- (b) *The origin is an equilibrium.*
- (c) *The positive U -axis and positive V -axis are forward invariant sets.*
- (d) *If $(U(0), V(0))$ is positive, then $(U(t), V(t))$ is positive for all time.*
- (e) *The origin is LAS and its basin of attraction includes \mathbb{R}_+^2 .*

Proof. The fact that the origin is an equilibrium is obvious. The equation for U is one that is described by Lemma 1.4.1, and so $U(t)$ is unique, non-negative, bounded, and exists for all time. Also, if $U(0) = 0$, then $U(t) = 0$ for $t \geq 0$, and if $U(0) > 0$ then $U(t) > 0$ for $t > 0$ with $U(t) \rightarrow 0$ as $t \rightarrow \infty$. The same comments hold for $V(t)$. Parts (c), (d), and (e) all follow immediately from these remarks. □

Lemma 1.4.3. *Let*

$$\begin{aligned} \dot{U} &= bV - U(\delta_1 + 2m), & U(0) &\geq 0 \\ \dot{V} &= mU - V(\delta_2 + c_{22}V), & V(0) &\geq 0 \end{aligned} \tag{1.4.1}$$

- (a) *The solution $(U(t), V(t))$ is unique, non-negative, bounded, and exists for all time.*
- (b) *The origin is an equilibrium.*
- (c) *If $(U(0), V(0))$ is on $\partial\mathbb{R}_+^2 - \{\mathbf{0}\}$, then $(U(t), V(t))$ immediately enters $\text{Int}(\mathbb{R}_+^2)$.*
- (d) *If $(U(0), V(0))$ is positive, then $(U(t), V(t))$ is positive for all time.*
- (e) *If $R_0 < 1$, then the origin is LAS and its basin of attraction includes \mathbb{R}_+^2 .*
- (f) *If $R_0 > 1$, then*
 - (i) *There is a second equilibrium $P(U^*, V^*)$ and it is positive*
 - (ii) *U^* and V^* satisfy $R_0\delta_2V^* = mU^*$ and $R_0\delta_2 = \delta_2 + c_{22}V^*$*
 - (iii) *$P(U^*, V^*)$ is LAS and its basin of attraction includes $\mathbb{R}_+^2 - \{\mathbf{0}\}$.*

Proof. The right side of system (1.4.1) is a continuously differentiable function of U and V . Therefore, a local solution exists starting from anywhere in \mathbb{R}_+^2 and is unique so long as it exists. Also, it is clear that the origin is an equilibrium. We now show that every solution that starts on $\partial\mathbb{R}_+^2 - \{\mathbf{0}\}$ immediately enters $\text{Int}(\mathbb{R}_+^2)$. It is clear from (1.4.1) that if $U(0) = 0$ and $V(0) > 0$, then $\dot{U}(0) = bV(0) > 0$. Thus, $U(t) > 0$ for small $t > 0$. Next, if $U(0) > 0$ and $V(0) = 0$, then $\dot{V}(0) = mU(0) > 0$. Hence, $V(t) > 0$ for small $t > 0$. It follows that if $(U(0), V(0))$ is on $\partial\mathbb{R}_+^2 - \{\mathbf{0}\}$, then $(U(t), V(t))$ immediately enters $\text{Int}(\mathbb{R}_+^2)$. Also, we

obtain that if $(U(0), V(0))$ is non-negative then $(U(t), V(t))$ remains non-negative so long as it exists.

System (1.4.1) forms a planar strictly cooperative system ($\partial\dot{U}/\partial V > 0$ and $\partial\dot{V}/\partial U > 0$) whose orbits either converge to an equilibrium or become unbounded [45]. It is useful to introduce the nullcline curves for U and V (in the UV -plane),

$$\gamma_1 = \{(U, V) : bV = U(\delta_1 + 2m)\} \quad (\text{along which } \dot{U} = 0)$$

$$\gamma_2 = \{(U, V) : mU = V(\delta_2 + c_{22}V)\} \quad (\text{along which } \dot{V} = 0)$$

The line γ_1 and the parabolic curve γ_2 both pass through the origin and are increasing functions of U . Suppose first that $R_0 \leq 1$. Equation (1.2.4) implies that the slope of γ_1 ($\frac{\delta_1 + 2m}{b}$) is no less than the slope of γ_2 at the origin ($\frac{m}{\delta_2}$). Therefore, the origin is the only point of intersection for γ_1 and γ_2 . In general, $\dot{U} > 0$ to the left of γ_1 , $\dot{U} = 0$ along γ_1 , and $\dot{U} < 0$ to the right of γ_1 . Also, $\dot{V} < 0$ to the left of γ_2 , $\dot{V} = 0$ along γ_2 , and $\dot{V} > 0$ to the right of γ_2 . The corresponding vector field configuration appears in Figure 1.5 (a). The figure suggests that any trajectory $(U(t), V(t))$ that starts in \mathbb{R}_+^2 is bounded and, based on the remarks above, approaches the origin. Toward this end, consider the candidate Lyapunov function

$$E(U, V) = \frac{1}{2}mU^2 + \frac{1}{2}bV^2$$

It is clear that $E \geq 0$ on \mathbb{R}_+^2 and that $E = 0$ if and only if $(U, V) = (0, 0)$ (E is positive definite). Also, notice that $E(U, V) \rightarrow \infty$ whenever $U \rightarrow \infty$ or $V \rightarrow \infty$ (E is radially unbounded). Next,

we calculate

$$\begin{aligned}
\dot{E} &= mU \cdot \dot{U} + bV \cdot \dot{V} \\
&= mU[bV - U(\delta_1 + 2m)] + bV[mU - V(\delta_2 + c_{22}V)] \\
&= -m(\delta_1 + 2m)U^2 + 2bmUV - b\delta_2V^2 - bc_{22}V^3 \\
&= -[\sqrt{m(\delta_1 + 2m)}U - \sqrt{b\delta_2}V]^2 - 2\sqrt{bm}[\sqrt{(\delta_1 + 2m)\delta_2} - \sqrt{bm}]UV - bc_{22}V^3 \\
&\leq -bc_{22}V^3
\end{aligned}$$

The final inequality follows from the assumption $R_0 \leq 1$ and (1.2.4) which together imply that $bm \leq (\delta_1 + 2m)\delta_2$. If $V > 0$, then $V^3 > 0$ which implies that $\dot{E} < 0$. If $V = 0$ and $U > 0$, then $\dot{E} = -m(\delta_1 + 2m)U^2 < 0$. Hence, $\dot{E} < 0$ on $\mathbb{R}_+^2 - \{\mathbf{0}\}$ (\dot{E} is negative definite). As E is a strict Lyapunov function, the origin is LAS and its basin of attraction includes \mathbb{R}_+^2 . As a consequence, every trajectory $(U(t), V(t))$ exists for all time. Now we show that if $(U(0), V(0))$ is positive, then $(U(t), V(t))$ remains positive for all time. Let $(U_*(t), V_*(t))$ be the system described in Lemma 1.4.2 with $U_*(t) = U(0) > 0$ and $V_*(t) = V(0) > 0$. According to Theorem B.1 in [48], we have that $U(t) \geq U_*(t)$ and $V(t) \geq V_*(t)$ for all time. As $U_*(t)$ and $V_*(t)$ are positive for all time, it follows that $U(t)$ and $V(t)$ are also positive for all time.

Suppose now that $R_0 > 1$. In this case, the slope of γ_1 ($\frac{\delta_1 + 2m}{b}$) is less than the slope of γ_2 at the origin ($\frac{m}{\delta_2}$). Therefore, γ_1 and γ_2 intersect at the origin and at a second point $P(U^*, V^*)$ in $\text{Int}(\mathbb{R}_+^2)$. Again, $\dot{U} > 0$ to the left of γ_1 , $\dot{U} = 0$ along γ_1 , and $\dot{U} < 0$ to the right of γ_1 . Also, $\dot{V} < 0$ to the left of γ_2 , $\dot{V} = 0$ along γ_2 , and $\dot{V} > 0$ to the right

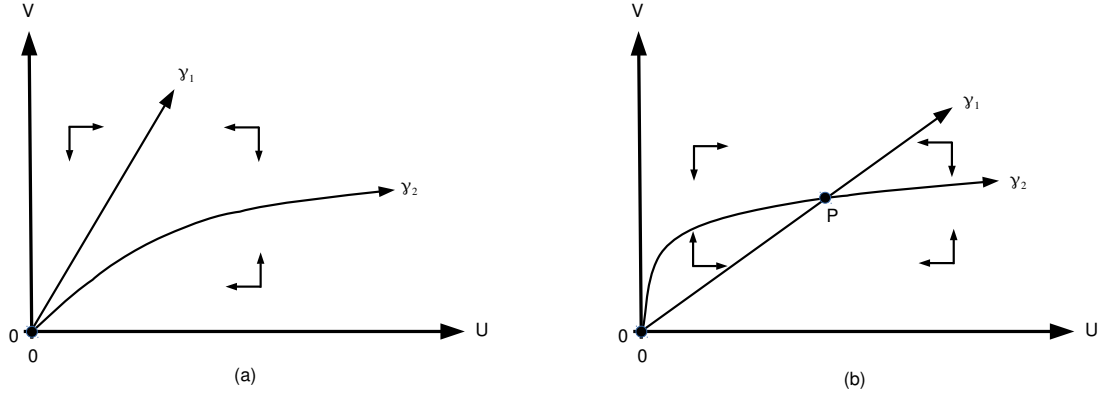


Figure 1.5: Vector field for U and V in the proof of Lemma 1.4.3 when (a) $R_0 \leq 1$ and (b) $R_0 > 1$.

of γ_2 . The corresponding vector field configuration appears in Figure 1.5 (b). The figure suggests that any trajectory $(U(t), V(t))$ that starts in $\mathbb{R}_+^2 - \{\mathbf{0}\}$ is bounded and approaches P. The coordinates of P satisfy $bV^* = U^*(\delta_1 + 2m)$ and $mU^* = V^*(\delta_2 + c_{22}V^*)$. Equation (1.2.4) implies that $R_0\delta_2V^* = mU^*$ and $R_0\delta_2 = \delta_2 + c_{22}V^*$. Consider the candidate Lyapunov function

$$E(U, V) = \frac{1}{2}bm(V^*U - U^*V)^2 + \frac{1}{6}bc_{22}U^*V^*(2V + V^*)(V - V^*)^2$$

on the set $\Omega = \mathbb{R}_+^2 - \{\mathbf{0}\}$. It is clear that $E \geq 0$ on Ω and that $E = 0$ if and only if $(U, V) = (U^*, V^*)$. Also, $E(U, V) \rightarrow \infty$ whenever $U \rightarrow \infty$ or $V \rightarrow \infty$. Next, we calculate

$$\begin{aligned} \frac{\partial E}{\partial U} &= bm(V^*U - U^*V)V^* \\ &= m(bV^*U - bU^*V)V^* \\ &= m[(\delta_1 + 2m)U^*U - bU^*V]V^* \\ &= mU^*V^*[(\delta_1 + 2m)U - bV] \end{aligned}$$

$$\begin{aligned}
&= mU^*V^*(-\dot{U}) \\
\frac{\partial E}{\partial V} &= bm(V^*U - U^*V)(-U^*) + \frac{1}{3}bc_{22}U^*V^*(V - V^*)^2 + \frac{1}{3}bc_{22}U^*V^*(2V + V^*)(V - V^*) \\
&= bU^*[m(U^*V - V^*U) + \frac{1}{3}c_{22}V^*(V - V^*)^2 + \frac{1}{3}c_{22}V^*(2V + V^*)(V - V^*)] \\
&= bU^*[m(U^*V - V^*U) + c_{22}V^*V(V - V^*)] \\
&= bU^*[mU^*V - mV^*U + c_{22}V^*V^2 - c_{22}(V^*)^2V] \\
&= bU^*[V^*(\delta_2 + c_{22}V^*)V - mV^*U + c_{22}V^*V^2 - c_{22}(V^*)^2V] \\
&= bU^*V^*[V(\delta_2 + c_{22}V) - mU] \\
&= bU^*V^*(-\dot{V})
\end{aligned}$$

It follows that

$$\dot{E} = \frac{\partial E}{\partial U}\dot{U} + \frac{\partial E}{\partial V}\dot{V} = mU^*V^*(-\dot{U}^2) + bU^*V^*(-\dot{V}^2) = -U^*V^*(m\dot{U}^2 + b\dot{V}^2)$$

Thus, $\dot{E} < 0$ on $\Omega - \{(U^*, V^*)\}$. As E is a strict Lyapunov function on Ω , we conclude that $P(U^*, V^*)$ is LAS and that its basin of attraction includes Ω . This result also implies that every trajectory $(U(t), V(t))$ exists for all time. The argument that if $(U(0), V(0))$ is positive, then $(U(t), V(t))$ remains positive for all time is the same as when $R_0 \leq 1$. \square

Lemma 1.4.4. *Let*

$$\begin{aligned}
\dot{U} &= bV + a_1 - U(\delta_1 + 2m), & U(0) &\geq 0 \\
\dot{V} &= mU + a_2 - V(\delta_2 + c_{22}V), & V(0) &\geq 0
\end{aligned} \tag{1.4.2}$$

with $a_1 > 0$ or $a_2 > 0$.

(a) *The solution $(U(t), V(t))$ is unique, non-negative, bounded, and exists for all time.*

(b) If $(U(0), V(0))$ is on $\partial\mathbb{R}_+^2$, then $(U(t), V(t))$ immediately enters $\text{Int}(\mathbb{R}_+^2)$.

(c) If $(U(0), V(0))$ is positive, then $(U(t), V(t))$ is positive for all time.

(d) There is a unique equilibrium $P(U^*, V^*)$ and it is positive.

(e) U^* and V^* satisfy $bV^* + a_1 = U^*(\delta_1 + 2m)$ and $mU^* + a_2 = V^*(\delta_2 + c_{22}V^*)$.

(f) $P(U^*, V^*)$ is LAS and its basin of attraction includes \mathbb{R}_+^2 .

Proof. The right side of system (1.4.2) is a continuously differentiable function of U and V . Therefore, a local solution exists starting from anywhere in \mathbb{R}_+^2 and is unique so long as it exists. We now show that every solution that starts on $\partial\mathbb{R}_+^2$ immediately enters $\text{Int}(\mathbb{R}_+^2)$. Suppose first that $a_1 > 0$. It is clear from (1.4.2) that if $U(0) = 0$, then $\dot{U}(0) = bV(0) + a_1 > 0$. Thus, $U(t) > 0$ for small $t > 0$. Next, if $V(0) = 0$, then $\dot{V}(0) = mU(0) + a_2$. If $U(0) > 0$ or $a_2 > 0$, then $\dot{V}(0) > 0$ which implies that $V(t) > 0$ for small $t > 0$. However, if $U(0) = 0$ and $a_2 = 0$, then $\dot{V}(0) = 0$. In this case, $\ddot{V}(0) = m\dot{U}(0) > 0$. Here, we have used the fact that $V(0) = 0$ and $\dot{V}(0) = 0$. Again, we obtain that $V(t) > 0$ for small $t > 0$. Suppose now that $a_1 = 0$. Then $a_2 > 0$. If $V(0) = 0$, then $\dot{V}(0) = mU(0) + a_2 > 0$ and so $V(t) > 0$ for small $t > 0$. If $U(0) = 0$, then $\dot{U}(0) = bV(0)$. If $V(0) > 0$, then $\dot{U}(0) > 0$ and so $U(t) > 0$ for small $t > 0$. If $V(0) = 0$, then $\dot{U}(0) = 0$ and $\ddot{U}(0) = b\dot{V}(0) > 0$. Again, $U(t) > 0$ for small $t > 0$. Hence, in all cases, if $(U(0), V(0))$ is on $\partial\mathbb{R}_+^2$, then $(U(t), V(t))$ immediately enters $\text{Int}(\mathbb{R}_+^2)$. Also, it follows from these remarks that if $(U(0), V(0))$ is non-negative, then $(U(t), V(t))$ remains non-negative so long as it exists.

As was the case for system (1.4.1) in the proof of Lemma 1.4.3, system (1.4.2) forms a planar strictly cooperative system ($\partial\dot{U}/\partial V > 0$ and $\partial\dot{V}/\partial U > 0$) whose orbits either converge to an equilibrium or become unbounded. Consider the nullcline curves for U and V (in the UV -plane),

$$\gamma_1 = \{(U, V) : bV + a_1 = U(\delta_1 + 2m)\} \quad (\text{along which } \dot{U} = 0)$$

$$\gamma_2 = \{(U, V) : mU + a_2 = V(\delta_2 + c_{22}V)\} \quad (\text{along which } \dot{V} = 0)$$

The line γ_1 is an increasing function of U and has a non-negative U -intercept. The parabolic curve γ_2 is an increasing function of U and has one non-negative V -intercept. The assumption $a_1 > 0$ or $a_2 > 0$ implies that γ_1 and γ_2 cannot both pass through the origin. Therefore, γ_1 and γ_2 meet at a single point $P(U^*, V^*)$ in $\text{Int}(\mathbb{R}_+^2)$. In general, $\dot{U} > 0$ to the left of γ_1 , $\dot{U} = 0$ along γ_1 , and $\dot{U} < 0$ to the right of γ_1 . Also, $\dot{V} < 0$ to the left of γ_2 , $\dot{V} = 0$ along γ_2 , and $\dot{V} > 0$ to the right of γ_2 . The corresponding vector field configuration appears in Figure 1.6.

$U - V$ vector field

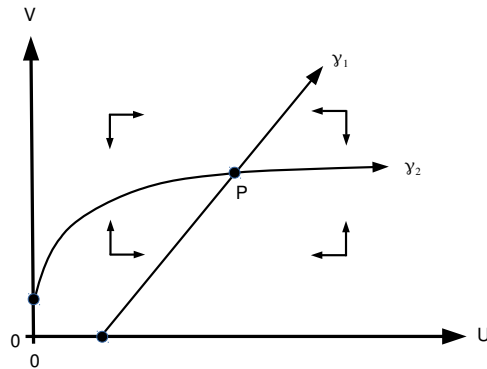


Figure 1.6: The vector field for U and V in the proof of Lemma 1.4.4.

The figure suggests that any trajectory $(U(t), V(t))$ that starts in \mathbb{R}_+^2 is bounded and, therefore, approaches the equilibrium point P. The coordinates of P satisfy $bV^* + a_1 = U^*(\delta_1 + 2m)$ and $mU^* + a_2 = V^*(\delta_2 + c_{22}V^*)$. Consider the candidate Lyapunov function

$$E(U, V) = \frac{1}{2}bm(V^*U - U^*V)^2 + \frac{1}{6}bc_{22}U^*V^*(2V + V^*)(V - V^*)^2 + \frac{1}{2}ma_1V^*(U - U^*)^2 + \frac{1}{2}ba_2U^*(V - V^*)^2$$

Observe that $E \geq 0$ on \mathbb{R}_+^2 and that $E = 0$ if and only if $(U, V) = (U^*, V^*)$. Also, notice that $E(U, V) \rightarrow \infty$ whenever $U \rightarrow \infty$ or $V \rightarrow \infty$. Next, we calculate

$$\begin{aligned} \frac{\partial E}{\partial U} &= bm(V^*U - U^*V)V^* + ma_1V^*(U - U^*) \\ &= mV^*[bV^*U - bU^*V + a_1U - a_1U^*] \\ &= mV^*[(bV^* + a_1)U - bU^*V - a_1U^*] \\ &= mV^*[U^*(\delta_1 + 2m)U - bU^*V - a_1U^*] \\ &= mU^*V^*[(\delta_1 + 2m)U - bV - a_1] \\ &= mU^*V^*(-\dot{U}) \end{aligned}$$

$$\begin{aligned} \frac{\partial E}{\partial V} &= bm(V^*U - U^*V)(-U^*) + \frac{1}{3}bc_{22}U^*V^*(V - V^*)^2 \\ &\quad + \frac{1}{3}bc_{22}U^*V^*(2V + V^*)(V - V^*) + ba_2U^*(V - V^*) \\ &= bU^*[mU^*V - mV^*U + \frac{1}{3}c_{22}V^*(V - V^*)^2 + \frac{1}{3}c_{22}V^*(2V + V^*)(V - V^*) + a_2V - a_2V^*] \\ &= bU^*[(mU^* + a_2)V - (mU + a_2)V^* + \frac{1}{3}c_{22}V^*\{(V - V^*)^2 + (2V + V^*)(V - V^*)\}] \\ &= bU^*[V^*(\delta_2 + c_{22}V^*)V - (mU + a_2)V^* + c_{22}V^*V(V - V^*)] \\ &= bU^*V^*[(\delta_2 + c_{22}V^*)V - mU - a_2 + c_{22}V^2 - c_{22}V^*V] \\ &= bU^*V^*[(\delta_2 + c_{22}V)V - mU - a_2] \end{aligned}$$

$$= bU^*V^*(-\dot{V})$$

It follows that

$$\dot{E} = \frac{\partial E}{\partial U}\dot{U} + \frac{\partial E}{\partial V}\dot{V} = mU^*V^*(-\dot{U}^2) + bU^*V^*(-\dot{V}^2) = -U^*V^*(m\dot{U}^2 + b\dot{V}^2)$$

Thus, $\dot{E} < 0$ on $\mathbb{R}_+^2 - \{(U^*, V^*)\}$. As E is a strict Lyapunov function on \mathbb{R}_+^2 , we conclude that $P(U^*, V^*)$ is LAS and that its basin of attraction includes \mathbb{R}_+^2 . Moreover, every trajectory $(U(t), V(t))$ exists for all time. It remains to show that if $(U(0), V(0))$ is positive, then $(U(t), V(t))$ remains positive for all time. Let $(U_*(t), V_*(t))$ be the system described in Lemma 1.4.2 with $U_*(t) = U(0) > 0$ and $V_*(t) = V(0) > 0$. According to Theorem B.1 in [48], we have that $U(t) \geq U_*(t)$ and $V(t) \geq V_*(t)$ for all time. As $U_*(t)$ and $V_*(t)$ are positive for all time, it follows that $U(t)$ and $V(t)$ are also positive for all time. \square

Lemma 1.4.5. *Let $X(t)$ and $Y(t)$ be functions with $\dot{X} = bY - X(\delta_1 + 2m)$, $X(T) \geq 0$, and $Y(T) \geq 0$. Let $U(t)$ and $V(t)$ be as in (1.4.1) in Lemma 1.4.3 with $U(T) = X(T)$ and $V(T) = Y(T)$.*

- (a) *If $\dot{Y} \leq mX - Y(\delta_2 + c_{22}Y)$ and $Y(t)$ exists for $t \geq T$, then $(X(t), Y(t)) \leq (U(t), V(t))$ for $t \geq T$.*
- (b) *If $\dot{Y} \geq mX - Y(\delta_2 + c_{22}Y)$ and $Y(t)$ exists for $t \geq T$, then $(X(t), Y(t)) \geq (U(t), V(t))$ for $t \geq T$.*

Proof. These results follow from Theorem B.1 in [48] together with the fact that system (1.4.1) is a cooperative system ($\partial\dot{U}/\partial V \geq 0$ and $\partial\dot{V}/\partial U \geq 0$). \square

1.5 Proofs of all theorems

1.5.1 Proof of Theorem 1.2.1

Let $a_1 = 0$ and $a_2 = 0$. The right side of system (1.2.1) is a continuously differentiable function of the state variables x_1 , x_2 , and x_3 . Therefore, a local solution exists starting from anywhere in \mathbb{R}_+^3 and is unique so long as it exists. Now, we show that the non-negative x_3 -axis is a forward invariant set. Let $\mathbf{x}(t)$ be the unique solution of (1.2.1) that starts at $(0, 0, x_3(0))$ with $x_3(0) \geq 0$ and consider the initial value problem $\dot{z} = a_3 - z(\delta_3 + c_{33}z)$ with $z(0) = x_3(0)$. Lemma 1.4.1 implies that $z(t)$ is non-negative and exists for all time. A direct substitution shows that $(0, 0, z(t))$ is a solution of (1.2.1). Therefore, $\mathbf{x}(t) = (0, 0, z(t))$ for $t \geq 0$ and the non-negative x_3 -axis is a forward invariant set.

Next, we show that if $\mathbf{x}(0)$ is on the boundary but not on the non-negative x_3 -axis, then $\mathbf{x}(t)$ immediately enters the positive cone. Suppose first that $x_1(0) = 0$. Then $x_2(0) > 0$ and $\dot{x}_1(0) = bx_2(0) > 0$. Thus, $x_1(t) > 0$ for small $t > 0$. Similarly, if $x_2(0) = 0$, then $x_1(0) > 0$ and $\dot{x}_2(0) = mx_1(0) > 0$. In this case, $x_2(t) > 0$ for small $t > 0$. Finally, if $x_3(0) = 0$, then $\dot{x}_3(0) = mx_1(0) + a_3$. If $x_1(0) > 0$ or $a_3 > 0$, then $\dot{x}_3(0) > 0$ which implies that $x_3(t) > 0$ for small $t > 0$. However, if $x_1(0) = 0$ and $a_3 = 0$, then $\dot{x}_3(0) = 0$ and $\ddot{x}_3(0) = m\dot{x}_1(0) > 0$. Here, we have used the fact that $x_3(0) = 0$, $\dot{x}_3(0) = 0$, and $\dot{x}_1(0) > 0$. We conclude that $x_3(t) > 0$ for small $t > 0$. In all cases, $\mathbf{x}(t)$ immediately enters the positive cone. The forward

invariance of the non-negative x_3 -axis implies that if $\mathbf{x}(0)$ is non-negative, then $\mathbf{x}(t)$ remains non-negative so long as it exists.

Next, we show that every solution $\mathbf{x}(t)$ is bounded and hence exists for all time.

Consider the comparison system from above

$$\begin{aligned} \dot{v}_1 &= bv_2 - v_1(\delta_1 + 2m), & v_1(0) &= x_1(0) \\ \dot{v}_2 &= mv_1 - v_2(\delta_2 + c_{22}v_2), & v_2(0) &= x_2(0) \\ \dot{v}_3 &= mv_1 + a_3 - v_3(\delta_3 + c_{33}v_3), & v_3(0) &= x_3(0) \end{aligned} \tag{1.5.1}$$

and note that it is cooperative ($\partial \dot{v}_i / \partial v_j \geq 0$ when $i \neq j$). Let $\mathbf{v}(t) = (v_1(t), v_2(t), v_3(t))$.

According to Theorem B.1 in [48], we have that $\mathbf{x}(t) \leq \mathbf{v}(t)$ so long as both functions exist.

We now bound $\mathbf{v}(t)$. Observe that the equations for v_1 and v_2 in (1.5.1) are described by

Lemma 1.4.3. Thus, $v_1(t)$ and $v_2(t)$ exist for all time and given any $(x_1(0), x_2(0))$ in \mathbb{R}_+^2 ,

there exists some $M > 0$ (depending on the initial condition) such that $0 \leq v_1(t) \leq M$ and

$0 \leq v_2(t) \leq M$ for $t \geq 0$. Next, observe that $-v_3(\delta_3 + c_{33}v_3) \leq \dot{v}_3 \leq mM + a_3 - v_3(\delta_3 + c_{33}v_3)$.

Also, \dot{v}_3 is a continuous function of v_1 (which is itself a continuous function of t) and v_3 .

According to Lemma 1.4.1, $v_3(t)$ exists for all time and is bounded. Based on the remarks

above, $\mathbf{v}(t)$ is bounded and exists for all time. Recall that $0 \leq \mathbf{x}(t) \leq \mathbf{v}(t)$ so long as $\mathbf{x}(t)$

exists. A non-negative and bounded solution to a system of differential equations whose

domain includes the non-negative cone must exist for all time. Thus, $\mathbf{x}(t)$ exists for all time,

and it is bounded. Note that the upper bounds for $v_1(t)$, $v_2(t)$, and $v_3(t)$ all depend on M

(which in turn depends on the initial condition).

It remains only to show that if $\mathbf{x}(0)$ is positive, then $\mathbf{x}(t)$ remains positive for all time. The argument above implies that there exists some $N > 0$ (depending on the initial condition) such that $0 \leq x_i(t) \leq N$ for $i = 1, 2, 3$ and $t \geq 0$. Consider the comparison system from below

$$\dot{u}_1 = -u_1(\delta_1 + 2m), \quad u_1(0) = x_1(0)$$

$$\dot{u}_2 = -u_2(\delta_2 + c_{22}u_2 + c_{23}N), \quad u_2(0) = x_2(0)$$

$$\dot{u}_3 = -u_3(\delta_3 + c_{32}N + c_{33}u_3), \quad u_3(0) = x_3(0)$$

whose equations completely decouple. Let $\mathbf{u}(t) = (u_1(t), u_2(t), u_3(t))$. According to Theorem B.1 in [48], we have that $\mathbf{x}(t) \geq \mathbf{u}(t)$ so long as $\mathbf{u}(t)$ exists. Lemma 1.4.1 implies that each $u_i(t) > 0$ for $t > 0$ with $u_i(t) \rightarrow 0$ as $t \rightarrow \infty$. As $\mathbf{u}(t)$ is positive for all time, it follows that $\mathbf{x}(t)$ is also positive for all time.

1.5.2 Proof of Theorem 1.2.2

Let $a_1 > 0$ or $a_2 > 0$. Again, the right side of system (1.2.1) is a continuously differentiable function of the state variables x_1 , x_2 , and x_3 . Therefore, a local solution exists starting from anywhere in \mathbb{R}_+^3 and is unique so long as it exists. We now show that every solution that starts on the boundary (of the non-negative cone) immediately enters the positive cone. Suppose first that $a_1 > 0$. It is clear from (1.2.1) that if $x_1(0) = 0$, then $\dot{x}_1(0) = bx_2(0) + a_1 > 0$. Thus, $x_1(t) > 0$ for small $t > 0$. Next, if $x_2(0) = 0$, then $\dot{x}_2(0) = mx_1(0) + a_2$. If $x_1(0) > 0$ or $a_2 > 0$, then $\dot{x}_2(0) > 0$ which implies that $x_2(t) > 0$ for small $t > 0$. However, if $x_1(0) = 0$

and $a_2 = 0$, then $\dot{x}_2(0) = 0$. In this case, $\ddot{x}_2(0) = m\dot{x}_1(0) > 0$. Here, we have used the fact that $\dot{x}_1(0) > 0$ when $x_1(0) = 0$. Again, we obtain that $x_2(t) > 0$ for small $t > 0$. Finally, if $x_3(0) = 0$, then $\dot{x}_3(0) = mx_1(0) + a_3$. A similar argument to the one just used shows that $x_3(t) > 0$ for small $t > 0$.

Suppose now that $a_1 = 0$. Then $a_2 > 0$. If $x_2(0) = 0$, then $\dot{x}_2(0) = mx_1(0) + a_2 > 0$ and so $x_2(t) > 0$ for small $t > 0$. If $x_1(0) = 0$, then $\dot{x}_1(0) = bx_2(0)$. If $x_2(0) > 0$, then $\dot{x}_1(0) > 0$ and so $x_1(t) > 0$ for small $t > 0$. If $x_2(0) = 0$, then $\dot{x}_1(0) = 0$ and $\ddot{x}_1(0) = b\dot{x}_2(0) > 0$. Here, we have used the fact that $\dot{x}_2(0) > 0$ when $x_2(0) = 0$. Again, $x_1(t) > 0$ for small $t > 0$. Finally, if $x_3(0) = 0$, then $\dot{x}_3(0) = mx_1(0) + a_3$. If $x_1(0) > 0$ or $a_3 > 0$, then $\dot{x}_3(0) > 0$ which implies that $x_3(t) > 0$ for small $t > 0$. However, if $x_1(0) = 0$ and $a_3 = 0$, then $\dot{x}_3(0) = 0$ and $\ddot{x}_3(0) = m\dot{x}_1(0)$. As argued above, $\dot{x}_1(0) \geq 0$. If $\dot{x}_1(0) > 0$, then $\ddot{x}_3(0) > 0$ and so $x_3(t) > 0$ for small $t > 0$. However, if $\dot{x}_1(0) = 0$, then $\ddot{x}_3(0) = 0$. In this case, $\dddot{x}_3(0) = m\ddot{x}_1(0) > 0$. Here, we have used the fact that $\ddot{x}_1(0) > 0$ when $x_1(0) = 0$ and $\dot{x}_1(0) = 0$. We conclude that $x_3(t) > 0$ for small $t > 0$. In all cases, if $\mathbf{x}(0)$ is on the boundary, then $\mathbf{x}(t)$ immediately enters the positive cone. Also, it follows from these remarks that if $\mathbf{x}(0)$ is non-negative, then $\mathbf{x}(t)$ remains non-negative so long as it exists.

The argument establishing that every solution $\mathbf{x}(t)$ is bounded and exists for all time is the same as the one presented in the proof of Theorem 1.2.1 but with two minor differences.

The first difference is that it involves a slightly different comparison system from above:

$$\begin{aligned}
\dot{v}_1 &= bv_2 + a_1 - v_1(\delta_1 + 2m), & v_1(0) &= x_1(0) \\
\dot{v}_2 &= mv_1 + a_2 - v_2(\delta_2 + c_{22}v_2), & v_2(0) &= x_2(0) \\
\dot{v}_3 &= mv_1 + a_3 - v_3(\delta_3 + c_{33}v_3), & v_3(0) &= x_3(0)
\end{aligned} \tag{1.5.2}$$

The second difference is that the equations for v_1 and v_2 in (1.5.2) are now described by Lemma 1.4.4 (previously there were described by Lemma 1.4.3). The argument showing that if $\mathbf{x}(0)$ is positive, then $\mathbf{x}(t)$ remains positive for all time remains unchanged.

We conclude by showing that system (1.2.1) is strongly persistent. There exists some $N > 0$ (depending on the initial condition) such that $0 \leq x_i(t) \leq N$ for $i = 1, 2, 3$ and $t \geq 0$. Suppose first that $a_1 > 0$. Observe that $\dot{x}_1 \geq a_1 - x_1(\delta_1 + 2m)$ for $t \geq 0$. According to Lemma 1.4.1, $0 < \bar{w}_1 \leq \liminf_{t \rightarrow \infty} x_1(t)$, where \bar{w}_1 is the unique positive solution of $a_1 = w_1(\delta_1 + 2m)$. Moreover, given $0 < w_1^* < \bar{w}_1$ there exists some $T > 0$ such that $x_1(t) \geq w_1^*$ for $t \geq T$. Next, observe that $\dot{x}_2 \geq mw_1^* + a_2 - x_2(\delta_2 + c_{22}x_2 + c_{23}N)$ for $t \geq T$. Lemma 1.4.1 implies that $\liminf_{t \rightarrow \infty} x_2(t) \geq \bar{w}_2 > 0$ where \bar{w}_2 is the unique positive solution of $mw_1^* + a_2 = w_2(\delta_2 + c_{22}w_2 + c_{23}N)$. A similar argument shows that $\liminf_{t \rightarrow \infty} x_3(t) \geq \bar{w}_3 > 0$ where \bar{w}_3 is the unique positive solution of $mw_1^* + a_3 = w_3(\delta_3 + c_{32}N + c_{33}w_3)$. That is, $\liminf_{t \rightarrow \infty} x_i(t) \geq \bar{w}_i > 0$ for $i = 1, 2, 3$. As \bar{w}_i depends on N for $i = 2, 3$ and N depends on the initial condition, it follows that system (1.2.1) is strongly persistent.

Suppose now that $a_1 = 0$ and $a_2 > 0$. Here, we observe that $\dot{x}_2 \geq a_2 - x_2(\delta_2 + c_{22}x_2 + c_{23}N)$ for $t \geq 0$. Lemma 1.4.1 implies that $\liminf_{t \rightarrow \infty} x_2(t) \geq \bar{y}_2 > 0$ where \bar{y}_2 is the unique positive solution of $a_2 = y_2(\delta_2 + c_{22}y_2 + c_{23}N)$. Moreover, given $0 < y_2^* < \bar{y}_2$ there exists some $T >$

0 such that $x_2(t) \geq y_2^*$ for $t \geq T$. Next, observe that $\dot{x}_1 \geq by_2^* - x_1(\delta_1 + 2m)$ for $t \geq T$. According to Lemma 1.4.1, $\liminf_{t \rightarrow \infty} x_1(t) \geq \bar{y}_1 > 0$ where \bar{y}_1 is the unique positive solution of $by_2^* = y_1(\delta_1 + 2m)$. Moreover, given $0 < y_1^* < \bar{y}_1$ there exists some $U > T$ such that $x_1(t) \geq y_1^*$ for $t \geq U$. Finally, observe that $\dot{x}_3 \geq my_1^* + a_3 - x_3(\delta_3 + c_{32}N + c_{33}x_3)$ for $t \geq U$. Lemma 1.4.1 implies that $\liminf_{t \rightarrow \infty} x_3(t) \geq \bar{y}_3 > 0$ where \bar{y}_3 is the unique positive solution of $my_1^* + a_3 = y_3(\delta_3 + c_{32}N + c_{33}y_3)$. Again, $\liminf_{t \rightarrow \infty} x_i(t) \geq \bar{y}_i > 0$ for $i = 1, 2, 3$ and system (1.2.1) is strongly persistent.

1.5.3 Proof of Theorems 1.2.3, 1.2.4, and 1.2.5

Let $a_1 = 0$ and $a_2 = 0$. Recall that a constant vector $\bar{\mathbf{x}} = (\bar{x}_1, \bar{x}_2, \bar{x}_3)$ in \mathbb{R}_+^3 is an equilibrium provided that it satisfies (1.2.2). In the case studied here, those equations become

$$b\bar{x}_2 = \bar{x}_1(\delta_1 + 2m), \quad m\bar{x}_1 = \bar{x}_2(\delta_2 + c_{22}\bar{x}_2 + c_{23}\bar{x}_3), \quad \text{and} \quad m\bar{x}_1 + a_3 = \bar{x}_3(\delta_3 + c_{32}\bar{x}_2 + c_{33}\bar{x}_3) \quad (1.5.3)$$

First, we establish that $\bar{\mathbf{z}} = (0, 0, \bar{z}_3)$ is the only boundary equilibrium, where \bar{z}_3 is the unique non-negative solution of (1.5.3). A direct substitution of $\bar{\mathbf{z}}$ into (1.2.2) demonstrates that $\bar{\mathbf{z}}$ is an equilibrium, and the uniqueness of \bar{z}_3 implies that $\bar{\mathbf{z}}$ is the only equilibrium on the x_3 -axis. For sake of contradiction, let $\bar{\mathbf{x}}$ be a second boundary equilibrium (different from $\bar{\mathbf{z}}$). Since $\bar{\mathbf{x}}$ cannot be on the x_3 -axis, it must be that $\bar{x}_1 > 0$ or $\bar{x}_2 > 0$. If $\bar{x}_1 = 0$, then (1.5.3) implies that $\bar{x}_2 = 0$, a contradiction. Similarly, if $\bar{x}_2 = 0$ then (1.5.3) implies that $\bar{x}_1 = 0$, again a contradiction. We conclude that $\bar{\mathbf{z}}$ is the only boundary equilibrium.

We now consider the existence (and possible uniqueness) of a positive equilibrium $\bar{\mathbf{x}} = (\bar{x}_1, \bar{x}_2, \bar{x}_3)$. Equations (1.2.4) and (1.5.3) together imply that

$$R_0 \delta_2 \bar{x}_2 = m \bar{x}_1, \quad R_0 \delta_2 = \delta_2 + c_{22} \bar{x}_2 + c_{23} \bar{x}_3, \quad \text{and} \quad R_0 \delta_2 \bar{x}_2 + a_3 = \bar{x}_3 (\delta_3 + c_{32} \bar{x}_2 + c_{33} \bar{x}_3) \quad (1.5.4)$$

The first two equations imply that \bar{x}_1 and \bar{x}_2 are uniquely determined by the expression $c_{23} \bar{x}_3$. Moreover, necessary and sufficient conditions for a positive equilibrium to exist are that

$$\bar{x}_3 > 0 \quad \text{and} \quad R_0 \delta_2 > \delta_2 + c_{23} \bar{x}_3 \quad (1.5.5)$$

If $R_0 \leq 1$, then the second condition in (1.5.5) cannot be met. In this case, $\bar{\mathbf{x}}$ does not exist.

Suppose now (and for the remainder of the argument) that $R_0 > 1$. If $c_{23} > 0$ then (1.2.5) implies that the necessary and sufficient conditions in (1.5.5) for a positive equilibrium to exist are equivalent to

$$0 < \bar{x}_3 < k^* \quad (1.5.6)$$

If $c_{23} = 0$, then the second condition in (1.5.5) is always met. If we make the convention that $k^* = \infty$ in this case, then (1.5.6) again forms the necessary and sufficient conditions for a positive equilibrium to exist. We seek now to discover exactly when (1.5.6) occurs. The second and third equations of (1.5.4) together imply that \bar{x}_3 must satisfy

$$R_0 \delta_2 \frac{1}{c_{22}} (R_0 \delta_2 - \delta_2 - c_{23} \bar{x}_3) + a_3 = \bar{x}_3 \left[\delta_3 + \frac{c_{32}}{c_{22}} (R_0 \delta_2 - \delta_2 - c_{23} \bar{x}_3) + c_{33} \bar{x}_3 \right]$$

Rearrangement produces a quadratic equation in \bar{x}_3

$$(c_{22} c_{33} - c_{23} c_{32}) \bar{x}_3^2 + [c_{22} \delta_3 + c_{23} R_0 \delta_2 + c_{32} (R_0 - 1) \delta_2] \bar{x}_3 - R_0 \delta_2 (R_0 - 1) \delta_2 = c_{22} a_3$$

Notice that the right side is a non-negative constant. Our aim is to find all solutions of

$$\Phi(\bar{x}_3) = c_{22}a_3 \quad \text{with} \quad 0 < \bar{x}_3 < k^* \quad (1.5.7)$$

where

$$\Phi(\xi) = (c_{22}c_{33} - c_{23}c_{32})\xi^2 + [c_{22}\delta_3 + c_{23}R_0\delta_2 + c_{32}(R_0 - 1)\delta_2]\xi - R_0\delta_2(R_0 - 1)\delta_2 \quad (1.5.8)$$

Observe from (1.2.4) and (1.5.8) that Φ does not depend on a_3 , and that the expressions $c_{22}\delta_3 + c_{23}R_0\delta_2 + c_{32}(R_0 - 1)\delta_2$ and $R_0\delta_2(R_0 - 1)\delta_2$ are both positive. Thus, $\Phi(0) < 0$ and $\Phi'(0) > 0$. If $c_{23} = 0$, then Φ is concave upward, which implies that (1.5.7) has a unique solution \bar{x}_3 (recall that in this case $k^* = \infty$). It follows, then, that a unique positive equilibrium \bar{x} exists. Suppose now (and for the remainder of the argument) that $c_{23} > 0$. Equations (1.2.5) and (1.5.8) imply that

$$\begin{aligned} \Phi(k^*) &= (c_{22}c_{33} - c_{23}c_{32})(k^*)^2 + [c_{22}\delta_3 + c_{23}R_0\delta_2 + c_{32}(R_0 - 1)\delta_2]k^* - R_0\delta_2(R_0 - 1)\delta_2 \\ &= (c_{22}c_{33} - c_{23}c_{32})(k^*)^2 + (c_{22}\delta_3 + c_{23}R_0\delta_2 + c_{23}c_{32}k^*)k^* - c_{23}R_0\delta_2k^* \\ &= c_{22}(\delta_3 + c_{33}k^*)k^* \\ &= c_{22}a_3^* \end{aligned}$$

If $c_{22}c_{33} \geq c_{23}c_{32}$ (i.e., $c_{32} \leq \frac{c_{22}c_{33}}{c_{23}}$), then Φ is concave upward (or possibly linear) and therefore increasing on $[0, k^*]$. Thus, if $a_3 < a_3^*$, then (1.5.7) has a unique solution and if $a_3 \geq a_3^*$, then it has no solution. The first inequality allows for a single positive equilibrium \bar{x} , and the second one does not. Suppose now (and for the remainder of the argument) that $c_{22}c_{33} < c_{23}c_{32}$ (i.e.,

$c_{32} > \frac{c_{22}c_{33}}{c_{23}}$). Then Φ is concave downward and attains its maximum at the positive number

$$\xi^* = \frac{c_{22}\delta_3 + c_{23}R_0\delta_2 + c_{32}(R_0 - 1)\delta_2}{2(c_{23}c_{32} - c_{22}c_{33})}$$

Observe from (1.2.5) that $c_{32}^* > \frac{c_{22}c_{33}}{c_{23}}$. If $c_{32} \leq c_{32}^*$, then

$$\begin{aligned} c_{32} &\leq \frac{2c_{22}c_{33}}{c_{23}} + \frac{c_{22}\delta_3 + c_{23}R_0\delta_2}{(R_0 - 1)\delta_2} \\ \implies c_{23}c_{32}(R_0 - 1)\delta_2 &\leq 2c_{22}c_{33}(R_0 - 1)\delta_2 + c_{23}(c_{22}\delta_3 + c_{23}R_0\delta_2) \\ \implies 2(c_{23}c_{32} - c_{22}c_{33})(R_0 - 1)\delta_2 &\leq c_{23}[c_{22}\delta_3 + c_{23}R_0\delta_2 + c_{32}(R_0 - 1)\delta_2] \\ \implies \frac{(R_0 - 1)\delta_2}{c_{23}} &\leq \frac{c_{22}\delta_3 + c_{23}R_0\delta_2 + c_{32}(R_0 - 1)\delta_2}{2(c_{23}c_{32} - c_{22}c_{33})} \\ \implies k^* &\leq \xi^* \end{aligned}$$

Again, Φ is increasing on $[0, k^*]$. As before, if $a_3 < a_3^*$, then (1.5.7) has a unique solution and if $a_3 > a_3^*$, then it has no solution. Again, the first inequality allows for a single positive equilibrium $\bar{\mathbf{x}}$, and the second one does not. The final case to consider is $c_{32} > c_{32}^*$. Reversing the inequalities in the argument above shows that $0 < \xi^* < k^*$. Recalling that Φ is a quadratic polynomial, its maximum value can be computed to be (using the vertex formula)

$$\Phi(\xi^*) = \frac{[c_{22}\delta_3 + c_{23}R_0\delta_2 + c_{32}(R_0 - 1)\delta_2]^2}{4(c_{23}c_{32} - c_{22}c_{33})} - R_0\delta_2(R_0 - 1)\delta_2 = c_{22}a_3^{**}$$

In the last step, we used (1.2.6). Recalling that $\Phi(k^*) = c_{22}a_3^*$, it must be that $a_3^{**} > a_3^*$. Based on the remarks above, if $a_3 \leq a_3^*$, then (1.5.7) has a unique solution, if $a_3^* < a_3 < a_3^{**}$, then it has two solutions (whose midpoint is ξ^*), if $a_3 = a_3^{**}$, then it has a unique solution, and if $a_3 > a_3^{**}$, then it has no solution. The first and third cases allow for a single positive equilibrium $\bar{\mathbf{x}}$, the second case produces two positive equilibrium points $\bar{\mathbf{x}} = (\bar{x}_1, \bar{x}_2, \bar{x}_3)$ and

$\bar{\mathbf{y}} = (\bar{y}_1, \bar{y}_2, \bar{y}_3)$ with $0 < \bar{x}_3 < \xi^* < \bar{y}_3 < k^*$, and the final case results in no positive equilibrium points.

1.5.4 Proof of Theorem 1.2.6

Let $a_1 > 0$ or $a_2 > 0$. Recall that a constant vector $\bar{\mathbf{x}} = (\bar{x}_1, \bar{x}_2, \bar{x}_3)$ in \mathbb{R}_+^3 is an equilibrium provided that it satisfies (1.2.2). First we establish that an equilibrium cannot reside on the boundary. Let $\bar{\mathbf{x}} = (\bar{x}_1, \bar{x}_2, \bar{x}_3)$ be any equilibrium, and suppose first that $a_1 > 0$. If $\bar{x}_1 = 0$, then $b\bar{x}_2 + a_1 = 0$, which is a contradiction. Therefore, $\bar{x}_1 > 0$. If $\bar{x}_2 = 0$, then $m\bar{x}_1 + a_2 = 0$ (a contradiction) and if $\bar{x}_3 = 0$, then $m\bar{x}_1 + a_3 = 0$ (also a contradiction). It follows that $\bar{\mathbf{x}}$ must be positive. Suppose now that $a_1 = 0$ and $a_2 > 0$. If $\bar{x}_2 = 0$, then $m\bar{x}_1 + a_2 = 0$, a contradiction. Thus, $\bar{x}_2 > 0$. Next, if $\bar{x}_1 = 0$ Then $b\bar{x}_2 = 0$, another contradiction. So $\bar{x}_1 > 0$. Finally, if $\bar{x}_3 = 0$, then $m\bar{x}_1 + a_3 = 0$ (a contradiction). Again, we conclude that $\bar{\mathbf{x}}$ must be positive. That is, there cannot be a boundary equilibrium.

We now establish the existence of at least one positive equilibrium $\bar{\mathbf{x}}$. The nullcline surfaces for system (1.2.1) are

$$\Gamma_1 = \{\mathbf{x} \in \mathbb{R}_+^3 : bx_2 + a_1 = x_1(\delta_1 + 2m)\} \quad (\text{along which } \dot{x}_1 = 0)$$

$$\Gamma_2 = \{\mathbf{x} \in \mathbb{R}_+^3 : mx_1 + a_2 = x_2(\delta_2 + c_{22}x_2 + c_{23}x_3)\} \quad (\text{along which } \dot{x}_2 = 0)$$

$$\Gamma_3 = \{\mathbf{x} \in \mathbb{R}_+^3 : mx_1 + a_3 = x_3(\delta_3 + c_{32}x_2 + c_{33}x_3)\} \quad (\text{along which } \dot{x}_3 = 0)$$

Notice that Γ_1 describes a plane. It is useful to let γ_1 and $\gamma_2(k)$ be the intersections, respectively, of Γ_1 and Γ_2 with the plane $x_3 = k$ for $k \geq 0$. The line γ_1 (which is independent

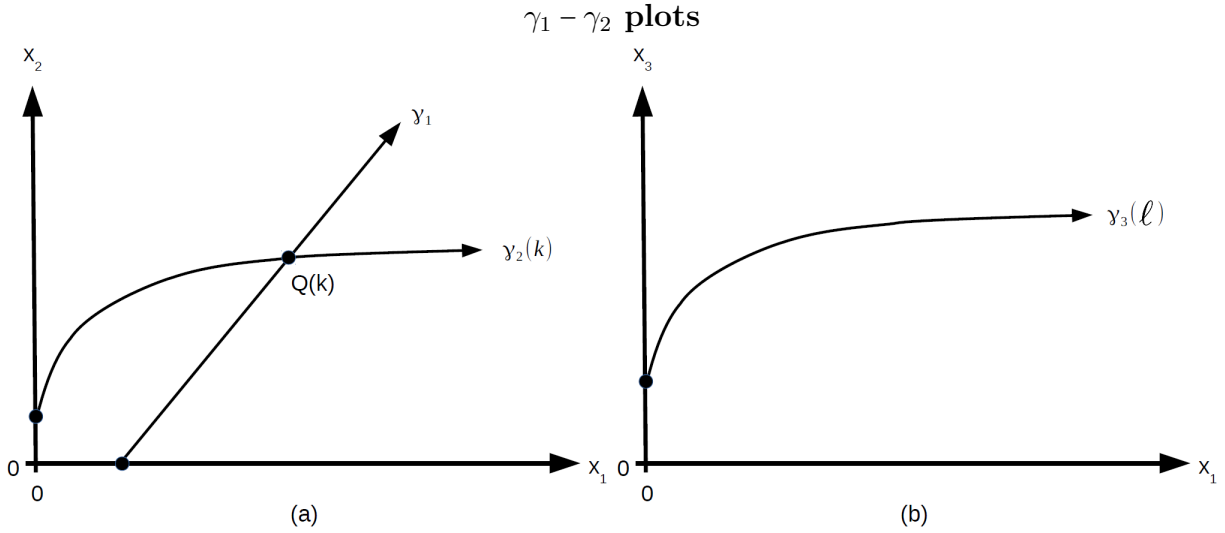


Figure 1.7: (a) The line γ_1 and the curve $\gamma_2(k)$ in the plane $x_3 = k$. (b) The curve $\gamma_3(\ell)$ in the plane $x_2 = \ell$.

of k) is an increasing function of x_1 and has a non-negative x_1 -intercept. The curve $\gamma_2(k)$, which satisfies

$$mx_1 + a_2 = x_2(\delta_2 + c_{22}x_2 + c_{23}k) \quad (1.5.9)$$

is described by a parabola that opens in the positive x_1 -direction and has a non-negative x_2 -intercept. The assumption $a_1 > 0$ or $a_2 > 0$ implies that γ_1 and $\gamma_2(k)$ cannot both pass through the origin. It follows that γ_1 and $\gamma_2(k)$ meet at a single point $Q(k)$ in $\text{Int}(\mathbb{R}_+^2)$ for each $k \geq 0$. See Figure 1.7 (a). Observe from (1.5.9) that, for a fixed value of $x_1 > 0$, an increase in k has no effect on x_2 when $c_{23} = 0$ and it results in a decrease in x_2 when $c_{23} > 0$. It follows that $Q(k)$ either remains fixed as k increases (when $c_{23} = 0$) or it moves “southwest” along γ_1 as k increases (when $c_{23} > 0$). Let Ω be the smallest rectangle in the x_1x_2 -plane whose diagonal includes $\{Q(k) : k \geq 0\}$. The related set $\{(Q(k), k) : k \geq 0\}$ defines

a continuous parametric curve $\mathbf{q}(k)$ residing on a subset of Γ_1 . Its tangent vector at every k has the form $(u_1, u_2, 1)$ with $u_1 \leq 0$ and $u_2 \leq 0$. We claim that the surface Γ_3 intersects $\mathbf{q}(k)$ at some $k > 0$. Let $\gamma_3(\ell)$ be the intersection of Γ_3 with the plane $x_2 = \ell$ for $\ell \geq 0$. The curve $\gamma_3(\ell)$, which satisfies

$$mx_1 + a_3 = x_3(\delta_3 + c_{32}\ell + c_{33}x_3)$$

is described by a parabola that opens in the positive x_1 -direction and has a non-negative x_3 -intercept. See Figure 1.7 (b). For a fixed value of $x_1 > 0$, an increase in ℓ has no effect on x_3 when $c_{32} = 0$ and it results in a decrease in x_3 when $c_{32} > 0$. The union of these parabolic curves $\gamma_3(\ell)$ forms the surface Γ_3 . The portion of the surface Γ_3 that overlies the compact set Ω attains its maximum in the x_3 -direction. However, the parametric curve $\mathbf{q}(k)$ is unbounded in the x_3 -direction. It follows from these geometric considerations that there exists at least one point of intersection between Γ_3 and $\mathbf{q}(k)$. This point occurs when $k > 0$ and corresponds to a positive equilibrium point $\bar{\mathbf{x}}$. Notice that if $c_{23} = 0$, then $\mathbf{q}(k)$ describes a vertical line emanating from the x_1x_2 -plane. In this case, the surface Γ_3 intersects $\mathbf{q}(k)$ exactly once. That is, there is a unique positive equilibrium point $\bar{\mathbf{x}}$.

Next, we establish an upper limit on the number of positive equilibrium points. Based on the remarks above, we may restrict attention to the case $c_{23} > 0$. The first equation in (1.2.2) implies that

$$\bar{x}_1 = \frac{b\bar{x}_2 + a_1}{\delta_1 + 2m} \tag{1.5.10}$$

Thus, \bar{x}_1 is uniquely determined by \bar{x}_2 . Equation (1.5.10) and the second equation in (1.2.2) together imply that

$$m \cdot \frac{b\bar{x}_2 + a_1}{\delta_1 + 2m} + a_2 = \bar{x}_2(\delta_2 + c_{22}\bar{x}_2 + c_{23}\bar{x}_3)$$

It is useful to rearrange this equation to get

$$\left\{ c_{22}\bar{x}_2 + c_{23}\bar{x}_3 - \frac{bm}{\delta_1 + 2m} + \delta_2 \right\} \bar{x}_2 = \frac{a_1m}{\delta_1 + 2m} + a_2 \quad (1.5.11)$$

Treating \bar{x}_3 as a fixed constant, the left side of (1.5.11) is a quadratic polynomial in \bar{x}_2 whose graph is concave upward and passes through the origin. Since the right side of (1.5.11) is a positive constant, there is one positive solution \bar{x}_2 . Based on these remarks, a necessary and sufficient condition for a positive equilibrium $\bar{\mathbf{x}}$ to exist is that $\bar{x}_3 > 0$. We seek now a single equation for \bar{x}_3 . Equation (1.5.10) and the third equation in (1.2.2) together imply that

$$m \cdot \frac{b\bar{x}_2 + a_1}{\delta_1 + 2m} + a_3 = \bar{x}_3(\delta_3 + c_{32}\bar{x}_2 + c_{33}\bar{x}_3) \implies \left\{ \frac{bm}{\delta_1 + 2m} - c_{32}\bar{x}_3 \right\} \bar{x}_2 = \bar{x}_3(\delta_3 + c_{33}\bar{x}_3) - \frac{a_1m}{\delta_1 + 2m} - a_3$$

Equation (1.5.11) implies that

$$\begin{aligned} & c_{22} \left\{ \bar{x}_3(\delta_3 + c_{33}\bar{x}_3) - \frac{a_1m}{\delta_1 + 2m} - a_3 \right\}^2 \\ & + \left\{ c_{23}\bar{x}_3 - \frac{bm}{\delta_1 + 2m} + \delta_2 \right\} \left\{ \frac{bm}{\delta_1 + 2m} - c_{32}\bar{x}_3 \right\} \left\{ \bar{x}_3(\delta_3 + c_{33}\bar{x}_3) - \frac{a_1m}{\delta_1 + 2m} - a_3 \right\} \\ & = \left\{ \frac{a_1m}{\delta_1 + 2m} + a_2 \right\} \left\{ \frac{bm}{\delta_1 + 2m} - c_{32}\bar{x}_3 \right\}^2 \end{aligned}$$

This fourth degree polynomial equation in \bar{x}_3 has at most four positive solutions and each such solution corresponds to a positive equilibrium $\bar{\mathbf{x}}$.

1.5.5 Proof of Theorem 1.2.7

Let $a_1 = 0$ and $a_2 = 0$. In general, the Jacobian matrix for system (1.2.1) at an equilibrium $\bar{\mathbf{x}}$ has the form

$$J(\bar{\mathbf{x}}) = \begin{bmatrix} -\delta_1 - 2m & b & 0 \\ m & -\delta_2 - 2c_{22}\bar{x}_2 - c_{23}\bar{x}_3 & -c_{23}\bar{x}_2 \\ m & -c_{32}\bar{x}_3 & -\delta_3 - c_{32}\bar{x}_2 - 2c_{33}\bar{x}_3 \end{bmatrix}$$

At $\bar{\mathbf{z}} = (0, 0, \bar{z}_3)$ this becomes

$$J(\bar{\mathbf{z}}) = \begin{bmatrix} -\delta_1 - 2m & b & 0 \\ m & -\delta_2 - c_{23}\bar{z}_3 & 0 \\ m & -c_{32}\bar{z}_3 & -\delta_3 - 2c_{33}\bar{z}_3 \end{bmatrix}$$

Because of its block triangular form, the eigenvalues of $J(\bar{\mathbf{z}})$ are those of the blocks

$$A = \begin{bmatrix} -\delta_1 - 2m & b \\ m & -\delta_2 - c_{23}\bar{z}_3 \end{bmatrix} \quad \text{and} \quad B = \begin{bmatrix} -\delta_3 - 2c_{33}\bar{z}_3 \end{bmatrix} \quad (1.5.12)$$

Notice that the matrix B is always a stable matrix (its spectral bound is negative). Therefore, $J(\bar{\mathbf{z}})$ is a stable matrix if and only if A is a stable matrix. It is well known that this occurs if and only if $\text{tr}(A) < 0$ and $\det(A) > 0$ [49]. Next, observe that $\text{tr}(A) = -\delta_1 - 2m - \delta_2 - c_{23}\bar{z}_3 < 0$ and $\det(A) = (\delta_1 + 2m)(\delta_2 + c_{23}\bar{z}_3) - bm$. We consider various cases:

1. If $R_0 < 1$, then $\det(A) \geq (\delta_1 + 2m)\delta_2 - bm > 0$ by (1.2.4). In this case, $\bar{\mathbf{z}}$ is LAS.
2. If $R_0 > 1$ and $c_{23} = 0$, then $\det(A) = (\delta_1 + 2m)\delta_2 - bm < 0$ by (1.2.4). In this case, $\bar{\mathbf{z}}$ is unstable.

3. Let $R_0 > 1$, $c_{23} > 0$, and $a_3 < a_3^*$. It follows from (1.2.3), (1.2.4), and (1.2.5), that

$$\begin{aligned}
\det(A) &< (\delta_1 + 2m)(\delta_2 + c_{23}k^*) - bm \\
&= (\delta_1 + 2m)[\delta_2 + (R_0 - 1)\delta_2] - bm \\
&= (\delta_1 + 2m)R_0\delta_2 - bm \\
&= bm - bm \\
&= 0
\end{aligned}$$

In this case, $\bar{\mathbf{z}}$ is unstable.

4. Let $R_0 > 1$, $c_{23} > 0$, and $a_3 > a_3^*$. Then an argument similar to the previous one shows that $\det(A) > 0$. In this case, $\bar{\mathbf{z}}$ is LAS.

Linear stability analysis is inconclusive in the two remaining borderline cases: (i) $R_0 = 1$ and (ii) $R_0 > 1$, $c_{23} > 0$, and $a_3 = a_3^*$.

1.5.6 Proof of Theorem 1.2.8

Let $a_1 = 0$ and $a_2 = 0$. Let $\bar{\mathbf{x}} = (\bar{x}_1, \bar{x}_2, \bar{x}_3)$ be any positive equilibrium point. In view of Theorem 1.2.3, we may assume that $R_0 > 1$. The Jacobian matrix for system (1.2.1) at $\bar{\mathbf{x}}$ is

$$J(\bar{\mathbf{x}}) = \begin{bmatrix} -\delta_1 - 2m & b & 0 \\ m & -\delta_2 - 2c_{22}\bar{x}_2 - c_{23}\bar{x}_3 & -c_{23}\bar{x}_2 \\ m & -c_{32}\bar{x}_3 & -\delta_3 - c_{32}\bar{x}_2 - 2c_{33}\bar{x}_3 \end{bmatrix}$$

For the sake of clarity, we have dropped the overline notation for the coordinates of $\bar{\mathbf{x}}$. Also, we recall the relations (1.5.4) that were obtained in an earlier proof:

$$\mathbf{R}_0\delta_2x_2 = mx_1, \quad \mathbf{R}_0\delta_2 = \delta_2 + c_{22}x_2 + c_{23}x_3, \quad \text{and} \quad \mathbf{R}_0\delta_2x_2 + a_3 = x_3(\delta_3 + c_{32}x_2 + c_{33}x_3) \quad (1.5.13)$$

Apart from sign, the characteristic polynomial for $J(\bar{\mathbf{x}})$ has the form $p_J(\bar{\mathbf{x}}) = \lambda^3 + A\lambda^2 + B\lambda + C$.

The positive equilibrium $\bar{\mathbf{x}}$ is stable provided that the Routh-Hurwitz conditions are satisfied:

$A, B, C > 0$ and $AB > C$. We calculate

$$\begin{aligned} A &= -(J_{11} + J_{22} + J_{33}) \\ &= (\delta_1 + 2m) + (\delta_2 + 2c_{22}x_2 + c_{23}x_3) + (\delta_3 + c_{32}x_2 + 2c_{33}x_3) \\ &> 0 \end{aligned}$$

$$\begin{aligned} B &= (J_{11}J_{22} - J_{12}J_{21}) + (J_{11}J_{33} - J_{13}J_{31}) + (J_{22}J_{33} - J_{23}J_{32}) \\ &= \{(\delta_1 + 2m)(\delta_2 + 2c_{22}x_2 + c_{23}x_3) - bm\} + \{(\delta_1 + 2m)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) - 0\} \\ &\quad + \{(\delta_2 + 2c_{22}x_2 + c_{23}x_3)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) - c_{23}x_2 \cdot c_{32}x_3\} \\ &= (\delta_1 + 2m)(\mathbf{R}_0\delta_2 + c_{22}x_2) - (\delta_1 + 2m)\mathbf{R}_0\delta_2 + (\delta_1 + 2m)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) \\ &\quad + (\delta_2 + 2c_{22}x_2 + c_{23}x_3)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) - c_{23}c_{32}x_2x_3 \quad (\text{by (1.2.4) and (1.5.13)}) \\ &= (\delta_1 + 2m)(\delta_3 + c_{22}x_2 + c_{32}x_2 + 2c_{33}x_3) \\ &\quad + (\delta_2 + 2c_{22}x_2)(\delta_3 + 2c_{33}x_3) + c_{23}x_3(\delta_3 + 2c_{33}x_3) + c_{32}x_2(\delta_2 + 2c_{22}x_2) \\ &> 0 \end{aligned}$$

$$\begin{aligned}
C &= -J_{11}(J_{22}J_{33} - J_{23}J_{32}) + J_{12}(J_{21}J_{33} - J_{31}J_{23}) - J_{13}(J_{21}J_{32} - J_{31}J_{22}) \\
&= (\delta_1 + 2m)\{(\delta_2 + 2c_{22}x_2 + c_{23}x_3)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) - c_{23}x_2 \cdot c_{32}x_3\} \\
&\quad + bm\{-\delta_3 - c_{32}x_2 - 2c_{33}x_3 + c_{23}x_2\} \\
&= (\delta_1 + 2m)\{(\delta_2 + 2c_{22}x_2 + c_{23}x_3)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) - c_{23}c_{32}x_2x_3 \\
&\quad + \frac{bm}{\delta_1+2m}(-\delta_3 - c_{32}x_2 - 2c_{33}x_3 + c_{23}x_2)\} \\
&= (\delta_1 + 2m)\{(\delta_2 + 2c_{22}x_2 + c_{23}x_3 - \frac{bm}{\delta_1+2m})(\delta_3 + c_{32}x_2 + 2c_{33}x_3) - c_{23}c_{32}x_2x_3 + \frac{bm}{\delta_1+2m}c_{23}x_2\} \\
&= (\delta_1 + 2m)\{(R_0\delta_2 + c_{22}x_2 - R_0\delta_2)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) - c_{23}c_{32}x_2x_3 + R_0\delta_2c_{23}x_2\} \\
&\hspace{25em} \text{(by (1.2.4), (1.5.13))} \\
&= (\delta_1 + 2m)\{c_{22}x_2(\delta_3 + c_{32}x_2 + 2c_{33}x_3) - c_{23}c_{32}x_2x_3 + R_0\delta_2c_{23}x_2\} \\
&= (\delta_1 + 2m)x_2\{c_{22}(\delta_3 + c_{32}x_2 + 2c_{33}x_3) - c_{23}c_{32}x_3 + R_0\delta_2c_{23}\} \\
&= (\delta_1 + 2m)x_2\{c_{22}(\delta_3 + 2c_{33}x_3) + c_{23}R_0\delta_2 + c_{32}c_{22}x_2 - c_{23}c_{32}x_3\} \\
&= (\delta_1 + 2m)x_2\{c_{22}(\delta_3 + 2c_{33}x_3) + c_{23}R_0\delta_2 + c_{32}(R_0\delta_2 - \delta_2 - c_{23}x_3) - c_{23}c_{32}x_3\} \text{ (by (1.5.13))} \\
&= (\delta_1 + 2m)x_2\{c_{22}\delta_3 + c_{23}R_0\delta_2 + c_{32}(R_0 - 1)\delta_2 + 2(c_{22}c_{33} - c_{23}c_{32})x_3\}
\end{aligned}$$

The sign of C will be found below. Omitting terms (some positive and some non-negative), we have

$$\begin{aligned}
AB &= \{(\delta_1 + 2m) + \dots\}\{\dots + (\delta_2 + 2c_{22}x_2)(\delta_3 + 2c_{33}x_3) + c_{23}x_3(\delta_3 + 2c_{33}x_3) + c_{32}x_2(\delta_2 + 2c_{22}x_2)\} \\
&> (\delta_1 + 2m)\{(\delta_2 + 2c_{22}x_2)(\delta_3 + 2c_{33}x_3) + c_{23}x_3(\delta_3 + 2c_{33}x_3) + c_{32}x_2(\delta_2 + 2c_{22}x_2)\} \\
&> (\delta_1 + 2m)\{c_{22}\delta_3x_2 + c_{23}x_3(\delta_3 + c_{33}x_3) + c_{32}x_2(\delta_2 + c_{22}x_2) + 2c_{22}c_{33}x_2x_3\} \\
&= (\delta_1 + 2m)\{c_{22}\delta_3x_2 + c_{23}x_3(\delta_3 + c_{32}x_2 + c_{33}x_3) + c_{32}x_2(\delta_2 + c_{22}x_2 + c_{23}x_3)\}
\end{aligned}$$

$$\begin{aligned}
& + 2(c_{22}c_{33} - c_{23}c_{32})x_2x_3 \} \\
& \geq (\delta_1 + 2m) \{ c_{22}\delta_3x_2 + c_{23}R_0\delta_2x_2 + c_{32}x_2R_0\delta_2 + 2(c_{22}c_{33} - c_{23}c_{32})x_2x_3 \} \quad (\text{by (1.5.13)}) \\
& = (\delta_1 + 2m)x_2 \{ c_{22}\delta_3 + c_{23}R_0\delta_2 + c_{32}R_0\delta_2 + 2(c_{22}c_{33} - c_{23}c_{32})x_3 \} \\
& > (\delta_1 + 2m)x_2 \{ c_{22}\delta_3 + c_{23}R_0\delta_2 + c_{32}(R_0 - 1)\delta_2 + 2(c_{22}c_{33} - c_{23}c_{32})x_3 \} \\
& = C
\end{aligned}$$

The Routh-Hurwitz conditions are satisfied whenever $C > 0$. Recall from Theorems 1.2.3, 1.2.4, and 1.2.5 that \bar{x} exists in these cases: (i) $c_{23} = 0$, (ii) $c_{23} > 0$, $c_{32} \leq c_{32}^*$, and $a_3 < a_3^*$, and (iii) $c_{23} > 0$, $c_{32} > c_{32}^*$, and $a_3 \leq a_3^{**}$. We examine each case separately.

1. If $c_{23} = 0$, then there is one positive equilibrium \bar{x} (see Theorem 1.2.3). Also,

$$C = (\delta_1 + 2m)x_2 \{ c_{22}\delta_3 + c_{23}R_0\delta_2 + c_{32}(R_0 - 1)\delta_2 + 2c_{22}c_{33}x_3 \} > 0$$

In this case, \bar{x} is LAS.

2. If $c_{23} > 0$, $c_{32} \leq c_{32}^*$, and $a_3 < a_3^*$, then there is one positive equilibrium \bar{x} (see Theorem 1.2.4). Observe from (1.2.5) that $0 < \frac{c_{22}c_{33}}{c_{23}} < c_{32}^*$. If $c_{32} \leq \frac{c_{22}c_{33}}{c_{23}}$, then

$$C \geq (\delta_1 + 2m)x_2 \{ c_{22}\delta_3 + c_{23}R_0\delta_2 + c_{32}(R_0 - 1)\delta_2 \} > 0$$

In this case, \bar{x} is LAS. Suppose now that $c_{32} > \frac{c_{22}c_{33}}{c_{23}}$. Recall from the proof of Theorem 1.2.4 that $x_3 < k^* \leq \xi^*$. Equation (1.2.6) implies that

$$C = (\delta_1 + 2m)x_2 \{ c_{22}\delta_3 + c_{23}R_0\delta_2 + c_{32}(R_0 - 1)\delta_2 + 2(c_{22}c_{33} - c_{23}c_{32})x_3 \}$$

$$\begin{aligned}
&= (\delta_1 + 2m)x_2 \{ 2(c_{23}c_{32} - c_{22}c_{33})\xi^* - 2(c_{23}c_{32} - c_{22}c_{33})x_3 \} \\
&= 2(\delta_1 + 2m)x_2(c_{23}c_{32} - c_{22}c_{33})(\xi^* - x_3) \\
&> 0
\end{aligned}$$

Again, \bar{x} is LAS.

3. Finally, let $c_{23} > 0$, $c_{32} > c_{32}^*$ and $a_3 < a_3^{**}$ (linear stability analysis is inconclusive in the borderline case $a_3 = a_3^{**}$). Then $c_{32} > \frac{c_{22}c_{33}}{c_{23}}$. If $a_3 \leq a_3^*$ then there is one positive equilibrium $\bar{x} = (x_1, x_2, x_3)$ and $x_3 < \xi^*$ (see Theorem 1.2.5). The second argument in the previous case applies to this situation and so \bar{x} is LAS. Suppose now that $a_3^* < a_3 < a_3^{**}$. Then there are two positive equilibrium points $\bar{x} = (x_1, x_2, x_3)$ and $\bar{y} = (y_1, y_2, y_3)$ and they satisfy $x_3 < \xi^* < y_3$ (see Theorem 1.2.5). The equilibrium \bar{x} is stable (the argument is the same as when $a_3 \leq a_3^*$). The equilibrium \bar{y} is not stable ($C < 0$ in this case).

1.5.7 Proof of Theorem 1.2.9

Let $a_1 > 0$ or $a_2 > 0$. Let $\bar{x} = (\bar{x}_1, \bar{x}_2, \bar{x}_3)$ be any positive equilibrium point. The Jacobian matrix for system (1.2.1) at \bar{x} is

$$J(\bar{x}) = \begin{bmatrix} -\delta_1 - 2m & b & 0 \\ m & -\delta_2 - 2c_{22}x_2 - c_{23}x_3 & -c_{23}x_2 \\ m & -c_{32}x_3 & -\delta_3 - c_{32}x_2 - 2c_{33}x_3 \end{bmatrix}$$

Again, we drop the overline notation for the coordinates of $\bar{\mathbf{x}}$. As in the proof of Theorem 1.2.8, the characteristic polynomial for $J(\bar{\mathbf{x}})$ has the form $p_J(\bar{\mathbf{x}}) = \lambda^3 + A\lambda^2 + B\lambda + C$ and $\bar{\mathbf{x}}$ is stable if and only if $A, B, C > 0$ and $AB > C$. We calculate

$$\begin{aligned} A &= -(J_{11} + J_{22} + J_{33}) \\ &= (\delta_1 + 2m) + (\delta_2 + 2c_{22}x_2 + c_{23}x_3) + (\delta_3 + c_{32}x_2 + 2c_{33}x_3) \\ &> 0 \end{aligned}$$

$$\begin{aligned} B &= (J_{11}J_{22} - J_{12}J_{21}) + (J_{11}J_{33} - J_{13}J_{31}) + (J_{22}J_{33} - J_{23}J_{32}) \\ &= \{(\delta_1 + 2m)(\delta_2 + 2c_{22}x_2 + c_{23}x_3) - bm\} + \{(\delta_1 + 2m)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) - 0\} \\ &\quad + \{(\delta_2 + 2c_{22}x_2 + c_{23}x_3)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) - c_{23}x_2 \cdot c_{32}x_3\} \\ &= \frac{bx_2 + a_1}{x_1} \left(\frac{mx_1 + a_2}{x_2} + c_{22}x_2 \right) - bm + (\delta_1 + 2m)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) \\ &\quad + (\delta_2 + 2c_{22}x_2 + c_{23}x_3)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) - c_{23}c_{32}x_2x_3 \quad (\text{by (1.2.2)}) \\ &= \frac{bx_2}{x_1} \left(\frac{a_2}{x_2} + c_{22}x_2 \right) + \frac{a_1}{x_1} \left(\frac{mx_1 + a_2}{x_2} + c_{22}x_2 \right) + (\delta_1 + 2m)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) \\ &\quad + (\delta_2 + 2c_{22}x_2)(\delta_3 + 2c_{33}x_3) + c_{23}x_3(\delta_3 + 2c_{33}x_3) + c_{32}x_2(\delta_2 + 2c_{22}x_2) \\ &> 0 \end{aligned}$$

$$\begin{aligned} C &= -J_{11}(J_{22}J_{33} - J_{23}J_{32}) + J_{12}(J_{21}J_{33} - J_{31}J_{23}) - J_{13}(J_{21}J_{32} - J_{31}J_{22}) \\ &= (\delta_1 + 2m) \{(\delta_2 + 2c_{22}x_2 + c_{23}x_3)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) - c_{23}x_2 \cdot c_{32}x_3\} \\ &\quad + bm(-\delta_3 - c_{32}x_2 - 2c_{33}x_3 + c_{23}x_2) \end{aligned}$$

$$\begin{aligned}
&= (\delta_1 + 2m) \left\{ (\delta_2 + 2c_{22}x_2 + c_{23}x_3)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) - c_{23}c_{32}x_2x_3 \right. \\
&\quad \left. - \frac{bm}{\delta_1+2m}(\delta_3 + c_{32}x_2 + 2c_{33}x_3 - c_{23}x_2) \right\} \\
&= (\delta_1 + 2m) \left\{ (\delta_2 + 2c_{22}x_2 + c_{23}x_3 - \frac{bm}{\delta_1+2m})(\delta_3 + c_{32}x_2 + 2c_{33}x_3) + \frac{bm}{\delta_1+2m}c_{23}x_2 - c_{23}c_{32}x_2x_3 \right\}
\end{aligned}$$

The sign of C will be found below. Omitting terms (some positive and some non-negative) yields

$$\begin{aligned}
AB &= \left\{ (\delta_1 + 2m) + (\delta_2 + 2c_{22}x_2 + c_{23}x_3) + \dots \right\} \left\{ \dots + (\delta_1 + 2m)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) \right. \\
&\quad \left. + c_{23}x_3(\delta_3 + 2c_{33}x_3) + \dots \right\} \\
&> (\delta_2 + 2c_{22}x_2 + c_{23}x_3)(\delta_1 + 2m)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) + (\delta_1 + 2m)c_{23}x_3(\delta_3 + 2c_{33}x_3) \\
&\geq (\delta_1 + 2m) \left\{ (\delta_2 + 2c_{22}x_2 + c_{23}x_3)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) + c_{23}x_3(\delta_3 + c_{33}x_3) \right\} \\
&= (\delta_1 + 2m) \left\{ (\delta_2 + 2c_{22}x_2 + c_{23}x_3)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) + c_{23}x_3(\delta_3 + c_{32}x_2 + c_{33}x_3) \right. \\
&\quad \left. - c_{23}c_{32}x_2x_3 \right\} \\
&= (\delta_1 + 2m) \left\{ (\delta_2 + 2c_{22}x_2 + c_{23}x_3)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) + c_{23}(mx_1 + a_3) - c_{23}c_{32}x_2x_3 \right\} \\
&\hspace{20em} \text{(by (1.2.2))} \\
&\geq (\delta_1 + 2m) \left\{ (\delta_2 + 2c_{22}x_2 + c_{23}x_3)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) + c_{23}mx_1 - c_{23}c_{32}x_2x_3 \right\} \\
&\geq (\delta_1 + 2m) \left\{ (\delta_2 + 2c_{22}x_2 + c_{23}x_3)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) + \frac{bx_2}{bx_2+a_1}c_{23}mx_1 - c_{23}c_{32}x_2x_3 \right\} \\
&= (\delta_1 + 2m) \left\{ (\delta_2 + 2c_{22}x_2 + c_{23}x_3)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) + \frac{bmx_1}{bx_2+a_1}c_{23}x_2 - c_{23}c_{32}x_2x_3 \right\} \\
&= (\delta_1 + 2m) \left\{ (\delta_2 + 2c_{22}x_2 + c_{23}x_3)(\delta_3 + c_{32}x_2 + 2c_{33}x_3) + \frac{bm}{\delta_1+2m}c_{23}x_2 - c_{23}c_{32}x_2x_3 \right\} \\
&> (\delta_1 + 2m) \left\{ (\delta_2 + 2c_{22}x_2 + c_{23}x_3 - \frac{bm}{\delta_1+2m})(\delta_3 + c_{32}x_2 + 2c_{33}x_3) + \frac{bm}{\delta_1+2m}c_{23}x_2 - c_{23}c_{32}x_2x_3 \right\} \\
&= C
\end{aligned}$$

The Routh-Hurwitz conditions are satisfied whenever $C > 0$. Recall from Theorem 1.2.6 that

\bar{x} always exists. Observe that

$$\begin{aligned}
C &= (\delta_1 + 2m) \left\{ (\delta_2 + 2c_{22}x_2 + c_{23}x_3 - \frac{bm}{\delta_1 + 2m}) (\delta_3 + c_{32}x_2 + 2c_{33}x_3) + \frac{bm}{\delta_1 + 2m} c_{23}x_2 - c_{23}c_{32}x_2x_3 \right\} \\
&= (\delta_1 + 2m) \left\{ \left(\frac{mx_1 + a_2}{x_2} + c_{22}x_2 - \frac{bmx_1}{bx_2 + a_1} \right) (\delta_3 + c_{32}x_2 + 2c_{33}x_3) - c_{23}c_{32}x_2x_3 + \frac{bm}{\delta_1 + 2m} c_{23}x_2 \right\} \\
&\hspace{25em} \text{(by (1.2.2))} \\
&= (\delta_1 + 2m) \left\{ \left(\frac{mx_1 + a_2}{x_2} - \frac{bmx_1}{bx_2 + a_1} \right) (\delta_3 + c_{32}x_2 + 2c_{33}x_3) + c_{22}x_2 (\delta_3 + c_{32}x_2 + c_{33}x_3) \right. \\
&\hspace{15em} \left. + \frac{bm}{\delta_1 + 2m} c_{23}x_2 + (c_{22}c_{33} - c_{23}c_{32})x_2x_3 \right\} \\
&= (\delta_1 + 2m) \left\{ \left(\frac{bmx_1}{bx_2} - \frac{bmx_1}{bx_2 + a_1} + \frac{a_2}{x_2} \right) (\delta_3 + c_{32}x_2 + 2c_{33}x_3) + c_{22}x_2 (\delta_3 + c_{32}x_2) \right. \\
&\hspace{15em} \left. + \frac{bm}{\delta_1 + 2m} c_{23}x_2 + (2c_{22}c_{33} - c_{23}c_{32})x_2x_3 \right\} \\
&= (\delta_1 + 2m) \left\{ \left(\frac{a_1mx_1}{x_2(bx_2 + a_1)} + \frac{a_2}{x_2} \right) (\delta_3 + c_{32}x_2 + 2c_{33}x_3) + c_{22}x_2 (\delta_3 + c_{32}x_2) \right. \\
&\hspace{15em} \left. + \frac{bm}{\delta_1 + 2m} c_{23}x_2 + (2c_{22}c_{33} - c_{23}c_{32})x_2x_3 \right\}
\end{aligned}$$

If (i) $c_{23} = 0$ or (ii) $c_{23} > 0$ and $c_{32} \leq \frac{2c_{22}c_{33}}{c_{23}}$, then $C > 0$. In these cases \bar{x} is LAS. Suppose now that $c_{32} > \frac{2c_{22}c_{33}}{c_{23}}$. Then

$$\begin{aligned}
C &= (\delta_1 + 2m) \left\{ \left(\frac{a_1mx_1}{x_2(bx_2 + a_1)} + \frac{a_2}{x_2} \right) (\delta_3 + c_{32}x_2 + 2c_{33}x_3) + c_{22}x_2 (\delta_3 + c_{32}x_2) + \frac{bm}{\delta_1 + 2m} c_{23}x_2 \right. \\
&\hspace{15em} \left. + (2c_{22}c_{33} - c_{23}c_{32})x_2x_3 \right\} \\
&= (\delta_1 + 2m) \left\{ \frac{a_2(bx_2 + a_1) + a_1mx_1}{x_2(bx_2 + a_1)} (\delta_3 + c_{32}x_2 + 2c_{33}x_3) + c_{22}x_2 (\delta_3 + c_{32}x_2) + \frac{bmx_1}{bx_2 + a_1} c_{23}x_2 \right. \\
&\hspace{15em} \left. + (2c_{22}c_{33} - c_{23}c_{32})x_2x_3 \right\} \\
&= (\delta_1 + 2m) \left\{ \frac{ba_2x_2 + a_1(mx_1 + a_2)}{x_2(bx_2 + a_1)} \left(\frac{mx_1 + a_3}{x_3} + c_{33}x_3 \right) + c_{22}x_2 \cdot \frac{mx_1 + a_3}{x_3} + \frac{bmx_1}{bx_2 + a_1} \cdot c_{23}x_2 \right. \\
&\hspace{15em} \left. + (c_{22}c_{33} - c_{23}c_{32})x_2x_3 \right\}
\end{aligned}$$

$$\begin{aligned}
&= (\delta_1 + 2m) \left\{ \frac{ba_2x_2+a_1(mx_1+a_2)}{x_2(bx_2+a_1)} \left(\frac{mx_1+a_3}{x_3} + C_{33}x_3 \right) + \frac{mx_1+a_3}{x_3} \left(C_{22}x_2 + \frac{x_3}{mx_1+a_3} \cdot \frac{bmx_1}{bx_2+a_1} \cdot C_{23}x_2 \right) \right. \\
&\quad \left. + (C_{22}C_{33} - C_{23}C_{32})x_2x_3 \right\} \\
&> (\delta_1 + 2m) \left\{ \frac{a_1}{bx_2+a_1} \cdot \frac{mx_1+a_2}{x_2} \cdot C_{32}x_2 + C_{32}x_2 \cdot \left(\frac{x_3}{mx_1+a_3} \cdot \frac{bmx_1}{bx_2+a_1} \cdot C_{23}x_2 \right) + (C_{22}C_{33} - C_{23}C_{32})x_2x_3 \right\} \\
&> (\delta_1 + 2m) \left\{ \frac{a_1}{bx_2+a_1} \cdot C_{23}x_3 \cdot C_{32}x_2 + C_{32}x_2 \cdot \left(\frac{x_2}{mx_1+a_3} \cdot \frac{bmx_1}{bx_2+a_1} \cdot C_{23}x_3 \right) + (C_{22}C_{33} - C_{23}C_{32})x_2x_3 \right\} \\
&= (\delta_1 + 2m) \left\{ \left(\frac{a_1}{bx_2+a_1} + \frac{x_2}{mx_1+a_3} \cdot \frac{bmx_1}{bx_2+a_1} - 1 \right) C_{23}C_{32}x_2x_3 + C_{22}C_{33}x_2x_3 \right\} \\
&= (\delta_1 + 2m) \left\{ \left(\frac{a_1}{bx_2+a_1} + \frac{bx_2}{bx_2+a_1} \cdot \frac{mx_1}{mx_1+a_3} - \frac{bx_2+a_1}{bx_2+a_1} \right) C_{23}C_{32} + C_{22}C_{33} \right\} x_2x_3 \\
&= (\delta_1 + 2m) \left\{ \left(\frac{bx_2}{bx_2+a_1} \cdot \frac{mx_1}{mx_1+a_3} - \frac{bx_2}{bx_2+a_1} \right) C_{23}C_{32} + C_{22}C_{33} \right\} x_2x_3 \\
&= (\delta_1 + 2m) \left\{ \frac{bx_2}{bx_2+a_1} \left(\frac{mx_1}{mx_1+a_3} - 1 \right) C_{23}C_{32} + C_{22}C_{33} \right\} x_2x_3 \\
&= (\delta_1 + 2m) \left\{ \frac{bx_2}{bx_2+a_1} \left(-\frac{a_3}{mx_1+a_3} \right) C_{23}C_{32} + C_{22}C_{33} \right\} x_2x_3
\end{aligned}$$

If $a_3 = 0$ or $a_3 > 0$ and is sufficiently small, then $C > 0$.

1.5.8 Proof of Theorem 1.2.10

Let $a_1 = 0$ and $a_2 = 0$. We first show that the basin of attraction for $\bar{\mathbf{z}} = (0, 0, \bar{z}_3)$ includes the non-negative x_3 -axis. Let $\mathbf{x}(t) = (x_1(t), x_2(t), x_3(t))$ be a solution of (1.2.1) that starts on the x_3 -axis. Theorem 1.2.1 implies that $\mathbf{x}(t)$ remains on the x_3 -axis for $t \geq 0$. Hence, $\dot{x}_3 = a_3 - x_3(\delta_3 + c_{33}x_3)$ for $t \geq 0$. Lemma 1.4.1 and equation (1.2.3) together imply that $x_3(t) \rightarrow \bar{z}_3$ as $t \rightarrow \infty$. Thus, $\mathbf{x}(t) \rightarrow \bar{\mathbf{z}}$ as $t \rightarrow \infty$. That is, the basin of attraction for $\bar{\mathbf{z}}$ includes the non-negative x_3 -axis.

Next, we show that system (1.2.1) is point dissipative, that is, there exists a compact subset \mathfrak{L} of \mathbb{R}_+^3 with the property that if $\mathbf{x}(t) = (x_1(t), x_2(t), x_3(t))$ is a solution of (1.2.1) with $\mathbf{x}(0) \geq \mathbf{0}$, then $\mathbf{x}(t) \in \mathfrak{L}$ for t sufficiently large. The argument above shows that if $\mathbf{x}(0)$ starts on the non-negative x_3 -axis, then $\mathbf{x}(t) \rightarrow \bar{\mathbf{z}}$ as $t \rightarrow \infty$. Also, Theorem 1.2.1 states that if $\mathbf{x}(0)$ is on the boundary but not on the x_3 -axis then $\mathbf{x}(t)$ immediately enters the positive cone. Thus, we may restrict attention to solutions $\mathbf{x}(t)$ that start inside the positive cone. Recall from the proof of Theorem 1.2.1 that $\mathbf{x}(t)$ is dominated from above by the solution $\mathbf{v}(t) = (v_1(t), v_2(t), v_3(t))$ of the comparison system

$$\begin{aligned}
\dot{v}_1 &= bv_2 - v_1(\delta_1 + 2m), & v_1(0) &= x_1(0) \\
\dot{v}_2 &= mv_1 - v_2(\delta_2 + c_{22}v_2), & v_2(0) &= x_2(0) \\
\dot{v}_3 &= mv_1 + a_3 - v_3(\delta_3 + c_{33}v_3), & v_3(0) &= x_3(0)
\end{aligned} \tag{1.5.14}$$

That is, $\mathbf{0} \leq \mathbf{x}(t) \leq \mathbf{v}(t)$ for $t \geq 0$ (it was also established that $\mathbf{v}(t)$ exists for all time). It suffices to show that the comparison system (1.5.14) has an equilibrium $\bar{\mathbf{v}}$ in \mathbb{R}_+^3 that attracts all solutions that start in the positive cone. The result that (1.2.1) is point dissipative will then follow by taking \mathfrak{L} to be the box having one corner at the origin and another corner at (M, M, M) with $M > \|\bar{\mathbf{z}}\|_\infty$ and $M > \|\bar{\mathbf{v}}\|_\infty$. Suppose first that $R_0 \leq 1$. Lemma 1.4.3 implies that every trajectory $(v_1(t), v_2(t))$ approaches $(0, 0)$ as $t \rightarrow \infty$. We now consider $v_3(t)$. Given a small $\epsilon > 0$ there exists $T > 0$ such that $0 \leq v_1(t) \leq \epsilon$ and $0 \leq v_2(t) \leq \epsilon$ for $t \geq T$. Therefore, $a_3 - v_3(\delta_3 + c_{33}v_3) \leq \dot{v}_3 \leq m\epsilon + a_3 - v_3(\delta_3 + c_{33}v_3)$ for $t \geq T$. Also, \dot{v}_3 is a continuous function of v_1 (which is itself a continuous function of t) and v_3 . Lemma 1.4.1 implies that $\bar{u} \leq \liminf_{t \rightarrow \infty} v_3(t) \leq \limsup_{t \rightarrow \infty} v_3(t) \leq \bar{w}$ where \bar{u} and \bar{w} are the unique nonnegative

numbers such that $a_3 = \bar{u}(\delta_3 + c_{33}\bar{u})$ and $m\epsilon + a_3 = \bar{w}(\delta_3 + c_{33}\bar{w})$. Since ϵ is arbitrary, it must be that $\bar{u} \leq \liminf_{t \rightarrow \infty} v_3(t) \leq \limsup_{t \rightarrow \infty} v_3(t) \leq \bar{u}$. That is, $v_3(t) \rightarrow \bar{u}$ as $t \rightarrow \infty$. Letting $\bar{\mathbf{v}} = (\bar{v}_1, \bar{v}_2, \bar{u})$, it follows from the remarks above that $\mathbf{v}(t) \rightarrow \bar{\mathbf{v}}$ as $t \rightarrow \infty$ whenever $\mathbf{x}(0)$ is in $\text{Int}(\mathbb{R}_+^3)$.

Suppose now that $R_0 > 1$. Lemma 1.4.3 implies that every trajectory $(v_1(t), v_2(t))$ approaches $P(\bar{v}_1, \bar{v}_2)$ as $t \rightarrow \infty$ where $\bar{v}_1 > 0$ and $\bar{v}_2 > 0$ satisfy $R_0\delta_2\bar{v}_2 = m\bar{v}_1$ and $R_0\delta_2 = \delta_2 + c_{22}\bar{v}_2$. It remains to determine the behavior of $v_3(t)$. Given a small $\epsilon > 0$ there exists $T > 0$ such that $\bar{v}_1 - \epsilon \leq v_1(t) \leq \bar{v}_1 + \epsilon$ and $\bar{v}_2 - \epsilon \leq v_2(t) \leq \bar{v}_2 + \epsilon$ for $t \geq T$. Therefore, $m(\bar{v}_1 - \epsilon) + a_3 - v_3(\delta_3 + c_{33}v_3) \leq \dot{v}_3 \leq m(\bar{v}_1 + \epsilon) + a_3 - v_3(\delta_3 + c_{33}v_3)$ for $t \geq T$. Also, \dot{v}_3 is a continuous function of v_1 (which is itself a continuous function of t) and v_3 . Lemma 1.4.1 implies that $\bar{u} \leq \liminf_{t \rightarrow \infty} v_3(t) \leq \limsup_{t \rightarrow \infty} v_3(t) \leq \bar{w}$ where \bar{u} and \bar{w} are the unique positive numbers such that $m(\bar{v}_1 - \epsilon) + a_3 = \bar{u}(\delta_3 + c_{33}\bar{u})$ and $m(\bar{v}_1 + \epsilon) + a_3 = \bar{w}(\delta_3 + c_{33}\bar{w})$. Since ϵ is arbitrary, it must be that $\bar{v}_3 \leq \liminf_{t \rightarrow \infty} v_3(t) \leq \limsup_{t \rightarrow \infty} v_3(t) \leq \bar{v}_3$ where \bar{v}_3 is the unique positive number such that $m\bar{v}_1 + a_3 = \bar{v}_3(\delta_3 + c_{33}\bar{v}_3)$. That is, $v_3(t) \rightarrow \bar{v}_3$ as $t \rightarrow \infty$. Letting $\bar{\mathbf{v}} = (\bar{v}_1, \bar{v}_2, \bar{v}_3)$, it follows from the remarks above that $\mathbf{v}(t) \rightarrow \bar{\mathbf{v}}$ as $t \rightarrow \infty$ whenever $\mathbf{x}(0)$ is in $\text{Int}(\mathbb{R}_+^3)$. This completes the argument that system (1.2.1) is point dissipative.

In some cases, we can ascertain the basin of attraction for an equilibrium. We treat those cases separately.

Case 1. Let $R_0 \leq 1$. We will show that $\bar{\mathbf{z}} = (0, 0, \bar{z}_3)$ is a global attractor (its basin of attraction is \mathbb{R}_+^3). Recall from the argument above that the basin of attraction for $\bar{\mathbf{z}}$ includes the x_3 -axis, and that if $\mathbf{x}(0)$ is somewhere else on the boundary, then $\mathbf{x}(t)$ immediately

enters the positive cone. Thus, we may restrict attention to solutions $\mathbf{x}(t)$ that start inside the positive cone. Recall from the argument above that $\mathbf{x}(t)$ is dominated from above by the solution $\mathbf{v}(t) = (v_1(t), v_2(t), v_3(t))$ of the comparison system (1.5.14). That is, $\mathbf{0} \leq \mathbf{x}(t) \leq \mathbf{v}(t)$ for $t \geq 0$. Again, Lemma 1.4.3 implies that $v_1(t) \rightarrow 0$ and $v_2(t) \rightarrow 0$ as $t \rightarrow \infty$, and therefore $x_1(t) \rightarrow 0$ and $x_2(t) \rightarrow 0$ as $t \rightarrow \infty$. We now show that $x_3(t) \rightarrow \bar{z}_3$ as $t \rightarrow \infty$. Given $\epsilon > 0$ there exists $T > 0$ such that $0 < x_1(t) \leq \epsilon$ and $0 < x_2(t) \leq \epsilon$ for $t \geq T$. Therefore, $a_3 - x_3(\delta_3 + c_{32}\epsilon + c_{33}x_3) \leq \dot{x}_3 \leq m\epsilon + a_3 - x_3(\delta_3 + c_{33}x_3)$ for $t \geq T$. Also, \dot{x}_3 is a continuous function of x_1 and x_2 (which are both itself a continuous function of t) and x_3 . According to Lemma 1.4.1, $\bar{u} \leq \liminf_{t \rightarrow \infty} x_3(t) \leq \limsup_{t \rightarrow \infty} x_3(t) \leq \bar{w}$ where \bar{u} is the unique non-negative number such that $a_3 = \bar{u}(\delta_3 + c_{32}\epsilon + c_{33}\bar{u})$ and \bar{w} is the unique non-negative number such that $m\epsilon + a_3 = \bar{w}(\delta_3 + c_{33}\bar{w})$. However, ϵ is arbitrary, so in fact $\bar{z}_3 \leq \liminf_{t \rightarrow \infty} x_3(t) \leq \limsup_{t \rightarrow \infty} x_3(t) \leq \bar{z}_3$. Here, we use the fact that the limiting equations for \bar{u} and \bar{w} as $\epsilon \rightarrow 0$ coincide with the equation for \bar{z}_3 in (1.2.3). Thus, $x_3(t) \rightarrow \bar{z}_3$ as $t \rightarrow \infty$. It follows from these considerations that $\mathbf{x}(t) \rightarrow \bar{\mathbf{z}}$ as $t \rightarrow \infty$ for all non-negative initial conditions. That is, $\bar{\mathbf{z}}$ is a global attractor. This result and Theorem 1.2.7 together imply that $\bar{\mathbf{z}}$ is GAS when $R_0 < 1$.

Case 2. Let $R_0 > 1$ and $c_{23} = 0$. Recall from Theorem 1.2.3 that there is a unique positive equilibrium $\bar{\mathbf{x}} = (\bar{x}_1, \bar{x}_2, \bar{x}_3)$ whose coordinates satisfy (1.2.2). We will show that the basin of attraction for $\bar{\mathbf{x}}$ is \mathbb{R}_+^3 minus the x_3 -axis. As before, if $\mathbf{x}(0)$ is on the boundary but not on the x_3 -axis, then $\mathbf{x}(t)$ immediately enters the positive cone. Thus, we may restrict attention to solutions $\mathbf{x}(t)$ that start in $\text{Int}(\mathbb{R}_+^3)$. As $c_{23} = 0$, the first two equations in system (1.2.1)

decouple from the third, and so we may consider them in isolation

$$\dot{x}_1 = bx_2 - x_1(\delta_1 + 2m), \quad x_1(0) \geq 0$$

$$\dot{x}_2 = mx_1 - x_2(\delta_2 + c_{22}x_2), \quad x_2(0) \geq 0$$

Lemma 1.4.3 implies that every trajectory $(x_1(t), x_2(t))$ approaches $P(\bar{x}_1, \bar{x}_2)$ as $t \rightarrow \infty$. That is, $x_1(t) \rightarrow \bar{x}_1$ and $x_2(t) \rightarrow \bar{x}_2$ as $t \rightarrow \infty$. We now show that $x_3(t) \rightarrow \bar{x}_3$ as $t \rightarrow \infty$. Given $\epsilon > 0$ there exists $T > 0$ such that $\bar{x}_1 - \epsilon \leq x_1(t) \leq \bar{x}_1 + \epsilon$ and $\bar{x}_2 - \epsilon \leq x_2(t) \leq \bar{x}_2 + \epsilon$ for $t \geq T$. Therefore, $m(\bar{x}_1 - \epsilon) + a_3 - x_3\{\delta_3 + c_{32}(\bar{x}_2 + \epsilon) + c_{33}x_3\} \leq \dot{x}_3 \leq m(\bar{x}_1 + \epsilon) + a_3 - x_3\{\delta_3 + c_{32}(\bar{x}_2 - \epsilon) + c_{33}x_3\}$ for $t \geq T$. Lemma 1.4.1 implies that $\bar{u} \leq \liminf_{t \rightarrow \infty} x_3(t) \leq \limsup_{t \rightarrow \infty} x_3(t) \leq \bar{w}$ where \bar{u} and \bar{w} are the unique positive numbers such that $m(\bar{x}_1 - \epsilon) + a_3 = \bar{u}\{\delta_3 + c_{32}(\bar{x}_2 + \epsilon) + c_{33}\bar{u}\}$ and $m(\bar{x}_1 + \epsilon) + a_3 = \bar{w}\{\delta_3 + c_{32}(\bar{x}_2 - \epsilon) + c_{33}\bar{w}\}$. However, ϵ is arbitrary, so it must be that $\bar{x}_3 \leq \liminf_{t \rightarrow \infty} x_3(t) \leq \limsup_{t \rightarrow \infty} x_3(t) \leq \bar{x}_3$. Here, we use the fact that the limiting equations for \bar{u} and \bar{w} as $\epsilon \rightarrow 0$ coincide with the equation for \bar{x}_3 in (1.2.2). Thus, $x_3(t) \rightarrow \bar{x}_3$ as $t \rightarrow \infty$. It follows from these considerations that $\mathbf{x}(t) \rightarrow \bar{\mathbf{x}}$ as $t \rightarrow \infty$. That is, the basin of attraction for $\bar{\mathbf{x}}$ is \mathbb{R}_+^3 minus the x_3 -axis. This result and Theorem 1.2.8 together imply that $\bar{\mathbf{x}}$ is GAS relative to \mathbb{R}_+^3 minus the x_3 -axis.

Case 3. Let $R_0 > 1$, $c_{23} > 0$, and $a_3 < a_3^\circ$ where a_3° satisfies (1.2.8). Here, we assume that $a_3^\circ > 0$ (this will always be the case when c_{22} is sufficiently large or c_{23} is sufficiently small).

Equations (1.2.5) and (1.2.8) together imply that

$$\begin{aligned} a_3^\circ &= \frac{(R_0 - 1)\delta_2}{c_{23}} \left\{ \delta_3 + \frac{c_{33}(R_0 - 1)\delta_2}{c_{23}} \right\} - \frac{R_0\delta_2(R_0 - 1)\delta_2}{c_{22}} \\ &= k^*(\delta_3 + c_{33}k^*) - \frac{R_0\delta_2(R_0 - 1)\delta_2}{c_{22}} \end{aligned}$$

$$= a_3^* - \frac{R_0 \delta_2 (R_0 - 1) \delta_2}{c_{22}}$$

Therefore, $a_3 < a_3^\circ < a_3^*$. Theorem 1.2.4 implies that there is a unique positive equilibrium $\bar{\mathbf{x}} = (\bar{x}_1, \bar{x}_2, \bar{x}_3)$. We will show that the basin of attraction for $\bar{\mathbf{x}}$ is \mathbb{R}_+^3 minus the x_3 -axis. As before, if $\mathbf{x}(0)$ is on the boundary but not on the x_3 -axis, then $\mathbf{x}(t)$ immediately enters the positive cone. Thus, we may restrict attention to solutions $\mathbf{x}(t)$ that start in $\text{Int}(\mathbb{R}_+^3)$. Fix such a solution $\mathbf{x}(t)$. As mentioned earlier, $\mathbf{x}(t)$ is dominated from above by the solution $\mathbf{v}(t) = (v_1(t), v_2(t), v_3(t))$ of the comparison system (1.5.14). That is, $\mathbf{0} \leq \mathbf{x}(t) \leq \mathbf{v}(t)$ for $t \geq 0$. In addition, it was shown that $\mathbf{v}(t)$ approaches a positive vector $\bar{\mathbf{v}}$. Let \mathbf{x}_* be the vector in \mathbb{R}_+^3 whose i th coordinate is $\liminf_{t \rightarrow \infty} x_i(t)$ for $i = 1, 2, 3$ and let \mathbf{x}^* be the vector in \mathbb{R}_+^3 whose i th coordinate is $\limsup_{t \rightarrow \infty} x_i(t)$ for $i = 1, 2, 3$. The remarks above imply that $\mathbf{0} \leq \mathbf{x}_* \leq \mathbf{x}^* \leq \bar{\mathbf{v}}$. Our goal is to construct sequences $\{\mathbf{u}^j\}_{j=1}^\infty$ and $\{\mathbf{w}^j\}_{j=1}^\infty$ in \mathbb{R}_+^3 such that

1. $\mathbf{0} \ll \mathbf{u}^1 \ll \mathbf{u}^2 \ll \mathbf{u}^3 \ll \dots \ll \bar{\mathbf{x}} \ll \dots \ll \mathbf{w}^3 \ll \mathbf{w}^2 \ll \mathbf{w}^1 \ll \bar{\mathbf{v}}$
2. $\mathbf{u}^j \leq \mathbf{x}_* \leq \mathbf{x}^* \leq \mathbf{w}^j$ for $j \geq 1$
3. $\mathbf{u}^j \rightarrow \bar{\mathbf{x}}$ and $\mathbf{w}^j \rightarrow \bar{\mathbf{x}}$ as $j \rightarrow \infty$

It will, then, follow that $\mathbf{x}_* = \mathbf{x}^* = \bar{\mathbf{x}}$. That is, $\mathbf{x}(t) \rightarrow \bar{\mathbf{x}}$ as $t \rightarrow \infty$. Recall that the coordinates of $\bar{\mathbf{v}} = (\bar{v}_1, \bar{v}_2, \bar{v}_3)$ satisfy

$$R_0 \delta_2 \bar{v}_2 = m \bar{v}_1, \quad R_0 \delta_2 = \delta_2 + c_{22} \bar{v}_2, \quad \text{and} \quad R_0 \delta_2 \bar{v}_2 + a_3 = \bar{v}_3 (\delta_3 + c_{33} \bar{v}_3) \quad (1.5.15)$$

Also, it follows from (1.2.2) and (1.2.4) that

$$R_0 \delta_2 \bar{x}_2 = m \bar{x}_1, \quad R_0 \delta_2 = \delta_2 + c_{22} \bar{x}_2 + c_{23} \bar{x}_3, \quad \text{and} \quad R_0 \delta_2 \bar{x}_2 + a_3 = \bar{x}_3 (\delta_3 + c_{32} \bar{x}_2 + c_{33} \bar{x}_3) \quad (1.5.16)$$

In view of (1.5.15) and the fact that $\bar{\mathbf{x}}$ is positive, it must be that

$$0 < \bar{x}_1 < \bar{v}_1, \quad 0 < \bar{x}_2 < \bar{v}_2, \quad \text{and} \quad 0 < \bar{x}_3 < \bar{v}_3 \quad (1.5.17)$$

Hence, $\mathbf{0} \ll \bar{\mathbf{x}} \ll \bar{\mathbf{v}}$. Recall also that

$$\frac{R_0 \delta_2 (R_0 - 1) \delta_2}{c_{22}} + a_3^\circ = a_3^* \implies \frac{R_0 \delta_2 (R_0 - 1) \delta_2}{c_{22}} + a_3 < a_3^*$$

It follows from this result and the second equation in (1.5.15) that $R_0 \delta_2 \bar{v}_2 + a_3 < a_3^*$. We obtain from the third equations each in (1.2.5) and (1.5.15) that $\bar{v}_3 < k^*$. This fact, together with the relation $R_0 \delta_2 = \delta_2 + c_{23} k^*$ (obtained from the first equation in (1.2.5)), implies that $R_0 \delta_2 > \delta_2 + c_{23} \bar{v}_3$. We proceed in four steps.

1. Select $\epsilon_1 > 0$ such that $R_0 \delta_2 > \delta_2 + c_{23}(\bar{v}_3 + \epsilon_1)$ and $T_1 > 0$ such that $x_3(t) \leq \bar{v}_3 + \epsilon_1$ for $t \geq T_1$. Then $\dot{x}_1 = bx_2 - x_1(\delta_1 + 2m)$ and $\dot{x}_2 \geq mx_1 - x_2\{\delta_2 + c_{22}x_2 + c_{23}(\bar{v}_3 + \epsilon_1)\}$ for $t \geq T_1$. Lemmas 1.4.3 and 1.4.5 together imply that $\liminf_{t \rightarrow \infty} x_1(t) \geq u_1$ and $\liminf_{t \rightarrow \infty} x_2(t) \geq u_2$ where u_1 and u_2 are the unique positive numbers such that $R_0 \delta_2 u_2 = mu_1$ and $R_0 \delta_2 = \delta_2 + c_{22}u_2 + c_{23}(\bar{v}_3 + \epsilon_1)$. Equations (1.5.16) and (1.5.17) imply that $0 < u_1 < \bar{x}_1 < \bar{v}_1$ and $0 < u_2 < \bar{x}_2 < \bar{v}_2$.
2. Select ϵ_2 in $(0, \epsilon_1)$ such that $u_1 > \epsilon_2$ and $T_2 > T_1$ such that $x_1(t) \geq u_1 - \epsilon_2$ and $x_2(t) \leq \bar{v}_2 + \epsilon_2$ for $t \geq T_2$. Then $\dot{x}_3 \geq m(u_1 - \epsilon_2) + a_3 - x_3\{\delta_3 + c_{32}(\bar{v}_2 + \epsilon_2) + c_{33}x_3\}$ for $t \geq T_2$. Lemma 1.4.1 implies that $\liminf_{t \rightarrow \infty} x_3(t) \geq u_3$ where u_3 is the unique positive number such that $m(u_1 - \epsilon_2) + a_3 = u_3\{\delta_3 + c_{32}(\bar{v}_2 + \epsilon_2) + c_{33}u_3\}$. In view of the fact that $0 < m(u_1 - \epsilon_2) = R_0 \delta_2 u_2 - m\epsilon_2 < R_0 \delta_2 \bar{x}_2$, it follows from (1.5.16) and (1.5.17) that $0 < u_3 < \bar{x}_3 < \bar{v}_3$. Also, the relation $u_3 < \bar{v}_3 < k^*$ implies that $R_0 \delta_2 > \delta_2 + c_{23}u_3$.

3. Select ϵ_3 in $(0, \epsilon_2)$ such that $u_3 > \epsilon_3$, and $T_3 > T_2$ such that $x_3(t) \geq u_3 - \epsilon_3$ for $t \geq T_3$.

Then $\dot{x}_1 = bx_2 - x_1(\delta_1 + 2m)$ and $\dot{x}_2 \leq mx_1 - x_2\{\delta_2 + c_{22}x_2 + c_{23}(u_3 - \epsilon_3)\}$ for $t \geq T_3$.

Lemmas 1.4.3 and 1.4.5 together imply that $\limsup_{t \rightarrow \infty} x_1(t) \leq w_1$ and $\limsup_{t \rightarrow \infty} x_2(t) \leq w_2$

where w_1 and w_2 are the unique positive numbers such that $R_0\delta_2w_2 = mw_1$ and $R_0\delta_2 = \delta_2 + c_{22}w_2 + c_{23}(u_3 - \epsilon_3)$. Equations (1.5.15) and (1.5.16) and the relation $u_3 < \bar{x}_3$ imply that $0 < u_1 < \bar{x}_1 < w_1 < \bar{v}_1$ and $0 < u_2 < \bar{x}_2 < w_2 < \bar{v}_2$.

4. Select ϵ_4 in $(0, \epsilon_3)$ such that $u_2 > \epsilon_4$ and $R_0\delta_2w_2 + m\epsilon_4 < R_0\delta_2\bar{v}_2$ and $T_4 > T_3$ such that

$x_1(t) \leq w_1 + \epsilon_4$ and $x_2(t) \geq u_2 - \epsilon_4$ for $t \geq T_4$. Then $\dot{x}_3 \leq m(w_1 + \epsilon_4) + a_3 - x_3\{\delta_3 + c_{32}(u_2 - \epsilon_4) + c_{33}x_3\}$ for $t \geq T_4$. Lemma 1.4.1 implies that $\limsup_{t \rightarrow \infty} x_3(t) \leq w_3$ where w_3 is the

unique positive number such that $m(w_1 + \epsilon_4) + a_3 = w_3\{\delta_3 + c_{32}(u_2 - \epsilon_4) + c_{33}w_3\}$. In view of the fact that $m(w_1 + \epsilon_4) + a_3 = R_0\delta_2w_2 + m\epsilon_4 \in (R_0\delta_2\bar{x}_2, R_0\delta_2\bar{v}_2)$, it follows from (1.5.15) and (1.5.16) and the relation $\epsilon_4 < u_2 < \bar{x}_2$ that $0 < u_3 < \bar{x}_3 < w_3 < \bar{v}_3$. Also, the relation $w_3 < \bar{v}_3 < k^*$ implies that $R_0\delta_2 > \delta_2 + c_{23}w_3$.

Let $\mathbf{u}^1 = (u_1, u_2, u_3)$ and $\mathbf{w}^1 = (w_1, w_2, w_3)$. Then $\mathbf{0} \ll \mathbf{u}^1 \ll \bar{\mathbf{x}} \ll \mathbf{w}^1 \ll \bar{\mathbf{v}}$ and $\mathbf{u}^1 \leq \mathbf{x}_* \leq \mathbf{x}^* \leq \mathbf{w}^1$. Letting $\epsilon_k^1 = \epsilon_k$ for $k = 1, 2, 3, 4$, we can repeat steps 1 to 4 indefinitely (but with ϵ_1^{j+1} in $(0, \frac{1}{2}\epsilon_4^j)$ and \mathbf{u}^j and \mathbf{w}^j in place of $\mathbf{0}$ and $\bar{\mathbf{v}}$) to obtain sequences of vectors $\{\mathbf{u}^j\}_{j=1}^\infty$ and $\{\mathbf{w}^j\}_{j=1}^\infty$ in \mathbb{R}_+^3 such that

1. $\mathbf{0} \ll \mathbf{u}^1 \ll \mathbf{u}^2 \ll \mathbf{u}^3 \ll \dots \ll \bar{\mathbf{x}} \ll \dots \ll \mathbf{w}^3 \ll \mathbf{w}^2 \ll \mathbf{w}^1 \ll \bar{\mathbf{v}}$

2. $\mathbf{u}^j \leq \mathbf{x}_* \leq \mathbf{x}^* \leq \mathbf{w}^j$ for $j \geq 1$

Explicitly, with $\mathbf{u}^0 = \mathbf{0}$ and $\mathbf{w}^0 = \bar{\mathbf{v}}$, we have

$$\begin{aligned} \mathbf{R}_0 \delta_2 u_2^j &= m u_1^j, & \mathbf{R}_0 \delta_2 &= \delta_2 + c_{22} u_2^j + c_{23} (w_3^{j-1} + \epsilon_1^j), & m(u_1^j - \epsilon_2^j) + a_3 &= u_3^j (\delta_3 + c_{32} (w_2^{j-1} + \epsilon_2^j) + c_{33} u_3^j) \\ \mathbf{R}_0 \delta_2 w_2^j &= m w_1^j, & \mathbf{R}_0 \delta_2 &= \delta_2 + c_{22} w_2^j + c_{23} (u_3^j - \epsilon_3^j), & m(w_1^j + \epsilon_4^j) + a_3 &= w_3^j \{ \delta_3 + c_{32} (u_2^j - \epsilon_4^j) + c_{33} w_3^j \} \end{aligned}$$

with $0 < \epsilon_4^j < \epsilon_3^j < \epsilon_2^j < \epsilon_1^j$ and $0 < \epsilon_1^{j+1} < \frac{1}{2} \epsilon_4^j$ for $j \geq 1$. It remains to show that $\mathbf{u}^j \rightarrow \bar{\mathbf{x}}$ and $\mathbf{w}^j \rightarrow \bar{\mathbf{x}}$ as $j \rightarrow \infty$. The sequences $\{\mathbf{u}^j\}_{j=1}^\infty$ and $\{\mathbf{w}^j\}_{j=1}^\infty$ are both bounded and strictly monotone. Therefore, they both converge. That is, there exist \mathbf{u}^∞ and \mathbf{w}^∞ in \mathbb{R}_+^3 such that $\mathbf{u}^j \rightarrow \mathbf{u}^\infty$ and $\mathbf{w}^j \rightarrow \mathbf{w}^\infty$ as $j \rightarrow \infty$. Moreover,

$$1. \quad \mathbf{0} \ll \mathbf{u}^\infty \leq \bar{\mathbf{x}} \leq \mathbf{w}^\infty \ll \bar{\mathbf{v}}$$

$$2. \quad \mathbf{u}^\infty \leq \mathbf{x}_* \leq \mathbf{x}^* \leq \mathbf{w}^\infty$$

It suffices to show that $\mathbf{u}^\infty = \mathbf{w}^\infty$ (for then $\mathbf{x}_* = \mathbf{x}^* = \bar{\mathbf{x}}$). Since $\max\{\|\epsilon_k^j\| : k = 1, 2, 3, 4\} \rightarrow 0$ as $j \rightarrow \infty$, we have in the limit

$$\begin{aligned} \mathbf{R}_0 \delta_2 u_2^\infty &= m u_1^\infty, & \mathbf{R}_0 \delta_2 &= \delta_2 + c_{22} u_2^\infty + c_{23} w_3^\infty, & m u_1^\infty + a_3 &= u_3^\infty (\delta_3 + c_{32} w_2^\infty + c_{33} u_3^\infty) \\ \mathbf{R}_0 \delta_2 w_2^\infty &= m w_1^\infty, & \mathbf{R}_0 \delta_2 &= \delta_2 + c_{22} w_2^\infty + c_{23} u_3^\infty, & m w_1^\infty + a_3 &= w_3^\infty (\delta_3 + c_{32} u_2^\infty + c_{33} w_3^\infty) \end{aligned} \tag{1.5.18}$$

Eliminating u_1^∞ , w_1^∞ , u_2^∞ , and w_2^∞ , we obtain

$$\begin{aligned} \frac{\mathbf{R}_0 \delta_2}{c_{22}} \left[(\mathbf{R}_0 - 1) \delta_2 - c_{23} w_3^\infty \right] + a_3 &= u_3^\infty \left\{ \delta_3 + \frac{c_{32}}{c_{22}} \left[(\mathbf{R}_0 - 1) \delta_2 - c_{23} u_3^\infty \right] + c_{33} u_3^\infty \right\} \\ \frac{\mathbf{R}_0 \delta_2}{c_{22}} \left[(\mathbf{R}_0 - 1) \delta_2 - c_{23} u_3^\infty \right] + a_3 &= w_3^\infty \left\{ \delta_3 + \frac{c_{32}}{c_{22}} \left[(\mathbf{R}_0 - 1) \delta_2 - c_{23} w_3^\infty \right] + c_{33} w_3^\infty \right\} \end{aligned}$$

That is, $\Psi(u_3^\infty, w_3^\infty) = c_{22} a_3$ and $\Psi(w_3^\infty, u_3^\infty) = c_{22} a_3$ where

$$\Psi(U, W) = (c_{22} c_{33} - c_{23} c_{32}) U^2 + [c_{22} \delta_3 + c_{32} (\mathbf{R}_0 - 1) \delta_2] U + c_{23} \mathbf{R}_0 \delta_2 W - \mathbf{R}_0 \delta_2 (\mathbf{R}_0 - 1) \delta_2 \tag{1.5.19}$$

We claim that if (U^+, W^+) in $\text{Int}(\mathbb{R}_+^2)$ is a solution of the system of quadratic equations

$$\Psi(U, W) = c_{22}a_3 \quad \text{and} \quad \Psi(W, U) = c_{22}a_3 \quad (1.5.20)$$

Then $U^+ = W^+$. Let $\Phi(\xi)$ be as in (1.5.8) in the proof of Theorems 1.2.4 and 1.2.5 (and recall its properties). Then $\Psi(\bar{x}_3, \bar{x}_3) = \Phi(\bar{x}_3) = c_{22}a_3$. Hence $(U, W) = (\bar{x}_3, \bar{x}_3)$ is a solution of (1.5.20).

Let γ_1 be the graph of the first equation in (1.5.20) in the UW -plane and suppose first that $c_{22}c_{33} > c_{23}c_{32}$. Then γ_1 is a parabola that opens downward with its vertex in the left half-plane. Let A be the W -intercept of γ_1 . Letting $U = 0$, we obtain

$$\Psi(0, A) = c_{22}a_3 \implies c_{23}R_0\delta_2A = R_0\delta_2(R_0 - 1)\delta_2 + c_{22}a_3 \quad (1.5.21)$$

Equation (1.2.5) and the relation $a_3 \geq 0$ imply that $A \geq k^*$. The positivity of A implies that the vertex of γ_1 lies in the second quadrant and that γ_1 has a unique positive U -intercept, say at B . The curve γ_1 meets the line $W = U$ at two points: (\bar{x}_3, \bar{x}_3) and (C, C) with $C < 0$. The second equation in (1.5.20) defines a second parabolic curve γ_2 . By symmetry, its graph is the reflection of γ_1 about the line $W = U$, and so it opens to the left, its vertex lies in the fourth quadrant, its U -intercept is at A , its positive W -intercept is at B , and it meets the line $W = U$ at (\bar{x}_3, \bar{x}_3) and (C, C) . Since γ_1 and γ_2 are distinct parabolas, they can meet at most four times (in general, $W = \alpha U^2 + \beta U + \gamma$ and $U = \alpha W^2 + \beta W + \gamma$ determine a fourth degree polynomial equation). There are three sub-cases to consider. If $A > B$, then γ_1 and γ_2 meet inside the interior of each quadrant. Since there can be at most four points of intersection, it must be that (\bar{x}_3, \bar{x}_3) is the unique intersection in $\text{Int}(\mathbb{R}_+^2)$. If $A < B$, then

γ_1 and γ_2 meet twice: once at (\bar{x}_3, \bar{x}_3) and once at (C, C) . Again, (\bar{x}_3, \bar{x}_3) is the unique intersection in $\text{Int}(\mathbb{R}_+^2)$. Finally, if $A = B$, then γ_1 and γ_2 meet at (\bar{x}_3, \bar{x}_3) , $(A, 0)$, $(0, A)$, and (C, C) . Since there can be at most four points of intersection, (\bar{x}_3, \bar{x}_3) is again the unique intersection in $\text{Int}(\mathbb{R}_+^2)$.

Suppose next that $c_{22}c_{33} = c_{23}c_{32}$. Then γ_1 is a line with negative slope and its W -intercept is again the number A in (1.5.21) satisfying $A \geq k^*$. Let B be the unique positive U -intercept of γ_1 . The second equation in (1.5.20) defines another line γ_2 . By symmetry, its graph is the reflection of γ_1 about the line $W = U$, and so it has negative slope, its U -intercept is at A and its positive W -intercept is at B . The relation $\Psi(B, 0) = c_{22}a_3$ implies that

$$[c_{22}\delta_3 + c_{32}(\mathbf{R}_0 - 1)\delta_2]B = \mathbf{R}_0\delta_2(\mathbf{R}_0 - 1)\delta_2 + c_{22}a_3 = c_{22}(a_3^* - a_3^\circ + a_3) < c_{22}a_3^*$$

Here, we used the fact that $a_3 < a_3^\circ$. On the other hand, the relation $c_{22}c_{33} = c_{23}c_{32}$ and (1.2.5) imply that

$$[c_{22}\delta_3 + c_{32}(\mathbf{R}_0 - 1)\delta_2]B = c_{22}\left[\delta_3 + c_{33}\frac{(\mathbf{R}_0 - 1)\delta_2}{c_{23}}\right]B = (\delta_3 + c_{33}k^*)B$$

Thus, $B(\delta_3 + c_{33}k^*) < a_3^*$. In view of (1.2.5), it must be that $B < k^*$. That is, $B < A$. Hence, the lines γ_1 and γ_2 meet exactly once in $\text{Int}(\mathbb{R}_+^2)$. By the previous remarks, it must be that they meet at (\bar{x}_3, \bar{x}_3) .

It follows from these considerations that $u_3^\infty = w_3^\infty$. Equation (1.5.18) implies that $u_1^\infty = w_1^\infty$ and $u_2^\infty = w_2^\infty$. That is, $\mathbf{u}^\infty = \mathbf{w}^\infty$. As mentioned earlier, it follows that $\mathbf{x}_* = \mathbf{x}^* = \bar{\mathbf{x}}$ and hence $\mathbf{x}(t) \rightarrow \bar{\mathbf{x}}$ as $t \rightarrow \infty$. That is, the basin of attraction for $\bar{\mathbf{x}}$ is \mathbb{R}_+^3 minus the x_3 -axis. This result and Theorem 1.2.8 together imply that $\bar{\mathbf{x}}$ is GAS relative to \mathbb{R}_+^3 minus the x_3 -axis.

1.5.9 Proof of Theorem 1.2.11

Let $a_1 > 0$ or $a_2 > 0$. We first show that system (1.2.1) is point dissipative, i.e., there exists a compact subset \mathfrak{L} of \mathbb{R}_+^3 with the property that if $\mathbf{x}(t) = (x_1(t), x_2(t), x_3(t))$ is a solution of (1.2.1) with $\mathbf{x}(0) \geq 0$, then $\mathbf{x}(t) \in \mathfrak{L}$ for t sufficiently large. Theorem 1.2.2 states that if $\mathbf{x}(0)$ is on the boundary, then $\mathbf{x}(t)$ immediately enters the positive cone. Thus, we may restrict attention to solutions $\mathbf{x}(t)$ that start inside the positive cone. Recall from the proof of Theorem 1.2.2 that $\mathbf{x}(t)$ is dominated from above by the solution $\mathbf{v}(t) = (v_1(t), v_2(t), v_3(t))$ of the comparison system

$$\begin{aligned} \dot{v}_1 &= bv_2 + a_1 - v_1(\delta_1 + 2m), & v_1(0) &= x_1(0) \\ \dot{v}_2 &= mv_1 + a_2 - v_2(\delta_2 + c_{22}v_2), & v_2(0) &= x_2(0) \\ \dot{v}_3 &= mv_1 + a_3 - v_3(\delta_3 + c_{33}v_3), & v_3(0) &= x_3(0) \end{aligned} \tag{1.5.22}$$

That is, $\mathbf{0} \leq \mathbf{x}(t) \leq \mathbf{v}(t)$ for $t \geq 0$ (it was also established that $\mathbf{v}(t)$ exists for all time). It suffices to show that the comparison system (1.5.22) has a positive equilibrium $\bar{\mathbf{v}}$ in \mathbb{R}_+^3 that attracts all solutions that start in the positive cone. The result that (1.2.1) is point dissipative will then follow by taking \mathfrak{L} to be the box having one corner at the origin and another corner at $\bar{\mathbf{v}} + (\epsilon, \epsilon, \epsilon)$ with $\epsilon > 0$. Lemma 1.4.4 implies that every trajectory $(v_1(t), v_2(t))$ approaches $P(\bar{v}_1, \bar{v}_2)$ as $t \rightarrow \infty$ where $\bar{v}_1 > 0$ and $\bar{v}_2 > 0$ satisfy $b\bar{v}_2 + a_1 = \bar{v}_1(\delta_1 + 2m)$ and $m\bar{v}_1 + a_2 = \bar{v}_2(\delta_2 + c_{22}\bar{v}_2)$. It remains to determine the behavior of $v_3(t)$. Given a small $\epsilon > 0$ there exists $T > 0$ such that $\bar{v}_1 - \epsilon \leq v_1(t) \leq \bar{v}_1 + \epsilon$ and $\bar{v}_2 - \epsilon \leq v_2(t) \leq \bar{v}_2 + \epsilon$ for $t \geq T$. Therefore, $m(\bar{v}_1 - \epsilon) + a_3 - v_3(\delta_3 + c_{33}v_3) \leq \dot{v}_3 \leq m(\bar{v}_1 + \epsilon) + a_3 - v_3(\delta_3 + c_{33}v_3)$ for $t \geq T$. Also,

\dot{v}_3 is a continuous function of v_1 (which is itself a continuous function of t) and v_3 . Lemma 1.4.1 implies that $\bar{u} \leq \liminf_{t \rightarrow \infty} v_3(t) \leq \limsup_{t \rightarrow \infty} v_3(t) \leq \bar{w}$ where \bar{u} and \bar{w} are the unique positive numbers such that $m(\bar{v}_1 - \epsilon) + a_3 = \bar{u}(\delta_3 + c_{33}\bar{u})$ and $m(\bar{v}_1 + \epsilon) + a_3 = \bar{w}(\delta_3 + c_{33}\bar{w})$. Since ϵ is arbitrary, it must be that $\bar{v}_3 \leq \liminf_{t \rightarrow \infty} v_3(t) \leq \limsup_{t \rightarrow \infty} v_3(t) \leq \bar{v}_3$ where \bar{v}_3 is the unique positive number such that $m\bar{v}_1 + a_3 = \bar{v}_3(\delta_3 + c_{33}\bar{v}_3)$. That is, $v_3(t) \rightarrow \bar{v}_3$ as $t \rightarrow \infty$. Letting $\bar{\mathbf{v}} = (\bar{v}_1, \bar{v}_2, \bar{v}_3)$, it follows from the remarks above that $\mathbf{v}(t) \rightarrow \bar{\mathbf{v}}$ as $t \rightarrow \infty$ whenever $\mathbf{x}(0)$ is in $\text{Int}(\mathbb{R}_+^3)$. This completes the argument that system (1.2.1) is point dissipative.

We now restrict attention to the situation in which $c_{23} = 0$. In this case, recall from Theorem 1.2.6 that there is a unique positive equilibrium $\bar{\mathbf{x}} = (\bar{x}_1, \bar{x}_2, \bar{x}_3)$ whose coordinates satisfy (1.2.2). We will show that the basin of attraction for $\bar{\mathbf{x}}$ is \mathbb{R}_+^3 . As before, if $\mathbf{x}(0)$ is on the boundary, then $\mathbf{x}(t)$ immediately enters the positive cone. Thus, we may restrict attention to solutions $\mathbf{x}(t)$ that start in $\text{Int}(\mathbb{R}_+^3)$. As $c_{23} = 0$, the first two equations in system (1.2.1) decouple from the third, and so we may consider them in isolation

$$\begin{aligned} \dot{x}_1 &= bx_2 + a_1 - x_1(\delta_1 + 2m), & x_1(0) &\geq 0 \\ \dot{x}_2 &= mx_1 + a_2 - x_2(\delta_2 + c_{22}x_2), & x_2(0) &\geq 0 \end{aligned}$$

Lemma 1.4.4 implies that every trajectory $(x_1(t), x_2(t))$ approaches $P(\bar{x}_1, \bar{x}_2)$ as $t \rightarrow \infty$. That is, $x_1(t) \rightarrow \bar{x}_1$ and $x_2(t) \rightarrow \bar{x}_2$ as $t \rightarrow \infty$. We now show that $x_3(t) \rightarrow \bar{x}_3$ as $t \rightarrow \infty$. Given $\epsilon > 0$ there exists $T > 0$ such that $\bar{x}_1 - \epsilon \leq x_1(t) \leq \bar{x}_1 + \epsilon$ and $\bar{x}_2 - \epsilon \leq x_2(t) \leq \bar{x}_2 + \epsilon$ for $t \geq T$. Therefore, $m(\bar{x}_1 - \epsilon) + a_3 - x_3\{\delta_3 + c_{32}(\bar{x}_2 + \epsilon) + c_{33}x_3\} \leq \dot{x}_3 \leq m(\bar{x}_1 + \epsilon) + a_3 - x_3\{\delta_3 + c_{32}(\bar{x}_2 - \epsilon) + c_{33}x_3\}$ for $t \geq T$. Lemma 1.4.1 implies that $\bar{u} \leq \liminf_{t \rightarrow \infty} x_3(t) \leq \limsup_{t \rightarrow \infty} x_3(t) \leq \bar{w}$ where \bar{u} and \bar{w} are the unique positive numbers such that $m(\bar{x}_1 - \epsilon) + a_3 = \bar{u}\{\delta_3 + c_{32}(\bar{x}_2 + \epsilon) + c_{33}\bar{u}\}$ and

$m(\bar{x}_1 + \epsilon) + a_3 = \bar{w}\{\delta_3 + c_{32}(\bar{x}_2 - \epsilon) + c_{33}\bar{w}\}$. However, ϵ is arbitrary, so it must be that $\bar{x}_3 \leq \liminf_{t \rightarrow \infty} x_3(t) \leq \limsup_{t \rightarrow \infty} x_3(t) \leq \bar{x}_3$. Here, we use the fact that the limiting equations for \bar{u} and \bar{w} as $\epsilon \rightarrow 0$ coincide with the equation for \bar{x}_3 in (1.2.2). Thus, $x_3(t) \rightarrow \bar{x}_3$ as $t \rightarrow \infty$. It follows from these considerations that $\mathbf{x}(t) \rightarrow \bar{\mathbf{x}}$ as $t \rightarrow \infty$. That is, the basin of attraction for $\bar{\mathbf{x}}$ is \mathbb{R}_+^3 . This result and Theorem 1.2.9 together imply that $\bar{\mathbf{x}}$ is GAS.

1.6 Discussion

We have assumed that all parameters are time-independent. While this is common among the cited models, most feral populations do experience seasonally varying environments [28, 42]. During winter, birth and death rates may change, decreasing and increasing respectively. During non-breeding seasons territoriality decreases [28]. Since many of the colonies we hope to model are urban in nature, many of the parameters could potentially be functions of human intervention. Pet cats may be kept inside more (and so decrease their influence). Control efforts might slow down during seasons where that work is more difficult. Humans may be more likely to abandon their pets during specific times of year (perhaps at the end of an academic year) and so influence abandonment rates. The schedules of trash pick-up would influence the availability of food and so influence competition (c_{ij}). Increases in road traffic during tourist seasons may increase death rates (d_i). Future work may incorporate time-dependent parameters to attempt to account for these complexities.

Literature suggests that while an equal numbers of males and females are born [28], male and female kittens do not reach reproductive maturity at the same age [28]. In this work, assumptions (A1) and (A3), imply that kittens are born effectively genderless and leave the kitten class at equal rates. This replicates the former detail but not the latter. Future work may have two classes of kitten, one for each gender, each of which with its own maturation rate.

We have assumed that adult females will always find mates. This justifies assumptions (A1), that is, that the birth rate is proportional to the adult female density and independent of the density of adult males. Assumption (A7) implies that adult male house cats are constantly present, which enforces assumption (A1), even in the case where the initial conditions include no adult males. In very small populations or in populations with no native house cats (a case not covered in our model), this assumption may fail. Thus our results are not expected to be observed in populations within cases [30,50]. Future work may utilize a more complex birth rate, such as a rate which is an increasing but saturating function of x_3 such that the birth rate is zero if $x_3 = 0$. An example of such a birth rate is $b = \tilde{b} \frac{x_3}{x_3 + v}$ for $\tilde{b}, v > 0$.

Assumption (A8) states that abandoned house-cats immediately become feral. In reality, these members may never fully integrate with the population of ferals. They may live longer or be less aggressive than their feral counterparts and their friendlier nature may even make them more susceptible to control methods. Future work may include additional compartments for these semi-feral cats.

Assumption (A3) implies that death rates of adults include the density-dependent Lotka-Volterra type interaction terms, which is common in the cited models. Our model has four such terms. As with all Lotka-Volterra based models, it is difficult to measure the introduced coefficients from biological data. Moreover, it is unclear if this form is sufficiently accurate or whether these interactions can be modeled simultaneously using the same types of terms. In addition, we have assumed that competition rates for kittens is negligible. This may not be the case, and a more general model may include this term. To complicate matters further, familiar females have been known to act collaboratively, such as group defense of resources or communal litters. Hence, it is possible that death rates of kittens may be a decreasing function of the number of adult females and the per-capita death and competition rates of adult females may be a more complicated function of the state variables [31].

The only form of control this model addresses is that of removal, wherein an animal is removed from the population, which manifests as an increase in the effective death rates of the sub-population being targeted. Two issues arise here. First, assumption (A4) states that the per-capita removal rates (s_i) are independent of the feral populations they affect. However, the ability of humans to handle large populations in this way may not be realistic. In addition, when populations are very small, enacting control on the remaining residents might become implausible. Future work could incorporate a more complex per-capita which addresses these concerns. We suggest that the per-capita removal rate be an increasing but saturating function of the targeted population. An example might be $s_i = \frac{\tilde{s}_i x_i}{x_i + v}$ for some positive v . The second issue is that other forms of control are common, such as prophylaxis,

which functionally exchanges a reproductive member for a non-reproductive one. A possible approach might be to include additional compartments for non-reproductive members. The most common form of prophylaxis, spay and neuter, has been noted to change the behavior of the animals markedly, and so these members might have lower competition coefficients than their unaltered counterparts. We conjecture that the impact of these changes would be to increase the net population, in accordance with other models and observations of real populations [40, 51, 52].

The colonies addressed in this work often do not exist in isolation and the model does not account for the mobile nature of males, who may interact with two or more groups of females who themselves never interact [28, 31, 41]. Chapter 2 will address this by including a patch-structure in which males are permitted to interact with multiple patches while females and their young remain in their native patch. Questions regarding the persistence of a patch in the presence of other patches will be addressed.

A main objective of this study is to support a larger study of disease ecology in the population. Chapter 3 will begin this discussion by introducing an SIR-type model with three state variables to track the infection status for each state variable presented in this work. There has been extensive work on the modeling of disease in this population [34–38], but the majority of these works described the population with a single state variable, with the few exceptions [39]. Since life-stage and gender are strong indicators of behavior which may be relevant to disease modeling, using the model presented here as the underlying ecology

model may allow for vaccination strategies which one gender is favored over another in what we are referring to as a “gender-informed” strategy.

If both the epidemiological and spatial aspect are addressed, future work might be to construct a hybrid model of both extensions. Questions regarding the interplay between spatial and social behavior with the spread of disease could be addressed. Moreover, it could be seen if the strategies developed in the single-patch disease model would still apply in the presence of other patches or if a network would promote the disease, as is common in such disease models. The effectiveness of single-population vaccination strategies could be explored when applied to a set of populations. Ultimately, a strategy for a larger set of patches, such as a large city, could be explored.

CHAPTER 2

THE PATCH MODEL

2.1 Introduction

As was discussed in Chapter 1, populations of feral cats around the world have had tremendous impacts on local ecologies (in particular on islands) [2, 13]. These animals are thought to pose threats as predators on local wildlife as well as competitors with local predators for shared prey. Feral cats have played a part in numerous population extinctions and near extinctions. A recent meta-analysis of the impacts of invasive mammalian predators established a link between free-roaming cats to the extinction of 63 different animals and the endangered status of 430 more [9]. For example, since their introduction in 1810, free-roaming cats (along with rabbits) are blamed for eliminating a native parakeet on the Australian territory of Macquarie Island (though other animals may have also played a role) [10]. Since their introduction in 1888, free-roaming cats (along with black rats and yellow crazy ants) have been blamed for the extinction four or five species of mammal on the Australian territory of Christmas Island [11]. Numerous other examples also exist [5–8, 12, 13]. Estimates to the economical impact of the presence of free-roaming cats to the US has been estimated to be as high as \$17 billion per year [13]. In addition to all this, free-roaming these animals also pose

an indirect threat as vectors of diseases, which affect local wildlife [14, 15], pet animals [1], and humans [1, 3, 16–19].

Concerns over the impact of free-roaming cats have lead many communities to enact plans to remove them entirely. The removal techniques which tend to be fastest are typically lethal (e.g., hunting, trapping [21], and poisoning [22]), though they are difficult to justify to the public who view them as pet animals. Conversely the techniques which are regarded as more humane (e.g., trap-neuter-release or trap-adopt) take much longer and are more expensive. In addition, debate continues on efficacy of these methods. [4, 13, 21, 23–26]. The key to appropriately managing these populations is understanding their dynamics.

Consider the Swedish population described in [44]. In this population, females were described to live in alone or in matrilineal colonies. These adult females remained in their colonies and rarely interacted with the members of other colonies. These colonies were described as small, localized around some human settlement or some “clumped” resource such as food or shelter. Adult males, however, were seen to have much larger home-ranges which included one or more groups of females, presumably to maximize reproductive success [28, 53]. Similarly, a population on the Japanese territory of of Ainoshima Island which has over 200 members in two large colonies, centralized around fish dumps. As above, adult males were the only individuals who were found to move between patches. In this work, we shall consider similar similar populations.

These cases illustrate common trends in feral cat behavior. Adult females, along with their immature offspring, tend to form groups around a shared resource such as shelter or

sources of food (e.g., trash containing food waste or food-providing well-wishers). These cats have a large degree of overlap with each other, but very little with members of other groups. Adult males are more nomadic, and tend to have home ranges which include one or more such groups of females [31, 41, 54–57].

Here, we build upon the work in Chapter 1 and propose a spatial model for feral cat population dynamics in the absence of abandonment of house-cats. In Section 2.2 we describe the assumptions of the model and the system of differential equations they imply as well as the the main results of our analysis with a focus on the existence, uniqueness and stability of steady states. In Section 2.3 we interpret selected composite parameters and theorems biologically. In Section 2.4 we provide proofs for the selected theorems. In Section 2.5 we detail the weaknesses of the model as well possible directions for future work to address those weaknesses.

2.2 Mathematical model

2.2.1 Description

As in Chapter 1, there are kittens ($i = 1$), adult females ($i = 2$), and adult males ($i = 3$). Let $x_{ij}(t)$ be the density of feral cats of type $i = 1, 2$ in patch $j = 1, 2, \dots, p$ (or ij -cats) at time $t \geq 0$ and let $x_3(t)$ be the density of feral adult males at time $t \geq 0$. We assume there are $p \geq 2$ patches and we denote the set of patches as $\Omega = \{1, 2, \dots, p\}$. Assume the following:

(B1) Only feral adult males move between patches.

(B2) A fixed proportion $g_j \in (0, 1)$ of feral adult males are in patch j at all times.

(B3) A fixed proportion $g_0 \in [0, 1)$ of feral adult males are in transit between patches at all times.

(B4) The constants g_j satisfy: $g_0 + g_1 + g_2 + \cdots + g_p = 1$.

Assumptions (B1) through (B4) detail the special way in which adult males move between patches. Specifically, when there are a total of x_3 males in the system, a fixed proportion g_j of these feral adult males will always be present in patch j , experiencing the competition, the removal and death rates of that patch. For convenience, we refer to adult males in patch j as $3j$ -cats.

(B5) Feral adult females in patch j produce feral kittens at rate $b_j > 0$.

(B6) The intrinsic death rate for feral ij -cats is $d_{ij} > 0$ for $i = 1, 2, 3$.

(B7) Feral kittens mature into feral adults of each sex at per-capita rate $m > 0$.

(B8) Feral ij -cats are removed from the population at per-capita rate $s_{ij} \geq 0$ for $i = 1, 2, 3$.

(B9) The competitive effect of feral adult ij -cats on feral adult kj -cats is $c_{ikj} \geq 0$ for $i, k = 2, 3$.

(B10) The competition coefficient $c_{iij} > 0$ for $i = 2, 3$.

(B11) The density of house ij -cats is $n_{ij} > 0$.

(B12) The competitive effect of adult house kj -cats on feral adult ij -cats is $e_{ikj} \geq 0$ for $i, k = 2, 3$.

The comments in Chapter 1 with regard to the analogous assumptions are still generally applicable. Assumptions (B1) to (B12) produce an initial value problem

$$\begin{aligned} \dot{x}_{1j} &= b_j x_{2j} - x_{1j} (d_{1j} + s_{1j} + 2m), & x_{1j}(0) &\geq 0 \\ \dot{x}_{2j} &= m x_{1j} - x_{2j} (d_{2j} + s_{2j} + c_{22j} x_{2j} + c_{23j} g_j x_3 + e_{22j} n_{2j} + e_{23j} n_{3j}), & x_{2j}(0) &\geq 0 \\ \dot{x}_3 &= \sum_{j=1}^p \{m x_{1j} - g_j x_3 (d_{3j} + s_{3j} + c_{32j} x_{2j} + c_{33j} g_j x_3 + e_{32j} n_{2j} + e_{33j} n_{3j})\}, & x_3(0) &\geq 0 \end{aligned} \quad (\text{C})$$

There are total of $2p + 1$ equations (the first 2 hold for $j \in \Omega$). See Table 2.1 for a description of all variables and parameters.

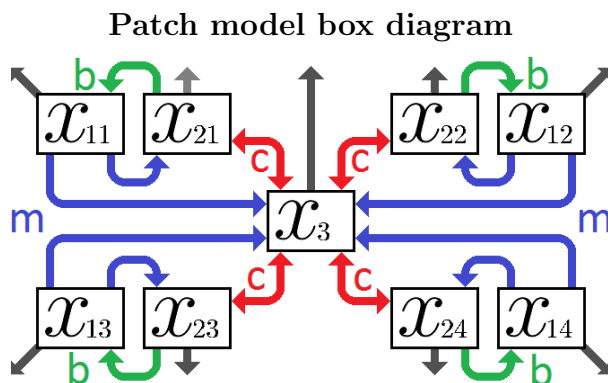


Figure 2.1: A box-diagram visualization of system (2.2.1) with $p = 4$.

In keeping with Chapter 1, we introduce a notation for the effective death rate for each category

$$\delta_{1j} = d_{1j} + s_{1j}, \quad \delta_{2j} = d_{2j} + s_{2j} + e_{22j} n_{2j} + e_{23j} n_{3j}, \quad \text{and} \quad \delta_3 = d_{3j} + s_{3j} + e_{32j} n_{2j} + e_{33j} n_{3j} \quad (\text{D})$$

The initial value problem can thus be stated as

$$\dot{x}_{1j} = b_j x_{2j} - x_{1j}(\delta_{1j} + 2m), \quad x_{1j}(0) \geq 0 \quad (2.2.1a)$$

$$\dot{x}_{2j} = m x_{1j} - x_{2j}(\delta_{2j} + c_{22j} x_{2j} + c_{23j} g_j x_3), \quad x_{2j}(0) \geq 0 \quad (2.2.1b)$$

$$\dot{x}_3 = \sum_{j=1}^p \{m x_{1j} - g_j x_3(\delta_{3j} + c_{32j} x_{2j} + c_{33j} g_j x_3)\}, \quad x_3(0) \geq 0 \quad (2.2.1c)$$

Again, this represents a total of $2p + 1$ equations. Table 2.1 describes the variables and parameters (and see Figure 2.1).

Numerical simulations of system (2.2.1)

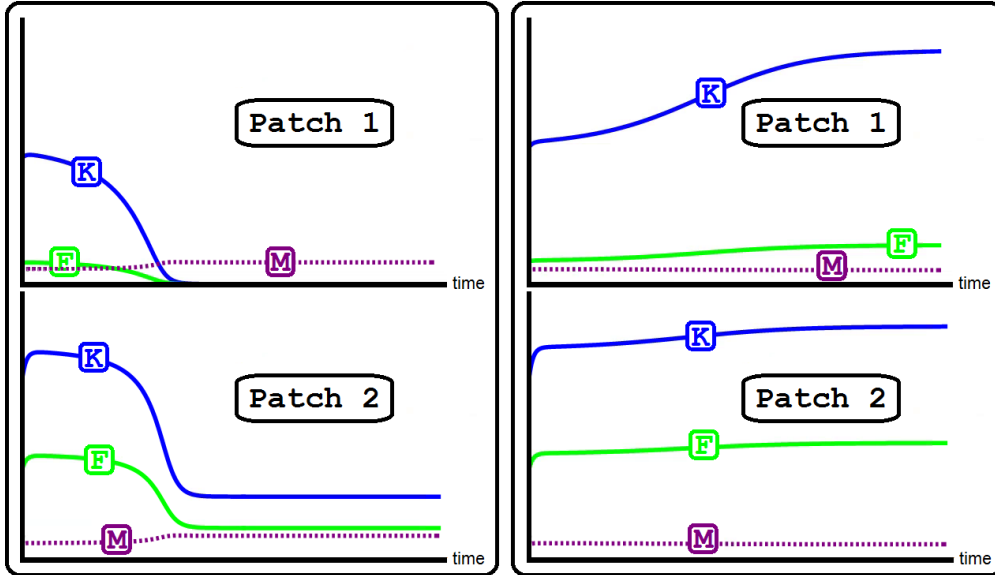


Figure 2.2: Small changes in initial conditions can alter the asymptotic behavior of System (2.2.1). The parameter values used here are:

$m = 10, \delta_{11} = 16, \delta_{12} = 5, \delta_{21} = 59.3, \delta_{22} = 19.3, \delta_{31} = .4, \delta_{32} = .02, c_{221} = 0.00482736, c_{222} = 0.02,$
 $c_{231} = 0.075, c_{232} = 0.2, c_{321} = 9, c_{322} = 0.9, c_{331} = 0.117188, c_{332} = 5, g_1 = .8, g_2 = .2$

Table 2.1: Quantities associated with models (C) and (2.2.1)

Quantity	Description (type)	Units	Equation
t	time	time	(C)
p	number of patches	none	(C)
Ω	set of patches: $\{1, 2, \dots, p\}$	none	(C)
x_{ij}	density of feral ij -cats ($i = 1, 2$)	cat	(C)
x_3	density of feral adult males	cat	(C)
n_i	density of house ij -cats	cat	(C)
g_0	proportion of feral adult males in transit	none	(C)
g_j	proportion of feral adult males in patch j	none	(C)
b_j	kitten birth rate in patch j	kitten \cdot adult $^{-1} \cdot$ time $^{-1}$	(C)
m	kitten maturation rate	adult \cdot kitten $^{-1} \cdot$ time $^{-1}$	(C)
d_{ij}	intrinsic death rate of feral adult ij -cats	time $^{-1}$	(C)
s_{ij}	control rate of feral ij -cats	time $^{-1}$	(C)
c_{ikj}	effect of feral adult kj -cats on feral adult ij -cats	adult $^{-1} \cdot$ time $^{-1}$	(C)
e_{ikj}	effect of house adult kj -cats on feral adult ij -cats	adult $^{-1} \cdot$ time $^{-1}$	(C)
δ_{ij}	effective death rate of feral ij -cats	time $^{-1}$	(D)

Table 2.2: Quantities associated with models (C) and (2.2.1).

Quantity	Description (type)	Units	Equation
\bar{x}_{ij}	equilibrium density of ij -cats	cat	(2.4.1)
\bar{x}_3	equilibrium density of adult males	cat	(2.4.1c)
R_j	patch reproduction number	none	(2.2.2a)
Q	a subset of Ω	none	
\bar{Q}	set of steady states with support Q	none	(2.2.2c)
$\overline{\bar{Q}}$	set of LAS steady states with support Q	none	(2.2.2c)
$k_j^*, k_Q^{*-}, k_Q^{*+}$	threshold equilibrium density of adult males	cat	(2.2.2a) and (2.2.2b)
$\phi_j(Q)$	indicator function for subset Q	none	(2.2.2c)
$A(Q), B(Q), C(Q)$	composite parameters	(cat · time) ⁻¹	(2.2.3a)

2.2.2 Statement of main results

This section is dedicated to the main properties of system (2.2.1). Their biological interpretations appear in Section 2.3 and their proofs are found in Section 2.4. First we introduce notation for some necessary sets. Define

$$\mathbb{R}^n = \{(u_1, u_2, \dots, u_n) : u_1, u_2, \dots, u_n \in \mathbb{R}\},$$

$$\mathbb{R}_+^n = \{(u_1, u_2, \dots, u_n) : u_1 \geq 0, u_2 \geq 0, \dots, u_n \geq 0\},$$

$$\text{Int}(\mathbb{R}_+^n) = \{(u_1, u_2, \dots, u_n) : u_1 > 0, u_2 > 0, \dots, u_n > 0\}.$$

We refer to the set \mathbb{R}_+^n as the *non-negative cone* and to its elements as *non-negative*.

We refer to $\text{Int}(\mathbb{R}_+^n)$ as the *positive cone* and to its elements as *positive*. We refer to the set

$\partial\mathbb{R}_+^n$ as the *boundary*. For $\mathbf{u}, \mathbf{v} \in \mathbb{R}^n$, we say that $\mathbf{u} \geq \mathbf{v}$ if $\mathbf{u} - \mathbf{v} \in \mathbb{R}_+^n$, $\mathbf{u} > \mathbf{v}$ if $\mathbf{u} - \mathbf{v} \in \mathbb{R}_+^n - \{\mathbf{0}\}$ and $\mathbf{u} \gg \mathbf{v}$ if $\mathbf{u} - \mathbf{v} \in \text{Int}(\mathbb{R}_+^n)$. Since our attention will be focused mostly on $n = 2p + 1$, we enumerate the elements of a vector $\mathbf{u} \in \mathbb{R}^{2p+1}$ in the following (non-standard) way:

$$\mathbf{u} = (u_{11}, u_{21}, u_{12}, u_{22}, \dots, u_{1p}, u_{2p}, u_3).$$

Notice that such a vector has the form (kittens, adult females, kittens, adult females, ... kittens, adult females, adult males). That is, the first subscript refers to the type of cat the state variable represents ($i = 1, 2, 3$) and the second subscript, if any, refers to the patch (j). Define the set $T_{ij} = \{\mathbf{u} \in \mathbb{R}_+^{2p+1} : u_{ij} = 0\}$ for $i = 1, 2$ and $j \in \Omega$. Note that T_{ij} is the set in which ij -cats are absent. Let $\mathbf{x}(t) = (x_{11}, x_{21}, x_{12}, x_{22}, \dots, x_{1p}, x_{2p}, x_3)(t)$ denote a solution to (2.2.1).

Theorem 2.2.1. *For system (2.2.1), the following results hold:*

- (a) *A solution $\mathbf{x}(t)$ exists for all time. Moreover, it is unique, non-negative, and bounded.*
- (b) *The non-negative x_3 -axis is a forward invariant set.*
- (c) *If $\mathbf{x}(0) \in T_{1j} \cap T_{2j}$, then the solution $\mathbf{x}(t)$ remains there for all time.*
- (d) *If $\mathbf{x}(0) \in (T_{1j} \cup T_{2j}) \setminus (T_{1j} \cap T_{2j})$, then the solution $\mathbf{x}(t)$ immediately leaves $T_{1j} \cup T_{2j}$.*
- (e) *If $\mathbf{x}(0)$ is positive, then the solution $\mathbf{x}(t)$ remains positive for all time.*

The proof of this theorem is essentially the same as that of the proof of Theorem 1.2.1, found in Chapter 1. The next several theorems describe the number of steady states

and their properties. A *steady state* is a constant vector $\bar{\mathbf{x}} = (\bar{x}_{11}, \bar{x}_{21}, \bar{x}_{12}, \bar{x}_{22}, \dots, \bar{x}_{1p}, \bar{x}_{2p}, \bar{x}_3)$ in \mathbb{R}_+^{2p+1} that is a solution of (2.2.1). We refer to a steady state $\bar{\mathbf{x}}$ as *trivial* if $\bar{\mathbf{x}} = \mathbf{0}$ and we refer to $\bar{\mathbf{x}}$ as *nontrivial* otherwise. As in Chapter 1, we continue to refer to locally asymptotically stable steady states as LAS. For a steady state $\bar{\mathbf{x}}$, we define the support of $\bar{\mathbf{x}}$ as $\text{supp}(\bar{\mathbf{x}}) = \{j : \bar{\mathbf{x}} \notin T_{1j} \cap T_{2j}\}$. Define the composite parameters:

$$R_j = \frac{b_j m}{(\delta_{1j} + 2m)\delta_{2j}} \quad \text{and} \quad k_j^* = \frac{(R_j - 1)\delta_{2j}}{c_{23j}g_j} \quad \text{for } j \in \Omega \quad (2.2.2a)$$

If $c_{23j} = 0$, then we make the convention that if $R_j < 1$, then $k_j^* = -\infty$; if $R_j = 1$, then $k_j^* = 0$; and if $R_j > 1$, then $k_j^* = \infty$.

For a subset $Q \subset \Omega$, define

$$k_Q^{*-} = \min \{k_j^* : j \in Q\}, \quad k_Q^{*+} = \max \{k_j^* : j \notin Q\}. \quad (2.2.2b)$$

If $Q = \emptyset$, we define $k_Q^{*-} = \infty$ and if $Q = \Omega$, we define $k_Q^{*+} = -\infty$.

Given a subset $Q \subset \Omega$, define

$$\bar{Q} = \{\bar{\mathbf{x}} \in \mathbb{R}_+^{2p+1} : \text{supp}(\bar{\mathbf{x}}) = Q\} \quad \text{and} \quad \overline{\bar{Q}} = \{\bar{\mathbf{x}} \in \bar{Q} : \bar{\mathbf{x}} \text{ is LAS}\} \quad (2.2.2c)$$

and

$$A(Q) = \sum_{j=1}^p \left(\frac{c_{22j}c_{33j} - \phi_j(Q)c_{23j}c_{32j}}{c_{22j}} \right) g_j^2, \quad (2.2.3a)$$

$$B(Q) = \sum_{j=1}^p \left(\delta_{3j} + \phi_j(Q) \frac{c_{32j}(R_j - 1)\delta_{2j} + c_{23j}R_j\delta_{2j}}{c_{22j}} \right) g_j, \quad (2.2.3b)$$

$$C(Q) = \sum_{j=1}^p \phi_j(Q) \frac{R_j\delta_{2j}(R_j - 1)\delta_{2j}}{c_{22j}}. \quad (2.2.3c)$$

where $\phi_j(Q)$ is the indicator function for Q : $\phi_j(Q) = 1$ for $j \in Q$ and $\phi_j(Q) = 0$ for $j \notin Q$.

Theorem 2.2.2. *For system (2.2.1), the following results hold:*

- (a) *The system always admits a trivial steady state $\bar{\mathbf{x}} = \mathbf{0}$.*
- (b) *If $\bar{\mathbf{x}}$ is a steady state and $\bar{x}_3 = 0$, then $\bar{\mathbf{x}} = \mathbf{0}$.*
- (c) *If $\bar{\mathbf{x}}$ is a steady state and $\text{supp}(\bar{\mathbf{x}}) = \emptyset$, then $\bar{\mathbf{x}} = \mathbf{0}$.*
- (d) *If $\bar{\mathbf{x}}$ is a steady state, then $R_j > 1$ for all $j \in \text{supp}(\bar{\mathbf{x}})$.*
- (e) *If $R_j \leq 1$ for all $j \in \Omega$, then $\bar{\mathbf{x}} = \mathbf{0}$ is the unique steady state.*
- (f) *If $Q \subseteq \Omega$ and $\bar{\mathbf{x}} \in \bar{Q}$, then $0 \leq \bar{x}_3 < k_Q^-$.*
- (g) *If $Q \subseteq \Omega$ and $c_{23j} = 0$ for all $j \in Q$, then $|\bar{Q}| = 1$.*
- (h) *If $\emptyset \neq Q \subset \Omega$, $A(Q) \geq 0$ and $A(Q)(k_Q^{**})^2 + B(Q)k_Q^{**} > C(Q)$, then $|\bar{Q}| = 1$.*
- (i) *If $\emptyset \neq Q \subset \Omega$, $A(Q) \geq 0$ and $A(Q)(k_Q^{**})^2 + B(Q)k_Q^{**} \leq C(Q)$, then $|\bar{Q}| = 0$.*
- (j) *If $\emptyset \neq Q \subset \Omega$, $A(Q) < 0$ and $A(Q)(k_Q^{**})^2 + B(Q)k_Q^{**} > C(Q)$, then $|\bar{Q}| = 1$.*
- (k) *If $\emptyset \neq Q \subset \Omega$, $A(Q) < 0$ and $A(Q)(k_Q^{**})^2 + B(Q)k_Q^{**} < C(Q)$, then $|\bar{Q}| \leq 2$.*
- (l) *If $\emptyset \neq Q \subset \Omega$, $A(Q) < 0$ and $A(Q)(k_Q^{**})^2 + B(Q)k_Q^{**} = C(Q)$, then $|\bar{Q}| \leq 1$.*

Theorem 2.2.3. *The following stability results hold for system (2.2.1):*

- (a) *If $R_j < 1$ for all $j \in \Omega$, then $\bar{\mathbf{x}} = \mathbf{0}$ is LAS.*
- (b) *If $R_j > 1$ for some $j \in \Omega$, then $\bar{\mathbf{x}} = \mathbf{0}$ is unstable.*

(c) If $Q \subseteq \Omega$ and $\bar{\mathbf{x}} \in \overline{Q}$, then $k_Q^{*+} < \bar{x}_3 < k_Q^{*-}$.

(d) There are at most $p + 1$ subsets $Q \subseteq \Omega$ such that $|\overline{Q}| \geq 1$ and $\sum_{Q \in \Omega} |\overline{Q}| \leq 2(p + 1)$

(e) If $Q \subseteq \Omega$, $\bar{\mathbf{x}} \in \overline{Q}$, and

(i) $b_j < \delta_{j1} + 2m$ for all $j \in Q$,

(ii) $m + c_{23j}g_j\bar{x}_{2j} < \delta_{2j} + 2c_{22j}x_{2j} + c_{23j}g_j\bar{x}_3$ for all $j \in Q$,

(iii) $pm + \sum_{j=1}^p c_{32j}g_j\bar{x}_3 < \sum_{j=1}^p \{\delta_{3j} + c_{32j}g_j\bar{x}_{2j} + 2c_{33j}g_j^2\bar{x}_3\}\bar{x}_3$

then $\bar{\mathbf{x}} \in \overline{Q}$.

We appeal to the same definitions presented in Chapter 1 for classifying steady states as *globally attracting* (GA) and as *globally asymptotically stable* (GAS).

Theorem 2.2.4. *The following results hold:*

(a) If $R_j \leq 1$ for all $j \in \Omega$, then $\bar{\mathbf{x}} = \mathbf{0}$ is GA.

(b) If $R_j < 1$ for all $j \in \Omega$, then $\bar{\mathbf{x}} = \mathbf{0}$ is GAS.

The proof of this theorem is essentially the same as that of Theorem 1.2.3 in the case of $a_3 = 0$ (i.e., $\bar{\mathbf{z}} = \mathbf{0}$). For the final theorem, we consider a system of identical patches. We will also assume adult males spend an equal proportion of their time in every patch. By *identical* we mean that all parameters are equal amongst the patches. For these reason, this theorem, and it's proof, shall omit subscripts, with the exception of R_j , which will be

denoted R_0 . Since we assume that adult males will spend an equal proportion of their time in each patch, $g_j = \frac{1-g_0}{p}$ for all j .

Theorem 2.2.5. *Let $Q \subseteq \Omega$ in a system of identical patches. Then the following results hold:*

(a) *If $Q = \emptyset$ and $R_0 \leq 1$, then $\overline{\overline{Q}} = \{\mathbf{0}\}$.*

(b) *If $Q = \emptyset$ and $R_0 > 1$, then $\overline{\overline{Q}} = \emptyset$.*

(c) *If $Q \neq \emptyset$ and $Q \neq \Omega$, then $\overline{\overline{Q}} = \emptyset$.*

2.3 Biological interpretation of results

Here we interpret the results of the previous section biologically.

2.3.1 The sets Q , \overline{Q} and $\overline{\overline{Q}}$

For a given steady state, let Q be the set of patches which have a positive population of adult females or kittens. This set of patches is called the support of that steady state. Multiple steady states may share a support, and so we denote the set of steady states with support Q as \overline{Q} . We denote the set of stable steady states with support Q as $\overline{\overline{Q}}$.

2.3.2 The sets T_{ij} , $T_{1j} \cup T_{2j}$ and $(T_{1j} \cup T_{2j}) \setminus (T_{1j} \cap T_{2j})$

The set T_{ij} is the set of states for which the density of ij -cats is zero, that is, the density of i -cats in patch j is zero. The set $T_{1j} \cup T_{2j}$ is the set of states for which the density of either adult females or kittens in patch j is zero. The set $(T_{1j} \cup T_{2j}) \setminus (T_{1j} \cap T_{2j})$ is the set of states for which the density of either adult females or kittens (but not both) in patch j is zero.

2.3.3 The patch reproduction number R_j

The role of the patch reproductive number R_j here is analogous to the net reproduction number R_0 in Section 1.3.1. This can be viewed as the maximum number of adult females a single adult female in patch j is capable of producing in the course of her life. This number has similar implications as in Chapter 1. For instance, in Chapter 1, if $R_0 \leq 1$, there was no steady state which had a positive population of adult females or kittens. If, for some j , $R_j \leq 1$ then there is no steady state for which patch j has a positive population of adult females or kittens.

2.3.4 The composite parameters k_j^* , k_Q^{*+} , and k_Q^{*-}

Similar to k^* in Chapter 1, the parameter k_j^* is the number of adult males at equilibrium which prohibits patch j from supporting adult females or kittens. For a given steady state,

k_Q^{*-} is the smallest value of k_j^* of all the patches in the support. Similarly, the largest value of k_j^* of the patches not in the support is denoted k_Q^{*+} .

2.3.5 Theorem 2.2.1

Theorem 2.2.1 confirms that no model population can become negative, or can experience an unending population explosion. If the initial population is composed entirely of adult males (i.e., no patch has a positive population density of adult females or kittens), then these population densities will remain zero. Moreover, if the initial population in any patch has neither adult females nor kittens, that patch's populations will remain this way. However, if an initial population in a patch has only adult females, the density of kittens will immediately become positive. The same holds for an initial population in a patch which has only kittens. Finally, if the initial population is such that all subpopulations are positive, all subpopulations will remain positive.

2.3.6 Theorem 2.2.2 and the composite parameters \mathbf{R}_j , $A(Q)$, $B(Q)$, and $C(Q)$

Theorem 2.2.2 places restrictions on the number and types of steady states which can exist. This theorem focuses attention on the trivial and on nontrivial steady states. The trivial steady state ($\bar{\mathbf{x}} = \mathbf{0}$) is the steady state for which all population densities are zero. These steady states have an empty support. Nontrivial steady states have a nonempty support.

Theorem 2.2.2 states that the model always permits the trivial steady state. Moreover, it is the only steady state for which the density of adult males is zero. A steady state has a zero population density of males must be the trivial steady state. This has several biological interpretations. First, it implies that adult males will be present so long as any other population density is positive.

Theorem 2.2.2 also states that the only patches which can have positive densities at some steady state are those for which the patch reproduction number is large ($R_j > 1$). A direct result of this is that if all patch reproduction numbers are small ($R_j \leq 1$ for all j) then there is no steady state besides the trivial steady state. For any steady state $(\bar{\mathbf{x}})$ the density of adult males (\bar{x}_3) cannot exceed k_Q^{*-} .

The remaining result of the theorem places upper limits on the number of steady states which can exist with support Q . First, if adult females suffer no competition for every patch in the support ($j \in Q$), then there is exactly one positive steady state with support Q . The remaining cases are governed by the relative magnitudes of $A(Q)(k_Q^{*-})^2 + B(k_Q^{*-})$ and $C(Q)$. Specifically, if $A(Q)(k_Q^{*-})^2 + B(k_Q^{*-}) > C(Q)$, then a single nontrivial steady state exists with support Q . If $A(Q)(k_Q^{*-})^2 + B(k_Q^{*-}) = C(Q)$, then a nontrivial steady state exists only if $A(Q) < 0$. If $A(Q)(k_Q^{*-})^2 + B(k_Q^{*-}) < C(Q)$, then no nontrivial steady states exist if $A(Q) \geq 0$ and up to two exist if $A(Q) < 0$.

2.3.7 Theorem 2.4.3 and 2.2.4

Theorems 2.4.3 and 2.2.4 state that if the patch reproduction number is too small ($R_j < 1$) for every patch, then all population densities will tend toward the trivial steady state, e.g. extinction. However, if this condition fails, the trivial steady state will be unstable. Biologically, this implies that a control effort as described in the assumptions which is large enough to bring the patch reproduction number below that threshold for every patch, then the population will tend toward extinction. Theorem 2.4.3 also states that, for any stable steady state, the density of males must be between the composite parameters k_Q^{*+} and k_Q^{*-} and states that there are at most $p+1$ supports Q which correspond to a stable steady state. Finally, Theorem 2.4.3 provides sufficient conditions for a steady state to be stable.

2.3.8 Theorem 2.2.5

Theorem 2.2.5 discusses some features of a set of identical patches. It states that the only types of steady states which can be stable are the trivial steady state and the steady state where all patches have positive population densities.

2.4 Proofs of selected theorems

2.4.1 Proof of Theorem 2.2.2

Recall that a steady state is a constant vector $\bar{\mathbf{x}} = (\bar{x}_{11}, \bar{x}_{21}, \bar{x}_{12}, \bar{x}_{22}, \dots, \bar{x}_{1p}, \bar{x}_{2p}, \bar{x}_3)$ solution to system (2.2.1). Such a steady state $\bar{\mathbf{x}}$ must satisfy the following $2p + 1$ equations:

$$b_j \bar{x}_{2j} = \bar{x}_{1j} (\delta_{1j} + 2m), \quad \forall j \in \Omega \quad (2.4.1a)$$

$$m \bar{x}_{1j} = \bar{x}_{2j} (\delta_{2j} + c_{22j} \bar{x}_{2j} + c_{23j} g_j \bar{x}_3), \quad \forall j \in \Omega \quad (2.4.1b)$$

$$\sum_{j=1}^p m \bar{x}_{1j} = \sum_{j=1}^p g_j \bar{x}_3 (\delta_{3j} + c_{32j} \bar{x}_{2j} + c_{33j} g_j \bar{x}_3) \quad (2.4.1c)$$

The proof of part (a) is clear by means of a direct substitution of $\bar{\mathbf{x}} = \mathbf{0}$ into the above equations. Let, let $\bar{\mathbf{x}}$ be a steady state with $\bar{x}_3 = 0$. Equation (2.4.1c) implies that $\sum_{j=1}^p m \bar{x}_{1j} = 0$. Since $m > 0$ and $\bar{x}_{1j} \geq 0$ for all $j \in \Omega$, the only solution is $\bar{x}_{1j} = 0$ for all $j \in \Omega$. Equation (2.4.1a) implies that $\bar{x}_{2j} = 0$ for all $j \in \Omega$. Thus $\bar{\mathbf{x}} = \mathbf{0}$. This proves part (b).

Let $\bar{\mathbf{x}}$ be a steady state with $\text{supp}(\bar{\mathbf{x}}) = \emptyset$. Then $\bar{x}_{1j} = \bar{x}_{2j} = 0$. Equation (2.4.1c) implies that $\bar{x}_3 = 0$ as well. Thus $\bar{\mathbf{x}} = \mathbf{0}$. This proves part (c) of the theorem.

Let $Q \subseteq \Omega$, let $\bar{\mathbf{x}} \in \bar{Q}$ and suppose that $R_i < 1$ for some $i \in Q$. Then, equations (2.2.2a), (2.4.1a) and (2.4.1b) jointly imply that

$$R_i \delta_{2i} \bar{x}_{2i} = m \bar{x}_{1i} \quad \text{and} \quad (R_i - 1) \delta_{2i} \bar{x}_{2i} = \bar{x}_{2i} (c_{22i} \bar{x}_{2i} + c_{23i} g_i \bar{x}_3).$$

Since $i \in Q$, we have that either $\bar{x}_{1i} > 0$ or $\bar{x}_{2i} > 0$. The first equation above implies these are equivalent, and so $\bar{x}_{2i} > 0$. However, the second equation above implies that $\bar{x}_{2i} = 0$, since $R_i < 1$. This is a contradiction and it proves part (d).

Let $\bar{\mathbf{x}}$ be a steady state such that $R_j \leq 1$ for all $j \in \Omega$. Equation (2.4.2) implies that $x_{1j} = x_{2j} = 0$ for all $j \in \Omega$. Then $\text{supp}(\bar{\mathbf{x}}) = \emptyset$. By part (c), this implies that $\bar{\mathbf{x}} = \mathbf{0}$. This proves part 2.4.3.

We prove the remaining parts of this theorem together. Since the number of steady states is already determined if $Q = \emptyset$ by part (c), we shall assume Q is nonempty for the remainder of the proof.

Let $Q \subseteq \Omega$ and let $\bar{\mathbf{x}} \in \bar{Q}$. Then (2.2.2a), (2.4.1a), and (2.4.1b) jointly imply that $\bar{\mathbf{x}}$ must satisfy

$$R_j \delta_{2j} \bar{x}_{2j} = m \bar{x}_{1j} \quad \text{and} \quad (R_j - 1) \delta_{2j} \bar{x}_{2j} = \bar{x}_{2j} (c_{22j} \bar{x}_{2j} + c_{23j} g_j \bar{x}_3), \quad \text{for } j \in Q. \quad (2.4.2)$$

In view of earlier remarks, this gives

$$\bar{x}_{1j} = 0 \quad \text{and} \quad \bar{x}_{2j} = 0 \quad \text{for } j \notin Q, \quad (2.4.3a)$$

$$\bar{x}_{1j} > 0 \quad \text{and} \quad \bar{x}_{2j} > 0 \quad \text{for } j \in Q, \quad (2.4.3b)$$

$$\bar{x}_{1j} = \frac{R_j \delta_{2j}}{m} \bar{x}_{2j} \quad \text{and} \quad \bar{x}_{2j} = \frac{(R_j - 1) \delta_{2j} - c_{23j} g_j \bar{x}_3}{c_{22j}} \quad \text{for } j \in Q. \quad (2.4.3c)$$

Let $j \in Q$. If $c_{23j} > 0$, then (2.2.2a) and (2.4.3c) implies that $\bar{x}_{2j} = \frac{c_{23j} g_j}{c_{22j}} (k_j^* - \bar{x}_3) > 0$. Since Q is nonempty, $\bar{x}_3 > 0$. Then, the positivity of \bar{x}_{2j} implies that $\bar{x}_3 < k_j^*$. Thus, $0 < \bar{x}_3 < k_j^*$ for $j \in Q$. If $c_{23j} = 0$, then $k_j^* = \infty$, and so the inequality $0 < \bar{x}_3 < k_j^*$ still holds. This proves part

(f) of the theorem. Equations (2.4.1c) and (2.4.3) implies that $\bar{\mathbf{x}}$ must satisfy

$$\begin{aligned}
& \sum_{j=1}^p \{g_j \bar{x}_3 (\delta_{3j} + c_{32j} \bar{x}_{2j} + c_{33j} g_j \bar{x}_3) - m \bar{x}_{1j}\} = 0 \\
& \implies \sum_{j=1}^p \{ \delta_{3j} g_j \bar{x}_3 + c_{33j} g_j^2 \bar{x}_3^2 + (c_{32j} g_j \bar{x}_3 - R_j \delta_{2j}) \bar{x}_{2j} \} = 0 \\
& \implies \sum_{j=1}^p \left\{ \delta_{3j} g_j \bar{x}_3 + c_{33j} g_j^2 \bar{x}_3^2 + \phi_j(Q) (c_{32j} g_j \bar{x}_3 - R_j \delta_{2j}) \frac{(R_j - 1) \delta_{2j} - c_{23j} g_j \bar{x}_3}{c_{22j}} \right\} = 0 \\
& \implies A(Q) \bar{x}_3^2 + B(Q) \bar{x}_3 - C(Q) = 0
\end{aligned}$$

where

$$\begin{aligned}
A(Q) &= \sum_{j=1}^p \left\{ \frac{c_{22j} c_{33j} - \phi_j(Q) c_{23j} c_{32j}}{c_{22j}} \right\} g_j^2, \\
B(Q) &= \sum_{j=1}^p \left\{ \delta_{3j} + \phi_j(Q) \frac{c_{32j} (R_j - 1) \delta_{2j} + c_{23j} R_j \delta_{2j}}{c_{22j}} \right\} g_j, \\
C(Q) &= \sum_{j=1}^p \phi_j(Q) \frac{R_j \delta_{2j} (R_j - 1) \delta_{2j}}{c_{22j}}.
\end{aligned}$$

Observe that $B(Q)$ is positive and $C(Q)$ is positive. Let $\Lambda(z, Q) = A(Q)z^2 + B(Q)z - C(Q)$. Equations (2.4.3) imply that solutions z to $\Lambda(z, Q) = 0$ correspond to $\bar{\mathbf{x}} \in \bar{Q}$ for which $\bar{x}_3 = z$ if and only if $\bar{x}_3 < k_j^*$ for all $j \in Q$, that is, if $\bar{x}_3 < k_Q^{*-}$, where k_Q^{*-} is as in (2.2.2b). If such an \bar{x}_3 exists, the remaining components of $\bar{\mathbf{x}}$ are uniquely determined by (2.4.3).

Assume $c_{23j} = 0$ for all $j \in Q$. Then $A(Q) = \sum_{j=1}^p \left\{ \frac{c_{22j} c_{33j}}{c_{22j}} \right\} g_j^2$, which implies that $\Lambda(z, Q)$ is an concave up parabola for which $\Lambda(0, Q)$ has a single solution. The values of x_{1j} and x_{2j} are given by (2.4.3c) (and are independent of the value of \bar{x}_3 . Thus $|\bar{Q}| = 1$. This proves part (g) of the theorem. For the remainder of the proof, we shall assume that there exists $j \in Q$ such that $c_{23j} > 0$, which implies k_Q^{*-} is finite.

First assume $A(Q) \geq 0$. Then $\Lambda(z, Q)$ is a quadratic in z which is concave up or a line with positive slope. Note that, since Q is nonempty, $\Lambda(0, Q) < 0$. If $\Lambda(k_Q^{*-}, Q) = A(Q)(k_Q^{*-})^2 + B(Q)k_Q^{*-} - C(Q) \leq 0$ then there are no values of \bar{x}_3 such that $\bar{x}_3 \in (0, k_Q^{*-})$ and $\Lambda(\bar{x}_3, Q) = 0$. Thus $|\bar{Q}| = 0$. This proves part (h) of the theorem

If instead $\Lambda(k_Q^{*-}, Q) = A(Q)(k_Q^{*-})^2 + B(Q)k_Q^{*-} - C(Q) > 0$ then there exists a unique $\bar{x}_3 \in (0, k_Q^{*-})$ such that $\Lambda(\bar{x}_3, Q) = 0$. Thus $|\bar{Q}| = 1$. This proves part (i) of the theorem.

Next assume $A(Q) > 0$. If $\Lambda(k_Q^{*-}, Q) = A(Q)(k_Q^{*-})^2 + B(Q)k_Q^{*-} - C(Q) \leq 0$ then the parabola $\Lambda(z, Q)$ may have 0, 1 or 2 solutions to the equation $\Lambda(z, Q) = 0$. Thus $|\bar{Q}| \leq 2$. This proves part (j) of the theorem.

If instead $\Lambda(k_Q^{*-}, Q) = A(Q)(k_Q^{*-})^2 + B(Q)k_Q^{*-} - C(Q) > 0$ then there exists a unique $\bar{x}_3 \in (0, k_Q^{*+})$ such that $\Lambda(\bar{x}_3, Q) = 0$. Thus $|\bar{Q}| = 1$. This proves part (k) of the theorem.

If instead $\Lambda(k_Q^{*-}, Q) = A(Q)(k_Q^{*-})^2 + B(Q)k_Q^{*-} - C(Q) = 0$ then there may exist at most one unique $\bar{x}_3 \in (0, k_Q^{*+})$ such that $\Lambda(\bar{x}_3, Q) = 0$. Thus $|\bar{Q}| = 1$. This proves part (l) of the theorem.

2.4.2 Proof of Theorem 2.4.3

We assume the patches are ordered in the following way. Fix a steady state $\bar{\mathbf{x}}$ and let $Q = \text{supp}(\bar{\mathbf{x}})$. Recall that $\bar{x}_{1j} = \bar{x}_{2j} = 0$ for $j \in Q^c$ and $\bar{x}_{1j}, \bar{x}_{2j} > 0$ for $j \in Q$. Without loss of generality, we may assume $\bar{x}_{1j} = \bar{x}_{2j} = 0$ for $j = 1, 2, \dots, q$ where $q = |Q^c|$, and that

$\bar{x}_{1j}, \bar{x}_{2j} > 0$ for $j = q + 1, q + 2, \dots, p$. In addition, we may assume $k_1^* \leq k_2^* \leq \dots \leq k_q^*$ and $k_{q+1}^* \leq k_{q+2}^* \leq \dots \leq k_p^*$. Define the composite parameters

$$h_{1j} = \delta_{1j} + 2m,$$

$$h_{2j} = \delta_{2j} + c_{22j}\bar{x}_{2j} + c_{23j}g_j\bar{x}_3,$$

$$h_{3j} = \delta_{3j}g_j + c_{32j}g_j\bar{x}_{2j} + c_{33j}g_j^2\bar{x}_3$$

and note that each is strictly positive. The Jacobian matrix for system (2.2.1) at $\bar{\mathbf{x}}$ is

$$J(\bar{\mathbf{x}}) = \begin{bmatrix} B_1 & & & & \mathbf{u}_1 \\ & B_2 & & & \mathbf{u}_2 \\ & & \ddots & & \vdots \\ & & & B_p & \mathbf{u}_p \\ * & * & \dots & * & B^* \end{bmatrix}$$

where

$$B_j = \begin{bmatrix} -h_{1j} & b_j \\ m & -h_{2j} - c_{22j}\bar{x}_{2j} \end{bmatrix}, \quad B^* = \left[-\sum_{j=1}^p \{h_{3j} + c_{33j}g_j^2\bar{x}_3\} \right], \quad \text{and } \mathbf{u}_j = \begin{bmatrix} 0 \\ -c_{23j}g_j\bar{x}_{2j} \end{bmatrix} \quad (2.4.4)$$

Since $\bar{x}_{2j} = 0$ for $j = 1, 2, \dots, q$, $\mathbf{u}_j = \mathbf{0}$ for $j = 1, 2, \dots, q$. Thus

$$J(\bar{\mathbf{x}}) = \left[\begin{array}{cccc|ccc} B_1 & & & & & & \mathbf{0} \\ & B_2 & & & & & \mathbf{0} \\ & & \ddots & & & & \vdots \\ & & & B_q & & & \mathbf{0} \\ \hline & & & & B_{q+1} & & \mathbf{u}_{q+1} \\ & & & & & \ddots & \vdots \\ & & & & & & B_p & \mathbf{u}_p \\ * & * & \dots & * & * & \dots & * & B^* \end{array} \right]$$

Observe that if $q > 0$, then $J(\bar{\mathbf{x}})$ is a block lower-triangular matrix and that first diagonal block is a block diagonal matrix (whose blocks are B_j).

Let $\bar{\mathbf{x}} = \mathbf{0}$. Then $Q = \text{supp}(\bar{\mathbf{x}}) = \emptyset$ and $q = p$. Moreover, the eigenvalues of $J(\mathbf{0})$ are the eigenvalues of its blocks B_1, B_2, \dots, B_p , and B^* . If $R_j < 1$ for all $j \in \Omega$ then each block B_j has a negative trace and (2.2.2a) implies that

$$\det(B_j) = h_{1j}h_{2j} - b_jm = (\delta_{1j} + 2m)h_{2j} - b_jm > (\delta_{1j} + 2m)\delta_{2j}(1 - R_j) > 0.$$

Hence, each B_j contributes two eigenvalues with negative real part. The final diagonal block, B^* , is a 1×1 matrix with the single element, $-\sum \delta_{3j}g_j$, which is clearly negative. Thus, all $2p + 1$ eigenvalues of $J(\mathbf{0})$ have negative real part and so $\bar{\mathbf{x}}$ is LAS. This proves part (a) of the theorem.

If $R_i > 1$ for some $i \in \Omega$, then (2.2.2a) implies that $\det(B_i) = (\delta_{1j} + 2m)\delta_{2j}(1 - R_j) < 0$.

Thus B_i contributes a positive eigenvalue and so $\bar{\mathbf{x}} = \mathbf{0}$ is unstable. This proves part (b) of the theorem.

If $Q = \emptyset$, then part 2.4.3 of the theorem follows directly from the (2.2.2a) and part(f) of Theorem 2.2.2. Next, let $Q \subseteq \Omega$ be nonempty such that \overline{Q} is also nonempty and let $\bar{\mathbf{x}} \in \overline{Q}$. Recall the definitions of k_Q^{*-} and k_Q^{*+} in (2.2.2a). For the sake of contradiction, suppose $\bar{x}_3 < k_i^*$ for some $i \in Q^c$. If $q = |Q^c|$, then $i \leq q$. Then

$$\det(B_i) = h_{1i} \left\{ h_{2i} - \frac{b_i m}{h_{1i}} \right\} = h_{1i} \left\{ \delta_{2i} + c_{23i} g_i \bar{x}_3 - \frac{b_i m}{h_{1i}} \right\} = h_{1i} c_{23i} g_i (\bar{x}_3 - k_i^*).$$

By assumption, $\bar{x}_3 < k_i^*$, and so $\bar{x}_3 - k_i^* < 0$. Then $\det(B_i) < 0$, and thus B_i contributes a positive eigenvalue which implies that $\bar{\mathbf{x}} \notin \overline{Q}$. This is a contradiction and so $\bar{x}_3 \geq k_Q^{*+}$. In the proof of Theorem 2.2.2, it was shown that $\bar{x}_3 < k_j^*$ for all $j \in Q$, which implies that $\bar{x}_3 < k_Q^{*-}$. This proves part 2.4.3 of the theorem.

To prove part (d) of this theorem, we will will, without loss of generality, assume that the patches are ordered in the following way: $k_1^* \leq k_2^* \leq \dots \leq k_p^*$. Note that this is a different ordering than was used previously in this theorem. Let $Q \subseteq \Omega$ and $\bar{\mathbf{x}} \in \overline{Q}$. Then either $\bar{x}_3 < k_1^*$, $\bar{x}_3 > k_p^*$ or there exists $j \in \Omega$ such that

$$k_1^* \leq \dots \leq k_{j-1}^* = k_Q^{*+} < \bar{x}_3 < k_Q^{*-} = k_j^* \leq \dots \leq k_p^*.$$

Since, $|\Omega| = p$, there are only $p + 1$ subsets $Q \subseteq \Omega$ which can satisfy part 2.4.3. For reference, they are $Q = \emptyset, \{p\}, \{p-1, p\}, \{p-2, p-1, p\}, \dots, \{1, 2, \dots, p\}$. Theorem 2.2.2 implies that for all $Q \subset \Omega$, $|\overline{Q}| \leq 2$. Then there are at most $2p + 2$ LAS steady states (i.e., $\sum_{Q \in \Omega} |\overline{Q}| \leq 2p + 2$).

This proves part (d) of the theorem. Let $Q \subseteq \Omega$ and $\bar{\mathbf{x}} \in \bar{Q}$. Conditions (i), (ii), and (iii) are the necessary conditions for the Jacobian $J(\bar{\mathbf{x}})$ to be diagonally dominant. Since each diagonal element is negative, we may apply Gershgorin's circle theorem to conclude that all eigenvalues have negative real part. This proves part (e) of the theorem.

2.4.3 Proof of Theorem 2.2.5

Part (a) of this proof is a direct result of part (a) of Theorem 2.4.3. Part (b) of this theorem is a direct result of part (b) of Theorem 2.4.3. For part (c), first assume $R_0 \leq 1$ and let $Q \subset \Omega$ such that $Q \neq \Omega$ and $Q \neq \emptyset$. Then there exists $j \in \Omega$ such that $R_j = R_0 \leq 1$. Then part of 2.2.2 implies that $\bar{Q} = \emptyset$. Since $\bar{\bar{Q}} \subseteq \bar{Q}$, then $\bar{\bar{Q}} = \emptyset$.

Next assume that $R_0 > 1$ and let $Q \subset \Omega$ such that $Q \neq \Omega$ and $Q \neq \emptyset$. Assume that $c_{23} = 0$. Then $k_Q^{*+} = k_Q^{*-} = \infty$. However, part of Theorem implies this is a contradiction.

2.5 Discussion

The issue of the stability of all steady states was not addressed completely. We conjecture that any steady state which satisfies the converse of part (c) of Theorem 2.4.3 will be stable. Moreover, we suspect and that the proof may involve viewing the appropriate Jacobian as a block matrix and establishing a form of block diagonally dominance.

Many of the same comments from Chapter 1 are still relevant, in particular with regard to time-independent parameters. We will focus on comments specific to the features unique to Chapter 2, specifically, the spatial nature of the model. We have chosen a patch-based model to describe the clumped distribution of resources noted in the literature. We have included a single category for adult males which interact with all patches to simulate the manner in which males will often move between these patches. Several issues arise.

Though this work is built upon the model in Chapter 1, it did not include the effects of abandonment. In Chapter 1, the inclusion of abandonment dramatically influenced the form and number of equilibria. Future work may include abandonment terms for one or more patch.

We have assumed that only adult males leave the patch of their birth. This is not entirely accurate as the movement of adult females cannot be ruled out. Future work may include a manner in which (a small number of) adult females can also move. We conjecture that this change would strongly impact the stability of the semitrivial steady states.

We have assumed that, at maturity, all males become semi-nomadic and spend a proportion of their time in every patch and that all adult males adopt the same constant strategy. This would seem to imply that adult males maintain a spatial distribution without regard for the relative densities of adult females. This does not agree with the literature on two fronts. First, some adult males may become residents to a patch (in the same way that adult females are residents to a patch). This behavior was noted in [41]. Second, classical mating system theory suggests that males will distribute themselves first by the relative

populations of potential mates [53]. Future work may include a distribution of adult males which reflects this. An example of this may be $g_j = \frac{x_{2j}}{c + \sum x_{2j}}$ and $g_0 = \frac{c}{c + \sum x_{2j}}$ for $c > 0$. We conjecture that this change would strongly impact the number and stability of semitrivial steady states. This distribution of adult males may also be influenced by seasons, and so future work may include time-dependent g_j .

A possible future direction, which is capable of addressing all of the previously raised issues is that of a network structure for the patches. If each patch had both resident adult males, adult females and kittens, a set of transition matrices could be constructed such that the elements are functions of time as well as the relative patch population densities. These transitions could also account for the varying dangers of specific routes. This would allow for animals to distribute themselves more realistically and allow for the consideration of resident adult males versus nomadic adult males. This would also allow adult females to populate patches with no residents. We conjecture that this would reduce or remove the possibility for semi-trivial steady states. Many of these ideas may also be implemented by means of partial differential equations, similar to [37].

We conjecture that many of these suggestions would destabilize or eliminate many semitrivial steady states, that is, it would promote the persistence of some patches. As such, we expect the inclusion of these changes may reduce the effectiveness of control strategies derived from this work. Our model would suggest that if the control parameter for a given patch (s_j) is sufficiently high (such that $R_j < 1$) then the population in that patch cannot persist. However, if adult females are permitted to relocate, it is possible that this result

will fail, and so a much broader strategy will be needed. These changes may also allow control strategies which the current model is not equipped to handle. For example, if the transition matrix is adopted, focusing control efforts on animals in transit between patches may decouple that patch from the system and so change the dynamics there. If there are patches through which many individuals pass, control implemented in this patch may have a strong influence on the populations of other patches.

CHAPTER 3

THE DISEASE MODEL

3.1 Introduction

The threat of zoonosis is a constant concern in the modern world. In a study of major diseases affecting humans, it was shown that an alarming percentage of those diseases were the result of zoonotic mutations and a major risk factor for zoonosis is the presence of large animal populations in cities [16]. For example, cows are known to have carried the rinderpest virus, which is believed to have evolved into measles in the 12th century [58]. In more recent history, rodents are believed to have spread various Hantaviruses which cause Hantavirus pulmonary syndrome in more than 1200 humans in Brazil between 1993 and 2003 [59].

In addition, there are numerous variants of the ‘highly pathogenic avian influenza virus’ (HPAIV), currently afflicting the world (e.g., bird flu and swine flu) [60,61].

Today, there are many examples of unowned, free-roaming cats (or *feral* cats as in [1]) living in large colonies in human population centers. In [28], a catalog of many such populations are cited. For example, in Jerusalem, a population with density over 18 cats per hectare is described in [43]. A population on the Japanese territory of Ainoshima Island is described to have a population density of over 23 cats per hectare is described

in [41]. Numerous other examples exist [32, 41–44], and so the feral cats pose a zoonotic threat [3, 16–18]. In addition to the threat of zoonosis these animals are generally regarded as an epidemiological threat to both local wildlife [14, 15], and pet animals [1], in particular by transmitting rabies, toxoplasmosis and the feline leukemia virus [62, 63].

The feline leukemia virus (or FeLV) is an immunosuppressive, oncogenic retrovirus. It is known to persist at endemic levels throughout the world [64]. This virus has been found to spread between feral cats and wild felids [14, 15] and can reproduce in human bone marrow in a lab setting [18]. Two great resources on this virus are [65] and [66] and the following short description is derived from those works. As many as two-thirds of cats exposed will clear the virus from their system and develop life-long immunity. Failing this, such animals develop life-long infections characterized by periods of viremia and a latent infection. Either of these periods may last years. Latently infected animals do not shed the virus and may have no outward symptoms. Viremic animals experience immunosuppression, lethargy, malaise, and increased death rates. The pregnancies of females in this state very often end in abortion [67]. During these periods, the virus is primarily found in the saliva, but can also be found in the blood and, if the infected is lactating, milk. Adult females can spread the virus vertically to their offspring or by grooming or nursing them. In dense settings, lactating females may groom and nurse kittens besides their own. The virus is more commonly spread by means of communal grooming among familiar adults and bites during territorial interactions with adversaries or during copulation. In addition to these modes of transmission, it has been

suggested that the virus can might be able to spread by means of sharing food and water sources or that fleas may be able to transmit the virus.

FeLV has been the study of numerous mathematical models [34–38]. In [34] an SIR model for FeLV is described which assumes no vertical transmission and logistic growth of sub-populations. That model was later expanded into four models in [36]. These models considered two different growth types (exponential and logistic) as well as two disease incidence terms (dependent and frequency dependent). Analysis and simulations on each of these models are also included. In [39], an SIRS model which distinguishes between social and asocial cats is described. The authors suggest that asocial cats engage in markedly different behavior, in particular with regard to the social habits that are thought to be the virus’s primary methods of transmission (e.g., social grooming, sharing food sources). Spatial aspects of the population are explored in [37], which utilizes partial differential equations and in [38], which uses a network structure to describe different types of habitat (i.e., “farms” and “villages”). Though efforts have been made to classify these feral cats by the behaviors which are more likely to cause contact with the disease [36,39], it may be that gender and life-stage are strong indicators for such behaviors. Indeed, since some disease-spreading behaviors are restricted to certain gender/life-stage combinations (e.g., nursing kittens), modeling efforts may benefit from this sort of grouping.

Here we propose a model with compartments for adult males, adult females and kittens, each of which may be susceptible, infected or recovered, for a total of 9 categories. Section 3.2 details the assumptions of the model, the system of differential equations they

imply, and the main results of our analysis. The main focus of these results focuses on the properties the disease-free equilibrium. In Section 3.3 we interpret selected composite parameters and theorems biologically. Section 3.4 describes proofs for selected theorems. Finally, Section 3.5 outlines weaknesses of the model and potential directions for future work to address these weaknesses.

3.2 Mathematical model

3.2.1 Description

Consider a population similar to that in Chapter 1 under the influence of feline leukemia. Unlike those in Chapter 1, this population will not interact with house-cats. The population includes kittens ($i = 1$), adult females ($i = 2$) and adult males ($i = 3$). We define the *status* of i -cats to be susceptible, infected or immune. For simplicity, we define *healthy* cats to be those that are uninfected. Let $x_i(t)$, $y_i(t)$ and $z_i(t)$ be the density of susceptible, infected and immune i -cats at time $t \geq 0$. Also define $\pi_i(t) = x_i(t) + y_i(t) + z_i(t)$. Assume the following:

- (C1) Healthy adult females produce susceptible kittens at per-capita rate $b > 0$.
- (C2) Infected adult females produce susceptible kittens and infected kittens at per-capita rates $\phi\epsilon b$ and $(1 - \phi)\epsilon b$, respectively, where $\epsilon \in [0, 1]$ and $\phi \in [0, 1]$.
- (C3) The intrinsic death rate for uninfected i -cats is $d_i > 0$.

- (C4) The intrinsic death rate for infected i -cats is $\theta_i d_i$ where $\theta_i \geq 1$.
- (C5) Kittens mature into adults of each sex (of the same infection status) at per-capita rate $m > 0$.
- (C6) Feral i -cats are removed from the population at per-capita rate $s_i \geq 0$.
- (C7) The competitive effect of adult j -cats on adult i -cats is $c_{ij} \geq 0$.
- (C8) The interaction coefficient $c_{ii} > 0$ for $i = 2, 3$.
- (C9) Susceptible i -cats become exposed to the disease at rate $B_i = \sum_{j=1}^3 \frac{\beta_{ij} y_j}{\pi_j}$ with $\beta_{ij} \geq 0$.
- (C10) The parameters $\beta_{11} = \beta_{13} = \beta_{31} = 0$.
- (C11) A fixed proportion α_i of exposed i -cats immediately become immune i -cats.
- (C12) A fixed proportion $1 - \alpha_i$ of exposed i -cats immediately become infected i -cats.
- (C13) Unexposed susceptible i -cats become immune i -cats at rate $\nu_i \geq 0$.

Many of these assumptions are similar in form and effect as those in Chapter 1 and comments there apply here as well. Assumption (C10) implies that kittens do not engage in the behaviors necessary to infect other kittens. Moreover, it reflects that observation that adult males do not interact with kittens, and so no transmission can occur between these two classes. Assumptions (C11) and (C12) represent the observation that some cats can mount a sufficient immune response to clear the virus before the infection becomes permanent (i.e., when target tissue is infected). These cats are never symptomatic nor infectious. Note

that outside of this initial event, there is no recovery from the disease. Assumption (C13) represents vaccination efforts. Assumptions (C1) to (C13) produce the initial value problem

$$\begin{aligned}
\dot{x}_1 &= b(x_2 + z_2) + \phi\epsilon by_2 - x_1(d_1 + s_1 + 2m) - \nu_1 x_1 - B_1 x_1, & x_1(0) &\geq 0 \\
\dot{x}_2 &= mx_1 - x_2(d_2 + s_2 + c_{22}\pi_2 + c_{23}\pi_3) - \nu_2 x_2 - B_2 x_2, & x_2(0) &\geq 0 \\
\dot{x}_3 &= mx_1 - x_3(d_3 + s_3 + c_{32}\pi_2 + c_{33}\pi_3) - \nu_3 x_3 - B_3 x_3, & x_3(0) &\geq 0 \\
\dot{y}_1 &= (1 - \phi)\epsilon by_2 - y_1(\theta_1 d_1 + s_1 + 2m) + (1 - \alpha_1)B_1 x_1, & y_1(0) &\geq 0 \\
\dot{y}_2 &= my_1 - y_2(\theta_2 d_2 + s_2 + c_{22}\pi_2 + c_{23}\pi_3) + (1 - \alpha_2)B_2 x_2, & y_2(0) &\geq 0 \\
\dot{y}_3 &= my_1 - y_3(\theta_3 d_3 + s_3 + c_{32}\pi_2 + c_{33}\pi_3) + (1 - \alpha_3)B_3 x_3, & y_3(0) &\geq 0 \\
\dot{z}_1 &= -z_1(d_1 + s_1 + 2m) + \nu_1 x_1 + \alpha_1 B_1 x_1, & z_1(0) &\geq 0 \\
\dot{z}_2 &= mz_1 - z_2(d_2 + s_2 + c_{22}\pi_2 + c_{23}\pi_3) + \nu_2 x_2 + \alpha_2 B_2 x_2, & z_2(0) &\geq 0 \\
\dot{z}_3 &= mz_1 - z_3(d_3 + s_3 + c_{32}\pi_2 + c_{33}\pi_3) + \nu_3 x_3 + \alpha_3 B_3 x_3, & z_3(0) &\geq 0
\end{aligned} \tag{E}$$

As in Chapter 1 we shall introduce notation for effective death rates.

$$\begin{aligned}
\delta_1 &= d_1 + s_1, & \delta_2 &= d_2 + s_2, & \delta_3 &= d_3 + s_3, \\
\delta_{y_1} &= \theta d_1 + s_1, & \delta_{y_2} &= \theta d_2 + s_2, & \delta_{y_3} &= \theta d_3 + s_3.
\end{aligned} \tag{F}$$

The simplified initial value problem is

$$\dot{x}_1 = b(x_2 + z_2) + \phi\epsilon by_2 - x_1(\delta_1 + 2m) - \nu_1 x_1 - B_1 x_1, \quad x_1(0) \geq 0 \tag{3.2.1a}$$

$$\dot{x}_2 = mx_1 - x_2(\delta_2 + c_{22}\pi_2 + c_{23}\pi_3) - \nu_2 x_2 - B_2 x_2, \quad x_2(0) \geq 0 \tag{3.2.1b}$$

$$\dot{x}_3 = mx_1 - x_3(\delta_3 + c_{32}\pi_2 + c_{33}\pi_3) - \nu_3 x_3 - B_3 x_3, \quad x_3(0) \geq 0 \tag{3.2.1c}$$

$$\dot{y}_1 = (1 - \phi)\epsilon by_2 - y_1(\delta_{y_1} + 2m) + (1 - \alpha_1)B_1 x_1, \quad y_1(0) \geq 0 \tag{3.2.1d}$$

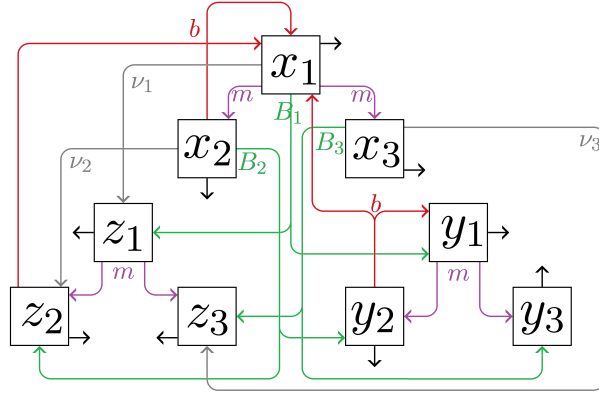


Figure 3.1: A box-diagram visualization of system (E).

$$\dot{y}_2 = my_1 - y_2(\delta_{y_2} + c_{22}\pi_2 + c_{23}\pi_3) + (1 - \alpha_2)B_2x_2, \quad y_2(0) \geq 0 \quad (3.2.1e)$$

$$\dot{y}_3 = my_1 - y_3(\delta_{y_3} + c_{32}\pi_2 + c_{33}\pi_3) + (1 - \alpha_3)B_3x_3, \quad y_3(0) \geq 0 \quad (3.2.1f)$$

$$\dot{z}_1 = -z_1(\delta_1 + 2m) + \nu_1x_1 + \alpha_1B_1x_1, \quad z_1(0) \geq 0 \quad (3.2.1g)$$

$$\dot{z}_2 = mz_1 - z_2(\delta_2 + c_{22}\pi_2 + c_{23}\pi_3) + \nu_2x_2 + \alpha_2B_2x_2, \quad z_2(0) \geq 0 \quad (3.2.1h)$$

$$\dot{z}_3 = mz_1 - z_3(\delta_3 + c_{32}\pi_2 + c_{33}\pi_3) + \nu_3x_3 + \alpha_3B_3x_3, \quad z_3(0) \geq 0 \quad (3.2.1i)$$

See Table 3.1 for a description of all variables and parameters.

3.2.2 Statement of main results

This section is dedicated to the main properties of system (2.2.1), which are in the vein of [46, 47] wherein the basic reproduction number for the disease (R_0) is defined in terms of the spectral radius of the next generation matrix.

Table 3.1: Quantities associated with model (E) and (3.2.1)

Quantity	Description	Units	Equation
t	time	time	(E)
x_i	density of susceptible i -cats	cat	(E)
y_i	density of infected i -cats	cat	(E)
z_i	density of immune i -cats	cat	(E)
π_i	sum density of all i -cats	cat	(E)
b	kitten birth rate for uninfected cats	kitten \cdot adult ⁻¹ \cdot time ⁻¹	(E)
ϵ	infected birth rate reduction factor	kitten \cdot adult ⁻¹ \cdot time ⁻¹	(E)
m	kitten maturation rate	adult \cdot kitten ⁻¹ \cdot time ⁻¹	(E)
d_i	intrinsic death rate of uninfected i -cats	time ⁻¹	(E)
θ_i	infected death rate increase factor for i -cats	time ⁻¹	(E)
s_i	control rate on i -cats	time ⁻¹	(E)
c_{ij}	effect of adult j -cats on adult i -cats	adult ⁻¹ \cdot time ⁻¹	(E)
α_i	probability exposure leads to immunity in i -cats	none	(E)
B_i	exposure rate of i -cats	time ⁻¹	(E)
β_{ij}	infective effect of j -cats on i -cats	time ⁻¹	(E)
ν_i	vaccination rate of i -cats	time ⁻¹	(E)
δ_i	effective death rate for uninfected i -cats	time ⁻¹	(F)
δ_{yi}	effective death rate for infected i -cats	time ⁻¹	(F)
H_0	net reproduction number for adult females	none	(3.2.2a)

Table 3.2: Quantities associated with model (E) and (3.2.1)

Quantity	Description	Units	Equation
R_0	basic reproduction number for FeLV	none	
$\bar{\mathbf{u}}$	disease-free equilibrium (DFE)	cat ⁹	(3.2.1)
h_i	effective removal rate of uninfected i -cats at DFE	time ⁻¹	(3.2.3c)
\bar{x}_i	density of susceptible i -cats at DFE	cat	(3.2.1)
\bar{z}_i	density of immune i -cats at DFE	cat	(3.2.1)
\bar{U}_i	density of healthy i -cats at DFE	cat	(3.4.3a)
\mathcal{F}_i	recruitment rate via infection of i -cats	cat · time ⁻¹	(3.4.4)
$\mathcal{V}_i^+, \mathcal{V}_i^-$	recruitment rate via noninfection of i -cats	cat · time ⁻¹	(3.4.4)
F	linearization of \mathcal{F} at the DFE		(3.4.4)
V^+, V^-	linearization of $\mathcal{V}^+, \mathcal{V}^-$ at the DFE		(3.4.4)

A *disease-free equilibrium* (DFE) of system (3.2.1) is defined to be a nontrivial equilibrium $\bar{\mathbf{u}} \in \mathbb{R}_+^9$ of the form

$$\bar{\mathbf{u}} = (\bar{x}_1, \bar{x}_2, \bar{x}_3, 0, 0, 0, \bar{z}_1, \bar{z}_2, \bar{z}_3).$$

We continue to use the notion of local asymptotic stability (LAS) established in Chapter 1 and used in Chapter 2. However, we now include the notion of stability *absence of disease*, that is, stable with regard to perturbations only in the healthy categories. Further details regarding this notion can be found in [47]. The statement of the first theorem requires the net reproduction number H_0 , given by

$$H_0 = \frac{bm}{(\delta_1 + 2m)\delta_2} \quad (3.2.2a)$$

Theorem 3.2.1. *The following results hold for system (3.2.1)*

(a) *If $H_0 \leq 1$, then no DFE exists.*

(b) *If $H_0 > 1$, then a unique DFE exists.*

(c) *When a DFE exists, its components satisfy*

$$\bar{x}_1 = \frac{h_1}{h_1 + \nu_1} \cdot \bar{U}_1, \quad \bar{x}_2 = \frac{h_1}{h_1 + \nu_1} \cdot \frac{h_2}{h_2 + \nu_2} \cdot \bar{U}_2, \quad \bar{x}_3 = \frac{h_1}{h_1 + \nu_1} \cdot \frac{h_3}{h_3 + \nu_3} \cdot \bar{U}_3 \quad (3.2.3a)$$

$$\bar{z}_1 = \frac{\nu_1}{h_1 + \nu_1} \cdot \bar{U}_1, \quad \bar{z}_2 = \frac{h_2\nu_1 + h_1\nu_2 + \nu_1\nu_2}{(h_1 + \nu_1)(h_2 + \nu_2)} \cdot \bar{U}_2, \quad \bar{z}_3 = \frac{h_3\nu_1 + h_1\nu_3 + \nu_1\nu_3}{(h_1 + \nu_1)(h_3 + \nu_3)} \bar{U}_3 \quad (3.2.3b)$$

$$h_1 = \delta_1 + 2m, \quad h_2 = \delta_2 + c_{22}\bar{U}_2 + c_{23}\bar{U}_3, \quad \text{and} \quad h_3 = \delta_3 + c_{32}\bar{U}_2 + c_{33}\bar{U}_3 \quad (3.2.3c)$$

where $(\bar{U}_1, \bar{U}_2, \bar{U}_3)$ is the unique solution to the system of equations

$$b\bar{U}_2 = \bar{U}_1(\delta_1 + 2m) \quad (3.2.4a)$$

$$m\bar{U}_1 = \bar{U}_2(\delta_2 + c_{22}\bar{U}_2 + c_{23}\bar{U}_3) \quad (3.2.4b)$$

$$m\bar{U}_1 = \bar{U}_3(\delta_3 + c_{32}\bar{U}_2 + c_{33}\bar{U}_3) \quad (3.2.4c)$$

(d) *When a DFE exists it is LAS in the absence of disease.*

Define the spectral radius of a square matrix A as

$$\rho(A) = \max \{ |\lambda| : \lambda \text{ is an eigenvalue of } A \}.$$

Theorem 3.2.2. *If a DFE exists, then it is LAS if and only $\rho(\mathbb{J}) < 1$, where*

$$\mathbb{J} = \begin{bmatrix} C_0(C_7 + C_1\bar{x}_1) & C_7 + C_1\bar{x}_1 & 0 \\ (C_2 + C_0(C_3 + C_4))\bar{x}_2 & C_3\bar{x}_2 & C_4\bar{x}_2 \\ C_0(C_5 + C_6)\bar{x}_3 & C_5\bar{x}_3 & C_6\bar{x}_3 \end{bmatrix} \quad (3.2.5)$$

where C_j 's are defined as in Table 3.3.

In holding with other works, when the DFE exists, we define $R_0 = \rho(\mathbb{J})$, where \mathbb{J} is the matrix in (3.2.5) and the values of C_j are given in Table 3.3.

Corollary 3.2.3. *Assume a DFE exists, and let the characteristic polynomial of the matrix in (3.2.5) be given by $p(\lambda) = \lambda^3 + \sigma_1\lambda^2 + \sigma_2\lambda + \sigma_3$. Then the DFE is LAS if and only if the following four conditions hold:*

$$1 + \sigma_1 + \sigma_2 + \sigma_3 > 0 \quad (3.2.6a)$$

$$1 - \sigma_1 + \sigma_2 - \sigma_3 > 0 \quad (3.2.6b)$$

$$1 - \sigma_3^2 + \sigma_2 - \sigma_1\sigma_3 > 0 \quad (3.2.6c)$$

$$1 - \sigma_3^2 - \sigma_2 + \sigma_1\sigma_3 > 0 \quad (3.2.6d)$$

The next theorem requires the composite parameters

$$r_1 = C_6\bar{x}_3 \quad (3.2.7a)$$

$$r_2 = (C_7 + C_2\bar{x}_2)(C_0 + C_1\bar{x}_1) + C_3\bar{x}_2 + \frac{C_0C_4(C_7 + C_2\bar{x}_2) + C_4C_5\bar{x}_2\bar{x}_3}{1 - C_6\bar{x}_3} \quad (3.2.7b)$$

Theorem 3.2.4. *The DFE is LAS if and only if $\max\{r_1, r_2\} < 1$.*

Table 3.3: Quantities associated with the matrix from (3.2.5)

and Theorem 3.2.4.

Quantity	Definition
C_0	mh_{y1}^{-1}
C_1	$\beta_{12}(1 - \alpha_1)(\bar{U}_1 h_{y1})^{-1}$
C_2	$\beta_{21}(1 - \alpha_2)(\bar{U}_1 h_{y1})^{-1}$
C_3	$\beta_{22}(1 - \alpha_2)(\bar{U}_2 h_{y2})^{-1}$
C_4	$\beta_{23}(1 - \alpha_2)(\bar{U}_3 h_{y3})^{-1}$
C_5	$\beta_{32}(1 - \alpha_3)(\bar{U}_2 h_{y2})^{-1}$
C_6	$\beta_{33}(1 - \alpha_3)(\bar{U}_3 h_{y3})^{-1}$
C_7	$(1 - \phi)\epsilon b h_{y2}^{-1}$
h_{y1}	$\delta_{y1} + 2m$
h_{y2}	$\delta_{y2} + c_{22}\bar{U}_2 + c_{23}\bar{U}_3$
h_{y3}	$\delta_{y3} + c_{32}\bar{U}_2 + c_{33}\bar{U}_3$
r_1	$C_6\bar{x}_3$
r_2	$(C_7 + C_2\bar{x}_2)(C_0 + C_1\bar{x}_1) + C_3\bar{x}_2 + \{C_0C_4(C_7 + C_2\bar{x}_2) + C_4C_5\bar{x}_2\bar{x}_3\}/\{1 - C_6\bar{x}_3\}$

Theorem 3.2.5. *If a DFE exists, then R_0 is a nonincreasing function of ν_1, ν_2 and ν_3 .*

The proofs of the remaining corollaries are direct results of the previous theorems. As such, their proofs have been omitted.

Corollary 3.2.6. *If $C_0C_7 > 1$ then $R_0 > 1$.*

Corollary 3.2.7. *$R_0 < 1$ if and only if the following conditions hold*

$$(a) \bar{x}_1 < \frac{1/C_0 - C_7}{C_1}$$

$$(b) \bar{x}_3 < \frac{1}{C_6}$$

$$(c) \bar{x}_2 < \frac{(1 - C_6x_3)(1 - C_7(C_1x_1 + C_0)) - C_0C_4C_7}{C_5C_4x_3 + (C_2(C_1x_1 + C_0) + C_3)(1 - C_6x_3) + C_0C_2C_4}$$

3.3 Biological interpretation of results

Here we interpret the results of the previous section biologically.

3.3.1 The net reproduction number H_0 and Theorem 3.2.1

The composite parameter H_0 is equivalent to the parameter R_0 in Chapter 1 and described in 1.3.1 (though this is not the same as the R_0 detailed in this chapter). This number is a theoretical maximum on the number of immediate adult female offspring a single adult female will have in her lifetime. Similar to the result in Chapter 1, if this number is small

($H_0 \leq 1$), then there is no DFE and if it is large ($H_0 > 1$) then a single DFE exists. Moreover, it is stable whenever it exists.

3.3.2 The composite parameters C_j

Each of these parameters can be viewed as a measure of how effectively infection passes between two classes. With the exception of C_0 and C_7 , each parameter contains a single factor of β_{ij} , which is a measure of how effectively disease is transmitted from infected j -cats to susceptible i -cats (see Table 3.3 for details). The composite parameters C_j can be viewed as a measure of the magnitude of new infections in i -cats that are caused by infected j -cats during their lifetimes by means of direct infection. For example, C_4 (which has a factor of β_{23}) can be viewed as a measure of new infections of adult females caused by infected adult males during their lifetimes. The composite parameter C_0 can be interpreted as a measure of infected adults (of both genders) which matured from infected kittens. The composite parameter C_7 can be viewed as a measure of infected newborn kittens an infected adult females will give birth to in their lifetimes.

3.3.3 The expressions basic reproduction number R_0

The basic reproduction number (R_0) is common to modern disease models. For a detailed description of its formulation and interpretation see [46,47]. In short, the basic reproduction

number for a disease R_0 can be viewed as a measure of virulence of the disease. In simple models, it may be the number of new infections a single infected individual can infect given a completely susceptible population. For further interpretations of R_0 for more complicated models (such as the one we have studied here) see the cited works. If this value is small ($R_0 < 1$), small introductions of the disease are not expected to produce an outbreak. If this number is large ($R_0 > 1$), then a small introduction of the disease is expected to produce an outbreak.

3.3.4 Theorems 3.2.4 and Corollaries 3.2.6 and 3.2.7

Theorem 3.2.4 provides precise conditions under which a DFE is locally stable. Given the values of the primary parameters, these conditions are easily calculable. Biologically, these could potentially be used to determine whether a certain level of vaccination would be effective and whether or not one type of cat should be more heavily vaccinated. In addition, this theorem, and subsequent corollaries, detail that there may be conditions for each type of cat which must be met in order to maintain the stability of the DFE. For example, if $C_0C_7 > 1$, then these conditions can never be met. Referring back to Section 3.3.2, we may interpret this as a measure of infected offspring who mature into infected adult females. It is intuitive that if this number is greater than 1 that the disease must persist, regardless of vaccination efforts.

3.3.5 Theorem 3.2.5

This theorem confirms the intuition that if the level of vaccination is increased, the virulence of the disease (R_0) cannot increase.

3.4 Proofs of selected theorems

3.4.1 Proof of Theorem 3.2.1

In the absence of disease, System (3.2.1) reduces to a system of 6 differential equations, given by

$$\dot{x}_1 = b(x_2 + z_2) - x_1(\delta_1 + 2m) - \nu_1 x_1 \quad (3.4.1a)$$

$$\dot{x}_2 = m x_1 - x_2(\delta_2 + c_{22}\mathbb{U}_2 + c_{23}\mathbb{U}_3) - \nu_2 x_2 \quad (3.4.1b)$$

$$\dot{x}_3 = m x_1 - x_3(\delta_3 + c_{32}\mathbb{U}_2 + c_{33}\mathbb{U}_3) - \nu_3 x_3 \quad (3.4.1c)$$

$$\dot{z}_1 = -z_1(\delta_1 + 2m) + \nu_1 x_1 \quad (3.4.1d)$$

$$\dot{z}_2 = m z_1 - z_2(\delta_2 + c_{22}\mathbb{U}_2 + c_{23}\mathbb{U}_3) + \nu_2 x_2 \quad (3.4.1e)$$

$$\dot{z}_3 = m z_1 - z_3(\delta_3 + c_{32}\mathbb{U}_2 + c_{33}\mathbb{U}_3) + \nu_3 x_3 \quad (3.4.1f)$$

where $\mathbb{U}_k = x_k + z_k$. Similarly, an equilibrium must satisfy

$$b\bar{\mathbb{U}}_2 = \bar{x}_1(\delta_1 + 2m) + \nu_1 \bar{x}_1 \quad (3.4.2a)$$

$$m\bar{x}_1 = \bar{x}_2(\delta_2 + c_{22}\bar{\mathbb{U}}_2 + c_{23}\bar{\mathbb{U}}_3) + \nu_2 \bar{x}_2 \quad (3.4.2b)$$

$$m\bar{x}_1 = \bar{x}_3(\delta_3 + c_{32}\bar{U}_2 + c_{33}\bar{U}_3) + \nu_3\bar{x}_3 \quad (3.4.2c)$$

$$\nu_1\bar{x}_1 = (\delta_1 + 2m)\bar{z}_1 \quad (3.4.2d)$$

$$m\bar{z}_1 + \nu_2\bar{x}_2 = \bar{z}_2(\delta_2 + c_{22}\bar{U}_2 + c_{23}\bar{U}_3) \quad (3.4.2e)$$

$$m\bar{z}_1 + \nu_3\bar{x}_3 = \bar{z}_3(\delta_3 + c_{32}\bar{U}_2 + c_{33}\bar{U}_3) \quad (3.4.2f)$$

where $\bar{U}_k = \bar{x}_k + \bar{z}_k$. Equations (3.4.2) imply that \bar{U}_1, \bar{U}_2 , and \bar{U}_3 must satisfy

$$b\bar{U}_2 = \bar{U}_1(\delta_1 + 2m) \quad (3.4.3a)$$

$$m\bar{U}_1 = \bar{U}_2(\delta_2 + c_{22}\bar{U}_2 + c_{23}\bar{U}_3) \quad (3.4.3b)$$

$$m\bar{U}_1 = \bar{U}_3(\delta_3 + c_{32}\bar{U}_2 + c_{33}\bar{U}_3) \quad (3.4.3c)$$

Theorem 1.2.4 in Chapter 1 with $a_1 = a_2 = a_3 = 0$, if $H_0 \leq 1$ that no positive solution $(\bar{U}_1, \bar{U}_2, \bar{U}_3)$ and if $H_0 > 1$ then there is exactly one positive solution $(\bar{U}_1, \bar{U}_2, \bar{U}_3)$. This proves parts (a) and (b) of the theorem.

Equations (3.4.2d) and (3.4.2a) together imply that $b(\bar{x}_2 + \bar{z}_2) - (\delta_1 + 2m)(\bar{x}_1 - \bar{z}_1) - 2\nu_1\bar{x}_1 = 0$. Substituting $\bar{z}_1 = \bar{U}_1 - \bar{x}_1$, and solving for \bar{x}_1 we find that $\bar{x}_1 = \frac{b\bar{U}_2 + \bar{U}_1(\delta_1 + 2m)}{2(\delta_1 + 2m + \nu_1)}$. Finally, along with (3.4.2a), this implies that $\bar{x}_1 = \frac{\delta_1 + 2m}{\delta_1 + 2m + \nu_1} \cdot \bar{U}_1 = \frac{h_1}{h_1 + \nu_1} \cdot \bar{U}_1$. Since $\bar{z}_1 + \bar{x}_1 = \bar{U}_1$, this also provides an explicit formula for \bar{z}_1 . The equilibrium values for $\bar{x}_2, \bar{x}_3, \bar{z}_2$ and \bar{z}_3 can be similarly calculated to find the remaining values given in the theorem. For reference, they are

$$\begin{aligned} \bar{x}_1 &= \frac{h_1}{h_1 + \nu_1} \cdot \bar{U}_1, & \bar{x}_2 &= \frac{h_1}{h_1 + \nu_1} \cdot \frac{h_2}{h_2 + \nu_2} \cdot \bar{U}_2, & \bar{x}_3 &= \frac{h_1}{h_1 + \nu_1} \cdot \frac{h_3}{h_3 + \nu_3} \cdot \bar{U}_3 \\ \bar{z}_1 &= \frac{\nu_1}{h_1 + \nu_1} \cdot \bar{U}_1, & \bar{z}_2 &= \frac{h_2\nu_1 + h_1\nu_2 + \nu_1\nu_2}{(h_1 + \nu_1)(h_2 + \nu_2)} \cdot \bar{U}_2, & \bar{z}_3 &= \frac{h_3\nu_1 + h_1\nu_3 + \nu_1\nu_3}{(h_1 + \nu_1)(h_3 + \nu_3)} \bar{U}_3 \end{aligned}$$

This proves (c) of the theorem.

For the remainder of the theorem, assume $H_0 > 1$. In part (b) it was shown that a unique DFE exists. The Jacobian of (3.4.1), expanded at the DFE is

$$J = \begin{bmatrix} -h_1 - \nu_1 & b & 0 & 0 & b & 0 \\ m & -h_2 - c_{22}\bar{x}_2 - \nu_2 & -c_{23}\bar{x}_2 & 0 & -c_{22}\bar{x}_2 & -c_{23}\bar{x}_2 \\ m & -c_{32}\bar{x}_3 & -h_3 - c_{33}\bar{x}_3 - \nu_3 & 0 & -c_{32}\bar{x}_3 & -c_{33}\bar{x}_3 \\ \nu_1 & 0 & 0 & -h_1 & 0 & 0 \\ 0 & \nu_2 - c_{22}\bar{z}_2 & -c_{23}\bar{z}_2 & m & -h_2 - c_{22}\bar{z}_2 & -c_{23}\bar{z}_2 \\ 0 & -c_{32}\bar{z}_3 & \nu_3 - c_{33}\bar{z}_3 & m & -c_{32}\bar{z}_3 & -h_3 - c_{33}\bar{z}_3 \end{bmatrix}$$

Define the matrices

$$U = \begin{bmatrix} 1 & 0 & 0 & -1 & 0 & 0 \\ 0 & 1 & 0 & 0 & -1 & 0 \\ 0 & 0 & 1 & 0 & 0 & -1 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \quad \text{and} \quad U^{-1} = \begin{bmatrix} 1 & 0 & 0 & 1 & 0 & 0 \\ 0 & 1 & 0 & 0 & 1 & 0 \\ 0 & 0 & 1 & 0 & 0 & 1 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

Similarity transformations preserve eigenvalues, and so the matrix $U^{-1}JU$ has the same eigenvalues as J . The effect of right-multiplying the matrix J by U is to subtract column i from column $i + 3$ for $i = 1, 2, 3$. and the effect of left-multiplying that product by the matrix

U^{-1} is to add row $j + 3$ to row j for $j = 1, 2, 3$. Then, the product is given by

$$U^{-1}JU = \left[\begin{array}{ccc|ccc} -h_1 & b & 0 & 0 & 0 & 0 \\ m & -h_2 - c_{22}\bar{U}_2 & -c_{23}\bar{U}_2 & 0 & 0 & 0 \\ m & -c_{32}\bar{U}_3 & -h_3 - c_{33}\bar{U}_3 & 0 & 0 & 0 \\ \hline \nu_1 & 0 & 0 & -h_1 - \nu_1 & 0 & 0 \\ 0 & \nu_2 - c_{22}\bar{z}_2 & -c_{23}\bar{z}_2 & m & -h_2 - \nu_2 & 0 \\ 0 & -c_{32}\bar{z}_3 & \nu_3 - c_{33}\bar{z}_3 & m & 0 & -h_3 - \nu_3 \end{array} \right]$$

This matrix is block lower-triangular, and so its eigenvalues are those of the diagonal blocks.

The first diagonal block is the same matrix obtained in Chapter 1 in the proof of Theorem 1.2.7 when analyzing the local stability of the positive equilibrium in the case where $a_1 = a_2 = a_3 = 0$. In the proof it was shown that all of the eigenvalues have negative real part whenever $H_0 > 1$ which, by part (b) of Theorem 3.2.1, is equivalent to assuming a DFE exists. The second diagonal block is a lower-triangular matrix with negative diagonal elements and so the eigenvalues of this block are strictly negative. Thus, if a DFE exists it is LAS in the absence of disease.

3.4.2 Proof of Theorem 3.2.2

We apply the next generation matrix method to show that the DFE is LAS as detailed in [46, 47]. The infected classes are governed by the differential equations

$$\dot{y}_1 = (1 - \phi)\epsilon by_2 - y_1(\delta_{y_1} + 2m) + (1 - \alpha_1)B_1x_1$$

$$\dot{y}_2 = my_1 - y_2(\delta_{y_2} + c_{22}\pi_2 + c_{23}\pi_3) + (1 - \alpha_2)B_2x_2$$

$$\dot{y}_3 = my_1 - y_3(\delta_{y_3} + c_{32}\pi_2 + c_{33}\pi_3) + (1 - \alpha_3)B_3x_3$$

The right-hand side of these equations are which are written in the form of $\mathcal{F}_i - (\mathcal{V}_i^- - \mathcal{V}_i^+)$, where the terms of each equation are grouped into one of \mathcal{F}_i , \mathcal{V}_i^- , or \mathcal{V}_i^+ where

$$\begin{aligned} \mathcal{F}_1 &= B_1(1 - \alpha_1)x_1 + (1 - \phi)\epsilon by_2 & \mathcal{V}_1^- &= y_1(\delta_{y_1} + 2m) & \mathcal{V}_1^+ &= 0 \\ \mathcal{F}_2 &= B_2(1 - \alpha_2)x_2 & \mathcal{V}_2^- &= y_2(\delta_{y_2} + c_{22}\pi_2 + c_{23}\pi_3) & \mathcal{V}_2^+ &= my_1 \\ \mathcal{F}_3 &= B_3(1 - \alpha_3)x_3 & \mathcal{V}_3^- &= y_3(\delta_{y_3} + c_{32}\pi_2 + c_{33}\pi_3) & \mathcal{V}_3^+ &= my_1 \end{aligned}$$

\mathcal{F}_i is the group of terms representing new infections in compartment i and \mathcal{V}_i^+ and \mathcal{V}_i^- are all other transitions into and out of compartment i , respectively. Define \mathcal{F} to be the vector whose i^{th} term is \mathcal{F}_i and \mathcal{V} to be the vector whose i^{th} term is $(\mathcal{V}_i^- - \mathcal{V}_i^+)$. We define the matrices F and V as the linearizations of \mathcal{F} and \mathcal{V} , with respect to the variables y_1, y_2 and y_3 . For system (3.2.1),

$$F = \begin{bmatrix} 0 & (C_7 + C_1\bar{x}_1)h_{y2} & 0 \\ C_2\bar{x}_2h_{y1} & C_3\bar{x}_2h_{y2} & C_4\bar{x}_2h_{y3} \\ 0 & C_5\bar{x}_3h_{y2} & C_6\bar{x}_3h_{y3} \end{bmatrix}, \quad (3.4.4a)$$

$$V = \begin{bmatrix} h_{y1} & 0 & 0 \\ -m & h_{y2} & 0 \\ -m & 0 & h_{y3} \end{bmatrix}, \quad V^{-1} = \begin{bmatrix} \frac{1}{h_{y1}} & 0 & 0 \\ \frac{m}{h_{y1}h_{y2}} & \frac{1}{h_{y2}} & 0 \\ \frac{m}{h_{y1}h_{y3}} & 0 & \frac{1}{h_{y3}} \end{bmatrix}. \quad (3.4.4b)$$

Where the values of C_i and h_{yi} are given in Table 3.3. Then the product of F and V^{-1} is given by

$$\mathbb{J} = FV^{-1} = \begin{bmatrix} C_0(C_7 + C_1\bar{x}_1) & C_7 + C_1\bar{x}_1 & 0 \\ (C_2 + C_0(C_3 + C_4))\bar{x}_2 & C_3\bar{x}_2 & C_4\bar{x}_2 \\ C_0(C_5 + C_6)\bar{x}_3 & C_5\bar{x}_3 & C_6\bar{x}_3 \end{bmatrix}$$

Theorem 2 of [47] states that the DFE is LAS if the eigenvalues of the next generation matrix \mathbb{J}^{-1} are inside the open unit disk. \square

3.4.3 Proof of Corollary 3.2.3

This theorem is a special case of the Jury Conditions (also known as the Schur-Cohn criteria), which can be found in [49]. For a characteristic polynomial of a 3×3 matrix of the form $p(\lambda) = \lambda^3 + \sigma_1\lambda^2 + \sigma_2\lambda + \sigma_3$, the solutions of the equation $p(\lambda) = 0$ all satisfy $|\lambda| < 1$ if and only if the following conditions holds

- $p(1) = 1 + \sigma_1 + \sigma_2 + \sigma_3 > 0$
- $-p(-1) = 1 - \sigma_1 + \sigma_2 - \sigma_3 > 0$
- $1 - \sigma_3^2 > |\sigma_2 - \sigma_1\sigma_3|$

These first two criteria are what we have cited in the statement of the corollary. The final condition is equivalent to the compound inequality $1 - \sigma_3^2 > \sigma_2 - \sigma_1\sigma_3 > -1 + \sigma_3^2$, which is itself equivalent to the inequalities $1 - \sigma_3^2 - \sigma_2 + \sigma_1\sigma_3 > 0$ and $1 - \sigma_3^2 + \sigma_2 - \sigma_1\sigma_3 > 0$. These are the four conditions stated in the theorem. □

3.4.4 Proof of Theorem 3.2.4

Before addressing the theorem, we introduce the partial ordering on the set of 3 matrices, \leq_3 . Define \leq_3 such that $\mathbf{0} \leq A \leq_3 B$ if $A_{ij} \leq B_{ij}$, for $i, j = 1, 2, 3$. Recall that $\rho(A)$ denotes the spectral radius of A . Let A and B be non-negative 3×3 matrices. If $A \leq_3 B$, then $\rho(A) \leq \rho(B)$ [68]. We will show the desired result by showing that the solutions to the equation $p(\lambda) = 0$ are inside the open unit disk if and only if both $r_1 < 1$ and $r_2 < 1$. First we show that $r_1 < 1$ is a necessary condition. Next, we show that if $r_1 < 1$, then $r_2 < 1$ is also necessary. We conclude by showing that the conditions $r_1 < 1$ and $r_2 < 1$ are together

sufficient. Define the matrix

$$\tilde{\mathbb{J}} = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & r_1 \end{bmatrix}.$$

Note that $r_1 = C_6\bar{x}_3$ implies that $\tilde{\mathbb{J}} \leq_3 \mathbb{J}$. Then $r_1 = \rho(\tilde{\mathbb{J}}) \leq \rho(\mathbb{J}) = R_0$. Thus, if $R_0 < 1$, then $r_1 < 1$. This establishes that $r_1 < 1$ is a necessary condition. Moreover,

$$\begin{aligned} r_2 &= C_3\bar{x}_2 + (C_7 + C_2\bar{x}_2)(C_0 + C_1\bar{x}_1) + \frac{C_0C_4(C_7 + C_2\bar{x}_2) + C_4C_5\bar{x}_2\bar{x}_3}{1 - C_6\bar{x}_3} \\ \iff 1 - r_2 &= 1 - C_3\bar{x}_2 - (C_7 + C_2\bar{x}_2)(C_0 + C_1\bar{x}_1) - \frac{C_0C_4(C_7 + C_2\bar{x}_2) + C_4C_5\bar{x}_2\bar{x}_3}{1 - C_6\bar{x}_3} \\ \iff (1 - r_1)(1 - r_2) &= \{1 - C_3\bar{x}_2 - (C_7 + C_2\bar{x}_2)(C_0 + C_1\bar{x}_1)\}(1 - C_6\bar{x}_3) \\ &\quad - C_0C_4(C_7 + C_2\bar{x}_2) - C_4C_5\bar{x}_2\bar{x}_3 \end{aligned}$$

Positivity of the right-hand side of this final equation is condition (3.2.6a). This proves the sufficiency part of the theorem. Next assume that $r_1 < 1$ and $r_2 < 1$. The expression in condition (3.2.6b) can be written as

$$\begin{aligned} &(1 + C_6\bar{x}_3)\{1 + C_3\bar{x}_2 + (C_1\bar{x}_1 + C_7)(C_0 - C_2\bar{x}_2)\} - C_4\bar{x}_2(C_0C_1\bar{x}_1 + C_5\bar{x}_3 + C_0C_7) \\ &= (1 + C_6\bar{x}_3)\{1 + C_3\bar{x}_2 - (C_1\bar{x}_1 + C_7)(C_2\bar{x}_2 - C_0)\} - C_4\bar{x}_2(C_0C_1\bar{x}_1 + C_5\bar{x}_3 + C_0C_7) \\ &= (1 + C_6\bar{x}_3)\{1 + C_3\bar{x}_2 - (C_1\bar{x}_1 + C_7)(C_2\bar{x}_2 + C_0 - 2C_0)\} - C_4\bar{x}_2(C_0C_1\bar{x}_1 + C_5\bar{x}_3 + C_0C_7) \\ &= (1 + C_6\bar{x}_3)\{1 + C_3\bar{x}_2 - (C_1\bar{x}_1 + C_7)(C_2\bar{x}_2 + C_0)\} - C_0C_4(C_7 + C_2\bar{x}_2) - C_4C_5\bar{x}_2\bar{x}_3 \\ &+ (1 + C_6\bar{x}_3)\{1 + C_3\bar{x}_2 + 2C_0(C_1\bar{x}_1 + C_7)\} \\ &> (1 - C_6\bar{x}_3)\{1 - C_3\bar{x}_2 - (C_7 + C_2\bar{x}_2)(C_0 + C_1\bar{x}_1)\} - C_0C_4(C_7 + C_2\bar{x}_2) - C_4C_5\bar{x}_2\bar{x}_3 \end{aligned}$$

$$\begin{aligned}
& + (1 + C_6\bar{x}_3)\{1 + C_3\bar{x}_2 + 2C_0(C_1\bar{x}_1 + C_7)\} \\
& = (1 - r_1)(1 - r_2) + (1 + C_6\bar{x}_3)\{1 + C_3\bar{x}_2 + 2C_0(C_1\bar{x}_1 + C_7)\} > 0
\end{aligned}$$

Thus the condition (3.2.6b) is always satisfied. Since the two remaining conditions ((3.2.6c) and (3.2.6d)) contain the common expression $\sigma_1\sigma_3 - \sigma_2$. We simplify this expression here before preceding.

$$\begin{aligned}
\sigma_1\sigma_3 - \sigma_2 &= C_0C_2C_6C_7^2\bar{x}_2\bar{x}_3 + C_2C_6^2C_7\bar{x}_2\bar{x}_3^2 - C_2C_7\bar{x}_2 - C_0C_4C_7\bar{x}_2 + C_2C_3C_6C_7\bar{x}_2^2\bar{x}_3 + C_0C_6C_7\bar{x}_3 \\
& + 2C_0C_1C_2C_6C_7\bar{x}_1\bar{x}_2\bar{x}_3 + C_1C_2C_6^2\bar{x}_1\bar{x}_2\bar{x}_3^2 - C_1C_2\bar{x}_1\bar{x}_2 - C_0C_1C_4\bar{x}_1\bar{x}_2 \\
& + C_1C_2C_3C_6\bar{x}_1\bar{x}_2^2\bar{x}_3 + C_0C_1C_6\bar{x}_1\bar{x}_3 + C_0C_1^2C_2C_6\bar{x}_1^2\bar{x}_2\bar{x}_3 - C_4C_5\bar{x}_2\bar{x}_3 + C_3C_6\bar{x}_2\bar{x}_3 \\
& = C_0C_2C_6C_7^2\bar{x}_2\bar{x}_3 + C_2C_6^2C_7\bar{x}_2\bar{x}_3^2 - C_2C_7\bar{x}_2 - C_0C_4C_7\bar{x}_2 + C_2C_3C_6C_7\bar{x}_2^2\bar{x}_3 + C_0C_6C_7\bar{x}_3 \\
& + 2C_0C_1C_2C_6C_7\bar{x}_1\bar{x}_2\bar{x}_3 + C_1C_2C_6^2\bar{x}_1\bar{x}_2\bar{x}_3^2 - C_1C_2\bar{x}_1\bar{x}_2 - C_0C_1C_4\bar{x}_1\bar{x}_2 \\
& + C_1C_2C_3C_6\bar{x}_1\bar{x}_2^2\bar{x}_3 + C_0C_1C_6\bar{x}_1\bar{x}_3 + C_0C_1^2C_2C_6\bar{x}_1^2\bar{x}_2\bar{x}_3 - C_4C_5\bar{x}_2\bar{x}_3 + C_3C_6\bar{x}_2\bar{x}_3 \\
& + (1 - C_0(C_1\bar{x}_1 + C_7) - C_3\bar{x}_2 - C_6\bar{x}_3)(1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7)) \\
& - (1 - C_0(C_1\bar{x}_1 + C_7) - C_3\bar{x}_2 - C_6\bar{x}_3)(1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7)) \\
& = 1 - C_2C_7\bar{x}_2 - C_0C_4C_7\bar{x}_2 + C_0C_6C_7\bar{x}_3 + C_2C_6C_7\bar{x}_2\bar{x}_3 - C_0C_1\bar{x}_1 - C_3\bar{x}_2 - C_1C_2\bar{x}_1\bar{x}_2 \\
& - C_0C_1C_4\bar{x}_1\bar{x}_2 - C_6\bar{x}_3 + C_0C_1C_6\bar{x}_1\bar{x}_3 - C_4C_5\bar{x}_2\bar{x}_3 + C_3C_6\bar{x}_2\bar{x}_3 + C_1C_2C_6\bar{x}_1\bar{x}_2\bar{x}_3 \\
& - C_0C_7 - (1 - C_0(C_1\bar{x}_1 + C_7) - C_3\bar{x}_2 - C_6\bar{x}_3)(1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7)) \\
& = 1 - C_0(C_1\bar{x}_1 + C_7) - C_2\bar{x}_2(C_1\bar{x}_1 + C_7) - C_3\bar{x}_2 - C_4C_5\bar{x}_2\bar{x}_3 - C_0C_4\bar{x}_2(C_1\bar{x}_1 + C_7) \\
& - C_6\bar{x}_3(1 - C_0(C_1\bar{x}_1 + C_7) - C_2\bar{x}_2(C_1\bar{x}_1 + C_7) - C_3\bar{x}_2) \\
& - (1 - C_0(C_1\bar{x}_1 + C_7) - C_3\bar{x}_2 - C_6\bar{x}_3)(1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7))
\end{aligned}$$

$$\begin{aligned}
&=(1 - C_6\bar{x}_3)(1 - (C_0 + C_2\bar{x}_2)(C_1\bar{x}_1 + C_7) - C_3\bar{x}_2) - C_4\bar{x}_2(C_5\bar{x}_3 + C_0(C_1\bar{x}_1 + C_7)) \\
&\quad - (1 - C_0(C_1\bar{x}_1 + C_7) - C_3\bar{x}_2 - C_6\bar{x}_3)(1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7)) \\
&=(1 - C_6\bar{x}_3)(1 - (C_0 + C_2\bar{x}_2)(C_1\bar{x}_1 + C_7) - C_3\bar{x}_2) - C_4\bar{x}_2(C_5\bar{x}_3 + C_0(C_1\bar{x}_1 + C_7)) \\
&\quad - (1 - C_0(C_1\bar{x}_1 + C_7) - C_3\bar{x}_2 - C_6\bar{x}_3)(1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7))
\end{aligned}$$

Using this simplification, we simplify condition (3.2.6c)

$$\begin{aligned}
1 - \sigma_3^2 + \sigma_2 - \sigma_1\sigma_3 &=(1 - C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7))(1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7)) \\
&\quad - (1 - C_0(C_1\bar{x}_1 + C_7) - C_3\bar{x}_2 - C_6\bar{x}_3)(1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7)) \\
&\quad + (1 - C_3\bar{x}_2 - (C_1\bar{x}_1 + C_7)(C_2\bar{x}_2 + C_0))(1 - C_6\bar{x}_3) \\
&\quad - C_4\bar{x}_2(C_0(C_1\bar{x}_1 + C_7) + C_5\bar{x}_3) \\
&=\{C_6\bar{x}_3 - C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7) + C_0(C_1\bar{x}_1 + C_7) + C_3\bar{x}_2\} \cdot \\
&\quad \{1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7)\} \\
&\quad + \{1 - C_3\bar{x}_2 - (C_1\bar{x}_1 + C_7)(C_2\bar{x}_2 + C_0)\}(1 - C_6\bar{x}_3) \\
&\quad - C_4\bar{x}_2(C_0(C_1\bar{x}_1 + C_7) + C_5\bar{x}_3) \\
&=\{C_6\bar{x}_3(1 - C_2\bar{x}_2(C_1\bar{x}_1 + C_7)) + C_0(C_1\bar{x}_1 + C_7) + C_3\bar{x}_2\} \cdot \\
&\quad (1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7)) \\
&\quad + \{1 - C_3\bar{x}_2 - (C_1\bar{x}_1 + C_7)(C_2\bar{x}_2 + C_0)\}(1 - C_6\bar{x}_3) \\
&\quad - C_4\bar{x}_2(C_0(C_1\bar{x}_1 + C_7) + C_5\bar{x}_3) \\
&=\{C_6\bar{x}_3(1 - C_2\bar{x}_2(C_1\bar{x}_1 + C_7)) + C_0(C_1\bar{x}_1 + C_7) + C_3\bar{x}_2\} \\
&\quad \cdot (1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7))
\end{aligned}$$

$$+ (1 - r_1)(1 - r_2) > 0.$$

This final expression is always positive, since the product $(1 - r_1)(1 - r_2) > 0$ and since $r_2 < 1 \implies C_2\bar{x}_2(C_1\bar{x}_1 + C_7) < 1$. For condition (3.2.6d), we again use the simplification of $\sigma_1\sigma_3 - \sigma_2$. We have,

$$\begin{aligned}
1 - \sigma_3^2 + \sigma_1\sigma_3 - \sigma_2 &= (1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7))(1 - C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7)) \\
&\quad + (1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7))(1 - C_0(C_1\bar{x}_1 + C_7) - C_3\bar{x}_2 - C_6\bar{x}_3) \\
&\quad + C_4\bar{x}_2\{C_0(C_1\bar{x}_1 + C_7) + C_5\bar{x}_3\} \\
&\quad - (1 - C_3\bar{x}_2 - (C_1\bar{x}_1 + C_7)(C_2\bar{x}_2 + C_0))(1 - C_6\bar{x}_3) \\
&= (1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7))(1 - (C_0 + C_2C_6\bar{x}_2\bar{x}_3)(C_1\bar{x}_1 + C_7) + 1 - C_6\bar{x}_3) \\
&\quad + C_4\bar{x}_2(C_0(C_1\bar{x}_1 + C_7) + C_5\bar{x}_3) \\
&\quad - (1 - C_3\bar{x}_2 - (C_1\bar{x}_1 + C_7)(C_2\bar{x}_2 + C_0))(1 - C_6\bar{x}_3) \\
&= (1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7))(1 - (C_0 + C_2C_6\bar{x}_2\bar{x}_3)(C_1\bar{x}_1 + C_7)) \\
&\quad - (1 - C_3\bar{x}_2 - (C_1\bar{x}_1 + C_7)(C_2\bar{x}_2 + C_0))(1 - C_6\bar{x}_3) \\
&\quad + (1 - C_6\bar{x}_3)(1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7)) + C_4\bar{x}_2(C_0(C_1\bar{x}_1 + C_7) + C_5\bar{x}_3) \\
&\geq (1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7))(1 - (C_0 + C_2\bar{x}_2)(C_1\bar{x}_1 + C_7)) \\
&\quad - (1 - C_3\bar{x}_2 - (C_1\bar{x}_1 + C_7)(C_2\bar{x}_2 + C_0))(1 - C_6\bar{x}_3) \\
&\quad + (1 - C_6\bar{x}_3)(1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7)) + C_4\bar{x}_2(C_0(C_1\bar{x}_1 + C_7) + C_5\bar{x}_3) \\
&\geq (1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7))(1 - C_3\bar{x}_2 - (C_0 + C_2\bar{x}_2)(C_1\bar{x}_1 + C_7)) \\
&\quad - (1 - C_3\bar{x}_2 - (C_1\bar{x}_1 + C_7)(C_2\bar{x}_2 + C_0))(1 - C_6\bar{x}_3)
\end{aligned}$$

$$\begin{aligned}
& + (1 - C_6\bar{x}_3)(1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7)) + C_4\bar{x}_2(C_0(C_1\bar{x}_1 + C_7) + C_5\bar{x}_3) \\
= & (C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7) + C_6\bar{x}_3)(1 - C_3\bar{x}_2 - (C_0 + C_2\bar{x}_2)(C_1\bar{x}_1 + C_7)) \\
& + (1 - C_6\bar{x}_3)(1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7)) + C_4\bar{x}_2(C_0(C_1\bar{x}_1 + C_7) + C_5\bar{x}_3) \\
= & (C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7) + C_6\bar{x}_3)(1 - C_3\bar{x}_2 - (C_0 + C_2\bar{x}_2)(C_1\bar{x}_1 + C_7)) \\
& + (1 - C_6\bar{x}_3)(1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7)) + C_4\bar{x}_2(C_0(C_1\bar{x}_1 + C_7) + C_5\bar{x}_3) \\
= & (C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7) + C_6\bar{x}_3)(1 - r_1)(1 - r_2) \\
& + (1 - r_1)(1 + C_2C_6\bar{x}_2\bar{x}_3(C_1\bar{x}_1 + C_7)) + C_4\bar{x}_2(C_0(C_1\bar{x}_1 + C_7) + C_5\bar{x}_3) > 0
\end{aligned}$$

Thus, by the Corollary 3.2.3, all roots of the characteristic polynomial of $p(\lambda)$, and so the eigenvalues of \mathbb{J} , lie exclusively within the unit disk. Then $R_0 < 1$ and by Theorem 3.2.2, the DFE is LAS. \square

3.4.5 Proof of Theorem 3.2.5

Recall that R_0 is given by the spectral radius of the matrix

$$\mathbb{J} = \begin{bmatrix} C_0(C_7 + C_1\bar{x}_1) & C_7 + C_1\bar{x}_1 & 0 \\ (C_2 + C_0(C_3 + C_4))\bar{x}_2 & C_3\bar{x}_2 & C_4\bar{x}_2 \\ C_0(C_5 + C_6)\bar{x}_3 & C_5\bar{x}_3 & C_6\bar{x}_3 \end{bmatrix}$$

The matrix \mathbb{J} is non-negative and so the spectral radius is a nondecreasing function of its entries so long as they remain non-negative [68]. Each C_j is constant with respect to ν_k , as each is a product of parameters which are also constant with respect to ν_k . Note that this

applies to \bar{U}_k . However, the formulae in Theorem 3.2.1 imply that each x_j is a nonincreasing function of ν_k . Thus, the elements of \mathbb{J} are nonincreasing functions of ν_k and so R_0 is a nonincreasing function of ν_k . \square

3.5 Discussion

Many of the comments of Chapter 1 still apply. We focus here on features unique to disease modeling.

As disease control measures are often enacted after the disease has invaded, a full treatment of this model should include analysis of the so-called endemic equilibria, specifically with regard to existence, uniqueness and stability. We conjecture that exactly one endemic equilibrium exists and is locally stable whenever the disease-free equilibrium is unstable.

Gender and age are strong indicators of behavior, but the model's treatment of age could be done on a finer level, with the addition of multiple age classes for both genders or the use of partial differential equations to track age-density. Gender and age are not the only indicators of behavior, however, and future work on the model may also include state variables for asocial cats (who live in a population without engaging in many of the behaviors which are thought to cause transmission) as in [39]. These animals would have lower values for some (or all) of the transmission terms.

As was stated in Sections 1.6 and 3.5, the assumption that parameters are independent of time is a weakness of the model. If the behavior of the animals is correlated to season, this may indirectly influence the incidence coefficients (β_{ij}) .

Though it is common among the cited works, this model neglects many of the more complicated features of the retrovirus [34–38]. For instance, in this model, cats who become infected remain. However, even after the virus infects the target tissue, the animal may eliminate the virus from their system, placing the animal in what is known as a *latent infection*. The animal may remain in this (undetectable) state for years. The host's cells may be provoked in the future to being production of the cells, making the animal viremic again. Future work may include state variables for these animals. In addition, it has been suggested that the immunity granted by the vaccine is not as effective as that granted by exposure to the virus [65]. Future work may include two categories to accommodate for this. In addition, the immunity granted by exposure is not externally obvious, and vaccines may be wasted on immune cats. Future work may modify the vaccination terms from ν_k to something incorporating the wasted vaccines, such as $\nu_k \frac{x_k}{x_k + z_k}$.

Finally, the permanency of the immunity granted by vaccination is considered not as effective as that granted by exposure to the disease [65]. Future work may include a terms to describe cats who lose their immunity and perhaps additional state variables for the immunity which cannot be lost.

Comments regarding spaying/neutering in Chapter 1 still apply and may have more significance in the context of disease. The resulting change in behavior from prophylaxis

could potentially influence the behavior of the animal and so indirectly influence the transmission terms [40]. Future work may include new state variables to track these animals to investigate the effect of prophylaxis on the disease's ability to invade.

Finally, Corollary 3.2.7 provides clear conditions on when the disease-free equilibrium is locally stable. Future work may use these conditions to construct a gender-informed vaccination strategy which ensures the disease-free equilibrium is locally stable while minimizing vaccination effort. In addition, the influence of removal rates (s_i) on the ability of the disease to invade could be analyzed as well as the interaction between these two approaches. Using Theorem 3.2.4 and subsequent corollaries, one might compare the effect of removing a cat rather than vaccinating it. If the issue of prophylaxis is also addressed, the interaction of the three different approaches could be analyzed.

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