Epidemiological modelling of bovine tuberculosis in badgers and cattle

John F. Rayman

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Department of Mathematics
Faculty of Engineering and Physical Science
University of Surrey
Guildford, Surrey

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Abstract

This thesis covers the formulation and analysis of a number of deterministic, continuous models of infection by a disease such as bovine tuberculosis in one species (essentially badgers) and in two mutually infective species (badgers and cattle). We examine the dynamics of the disease in each model and then consider the effects of the application of different badger culling strategies which have the objective of eliminating the disease in cattle. Chapter 1 sets out the broad background issues relating to the suggestion that tuberculosis in cattle is caused by infective badgers.

In Chapter 2 we study the behaviour of simple Susceptible - Infected - Susceptible (SIS) spatially homogeneous o.d.e. models with constant birth rates and establish the criteria for the existence and stability of equilibrium states. We then extend the population dynamics by utilising a logistic fecundity function in Chapter 3. In Chapter 4 we examine Susceptible - Exposed - Infected - Susceptible (SEIS) o.d.e. models both with an exponentially distributed latent period and delay differential equation models with a fixed length of latent period and analyse their equilibrium behaviour.

We study the application of both continuous and impulsive culling regimes in a spatially homogeneous SIS model on both a constant yield and a constant rate basis in Chapter 3 and the conditions in which an endemic equilibrium can be eliminated in cattle. We compare the effects of culling all the badger population and of culling the infective class only. We also look at culling in systems with net migration and in SEIS model systems.

Chapter 6 is concerned with spatially heterogeneous models of one and two species SIS and SEIS reaction-diffusion equation models on an infinite domain and the circumstances in which we would expect travelling wave solutions connecting different equilibria to be feasible. We then look at the effect of culling in spatially heterogeneous SIS models both on an infinite domain and also on a finite interval.

We introduce age structure to the population in Chapter 6, in one-species SIS and SEI models, using both a renewal equation and delay-differential equation approach. We study the existence and stability of age-structured equilibria.

Finally, we broaden our modelling of the infection process in the two species SIS model in Chapter 7 by introducing airborne and soil bacteria as another transmission route, both in the spatially homogeneous and heterogeneous cases.
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Chapter 1

Introduction

1.1 General context

For a number of years there has been considerable controversy about the cause of the bovine tuberculosis that is endemic within the British national cattle herd. The disease is a serious problem for the British agricultural industry and dealing with it is an urgent problem for government. Among the measures under active consideration, one is to deal with the badger population, regarded by many as mainly responsible for the transmission of the disease in cattle, by culling. This has led to a number of somewhat inconclusive culling trials as well as to vociferous protests about the culling strategy - both from animal lovers and from those who doubt the efficacy of, or the economic or biological basis for the idea.

1.2 Research objectives

The major objective of this research project is to consider different ways in which we can model key aspects of the dynamics of infection and epidemics (or, more properly epizootics - from the Greek zoon - animal) of a disease with the characteristics of bovine tuberculosis (mycobacterium bovis) in an animal species such as the badger (meles meles). The models will then be used to analyse the dynamics of disease infection and epidemics in two interacting animal species as well as the impact of culling as a control measure.

1.3 Bovine tuberculosis (m.bovis) in cattle

Over the past twenty years there has been an accelerating increase in the incidence of m.bovis in cattle herds in Great Britain and Ireland, particularly in the south west of England and in Wales.

A range of wild animals has been shown to be infected with m.bovis in Great Britain: moles (talpa europaeen), foxes (vulpus vulpus), rats (rattus norvegicus), various species of wild deer and, in particular, the European badger (meles meles). While no causation has been proved, and despite considerable uncertainty about the mechanism of transmission, recent research, [24], [40], [16], has shown that

- badgers can transmit infection to cattle in a closed field experiment.
• badgers forage for earthworms on cattle pasture and they can shed large quantities of the bacilli through urine and sputum.

• badgers' natural habitat frequently lies within or near cattle pasture and badgers are frequently found in farm buildings.

• there is a correlation between the geographical spread of badgers and the regional distribution of tuberculosis outbreaks in cattle herds.

• there has been a considerable growth in the badger population in Great Britain in recent years due perhaps both to their protected status and a warming climate.

• there is some correlation between removal of badgers and a reduction in herd breakdowns (defined as the presence of at least one infected animal in a herd).

There is considerable controversy in Great Britain on the question of whether badgers are indeed a reservoir of *m. bovis* and, if so, what action should be taken to deal with the problem. The powerful conservation lobby wants to continue the badgers' status as a protected species. Farmers want to eradicate the badgers to protect their cattle in TB-affected areas. Public health officials want to protect humans from a potentially very serious human disease.

*m. bovis* is closely related to *m. tuberculosis*, the principal cause of TB in humans. A Public Inquiry in 1934 found that 2000 of the annual deaths from TB in Great Britain (6% of all TB-related deaths) were due to bovine TB and that 40% of British dairy cows were infected. As a consequence, two key measures were introduced, which are still in force today. Milk was to be pasteurised and regular tuberculin testing of animals was to be introduced. Positive testing led to slaughter and restrictions on cattle movement. These measures had the effect of reducing the incidence of TB in the British herd to less than 0.5% in 1995, with only 32 cases of human TB attributed to *m. bovis* (apparently mostly among those who contracted it as children prior to the introduction of the control measures). Although the prevalence of TB in the British herd is still of the order of a few percentage points, the rate of growth, from fewer than 100 detected cases in 1985 to over 2000 in 2004, is a major cause of concern.

While cattle infected with *m. bovis* do not generally die from the disease, they do not thrive and so the production of meat and milk is substantially reduced. Moreover, countries where there is endemic tuberculosis in cattle find exporting fresh beef, beef products and dairy products a major problem. (In this context we note that vaccinating cattle against tuberculosis is not favoured by the farming industry, as there is currently no method of distinguishing between positive test results from vaccinated cattle and from those actually incubating tuberculosis.) Thus, for farmers, bovine tuberculosis is primarily an economic issue.
1.4 Population dynamics and behaviour of the badger

The badger population has a low intrinsic growth rate (0.2 per capita per year, the result of an annual birth rate of 0.6 per capita and an annual death rate of 0.4 per capita [2], these, as with all the data in this section are approximate values). There is a maturation delay of between one and two years to first breeding. Litters are small (2.7 cubs per litter) and the mortality in the first year of life is in the range 50% to 70%. Adult annual mortality is 0.25 per capita. Population abundance is largely determined by habitat suitability and there are density dependent effects on fecundity which are largely responsible for population stability. There may be cyclical fluctuations in the abundance of badgers in moderate to poor habitats. A typical badger population is 25% cubs, 25% immature animals and 50% adults. Population density ranges from as little as one to two adults per square kilometer to as much as 20, with the average in the range 6 to 8 adults per square kilometer. Density is dependant on soil type (which affects tunnelling), food availability and vegetation as well as seclusion from human activity. The badger has no other predator than humans. Badgers are essentially social and territorial, remaining within the boundaries of their social group territories. A small number of adult male badgers may disperse into neighbouring territories during the breeding season, and immature animals may disperse at the end of their first year of life and attempt to join new social groups, but dispersal is rather infrequent.

1.5 Epidemiology of tuberculosis in the badger

New infections in badgers arise when susceptible animals come into contact with \textit{m. bovis} bacilli, either directly from an infectious animal (through respiration or biting) or indirectly from the environment. Evidence suggests that the most common route of transmission is through inhaling or ingesting live bacilli from the environment. Diseased animals contaminate their environment heavily with faeces, urine and sputum. Their diet of earthworms (with a high water content) causes them to urinate frequently and they frequently visit the borders of the territory to defaecate (indeed this is a method of marking the territory). The chance of contact with bacilli and the chance of inhalation of the bacilli are all much increased as a result of the communal life that badgers live underground in their setts.

Once infected, there is a latent (incubation) period of 3 to 5 months. Infection may be life long and no immunity appears to be acquired. The infection may revert to being latent and the animal appear to recover, only to relapse later. It is unclear to what extent deaths due to the disease are an important factor in badger mortality.

1.6 General mathematical modelling considerations

It is evident that the systems we will be studying are both extremely complex and often relatively poorly understood from a biological or ecological point of view. Data in some cases exists to provide modellers with reasonable estimates
of key model parameters, but in other cases the data is either contradictory, poor or absent.

As a generalisation, there is little value in a mathematical model which is as complex as the system it is intended to explain, for if it were tractable so would be the system itself. We need to build models that are sufficiently simple to analyse with the mathematical techniques we have, focussing on specific key aspects of the system that we are studying, while identifying the inherent weaknesses and gaps in the model that are the inevitable result of doing so.

Whereas statistical models could be said to be diagnostic, (interpreting biological processes from measured data), deterministic models are prognostic, (proposing a descriptive model of a biological process and making predictions about what will be observed.) Evidently, deterministic models must be validated to be useful. We have adopted a deterministic, compartmentalised approach to model building in this research work and have attempted throughout to focus on analytical solutions of our model systems. Where this has not been possible we have used numerical simulations to illustrate what we are unable to prove analytically.

There have been relatively few papers published on the analysis of deterministic models to study the badger/cattle system [15],[6]; the majority of the work published has been numerical simulation with the emphasis on stochastic models, e.g. [53], [3].

While even relatively simple model systems are often very difficult to treat analytically, we can in many cases obtain at least a qualitative understanding of the explicit impact of the model parameters on the behaviour of solutions, in ways that cannot so straightforwardly be achieved with numerical analysis.

Finally, mathematical modelling provides the opportunity to "experiment" in a way that is not practical in the field.

1.7 General concepts and methods

We make use on many occasions of a few key concepts and theorems which we bring together for convenience in this section. The theorems are well-known and are stated, not proved.

Basic reproductive ratio

The basic reproductive ratio, usually given the symbol $R_0$ is defined as the number of secondary infections generated by the introduction of a single infective into a population consisting solely of susceptibles and is perhaps the most important quantity in epidemic modelling. A value greater than unity implies that each infected animal produces more than one secondary infection and thus the disease can spread and the infection-free equilibrium will become unstable. If $R_0 < 1$ then the number of secondary infections caused is sufficiently low that the disease dies out.
The first individual infects $R_0$ others, each of whom then infects $R_0$ others in turn, so that after two "generations" there are $1 + R_0 + R_0^2$ infected cases. After $n$ such "generations" the total number infected will be

$$\sum_{i=0}^{n} R_0^i = \frac{1 - R_0^{n+1}}{1 - R_0}.$$ 

If $R_0 < 1$ this series converges, to $\frac{1}{1-R_0}$, a finite number, while the size of the $n$th "generation" goes to zero as $n \to \infty$.

Epidemics and endemic states

In the progression of any disease in a system where the model does not allow for the appearance of more susceptibles after $t = 0$, we see either that the disease dies out without infecting large numbers of individuals, or that the evolution of the disease continues until there are insufficient susceptibles to maintain it and it consequently dies out. Which of the two outcomes we see depends on the size of $R_0$. If, however, new susceptibles appear, through births, recovery or migration, then we may see a third outcome, that of an endemic disease state, where the disease is always present in the population, for $R_0 > 1$. In the models we analyse, since the duration of infection is of the same order of magnitude as the lifetime of the individual animal, we will always have a recruitment function.

1.7.1 Next generation matrix and the basic reproductive ratio

We can describe a compartmental deterministic model in general as follows

$$\frac{du_i}{dt} = F_i(u, v) - V_i(u, v) \quad i = 1 \ldots n \quad (1.1)$$

$$\frac{dv_j}{dt} = g_j(u, v) \quad j = 1 \ldots m$$

where $u = (u_1, u_2 \ldots u_n)$ and $v = (v_1, v_2 \ldots v_n)$ with $u_i$ infective components and $v_j$ susceptible components. $F_i$ is the rate at which new infections increase $u_i$ and $V_i$ is the rate at which transfers between compartments reduce $u_i$. $g_i$ is the rate at which $v_i$ is reduced (by death or recovery). Clearly $F_i$ cannot be negative since it represents new infections. Let us assume that system (1.1) has an infection-free equilibrium (IFE) where $u = 0$.

If we linearise around this equilibrium we obtain the following differential equation for the vector $u$;

$$\frac{du}{dt} = (F - V)u$$

where $u$ is a $(1 \times n)^T$ vector and $F$ and $V$ are $n \times n$ constant matrices. We assume that, near to the IFE, the number of susceptibles is, effectively, large and constant. The length of time that an infectious individual remains infectious is then $\int_0^\infty \phi(u_0) dt$, where $\phi(u_0)$ is the solution to

$$\frac{du}{dt} = -Vu, \quad u(0) = u_0$$
We can solve this equation to give
\[ \phi(u_0) = e^{-vt}u_0. \]

The number of secondary infections produced by one infectious individual, \( N(t) \), will be given by
\[ N(t) = \int_0^\infty F\phi(u_0)dt. \]
If we substitute the expression for \( \phi(u_0) \) obtained above we obtain
\[ N(t) = \int_0^\infty Fe^{-vt}u_0dt = FV^{-1}u_0. \]

We term \( FV^{-1} \) the next generation matrix. All its entries are non-negative and as such (see [34]) it will have a non-negative eigenvalue, which we will term \( R_0 \), such that the magnitude of this eigenvalue is strictly greater than all the other eigenvalues of \( FV^{-1} \). Hence we can define, strictly, \( R_0 \) as the spectral radius \( \rho \) of the next generation matrix. Clearly, if \( \rho(FV^{-1}) < 1 \), each infectious individual produces fewer than one new secondary infection and the disease dies out.

### 1.7.2 A positivity theorem

We will need to verify that the models are well-posed, and in particular that all of the state variables will, provided that they start non-negative, remain non-negative. The following theorem will be useful in this context (see [51] p421).

**Theorem 1.7.1** Let \( \dot{x} = F(x) \), where
\[ x = (x_1, x_2, x_3 \ldots x_n) \quad \text{and} \quad F = (f_1, f_2, f_3 \ldots f_n), \]
and each of the \( f_i \) is Lipschitz continuous and let \( x(0) > 0 \). Then, if \( f_i(x) > 0 \) for all vectors \( x \) such that \( x_i = 0 \) and \( x_j > 0 \) where \( j \in \{1, 2, 3 \ldots n\} \) then \( x(t) > 0 \) for all \( t > 0 \).

### 1.7.3 Persistence

We are principally interested (apart from culling models) in situations where the population classes remain in being in the long term. We call this property persistence. We can define persistence for a population \( x(t) \) if there exist two real positive numbers \( m \) and \( M \) such that for large \( t \);
\[ m \leq x(t) \leq M. \]

A system of disease classes is persistent if each of the individual classes is persistent.

### 1.7.4 Non-existence of periodic orbits - The Dulac criterion

We may state the Dulac Criterion as follows (see, for instance [39]):

Let \( \Omega \) be a simply connected region of the plane. Let the functions \( f(u, v), g(u, v) \) \( \in C^1(\Omega) \) and \( B \in C^1(\Omega) \) be such that \( \frac{\partial (Bf)}{\partial u} + \frac{\partial (Bg)}{\partial v} \) is not identically zero and does not change sign in \( \Omega \). Then the system \( \dot{u} = f(u, v), \dot{v} = g(u, v) \) does
not have a periodic solution in $\Omega$.

This useful approach does not allow us of course to prove the existence of periodic orbits.

1.7.5 Routh Hurwitz stability criteria

We frequently want to test the linear stability of equilibria by examining the eigenvalues of Jacobian matrices of systems linearised about those equilibria. We make use of the Routh Hurwitz stability criteria (see for example [45]) and consider the signs of the real parts of the roots of the characteristic equation of such a matrix. We state the criteria as follows;

Theorem 1.7.2 A necessary and sufficient condition that all the roots of the $n^{th}$-degree polynomial equation in $\lambda$ with real coefficients $a_i, i = 1 \ldots n$,

$$\sum_{i=0}^{n} a_i \lambda^i = 0$$

have negative real parts is that all the principal leading minors of the following matrix are strictly positive:

$$
\begin{pmatrix}
a_1 & a_0 & 0 & 0 & 0 & 0 & \cdots & 0 \\
a_3 & a_2 & a_1 & a_0 & 0 & 0 & \cdots & 0 \\
a_5 & a_4 & a_3 & a_2 & a_1 & a_0 & \cdots & 0 \\
a_7 & a_6 & a_5 & a_4 & a_3 & a_2 & a_1 & \cdots & 0 \\
\vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \cdots & \vdots & \vdots \\
0 & 0 & 0 & 0 & 0 & 0 & \cdots & 0 & a_n
\end{pmatrix}
$$

Remark 1.7.3 If all of the roots of the characteristic equation obtained from the Jacobian of the linearisation of a system of o.d.e.s about an equilibrium are negative or have negative real parts then that equilibrium is said to be locally asymptotically stable. Small perturbations from the equilibrium die away and the system returns to the equilibrium.

The structure of the matrix for the Routh-Hurwitz conditions is obtained as follows. The coefficients of the polynomial from $a_1$ to $a_n$ are written out on the main diagonal. The columns consist in turn of coefficients with only odd or even subscripts, with the coefficient $a_0$ included among the latter. All the other entries of the matrix corresponding to coefficients with subscripts greater than $n$ or less than 0 are set equal to 0.

In practice we will apply the criteria for the most part to two and three dimensional systems. In the case of a $2 \times 2$ Jacobian matrix the criteria can be simplified to the requirement that the trace of the Jacobian be strictly negative and the determinant strictly positive in order that the equilibrium be locally stable.

For a $3 \times 3$ Jacobian matrix, if its characteristic equation is

$$\lambda^3 + b_1 \lambda^2 + b_2 \lambda + b_3 = 0$$
then we require \( b_1 > 0, \quad b_1 b_2 - b_3 > 0 \) and \( b_3 > 0 \) for the equilibrium to be locally stable. In general, for an \( n \times n \) matrix, the coefficient of \( \lambda^{n-1} \) is the trace of the Jacobian multiplied by \(-1\) (so that we require the trace to be negative whatever the order of the system) and the constant term is the determinant of the Jacobian multiplied by \((-1)^n\) (we require the determinant to be positive if the system is of even order and negative if it is of odd order).

It is worth pointing out that to prove that an equilibrium is unstable, it of course suffices merely to establish that any one of the Routh Hurwitz criteria is not met.

**Linearised systems**

Our justification for studying the properties of the linearised system rests on the Hartmann-Grobman Theorem (see [47] p 119) which may be stated as follows:

**Theorem 1.7.4** In the neighbourhood of a hyperbolic equilibrium \( x_0 \), a non-linear dynamical system \( \dot{x} = f(x, t) \) is topologically equivalent to its linearisation \( \dot{x} = Df(x_0)x \).

1.7.6 Reducing the dimension of a system of o.d.e.s

Many of the systems we are studying can be made more tractable by reducing their dimension. In many cases we can sum equations for the individual state variables to produce an o.d.e. for the overall population of a species, \( N(t) \), of the form

\[
\frac{dN}{dt} = B(N) - \mu N.
\]

Here \( B(\cdot) \) is a non-linear fecundity function (see Section 6.4.1 for the typical prescribed properties of \( B(\cdot) \)) and \( \mu \), which may or may not be constant, is a death function. Since \( B \) is non-negative by definition and \( \mu \) is positive, we must have an equilibrium \( N^* \) satisfying the equation \( N^* = \mu B(N^*) \). Thus, if we consider that \( t \) is sufficiently large then we may take \( N(t) = N^* \) and, provided that \( N^* > 0 \) and the equilibrium is stable, we can substitute for one of the state variables in terms of the others. This is not possible, of course, when there are, for example, additional deaths from disease or where there is migration of one of the disease classes.

1.7.7 Non-dimensionalisation

We non-dimensionalise many of the models we will be considering. The reasons for this approach are

- to reduce algebraic complexity
- to be able to focus on the impact of the key parameters and parameter groups, on the system
- to remove the dimensions from the system to permit exploitation of approximation techniques where small terms are neglected or used in expansions. We can only use terms like "small" where we are comparing quantities with the same dimension.
Chapter 2

An SIS model for one, two and three species

2.1 Introduction

We consider a deterministic compartmental model with inter-species and intra-species infectivity in a population of two or more separate species. The analysis considers the circumstances in which infection free equilibria and endemic disease states arise and their global stability.

For the analysis in this chapter we use an epidemic model in which susceptible animals ($S$) pass into an infective class ($I$) and, once recovered return to the susceptible class. This is known as an SIS model. We make the following assumptions

- Animal densities are continuous. Although the density of animals per unit area must be a discrete variable, continuity is of course mathematically convenient. However we make use of the so-called continuum hypothesis, quoted in [23], that the actual behaviour of a discrete variable such as population can be accurately represented by the evolution of a continuous variable. This arises from the “fine-grained” nature of the variable, i.e. in a large population, a change of one individual is a small relative change and can thus be regarded as a finite difference approximation to the infinitesimal change of differential and integral calculus. The impact of assuming continuity will be most serious when we are considering very small numbers of animals, when a discrete, stochastic model would be more appropriate.

- Recruitment of susceptibles is at a constant rate $\Lambda$.

This does not realistically model the population dynamics of a real animal species but suffices for our purposes in this first model, to look at the infection-free equilibria and endemic disease states only. In subsequent chapters we will consider firstly a logistic fecundity function and then a more general recruitment function. We note that the length of the infective period in tuberculosis is of a similar order to the length of the lifespan of the animals and that, in consequence, we must therefore introduce population dynamics. We can only consider populations to be constant at, or close to, equilibria.
• There is no latency period. Animals become immediately infectious once infected. In practice, tuberculosis does have a latent period and we shall investigate the effect of this in Chapter 4. For simplicity at this stage we ignore it.

• There is no vertical transmission of the disease. Newborn infants are immediately susceptible, they do not acquire the infection automatically from the mother. Both susceptible and infectious classes can produce offspring.

• Infection is through a mass action model. The rate of production of new infectives is proportional to the product of the densities of the susceptible and infectious classes - an approach borrowed from chemical reaction kinetics. Suppose that the density of susceptibles is \( S(t) \) and infectives \( I(t) \) in a population of density \( N(t) \). If an animal makes contact in unit time with \( c(N) \) other animals, where \( c \) is some appropriate function of \( N \), then \( \frac{S}{N} \) of these contacts will be with susceptibles. If the probability of transmission of the disease on contact is \( \pi(N) \) then the total rate of infectious contacts will be \( \pi(N)c(N)I\frac{S}{N} \) and we define \( \beta(N) = \pi(N)c(N)I\frac{S}{N} \). If \( c = cN \) and \( \pi \) is constant this reduces to the mass-action expression for the total rate of infectious contacts; \( \beta SI \). In a sufficiently geographically restricted animal population the proportionality of the rate of contacts to the population size appears a reasonable assumption and the mass action model is widely used in studying animal systems [45]. If \( c \) were constant, the resulting expression for the rate of infectious contact, \( \beta SI/N \), is known as the standard incidence model and is more appropriate, for example for human diseases.

• All the parameters are constant. At least some of the parameters, such as death rates, will be functions of age of the animal; others such as recovery rates, of the length of time since infection. Constant parameters are an obvious first approximation.

The exponential distribution

The processes of death and of recovery from the disease are modelled with an exponential distribution. If we consider a continuous random variable \( X \) with probability density function \( f(X = x) \) with parameter \( \lambda \) such that

\[
f(X = x) = \begin{cases} \lambda e^{-\lambda x} & : x \geq 0 \\ 0 & : \text{otherwise,} \end{cases}
\]

then the cumulative distribution function is \( F(x) \), where

\[
F(X \leq x) = \int_0^x f(\xi) d\xi = 1 - e^{-\lambda x}
\]

and this distribution has mean \( 1/\lambda \) and variance \( 1/\lambda^2 \).

Thus if \( \mu \) is the constant death rate, then the proportion of the population surviving from \( t = 0 \) to \( t = \tau \) is \( e^{-\mu \tau} \) and the mean life expectancy is \( \frac{1}{\mu} \). While the actual survival process is unlikely to be as simple, we
believe this to be an adequate basic model. Similarly, if the constant recovery rate is \( \gamma \) then the proportion of the infected population, infected at time \( t_1 \) still infected and alive at time \( t_2 \) will be \( e^{-(\mu+\gamma)(t_2-t_1)} \) and the mean length of time infected \( \frac{1}{\gamma} \). This illustrates a convenient property of the exponential distribution, the so-called "lack of memory property", that the probability of survival from any \( t_1 \) to any \( t_2 \) depends only on the length of the interval, not on the beginning or end values.

- There are no additional deaths due to the disease.
  In cattle this is true to the extent that tuberculosis itself is not a fatal disease. However since the cattle are slaughtered once they are found to be reactive, it could be considered as fatal. In badgers there may be a higher death rate among those found to be with the disease than in those without. However, ignoring extra deaths allows an equation for total population to be expressed in simple form.

- There is no immunity from the disease. Animals may recover from the infection but acquire neither complete nor partial immunity as a result.

- The populations are spatially homogeneous, isotropic and randomly mixed. This is clearly an unrealistic assumption and one that we will relax in Chapter 5.

- The state variables are functions of time only, in particular there is no age or maturity structure.

- In all of our models, except where we are modelling the effect of interventions such as culling, we consider in principle the introduction of an infinitesimally small number of infectious animals to a system initially in disease free equilibrium. If we started with no infectious animals then, of course, there would be no disease at any time and the model would be trivial.

We consider animal species \( c \) and \( b \), which we take as cattle and badgers respectively, with \( S_c \) the population density (in animals per unit area) of susceptible cattle, \( I_c \) the population density of infected cattle, \( N_c \) the total population of cattle and the corresponding variables for badgers have the subscript \( b \). The model we use here is developed from standard SIS models [45], [10]. The ordinary differential equations which describe the system are as follows

\[
\begin{align*}
\frac{dS_c}{dt} &= \Lambda_c - \mu_c S_c - \beta_c S_c I_c - \xi_{bc} S_c I_b + \gamma_c I_c, \\
\frac{dI_c}{dt} &= -\mu_c I_c + \beta_c S_c I_c + \xi_{bc} S_c I_b - \gamma_c I_c, \\
\frac{dS_b}{dt} &= \Lambda_b - \mu_b S_b - \beta_b S_b I_b - \xi_{bc} S_b I_c + \gamma_b I_b, \\
\frac{dI_b}{dt} &= -\mu_b I_b + \beta_b S_b I_b + \xi_{bc} S_b I_c - \gamma_b I_b,
\end{align*}
\]

(2.1)

together with the following definitions and constraints

\[ S_c + I_c = N_c, \quad S_b + I_b = N_b, \quad S_c > 0, \quad S_b > 0, \quad I_c \geq 0, \quad I_b \geq 0. \]
For initial conditions we assume that there is an infection free equilibrium (IFE) and that either $I_c(0) = \epsilon$ or $I_b(0) = \delta$, where $0 < \epsilon, \delta < 1$. A small number of infected animals is introduced at $t = 0$.

2.1.1 The parameters

The subscripts $c$ and $b$ refer to the parameters relating to cattle and badgers respectively, $\mu$ is the death rate, $\gamma$ is the recovery rate, returning from the infectious to the susceptible class, $\beta$ is the intra-species infection rate, $\xi$ is the inter-species infection rate with the direction of the infection in the order of the subscripts so $\xi_{bc}$ means badgers infecting cattle. We use asterisks for the endemic equilibrium values of the state variables. The quantity

$$R_c = \frac{\beta_c \Lambda_c}{\mu_c (\mu_c + \gamma_c)} \quad (2.2)$$

is the basic reproductive ratio for cattle in an environment alone and represents the number of secondary infections each infectious animal can be expected to produce, while it remains infectious, when introduced into a population consisting entirely of susceptibles. The quantity

$$R_b = \frac{\beta_b \Lambda_b}{\mu_b (\mu_b + \gamma_b)} \quad (2.3)$$

is the basic reproductive ratio for badgers alone. $R_{bc}$, which we define later, is the analogue of a basic reproductive ratio for the two-animal system.

2.1.2 A single species

For completeness we briefly review the dynamics of an SIS epidemic in a single animal species with the same assumptions as we have made for the two-animal system, using the following model;

$$\frac{dS}{dt} = \Lambda - \mu S - \beta S I + \gamma I$$

$$\frac{dI}{dt} = -\mu I + \beta S I - \gamma I \quad (2.4)$$

$S + I = N, \quad S > 0, \quad I \geq 0, \quad N(0) = N_0$.

Theorem 2.1.1 System (2.4) exhibits a transcritical bifurcation with bifurcation parameter $R_0 = \frac{\beta^*}{\mu (\mu + \gamma)}$. For $R_0 < 1$ the infection free equilibrium (IFE) is stable. For $R_0 > 1$ an endemic disease equilibrium exists and is stable, while the IFE is unstable.

Remark 2.1.2 The normal form of a transcritical bifurcation is $\frac{dx}{dt} = \mu x - x^2$ where $x$ is the state variable and $\mu$ the parameter. A transcritical bifurcation is characterised by an equilibrium having an eigenvalue whose real part passes through zero as the parameter increases. Both before and after the bifurcation, there is one unstable and one stable fixed point. However, their stability is exchanged when they coincide. The unstable fixed point becomes stable and vice versa.

A transcritical bifurcation thus occurs at a threshold value of some parameter. This section provides the proof of Theorem 2.1.1.
The whole population

By adding the equations in (2.4) we obtain \( \frac{dN}{dt} = \Lambda - \mu N \) which we can solve directly to obtain

\[
N(t) = N_0 e^{-\mu t} + \frac{\Lambda}{\mu} (1 - e^{-\mu t}),
\]

from which we see that \( N \) is both positive (for \( N_0 > 0 \)) and bounded (\( N(t) \leq \max\{N_0, \frac{\Lambda}{\mu}\} \)) and that there is a globally stable equilibrium at \( N^* = \frac{\Lambda}{\mu} \).

Disease classes

Firstly, we establish the well-posedness of system (2.4). We see immediately

\[
I(t) = I(0) e^{\int_0^t (\beta S(t) - (\mu + \gamma)) dt} > 0 \quad \text{for} \quad I(0) > 0,
\]

so that \( I(t) > 0 \) for all \( t > 0 \). It therefore follows that \( \left. \frac{dS}{dt} \right|_{S=0} > 0 \). If we suppose that \( S = 0 \) for the first time, at \( t = t_0 \) we see that \( \left. \frac{dS}{dt} \right|_{t=t_0} > 0 \), which, by continuity must imply \( S(\tilde{t}) < 0 \) for some \( \tilde{t} < t_0 \). This contradicts the assertion that \( t_0 \) was the first time that \( S = 0 \) and so we conclude that \( S(t) > 0 \) for all \( t > 0 \). Since \( N = S + I \) and \( N \) is bounded, \( S \) and \( I \) must also be bounded.

System (2.4) has an infection free equilibrium at \((S, I) = (\frac{\Lambda}{\mu}, 0)\) and an endemic disease equilibrium at \((S^*, I^*) = (\frac{\mu + \gamma}{\beta}, \frac{\Lambda \beta - \mu (\mu + \gamma)}{\beta \mu})\). We evidently require that the size of the endemic infectious class be positive. The Jacobian, \( J_0 \) of the linearisation of system (2.4) around the IFE (sometimes known as the community matrix) has eigenvalues \( \lambda_1, \lambda_2 \), where

\[
\lambda_1 = -\mu, \quad \lambda_2 = \frac{\Lambda \beta - \mu (\mu + \gamma)}{\mu}.
\]

The eigenvalues of the Jacobian, \( J^* \), of the linearisation around the endemic equilibrium are \( \lambda_3, \lambda_4 \) where

\[
\lambda_3 = -\mu, \quad \lambda_4 = -\frac{\Lambda \beta - \mu (\mu + \gamma)}{\mu}.
\]

The necessary and sufficient condition for each of the following

- the existence of the endemic equilibrium (i.e. \( I^* > 0 \), the only physically meaningful range,
- the negativity of \( \lambda_4 \) (which ensures that the endemic equilibrium is stable if it exists, since \( \lambda_3 < 0 \)) and
- the positivity of \( \lambda_2 \), thus ensuring the instability of the IFE

is that \( \frac{\Lambda \beta}{\mu (\mu + \gamma)} > 1 \). We define \( R_0 \), the basic reproductive ratio for the system as

\[
R_0 = \frac{\Lambda \beta}{\mu (\mu + \gamma)}. \tag{2.5}
\]

Conversely, \( R_0 < 1 \) ensures the stability of the IFE and the non-existence of the endemic disease equilibrium.
Remark 2.1.3 By analogy with the next generation matrix described in Section 1.7.1, in system (2.4), \( F = \frac{A_0}{\mu} \) and \( V = \mu + \gamma \) so that \( R_0 \) is simply the value of the \( 1 \times 1 \) matrix \( FV^{-1} \).

Solving the o.d.e.s

We cannot solve system (2.4) explicitly but we can substitute for \( S(t) \) knowing \( N(t) \) and obtain the following expression for \( I(t) \):

\[
I(t) = \frac{I(0)e^{-\frac{A(N_s)_t}{\mu} - \frac{\mu}{\mu^*}e^{-\frac{(\beta A_{\pm}(\mu + \gamma))t}{\mu^*}}}}{\beta I(0)\int_0^t e^{-\frac{A(N_s)_t}{\mu} - \frac{\mu}{\mu^*}e^{-\frac{(\beta A_{\pm}(\mu + \gamma))t}{\mu^*}}}d\tau + e^{-\frac{A(N_s)_t}{\mu} - \frac{\mu}{\mu^*}}}.
\]

For very large \( t \) and provided that \( \beta A > \mu(\mu + \gamma) \) we can approximate equation (2.6) with

\[
I(t) \approx \frac{e^{-\frac{A(N_s)_t}{\mu} - \frac{\mu}{\mu^*}e^{-\frac{(\beta A_{\pm}(\mu + \gamma))t}{\mu^*}}}}{\beta \int_0^t e^{-\frac{A(N_s)_t}{\mu} - \frac{\mu}{\mu^*}e^{-\frac{(\beta A_{\pm}(\mu + \gamma))t}{\mu^*}}}d\tau}.
\]

Carrying out the integration we obtain, for \( t \) very large

\[
I(t) = \frac{\beta A - \mu(\mu + \gamma)}{\mu\beta(1 - e^{-(\beta A - \mu(\mu + \gamma))t})},
\]

then

\[
\lim_{t \to \infty} I(t) = \frac{\beta A - \mu(\mu + \gamma)}{\mu\beta} = I^*, \text{ for } \beta A > \mu(\mu + \gamma).
\]

This suggests that the endemic equilibrium demonstrated by the one-species SIS model is globally stable. \( \square \)

Approximate solutions

If we consider system (2.4) at the IFE and we introduce one infective at \( t = 0 \), then for small \( t > 0 \) we can take \( S(t) \approx N^* \) and thus the second of the equations in system (2.4) becomes

\[
\frac{dI}{dt} = \beta N^*I - (\mu + \gamma)I, \quad I(0) = I_0,
\]

which solves straightforwardly to give \( I(t) = I_0e^{(R_0-1)t}, \quad a = \mu + \gamma \). We see immediately that for \( R_0 < 1, I(t) \) is always decreasing. If \( R_0 > 1 \) then the disease class is able to increase. This is of course in effect simply restating the result of evaluating the eigenvalues of the Jacobian at the IFE.

If we now take \( t \) large enough that we can consider that \( N(t) \approx N^* \), a constant, then we can substitute for \( S(t) \) in the second equation of system (2.4) to give

\[
\frac{dI}{dt} = \beta(N^* - I)I - (\mu + \gamma)I, \quad I(0) = I_0.
\]

We can solve this equation to give

\[
I(t) = \frac{I_0(R_0 - 1)N^*}{R_0I_0 - (R_0I_0 - N^*(R_0 - 1))e^{-(\mu + \gamma)(R_0 - 1)t}}.
\]
Hence
\[\text{if } R_0 < 1 \lim_{t \to \infty} I(t) = 0,\]

while if \( R_0 > 1 \lim_{t \to \infty} I(t) = N^* (1 - 1/R_0). \)

Thus we have proved Theorem 2.1.1 for the approximate model with \( N \) replaced by \( N^* \).

Global stability using a Lyapunov function

Lemma 2.1.4 The IFE of system (2.4) is globally asymptotically stable if \( R_0 < 1 \).

We introduce \( V(t) = \frac{1}{2} I^2 \), then \( V > 0 \) for all \( I \neq 0 \) and \( V = 0 \) only for \( I = 0 \).

By hypothesis, \( R_0 < 1 \), i.e. \( \frac{\beta N^*}{\mu + \gamma} < 1 \). We choose \( \epsilon > 0 \) sufficiently small that \( \frac{\beta (N^* + \epsilon)}{\mu + \gamma} < 1 \).

Now, \( S(t) + I(t) = N(t) \) so we must have \( S(t) \leq N(t) \). Hence
\[\limsup_{t \to \infty} S(t) \leq \lim_{t \to \infty} N(t) = N^*.\]

Therefore, there exists \( T > 0 \) such that for \( t \geq T \), we must have \( S(t) \leq N^* + \epsilon \).

Then for \( t \geq T \)
\[\frac{dV}{dt} = I \frac{dI}{dt} = (\beta S - (\gamma + \mu))I^2 \leq (\beta N^* + \beta \epsilon - (\gamma + \mu))I^2 = -\alpha I^2\]

where \( \alpha = (\gamma + \mu) - \beta N^* - \beta \epsilon > 0 \). Thus \( \dot{V} \leq 0 \) for \( R_0 < 1 \) and \( \dot{V} = 0 \) only for \( I = 0 \).

Integrating with respect to \( t \),
\[V(t) - V(0) + \alpha \int_0^t I^2(s) ds \leq 0.\]

Letting \( t \to \infty \) and using the positivity of \( V \)
\[\int_0^\infty I^2(s) ds \leq \infty,\]

hence \( I(t) \to 0 \) as \( t \to \infty \).

Now, \( S(t) = N(t) - I(t) \) so, by the rules for limits,
\[\lim_{t \to \infty} S(t) = \lim_{t \to \infty} N(t) - \lim_{t \to \infty} I(t)\]

and therefore
\[\lim_{t \to \infty} S(t) = \frac{\Lambda}{\mu}.\]

Thus the IFE is globally stable for \( R_0 < 1 \). \( \square \)
2.2 Some general comments about the two animal system

Proposition 2.2.1 If the initial values of the variables in system (2.1) are non-negative then the variables remain non-negative for all time.

For the proof of this proposition, we use Theorem 5.2.1 on p 81 of Smith [49]. We consider each of the equations in (2.1) in turn. If we set the variable the derivative of which appears on the left hand side equal to zero on the right hand side, and assume that the other variables are positive, we obtain in each case a positive quantity for the right hand side. Thus if the initial condition of the system of equation (2.1) is that all the variables lie in $\mathbb{R}^4_+$, then this positive cone is invariant for the system.

Observation 2.2.2 System (2.1) is co-operative in the two infectious species.

A co-operative system is one in which the derivative of any one variable with respect to any other variable is strictly positive. The partial derivative of the right hand side of equation (2.1) in one infective species with respect to the other infective species is positive in both cases. The larger the population of infectives in one species, the larger that in the other. This is an important element in establishing global stability. Thus,

$$\frac{\partial I_c}{\partial I_b} = \xi_{bc} S_c > 0 \quad \text{and} \quad \frac{\partial I_b}{\partial I_c} = \xi_{cb} S_b > 0$$

and system (2.1) is co-operative.

Proposition 2.2.3 An infection free equilibrium in one species and endemic disease state in the other is not an equilibrium solution of equation (2.1).

This follows logically from the previous proposition. We prove it as follows;

If $I_b = 0$, the only equilibrium solution is $I_c = 0$, $S_c = \frac{\Delta_s}{\mu_c}$ and $S_b = \frac{\Delta_b}{\mu_b}$. The same analysis will be true, mutatis mutandis, for $I_c = 0$.

If a single species has a stable disease-free state, the introduction of a second species susceptible to the same disease, but with no mutual infectivity, will evidently not affect the equilibrium in the first species. If there is mutual infectivity then the only stable equilibrium state in which the first species remains infection-free is if the second species is also infection-free, otherwise the first species will develop the endemic infection. Indeed, we shall see that, even for two species which both have stable infection-free states in the absence of the other species, as mutual infectivity increases from zero, there will eventually be a stable endemic disease state for the combined system. This coupling effect of mutual infectivity is key to understanding the dynamics of the system of equation (2.1).

2.2.1 Equilibria of the two animal system (2.1)

The existence and stability of equilibria of system (2.1) are governed by the following theorem;
Theorem 2.2.4 The infection-free equilibrium (IFE) always exists as an equilibrium which is globally stable in the absence of an endemic equilibrium. Whenever the endemic disease equilibrium state exists it is globally stable and the IFE becomes unstable. System (2.1) thus displays a transcritical bifurcation. More specifically:

- If \( R_b \in (0,1) \) and \( R_c \in (0,1) \) (\( R_b \) and \( R_c \) are defined in equations (2.3) and (2.2) respectively) and if, moreover \( R_{bc} < 1 \), where
  \[
  R_{bc} = \frac{\xi_c \xi_b N_c^* N_c^*}{(\mu_b + \gamma_b - \beta_b N_b^*)(\mu_c + \gamma_c - \beta_c N_c^*)},
  \]
  then the IFE is globally stable.

- If \( R_b < 1 \) and \( R_c < 1 \) and if, moreover \( R_{bc} > 1 \) then the IFE is unstable and a globally stable endemic equilibrium exists.

- If \( R_b > 1 \) and \( R_c > 1 \) then the IFE is unstable and a globally stable endemic equilibrium exists.

- If \( R_b < 1 \) and \( R_c > 1 \) or vice versa then the IFE is unstable and a globally stable endemic equilibrium exists.

The remainder of this chapter is concerned with the proof of Theorem 2.2.4.

2.3 Criss-cross infection only

As a way to gain an understanding of the system represented by equation (2.1), let us suppose that there is no intra-species infection, i.e. that \( \beta_b = 0 \) and \( \beta_c = 0 \) and the result is that the disease passes from cattle to badgers and vice versa but not between badgers and badgers or cattle and cattle.

We consider very large values of \( t \). We know that, because of its structure, the system approaches an equilibrium as \( t \to \infty \). We have, for cattle,

\[
\frac{dN_c}{dt} = \Lambda_c - \mu_c N_c,
\]

so that \( S_c + I_c \to \frac{\Lambda_c}{\mu_c} \) as \( t \to \infty \). We can thus replace \( S_c \) with \( \frac{\Lambda_c}{\mu_c} - I_c \). Since the equilibrium population is \( N_c^* = \frac{\Lambda_c}{\mu_c} \) we use the substitution \( S_c = N_c^* - I_c \). We can evidently make a similar substitution for badgers and can thus write the system, for \( t \) sufficiently large, in terms of the infected classes only as

\[
\frac{dI_c}{dt} = -(\mu_c + \gamma_c)I_c + \xi_{bc}(N_c^* - I_c)I_b,
\]

\[
\frac{dI_b}{dt} = -(\mu_b + \gamma_b)I_b + \xi_{cb}(N_b^* - I_b)I_c,
\]

where \( N_b^* = \frac{\Lambda_b}{\mu_b}, \quad N_c^* = \frac{\Lambda_c}{\mu_c} \).

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Proposition 2.3.1 System (2.7) exhibits a transcritical bifurcation with bifurcation parameter 

\[ R_0 = \frac{\xi_{bc}\xi_{cd}\lambda_b\lambda_c}{\mu_c\mu_b(\mu_c + \gamma_c)(\mu_b + \gamma_b)}. \]

For \( R_0 < 1 \) the IFE is the only equilibrium and is globally stable, for \( R_0 > 1 \) a globally stable endemic disease equilibrium appears and the IFE becomes unstable.

We demonstrate this proposition as follows: linearising this system around any equilibrium \((I^*_c, I^*_b)\) and computing the Jacobian matrix, \( J \), we obtain

\[
J = \begin{pmatrix}
-(\mu_c + \gamma_c) - \xi_{bc}I^*_b & \xi_{bc}(N^*_c - I^*_c) \\
\xi_{cd}(N^*_b - I^*_b) & -(\mu_b + \gamma_b) - \xi_{cb}I^*_b
\end{pmatrix}
\]

where the \( N^* \) terms are the equilibrium population sizes.

At the IFE, \((0,0)\) we have

\[
J_0 = \begin{pmatrix}
-(\mu_c + \gamma_c) & \xi_{bc}N^*_c \\
\xi_{cb}N^*_b & -(\mu_b + \gamma_b)
\end{pmatrix}.
\]

The Routh Hurwitz conditions (see Introduction) for local stability in two dimensions require the trace of the Jacobian to be negative and the determinant positive. By observation, \( \text{trace}(J_0) \) is always negative, while \( \text{det}(J_0) \) will be positive if

\[
R_0 = \frac{\xi_{bc}\xi_{cd}\lambda_b\lambda_c}{\mu_c\mu_b(\mu_c + \gamma_c)(\mu_b + \gamma_b)} < 1. \tag{2.8}
\]

This expression defines the basic reproductive ratio for the criss-cross system. It satisfactorily defines a threshold stability condition.

If an endemic equilibrium exists then the nullclines in the \((I_c, I_b)\) phase plane given by

\[
I_c = \frac{(\mu_b + \gamma_b)I_b}{\xi_{cb}(N^*_b - I_b)} = G(I_b), \quad I_b = \frac{(\mu_c + \gamma_c)I_c}{\xi_{bc}(N^*_c - I_c)} = F(I_c) \tag{2.9}
\]

must intersect in the first quadrant. The two curves always cross at \((0,0)\) (which represents the IFE) and thereafter once and only once again (which will be the endemic equilibrium) in the first quadrant if and only if

\[
\frac{dF(0)}{dI_c} < \left[ \frac{dG(0)}{dI_b} \right]^{-1}
\]

since \( F(I_c), F'(I_c), G(I_b) \) and \( G'(I_b) \) are monotone increasing in \( I_c, I_b < N^* \) (we prove this monotonicity property later in this chapter). Now,

\[
\frac{dF(0)}{dI_c} = \frac{(\mu_c + \gamma_c)}{\xi_{bc}N^*_c} \quad \text{and} \quad \frac{dG(0)}{dI_b} = \frac{(\mu_b + \gamma_b)}{\xi_{cb}N^*_b}
\]

so that the curves \( I_c = G(I_b) \) and \( I_b = F(I_c) \) cross in the open first quadrant if

\[
\frac{\xi_{cb}N^*_b}{\mu_b + \gamma_b} > \frac{\mu_c + \gamma_c}{\xi_{bc}N^*_c},
\]

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that is iff

$$R_0 = \frac{\xi_{bc} N^*_c N^*_b}{(\mu_c + \gamma_c)(\mu_b + \gamma_b)} > 1; \quad (2.10)$$

otherwise they intersect in the third quadrant. Thus $R_0 > 1$ is also the criterion for the existence of the endemic state.

If we solve (2.9) directly for $(I^*_c, I^*_b)$ we have

$$I^*_c = \frac{\xi_{bc} N^*_c - (\mu_b + \gamma_b)(\mu_c + \gamma_c)}{\xi_{bc}((\mu_c + \gamma_c) + N^*_c \xi_{bc})},$$

$$I^*_b = \frac{\xi_{bc} N^*_b - (\mu_b + \gamma_b)(\mu_c + \gamma_c)}{\xi_{bc}((\mu_b + \gamma_b) + N^*_b \xi_{bc})},$$

evidently $(I^*_c, I^*_b)$ are only positive if $R_0 > 1$.

We investigate the local linear asymptotic stability of the endemic equilibrium by substituting the expressions for $(I^*_c, I^*_b)$ into $J$ and computing the trace and determinant of the resulting matrix $J^*$ and then applying the Routh Hurwitz conditions. We find that

$$\text{det}(J^*) = -(\mu_b + \gamma_b)(\mu_c + \gamma_c) + \xi_{bc} N^*_c N^*_b > 0.$$  

Clearly, this condition is equivalent to $R_0 > 1$. Moreover,

$$\text{trace}(J^*) = -(\mu_b + \gamma_b) - (\mu_c + \gamma_c)$$

$$+ \frac{(\mu_b + \gamma_b)(\mu_c + \gamma_c) - \xi_{bc} N^*_c N^*_b}{(\mu_b + \gamma_b) + N^*_c \xi_{bc}} + \frac{\mu_c + \gamma_c) - \xi_{bc} N^*_c N^*_b}{(\mu_c + \gamma_c) + N^*_b \xi_{bc}}.$$  

The first two terms in the expression for $\text{trace}(J^*)$ are always negative and if $R_0 > 1$ then the last two terms are also negative, thus demonstrating that the endemic equilibrium is locally stable in the case that $R_0 > 1$. In the case that $R_0 < 1$ the endemic equilibrium does not exist.

So far we have only investigated local stability. We will use the theory of monotone dynamical systems at a later stage in this chapter to prove that this endemic disease equilibrium (whenever it exists) is globally stable and that the IFE is globally stable in the absence of an endemic equilibrium. The system thus exhibits a transcritical bifurcation with parameter $R_0$, where $R_0$ is given by equation (2.10).
2.4 The infection free equilibrium for inter and intra species infection

For convenience of reference we repeat the model set out in equation (2.1)

\[
\begin{align*}
\frac{dS_c}{dt} &= \Lambda_c - \mu_c S_c - \beta_c S_c I_c - \xi_c S_c I_b + \gamma_c I_c, \\
\frac{dI_c}{dt} &= -\mu_c I_c + \beta_c S_c I_c + \xi_c S_c I_b - \gamma_c I_c, \\
\frac{dS_b}{dt} &= \Lambda_b - \mu_b S_b - \beta_b S_b I_b - \xi_b S_b I_c + \gamma_b I_b, \\
\frac{dI_b}{dt} &= -\mu_b I_b + \beta_b S_b I_b + \xi_b S_b I_c - \gamma_b I_b,
\end{align*}
\]

together with the definitions of the variables and the constraints

\[
S_c + I_c = N_c, \quad S_b + I_b = N_b,
\]

\[
S_c > 0, \quad S_b > 0, \quad I_c \geq 0, \quad I_b \geq 0.
\]

These are four coupled differential equations; evidently if the \( \xi \) terms are zero the two species have independent dynamics.

If we put the right hand sides of each of equations (2.1) equal to zero we can solve to find the infection-free equilibrium, which is \( \left( \frac{\Lambda_c}{\mu_c}, 0, \frac{\Lambda_b}{\mu_b}, 0 \right) \) or \( (N_c^*, 0, N_b^*, 0) \).

Linearising around the infection-free equilibrium we compute the Jacobian matrix \( H_0 \) for system (2.1), where

\[
H_0 = \begin{pmatrix}
-\mu_c & \gamma_c - \beta_c N_c^* & 0 & -\xi_c N_c^* \\
0 & -(\mu_c + \gamma_c) + \beta_c N_c^* & 0 & \xi_c N_c^* \\
0 & -\xi_c N_b^* & -\mu_b & \gamma_b - \beta_b N_b^* \\
0 & \xi_c N_b^* & 0 & -(\mu_b + \gamma_b) + \beta_b N_b^*
\end{pmatrix}.
\]

We study the linear stability of the IFE by looking for the condition that all the eigenvalues have negative real parts. The eigenvalues of \( H_0 \) are

\[
\lambda_1 = -\mu_c, \quad \lambda_2 = -\mu_b, \quad \lambda_3 = \theta + \frac{1}{2} \sqrt{\psi}, \quad \lambda_4 = \theta - \frac{1}{2} \sqrt{\psi},
\]

where we define

\[
\theta = \frac{1}{2} \left( - (\mu_b + \gamma_b) - (\mu_c + \gamma_c) + \beta_b N_b^* + \beta_c N_c^* \right)
\]

\[
\psi = \left( \beta_c N_c^* \left( 1 - \frac{1}{R_c} \right) - \beta_b N_b^* \left( 1 - \frac{1}{R_b} \right) \right)^2 + 4 \xi_c \xi_b N_c^* N_b^*.
\]

\( \psi \) is clearly always positive so that the eigenvalues are real. We can equivalently also express \( \theta \) as

\[
\theta = \frac{1}{2} \left( \beta_c N_c^* \left( 1 - \frac{1}{R_c} \right) + \beta_b N_b^* \left( 1 - \frac{1}{R_b} \right) \right),
\]

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where \( \bar{R}_b \) and \( \bar{R}_c \) are defined in equations (2.3) and (2.2) respectively. It is evident that a sufficient but not necessary condition for \( \theta < 0 \) is that \( 0 < \bar{R}_c < 1 \) and \( 0 < \bar{R}_b < 1 \). Clearly if \( \bar{R}_c > 1 \) and \( 0 < \bar{R}_b < 1 \), or \( 0 < \bar{R}_c < 1 \) and \( \bar{R}_b > 1 \), then we may have \( \theta \) positive or negative. If \( \theta \) is positive, then \( \lambda_3 > 0 \) and the IFE will not be stable.

Now, \( \lambda_1, \lambda_2 < 0 \), so that for local linear stability of the IFE we need \( \lambda_3, \lambda_4 < 0 \), so that we require, in addition to \( \theta < 0 \) that

\[
\left( -(\mu_b + \gamma_b) - (\mu_c + \gamma_c) + \beta_b N_b^* + \beta_c N_c^* \right)^2 - \psi < 0,
\]

which is equivalent to

\[
0 \leq \frac{\xi_{bc} \xi_{bc} N_b^* N_c^*}{(\mu_b + \gamma_b - \beta_b N_b^*)\mu_c + \gamma_c - \beta_c N_c^*)} < 1,
\]

which we can express as

\[
0 < \frac{U_b U_c}{(1 - \bar{R}_c)(1 - \bar{R}_b)} < 1, \tag{2.11}
\]

where we have defined

\[
U_b = \frac{\xi_{cb} N_c^*}{\mu_c + \gamma_c}, \quad U_c = \frac{\xi_{bc} N_b^*}{\mu_b + \gamma_b}. \tag{2.12}
\]

These quantities in (2.12) are broadly analogous to basic reproductive ratios for the cross infections.

We also note, crucially, that \( 1 - R_c \) and \( 1 - R_b \) must both have the same sign for inequality (2.11) to hold. This therefore explicitly precludes the situation where one species alone could be infection free, the other alone has a stable endemic infection yet the whole system has an infection free equilibrium, as we have previously demonstrated.

The parameter \( R_{bc} \) could be thus considered to define a threshold value for the two animal system, however, we note that for \( R_b = 1 \) or \( R_c = 1 \), \( R_{bc} \) is not defined and that, paradoxically, \( R_{bc} \) can have large values when \( R_b \) and \( R_c \) are both very small and \( R_{bc} \) can take very small values when \( R_b \) and \( R_c \) are both very large. Thus although we shall see that this definition of the threshold value is mathematically satisfactory to explain the equilibrium behaviour of system (2.1) we need a more appropriate biologically significant definition of the basic reproductive ratio.

2.4.1 Next generation matrix and the basic reproductive ratio

To compute the next generation matrix (a concept we have summarised in the Introduction), we first non-dimensionalise system (2.1) for simplicity and
convenience.

\[ v = \frac{S_c}{N_c^*}, \quad w = \frac{I_c}{N_c^*}, \quad x = \frac{S_b}{N_b^*}, \quad y = \frac{I_b}{N_b^*} \]

\[ \alpha_c = \frac{\mu_c}{\mu_c + \gamma_c}, \quad \alpha_b = \frac{\mu_b}{\mu_b + \gamma_b}, \quad k = \frac{\mu_b + \gamma_b}{\mu_c + \gamma_c} \]

\[ U_b = \frac{N_b^* \xi b}{\mu_c + \gamma_c}, \quad U_c = \frac{N_c^* \xi bc}{\mu_b + \gamma_b} \]

\[ R_c = \frac{N_c^* \beta_c}{\mu_c + \gamma_c}, \quad R_b = \frac{N_b^* \beta_b}{\mu_b + \gamma_b}, \quad \hat{t} = (\mu_c + \gamma_c)t \]

so that equation (2.1) can now be written as follows, removing the caret from \( \hat{t} \),

\[ \frac{dv}{dt} = \alpha_c (1 - v) + w (1 - \alpha_c) - R_c w v - k U_c w y, \]

\[ \frac{dw}{dt} = -w + R_c w v + k U_c w y, \]

\[ \frac{dx}{dt} = k \alpha_b (1 - x) + k y (1 - \alpha_b) - k R_b x y - U_b x w, \]

\[ \frac{dy}{dt} = -k y + k R_b x y + U_b x w, \]

\[ v(0) > 0, w(0) \geq 0, x(0) > 0, y(0) \geq 0. \]

We define the matrices \( F \) and \( V \) as follows,

\[ F := \begin{pmatrix} R_c & k U_c \\ U_b & k R_b \end{pmatrix} \]

\[ V := \begin{pmatrix} 1 & 0 \\ 0 & k \end{pmatrix} \]

and the spectral radius \( \rho \) of the matrix \( F V^{-1} \) is then given by

\[ \rho(FV^{-1}) = \frac{1}{2} \left( R_b + R_c + \sqrt{(R_b - R_c)^2 + 4U_b U_c} \right). \] (2.15)

This is a better definition of the basic reproductive ratio for system (2.1) since the right hand side of equation (2.15) is continuous on \( \mathbb{R}_+^4 \) and, since it is increasing in all of its four variables, its behaviour is intuitively more meaningful. We term this expression \( \hat{R}_{bc} \). We see that, provided that \( R_b \) and \( R_c \) are both strictly less than unity, we can obtain one criterion from the other;

\[ \hat{R}_{bc} = \frac{1}{2} \left( R_b + R_c + \sqrt{(R_b - R_c)^2 + 4U_b U_c} \right) < 1 \]

\[ \iff R_b + R_c + \sqrt{(R_b - R_c)^2 + 4U_b U_c} < 2 \]

\[ \iff (R_b - R_c)^2 + 4U_b U_c < (2 - R_b - R_c)^2 \]

\[ \iff 4U_b U_c < 4 + 4R_b R_c - 4R_b - 4R_c \]

\[ \iff \frac{U_b U_c}{(R_b - 1)(R_c - 1)} < 1 \quad R_b \neq 1 \quad R_c \neq 1. \] (2.16)
The left hand side of the last inequality is $R_{bc}$, the previous formulation of the threshold parameter. Moreover, if $R_{bc} < 0$ then $(1 - R_c)(1 - R_b) < 0 < U_b U_c$, and by reversing the inequalities in (2.16) we obtain $R_{bc} > 1$. Finally, if $R_b$ and $R_c$ are both strictly greater than unity and $f_{bc} > 1$ then, by reversing the inequalities in (2.16), we obtain $R_{bc} > 1$. We are thus justified in using the original formulation of $R_{bc}$ as a threshold parameter, but in estimating values of the endemic equilibrium states or eigenvalues or eigenvectors of Jacobians of linearisations we should more appropriately use the form of $R_{bc}$.

The IFE is thus locally stable for $R_{bc} < 1$ provided that in addition both $1 - R_c < 1$ and $1 - R_b < 1$, i.e. $0 < R_c < 1$ and $0 < R_b < 1$. We note that the IFE is unstable if $R_c = 1$ and $R_b = 1$ since equality results in $\lambda_3 = \sqrt{\psi}$. □

2.4.2 Heuristic interpretation of the expression for $R_{bc}$

The number of secondary infections caused in cattle by a single infected cow introduced into a disease-free herd is $R_c$ and the number caused by a single infected badger introduced into a disease-free herd is $U_c$. If we assume that a cow can only sustain one infection at a time, the disease will die out in cattle if

$$R_c + U_c < 1 \iff \frac{U_c}{1 - R_c} < 1.$$  

For badgers, the disease will die out if $\frac{U_b}{1 - R_b} < 1$. For both situations to occur this implies

$$\frac{U_b U_c}{(1 - R_c)(1 - R_b)} < 1,$$

as we have already shown. Thus we can consider that $R_{bc}$ is an intuitively meaningful quantity, as the threshold at which the IFE becomes unstable.

2.5 Endemic disease equilibrium

In order to obtain analytical results about the endemic equilibrium, we need to simplify system (2.1). By using the same argument as in Section 2.3 we know that $N_c$ and $N_b$ tend to constants as $t \to \infty$. This reduces the dimension of system (2.1) from four to two. For large times the dynamics are determined by

$$\frac{dI_c}{dt} = -\beta_c I_c^2 + \beta_c N_c^* I_c \left(1 - \frac{1}{N_c^*}\right) + I_b \xi_{bc}(N_c^* - I_c)$$  

$$\frac{dI_b}{dt} = -\beta_b I_b^2 + \beta_b N_b^* I_b \left(1 - \frac{1}{N_b^*}\right) + I_c \xi_{cb}(N_b^* - I_b).$$ (2.17)

Putting the right hand sides of (2.17) equal to zero gives equilibria at the IFE, $(0,0)$ and the endemic state, $(I_c^*, I_b^*)$. We cannot obtain explicit or even useful implicit expressions for $I_c^*$ and $I_b^*$ since each is the solution of a non-factorisable cubic equation. We note that the constant term in this cubic is $U_b ((R_c - 1)(R_b - 1) - U_b U_c)$, so that the condition for zero roots is $R_{bc} = 1$, and while we would conjecture that the roots are increasing functions of $R_{bc}$, since we expect to have a transcritical bifurcation, we cannot prove this algebraically.
Numerical simulation to find the endemic equilibrium

Numerical simulation can give us some useful information about the sizes of the infective classes at the endemic equilibrium. From (2.14) we find the following system for $t$ very large, it is the non-dimensionalised version of (2.17).

\[
\begin{align*}
\frac{dw}{dt} &= -R_c w^2 + w(R_c - 1) + kU_c y - kU_c w y, \\
\frac{dy}{dt} &= -kR_b y^2 + ky(R_b - 1) + U_b w - U_b w y.
\end{align*}
\]

(2.18)

We take the parameter values $R_b = 2.2, R_c = 0.8, U_b = 0.7, U_c = 3, k = 1$ by way of illustration (so that cattle cannot cause an endemic equilibrium in badgers and the disease would die out in cattle alone). By letting one parameter at a time be considered as a variable with the others at these constant values we obtain expressions for the density of infected cattle $w$ as functions of each of the four parameters in turn as the appropriate root of the following cubic equations.

- as a function of $R_b$

\[-0.64R_b^3 + 1.68w^3 + (-2.72R_b + 7.44)w^2 + (1.76R_b - 14.82)w + 0.6R_b + 5.7 = 0\]

- as a function of $R_c$

\[-2.2R_c^3 + 2.1R_c w^3 + (4.4R_c^2 - 12.2R_c + 8.4)w^2 + (-2.2R_c^2 + 13.7R_c - 20.5)w - 3.6R_c + 9.9 = 0\]

- as a function of $U_b$

\[2.4U_b - 1.408)w^3 + (7.2U_b - 3.584)w^2 + (-18.6U_b + 2.072)w + 9U_b + 0.72 = 0\]

- as a function of $U_c$

\[(0.56U_c - 1.408)w^3 + (0.7U_c^2 - 1.38U_c - 0.704)w^2 + (-1.4U_c^2 + 0.58U_c - 0.088)w + 0.7U_c^2 + 0.24U_c = 0\]

We obtain more complicated expressions for the density of infected badgers, utilising the solutions to these cubic equations.

We compute values of $I_c$ and $I_b$ as functions of each of the four parameters in turn and plot the resulting graphs as in Figure 2.1. If we look for the equations which best fit these graphs using multiple regression, we obtain the following, the bracketed numbers are the $R^2$ values for the fit. ($R^2$ is the coefficient of determination, the fraction of the total variance that is explained by the model equation.) Since $R^2 = 1.0$ is, by definition a perfect fit, it is clear that
these are very highly significant. The coefficients are rounded to four decimal places.

\[
I_c(R_b) = 0.0005R_b^3 - 0.0098R_b^2 + 0.0704R_b + 0.5265 \quad (R^2 = 0.990),
\]

\[
I_b(R_b) = 0.0012R_b^3 - 0.0275R_b^2 + 0.2157R_b + 0.2860 \quad (R^2 = 0.997).
\]

While the size of both infected classes increase with \( R_b \), that of cattle increases very slowly and rapidly reaches a plateau.

\[
I_c(R_c) = 0.005R_c^2 - 0.0007R_c + 0.0067R_c + 0.6684 \quad (R^2 = 0.999),
\]

\[
I_b(R_c) = 0.0002R_c^3 - 0.006R_c^2 + 0.0617R_c + 0.6797 \quad (R^2 = 0.995).
\]

We see that the size of both infected classes increase with \( R_c \), that of badgers however is barely increasing. Thus we see that the increasing infectivity in one species does have a small positive effect on the size of the infective class in the other.

\[
I_c(U_b) = 0.0009U_b^3 - 0.0211U_b^2 + 0.1693U_b + 0.3707 \quad (R^2 = 0.996),
\]

\[
I_b(U_b) = 0.0005U_b^3 - 0.0022U_b^2 + 0.0191U_b + 0.6707 \quad (R^2 = 0.986),
\]

\[
I_c(U_c) = 0.0005U_b^3 - 0.0022U_b^2 + 0.0183U_b + 0.7116 \quad (R^2 = 0.997),
\]

\[
I_b(U_c) = 0.0004U_b^3 - 0.0102U_b^2 + 0.0873U_b + 0.6179 \quad (R^2 = 0.998).
\]
Increasing the cross-infectivity from badgers to cattle produces an increase in the numbers of infected cattle and also a smaller increase in the numbers of infected badgers (and vice versa).

These results illustrate the coupling of the system and that the key element that drives the level of the endemic equilibrium in cattle appears to be the cross-infectivity from badgers to cattle, not the number of infected badgers.

We can also study the nullclines of system (2.17) in the first quadrant in the \((I_c, I_b)\) phase plane. The nullclines are given by

\[
I_c = \frac{-\beta_b I_b^2 + \beta_b N_b^* I_b \left(1 - \frac{1}{R_c}\right)}{\xi_{cb} (I_b - N_b^*)} = g(I_b),
\]

\[
I_b = \frac{-\beta_c I_c^2 + \beta_c N_c^* I_c \left(1 - \frac{1}{R_b}\right)}{\xi_{bc} (I_c - N_c^*)} = f(I_c).
\]

Figure 2.2 shows two possible nullcline plots, on the left we have chosen parameters such that both species have basic reproductive ratios greater than unity and on the right they are both less than unity. In order to examine the existence and stability of the endemic disease states we need to consider the four possible different situations that may arise.

### 2.5.1 Trivial solution, \(R_c < 1, R_b < 1, R_{bc} < 1\)

System (2.17) will always have a trivial solution, the IFE. We have shown that system (2.17) has a transcritical bifurcation, with bifurcation parameter \(R_{bc}\), defined in equation (2.11). The IFE is stable for all values of \(R_{bc} < 1\), thereafter, as \(R_{bc}\) increases the IFE becomes unstable and a stable positive endemic disease state appears. There will be a critical value of \((\xi_{bc}, \xi_{cb})\) at which the IFE becomes unstable for a given pair of values of \(R_b < 1\) and \(R_c < 1\).
2.5.2 $R_b > 1, R_c > 1, R_{bc} > 1$

The two nullclines intersect at four points. One intersection is always at the origin (the IFE), a second is in the second quadrant and a third in the fourth quadrant (neither of which is relevant since we must have only non-negative values for the state variables). The fourth intersection will either be in the first or the third quadrant depending on the sizes of $R_b$ and $R_c$.

If $f(I_c) = 0$ then $I_c = 0$ or $I_c = N_c^*(1 - \frac{1}{R_c})$ while if $q(I_b) = 0$ then $I_b = 0$ or $I_b = N_b^*(1 - \frac{1}{R_b})$ so that the intercepts on the $I_b$ and $I_c$ axes represent the value of the size of the infected classes in the single species endemic disease states for cattle and badgers respectively, provided that $R_c > 1$ and $R_b > 1$.

In this case the nullclines intersect in the first quadrant at the endemic equilibrium and at the origin. There are two vertical asymptotes, $(I_c = N_c^*$ and $I_b = N_b^*)$. We have thus

$$N_c^* \left(1 - \frac{1}{R_c}\right) \leq I_c^* < N_c^* \quad \text{and} \quad N_b^* \left(1 - \frac{1}{R_b}\right) \leq I_b^* < N_b^*.$$  

Consequently we define a region $\Omega$ in which the endemic equilibrium must lie

$$(I_c^*, I_b^*) \in \Omega = \left( N_c^* \left(1 - \frac{1}{R_c}\right), N_c^* \right) \times \left( N_b^* \left(1 - \frac{1}{R_b}\right), N_b^* \right).$$

**Proposition 2.5.1** If $R_b > 1, R_c > 1$ the curves $I_b = f(I_c)$ and $I_c = g(I_b)$ as defined in equation (2.19) will necessarily intersect in $\Omega$.

We prove the proposition by showing that both $f(I_c)$ and $g(I_b)$ are convex.

Consider the case for $f(I_c)$, it is true for $g(I_b)$ mutatis mutandis. We write

$$f(I_c) = \frac{-\beta_c I_c}{\xi_{bc}} + \frac{\beta_c}{R_c \xi_{bc}} \left(\frac{N_c^*}{N_c^* - I_c} - 1\right),$$

$$f'(I_c) = \frac{-\beta_c}{\xi_{bc}} + \frac{\beta_c N_c^*}{R_c \xi_{bc}(N_c^* - I_c)^2},$$

$$f''(I_c) = \frac{2\beta_c N_c^*}{R_c \xi_{bc}(N_c^* - I_c)^3} > 0$$

Thus $f$ and $g$ are convex and there must be a unique endemic equilibrium. $\square$

**Proposition 2.5.2** $\Omega$ is an invariant set. Any solution trajectory which starts in $\Omega$ remains in $\Omega$.

This proposition is proved in Section 2.8.

Thus, for $R_c > 1, R_b > 1$ (2.17) has a unique endemic equilibrium state. In the absence of the inter-species infection terms, with $R_c > 1$ and $R_b > 1$, each single species endemic equilibrium will be stable. We can consider the inter-species term as having the effect of a perturbation from these equilibria simply driving the stable endemic equilibrium to higher levels of infected classes in both species.
Conjecture 2.5.3 The size of the infected classes at the endemic equilibrium of system (2.17), will depend directly on the magnitude of $R_{bc}$.

We cannot prove conjecture (2.5.3) analytically, however we can obtain some convincing numerical evidence for its being correct. We recall the definition of the basic reproductive ratio for the two-species system, the dominant eigenvalue of the next generation matrix, $\hat{R}_{bc}$ as

$$\hat{R}_{bc} = \frac{1}{2} \left( R_c + R_b + \sqrt{(R_c - R_b)^2 + 4U_c U_b} \right).$$

Dominant eigenvalue of the linearisation about the IFE

We have established that the dominant eigenvalue for the Jacobian of system (2.14), linearised about the IFE and with $R_{bc} > 1$ is

$$\lambda_{\text{max}} = \frac{1}{2} \left( k(R_b - 1) + (R_c - 1) + \sqrt{k(R_b - 1) - (R_c - 1))^2 + 4kU_c U_b} \right).$$

We substitute $U_b = 2, k = 1, U_c = 3, R_c = 5$ in both the expression for $\hat{R}_{bc}$ and that for $\lambda_{\text{max}}$ and then compute values for these expressions for different values of $R_b$. If we then plot the results we obtain Figure 2.3. It is clear that (over albeit a relatively narrow interval for $\lambda_{\text{max}}$) there is an approximately linear relationship between $\lambda_{\text{max}}$ and $\hat{R}_{bc}$. The greater $\hat{R}_{bc} - 1$ the more rapidly the system evolves away from the infection free equilibrium.

![Figure 2.3: Relationship between dominant IFE eigenvalue and system basic reproductive ratio](image-url)
Size of the equilibrium infected badger population

The size of the infected badger population, \( y^* \) is given by the largest positive root of the following non-factoriseable cubic equation in \( z \);

\[
\left( R_c R_b^2 - k U_c U_b R_b \right) z^3 + \left( R_c U_b R_b + 2 R_c k R_b + 2 k U_c U_b R_b - U_c U_b^2 - 2 R_c k R_b^2 - U_b R_b - k U_c U_b \right) z^2 + \left( 2 U_c U_b^2 - U_b + R_c U_b - 2 R_c U_b R_b + R_c k R_b^2 + R_c k - 2 k R_c R_b \right) z - U_b R_b + 2 U_c U_b R_b + k U_c U_b = 0.
\]

We make the same substitutions as before, \( U_b = 0.7, k = 1, U_c = 3, R_c = 0.8 \), and solve the cubic for various values of \( R_b \). We then plot the value of the largest roots against the value of \( \hat{R}_{bc} \) for the same values of \( R_b \) as shown in Figure 2.4. It is evident that \( y^* \) is increasing in \( \hat{R}_{bc} \). The form of the relationship is strongly qualitatively reminiscent of the expression \( y^* = 1 - \frac{1}{R_b} \) for the equilibrium infected class size of badgers in the absence of cattle.

Figure 2.4: Relationship between the size of the endemic infected badger population and system basic reproductive ratio

Dominant eigenvalue of the linearisation about the endemic equilibrium

In the same manner as before, we plot the value of the most negative eigenvalue of the Jacobian of the linearisation about the endemic equilibrium against \( \hat{R}_{bc} \) to obtain Figure 2.5. We see that the dominant eigenvalue is monotone.
Figure 2.5: Relationship between dominant endemic equilibrium eigenvalue and system basic reproductive ratio, $\hat{R}_{bc}$

decreasing in $\hat{R}_{bc}$ and we thus conclude that it is reasonable to consider that Conjecture 2.5.3 is correct.

2.5.3 $R_b < 1, R_c < 1, R_{bc} > 1$

This is the most interesting situation, where the cross-infection drives populations that are disease free in the absence of the other species into an endemic disease state. The two nullclines in equation (2.19) always intersect at the origin. They may intersect in the first quadrant once more, and only once more, with $R_b < 1, R_c < 1$ provided that

- $f(I_c)$ and $g(I_b)$ are monotone increasing (already shown),
- $f'(I_c)$ and $g'(I_b)$ are monotone increasing (shown below), and
- $f'(0) < g'(0)^{-1}$.

If these conditions are not met, then the intersection is in the third quadrant and there is no endemic equilibrium. Now

$$f''(I_c) = \frac{\beta_c N_c^*(1 + \frac{1}{R_c})}{\xi_{bc}(N_c^* - I_c)^2} + \frac{\beta_c \left(2I_c - N_c^*(1 - \frac{1}{R_c})\right) + 2(N_c^* - I_c)\beta_c I_c \left(I_c - N_c^*(1 - \frac{1}{R_c})\right)}{\xi_{bc}(N_c^* - I_c)^4},$$

and it is clear that for $R_b < 1, R_c < 1$ we have $I_c \geq N_c(1 - \frac{1}{R_c})$ so that the numerator of the second term is positive and thus $f''(0) > 0$. Once again the same argument applies mutatis mutandis to $g'(I_b^*)$. We have thus shown that $f'(I_c^*)$ and $g'(I_b^*)$ are monotone increasing.
Given that

\[ f'(0) = \frac{\beta_c(1 - \frac{1}{R_c})}{\xi_{bc}} \quad \text{and} \quad g'(0) = \frac{\beta_b(1 - \frac{1}{R_b})}{\xi_{cb}}, \]

the condition that they cross in the open first quadrant is

\[ \frac{\beta_c}{\xi_{bc}} \left( 1 - \frac{1}{R_c} \right) < \frac{\xi_{cb}}{\beta_b \left( 1 - \frac{1}{R_b} \right)}, \]

which we can rewrite as

\[ R_{bc} = \frac{\xi_{bc} \xi_{cb}}{\beta_b \beta_c \left( 1 - \frac{1}{R_b} \right) \left( 1 - \frac{1}{R_c} \right)} > 1. \]

As we would expect from a transcritical bifurcation, this is the condition that the IFE becomes unstable. This equilibrium endemic state occurs even though each of the individual species would reach an infection free equilibrium were they alone and thus results from the cross-infection term. There is great similarity between the structure of this equilibrium and that for the criss-cross epidemic, already analysed in Section 2.3. We have demonstrated that there can be no endemic equilibrium until the nullclines cross, which requires that \( R_{bc} > 1 \), which is tantamount to \( R_{bc} > 1 \), as \( R_{bc} \) increases so does the size of each of the infected populations, as we have already shown in the case of badgers.

2.5.4 \( R_b < 1, R_c > 1 \) or vice versa

We have demonstrated that the IFE cannot be stable in one species while the other has endemic disease, consequently an endemic disease equilibrium will exist if \( R_b < 1, R_c > 1 \) or vice versa, as we can see from an examination of the nullclines. In fact such a condition would make \( R_{bc} \) negative, so the IFE could not therefore be stable.

2.6 Local stability of the endemic disease state, with \( R_b > 1, R_c > 1 \)

Proposition 2.6.1 If the endemic state of system (2.17) exists with \( R_c > 1, R_b > 1 \) it is locally stable.

We prove that, for \( I_c, I_b, E \in \Omega \), the trace of the Jacobian of the linearisation of equation (2.17) is negative and the determinant is positive.

The Jacobian, \( L^* \), of system (2.17) at the endemic disease equilibrium, \( (I_c^*, I_b^*) \) is

\[
L^* := \begin{pmatrix}
-2\beta_c I_c^* + \beta_c N_c^* \left( 1 - \frac{1}{R_c} \right) - \xi_{bc} I_b^* & -\xi_{bc} I_c^* + \xi_{bc} N_c^* \\
-\xi_{cb} I_b^* + \xi_{cb} N_b^* & -2\beta_b I_b^* + \beta_b N_b^* \left( 1 - \frac{1}{R_b} \right) - \xi_{cb} I_c^* 
\end{pmatrix}.
\]
The trace is negative
We first show that \( \text{trace}(L^*) = T(I_c^*, I_b^*) < 0 \) by considering
\[
T(I_c^*, I_b^*) = -2\beta_c I_c^* + \beta_c N_c^* \left( 1 - \frac{1}{R_c} \right)
- \xi_{bc} I_b^* - 2\beta_b I_b^* + \beta_b N_b^* \left( 1 - \frac{1}{R_b} \right) - \xi_{bc} I_b^*
\]
\[
\frac{\partial T}{\partial I_c^*} = -2\beta_c - \xi_{bc} < 0 \quad \frac{\partial T}{\partial I_b^*} = -2\beta_b - \xi_{bc} < 0,
\]
so that \( T \) is strictly monotone decreasing in both \( I_c^* \) and \( I_b^* \) in \( \mathbb{R}^2 \).

Now, when
\[
I_c^* = N_c^* \left( 1 - \frac{1}{R_c} \right) \quad \text{and} \quad I_b^* = N_b \left( 1 - \frac{1}{R_b} \right)
\]
at the bottom left hand corner of \( \Omega \), after elementary algebra, we have
\[
T(I_c^*, I_b^*) = N_c^* \left( 1 - \frac{1}{R_c} \right) (\beta_c I_b^* - \xi_{bc} - N_c^* \left( 1 - \frac{1}{R_b} \right) (\beta_b I_b^* - \xi_{bc})
\]
and, once more, if \( R_c > 1, R_b > 1 \) then \( T(I_c^*, I_b^*) < 0 \). We thus conclude that \( \text{trace}(J^*) < 0 \) for all \( I_c^*, I_b^* \in \Omega \).

The determinant is positive
We now show that \( \det(L^*) = D(I_c^*, I_b^*) \geq 0 \). The determinant of the Jacobian matrix of the linearisation around the endemic equilibrium, \( D \), is given by
\[
D(I_c^*, I_b^*) = \left( \beta_b (N_b^* - 2I_b^*) - \frac{\beta_b N_b^*}{R_b} - \xi_{bc} I_b^* \right) \left( \beta_c (N_c^* - 2I_c^*) - \frac{\beta_c N_c^*}{R_c} - \xi_{bc} I_c^* \right)
\]
\[
- \frac{\beta_c N_c^*}{R_c} - \xi_{bc} I_c^* - \xi_{bc} (N_b^* - I_b^*) (N_c^* - I_c^*),
\]
(2.20)

If we restate the equations in system (2.17) at the endemic equilibrium we thus obtain
\[
\beta_b \left( N_b^* - I_b^* \right) - \frac{\beta_b N_b^*}{R_b} - \xi_{bc} I_b^* = -\frac{\xi_{bc} I_c^* N_b^*}{I_b^*},
\]
\[
\beta_c \left( N_c^* - I_c^* \right) - \frac{\beta_c N_c^*}{R_c} - \xi_{bc} I_c^* = -\frac{\xi_{bc} I_b^* N_c^*}{I_c^*}.
\]

Making the appropriate substitutions into the expression for \( D(I_c^*, I_b^*) \) in equation (2.20) we obtain
\[
D(I_c^*, I_b^*) = \left( \frac{-\xi_{bc} I_c^* N_b^*}{I_b^*} - \beta_b I_b^* \right) \left( \frac{-\xi_{bc} I_b^* N_c^*}{I_c^*} - \beta_c I_c^* \right)
- \xi_{bc} (N_b^* - I_b^*) (N_c^* - I_c^*).
\]

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Simplifying the above expression and using \( N_i^* > I_i^* \) we have \( D(I_i^*, I_i^*) > 0 \).

The Routh-Hurwitz conditions are thus satisfied and the endemic equilibrium state of the system defined by equation (2.17) is locally stable whenever it exists. This proves Proposition 2.6.1.

2.7 Local stability of the endemic disease state, with
\( R_b < 1, R_c < 1 \)

We have quite a different situation in this case, since all we can conclude about the location of the endemic equilibrium is that it must lie somewhere in the first quadrant of the \((I_c, I_b)\) phase plane. We consider two different approaches to analysing the local stability of this equilibrium. Firstly we employ a comparison method.

**Proposition 2.7.1** If the endemic state of the system of equations (2.1) exists with \( R_b < 1, R_c < 1 \), it is locally stable.

To prove this proposition we identify and analyse the behaviour of an upper solution and of a lower solution to system (2.17) with \( R_b < 1 \) and \( R_c < 1 \). We show that both solutions lead to stable equilibria and that thus the solution of equation (2.17) in this case must itself either tend to a stable equilibrium or to a periodic or quasi-periodic orbit (since there is no possibility of a chaotic solution of a system of ordinary differential equations in two dimensions). We then eliminate the possibility of a periodic or quasi-periodic orbit.

We take \( t \) sufficiently large that we can consider system (2.14) to have reached equilibrium. We derived the following equation in (2.18)

\[
\frac{dw}{dt} = -R_c w^2 + w(R_c - 1) + kU_c y - kU_c w y,
\]

\[
\frac{dy}{dt} = -kR_b y^2 + k y(R_b - 1) + U_b w - U_b w y.
\]

We note that, from equation (2.14), since \( v \geq 0 \) and \( x \geq 0 \), we must have \( w \leq 1 \) and \( y \leq 1 \) so that

\[-R_c w^2 + w(R_c - 1) \leq \frac{dw}{dt} \leq w(R_c - 1) + kU_c y - kU_c w y,\]

\[-kR_b y^2 + k y(R_b - 1) \leq \frac{dy}{dt} \leq k y(R_b - 1) + U_b w - U_b w y.\]

Let us define \( \dot{w}(t) \) and \( \dot{y}(t) \) such that

\[
\frac{d\dot{w}}{dt} = \dot{w}(R_c - 1) + kU_c \dot{y} - kU_c \dot{w} \dot{y},
\]

\[
\frac{d\dot{y}}{dt} = \dot{k} \dot{y}(R_b - 1) + U_b \dot{w} - U_b \dot{w} \dot{y}.
\]  (2.21)

Since the right hand side of the first equation in (2.21) is increasing in \( y \)
(since \( w \leq 1 \)) and the right hand side of the second increasing in \( w \) (since \( y \leq 1 \)) and if we suppose that the initial conditions are \( \hat{w}(0) = w(0) = \epsilon \) and \( \hat{y}(0) = y(0) = \delta \), where \( 0 \leq \epsilon \ll 1 \) and \( 0 \leq \delta \ll 1 \) then (applying the monotonicity arguments set out fully in Section 2.8) we can conclude that \( \hat{w}(t) \geq w(t) \) and that \( \hat{y}(t) \geq y(t) \) and so \( (\hat{w}(t), \hat{y}(t)) \) is an upper solution to system (2.18).

If we now define \( \hat{w}(t), \hat{y}(t) \) as follows

\[
\frac{d\hat{w}}{dt} = -Rc\hat{w}^2 + \hat{w}(Rc - 1), \\
\frac{d\hat{y}}{dt} = -kRb\hat{y}^2 + k\hat{y}(Rb - 1), \\
\hat{w}(0) = \epsilon, \hat{y}(0) = \delta,
\]

then \( \hat{w}(t) \leq w(t), \hat{y}(t) \leq y(t) \) and thus \( \hat{w}(t), \hat{y}(t) \) is lower solution. This latter set of equations we have already solved; it is the uncoupled model for separate species and we know that

- for \( Rb < 1 \) and \( Rc < 1 \), \( \lim_{t \to \infty} \hat{w}(t) = 0, \lim_{t \to \infty} \hat{y}(t) = 0 \), while
- for \( Rb > 1 \) and \( Rc > 1 \), a stable endemic equilibrium, \((\hat{w}^*, \hat{y}^*)\), exists.

We can solve the system for \( \hat{w}, \hat{y} \) straightforwardly. The endemic equilibrium is \((\hat{w}^*, \hat{y}^*)\), where

\[
\hat{w}^* = \frac{1 - \frac{1}{Rbc}}{1 + \frac{1}{kUc}}, \quad \hat{y}^* = \frac{1 - \frac{1}{Rbc}}{1 + \frac{k(1 - Rb)}{Ub}}.
\]

The denominator in each case is positive so we need \( Rbc > 1 \) for an endemic equilibrium to exist. We also note that \( \hat{w}^* \) and \( \hat{y}^* \) are both less than unity so the solutions fall into the acceptable range. The nullclines are thus

\[
\frac{d\hat{w}}{dt} = 0 \Rightarrow \hat{y} = \frac{\hat{w}(1 - Rc)}{kUc(1 - \hat{w})} = \phi(\hat{w}), \\
\frac{d\hat{y}}{dt} = 0 \Rightarrow \hat{w} = \frac{k\hat{y}(1 - Rb)}{Ub(1 - \hat{y})} = \psi(\hat{y}).
\]

Clearly the \( \hat{w} = 0 \) nullcline is displaced towards positive \( y \) and the \( \hat{y} = 0 \) nullcline towards positive \( w \) by comparison with the nullclines derived from equation (2.18) in the original variables. The equilibrium is thus displaced towards the top right hand corner of \( \Omega \) and we see that indeed

\( \hat{w}^* > w^* \) and \( \hat{y}^* > y^* \).

If we consider the gradients of \( \hat{y} = \phi(\hat{w}) \) and \( \hat{w} = \psi(\hat{y}) \), the condition that the nullclines, having crossed at the origin, cross again in the first quadrant is

\[
\phi_{\hat{w}} < \frac{1}{\psi_{\hat{y}}},
\]

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The partial derivatives have the following signs

\[ \phi_{\dot{w}} > 0, \quad \phi_{\dot{w}\dot{w}} > 0, \quad \phi_{\dot{y}} > 0, \quad \phi_{\ddot{y}\ddot{y}} > 0. \]

This once more requires (after some elementary algebra) that \( R_{bc} > 1 \). If we draw the phase diagram we see that the endemic equilibrium \((\dot{w}^*, \dot{y}^*)\) is stable. Since we have shown that \( \dot{w}(t) > w(t) > \dot{w}(t) > 0 \) and \( \dot{y}(t) > y(t) > \dot{w}(t) > 0 \) and that the equilibrium \((\ddot{w}^*, \ddot{y}^*)\) is stable, we can conclude that the endemic equilibrium \((w^*, y^*)\) is contained in the rectangle formed by the points \( w^*, y^*, \ddot{w}^*, \ddot{y}^* \). We can use Dulac’s criterion (see Introduction) to show that the equilibrium is not a periodic orbit. We can write system (2.18) as

\[
\frac{dw}{dt} = -R_c w^2 + w(R_c - 1) + kU_c y - kU_c wy = f(w, y),
\]

\[
\frac{dy}{dt} = -kR_b y^2 + ky(R_b - 1) + U_b w - U_bwy = g(w, y).
\]

If we define \( B(w, y) = \frac{1}{wy} \) then, for \( R_b < 1 \) and \( R_c < 1 \)

\[
\frac{\partial Bf}{\partial y} = \frac{R_c w + 1 - R_c}{y^2} > 0, \quad \frac{\partial Bg}{\partial w} = \frac{k(R_b y + 1 - R_b)}{w^2} > 0,
\]

\[
\frac{\partial Bf}{\partial w} + \frac{\partial Bg}{\partial y} > 0.
\]

Since \( y > 0 \) and \( w > 0 \), neither of these derivatives changes sign on \((0,1) \times (0,1)\). There is thus no periodic solution and by the Poincare-Bendixson Theorem (see for example [51] p425) there must exist a unique, globally stable equilibrium. In passing we note that for \( R_c < 1, R_b < 1 \) and \( R_{bc} > 1 \) every trajectory which starts at the origin reaches the endemic equilibrium.

### 2.7.1 An alternative proof of the local stability of the endemic equilibrium when \( R_c < 1 \) and \( R_b < 1 \) and \( R_{bc} > 1 \)

The linear stability of the endemic equilibrium which exists in this case is determined by the determinant of the Jacobian matrix, \( J \), for the system (2.18) linearised the equilibrium,

\[
\det(J) = \begin{vmatrix} f_w & f_y \\ g_w & g_y \end{vmatrix},
\]

where the equilibrium is locally stable (a node or a complex spiral) if the Routh Hurwitz conditions are met, i.e.

\[
f_w g_y - f_y g_w > 0, \quad f_w + g_y < 0.
\]

In order for the endemic equilibrium to exist we must have, at the intersection of the nullclines,

\[
\left. \frac{dy}{dw} \right|_{f=0} < \left. \frac{dy}{dw} \right|_{g=0}.
\]

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We compute
\[ f_w = -2R_cw + (R_c - 1) - kU_cy < 0, \quad f_y = kU_c(1 - y) > 0, \]
\[ g_w = U_b(1 - y) > 0, \quad g_y = -2kR_by + k(R_b - 1) - U_bw < 0. \]
The signs of the derivatives give the following sign pattern for the determinant
\[
\begin{vmatrix}
  - & + \\
  + & -
\end{vmatrix},
\]
from which it is clear that \( \text{trace}(J) < 0 \). Now,
\[
\begin{align*}
\left. \frac{dy}{dw} \right|_{g=0} &= -\frac{g_w}{g_y}, \\
\left. \frac{dy}{dw} \right|_{f=0} &= -\frac{f_w}{f_y},
\end{align*}
\]
(2.22)
since implicit differentiation of \( g(w, y) = 0 \) with respect to \( w \) gives \( g_w + g_y \frac{dw}{dw} = 0 \) and of \( f(w, y) = 0 \) with respect to \( w \) gives \( f_w + f_y \frac{dw}{dw} = 0 \).

Since \( g_w \) and \( g_y \) are of opposite sign and \( f_w \) and \( f_y \) are of opposite sign, the right hand sides of both equations (2.22) are positive and, since
\[
\left. \frac{dy}{dw} \right|_{f=0} < \left. \frac{dy}{dw} \right|_{g=0}
\]
for an endemic equilibrium to exist, we thus have
\[
\frac{g_w}{g_y} < \frac{f_w}{f_y},
\]
so that \( f_yg_w < f_wg_y \) and thus \( \text{det}(J) > 0 \), so the endemic equilibrium is locally asymptotically stable. Finally, the discriminant of the characteristic equation of the Jacobian determinant is
\[
(f_w + g_y)^2 - 4(f_wg_y - f_yg_w) = (f_w - g_y)^2 + 4f_yg_w > 0,
\]
so that the equilibrium is a stable node and the possibility of oscillatory approaches to the endemic equilibrium is excluded.

We can extend this analysis to the situation where \( R_b < 1 \) but \( R_c > 1 \), or vice versa; we consider \( R_c > 1 \). Then the endemic equilibrium exists and we see from the nullclines that \( w^* > 1 - \frac{1}{R_c} \). Thus,
\[
\begin{align*}
f_w &= -2R_cw + (R_c - 1) - kU_cy \\
&\leq -2R_c \left( 1 - \frac{1}{R_c} \right) + (R_c - 1) - kU_cy \\
&= 1 - R_c - kU_cy < 0
\end{align*}
\]
and all of the conditions in this case are precisely the same as for \( R_b < 1, R_c < 1 \) and the endemic equilibrium is locally stable.

2.8 Global stability of the endemic equilibrium with \( R_b > 1 \) and \( R_c > 1 \)

**Theorem 2.8.1** System (2.1) has a unique, globally stable endemic equilibrium in the case that \( R_b > 1, R_c > 1 \) and \( R_{bc} > 1 \).
We continue with the reduced, two dimensional system of equation (2.17) (with $N_c$ and $N_b$ constant and with $R_c > 1, R_b > 1$), since we have shown that this is the limit of system (2.1) as $t \to \infty$. We will show that that system (2.17) is monotone and co-operative and hence has a unique, globally stable, endemic equilibrium. We state the following definitions and result adapted from Smith [49] p 33.

Definition 2.8.2 Let $\Phi_t(x_0)$ be the solution of the ode $x' = f(x)$, where $f = (f_1, f_2, f_3, \ldots)$ is continuously differentiable on an open subset $D \subset \mathbb{R}^n$, starting at the point $x_0$ when $t = 0$. Then $\Phi$ is termed the flow corresponding to $x' = f(x)$ and $f$ is the vector field generating the flow. $f$ is said to be "type K" (for Kamke) if, for each $i$, $f_i(a) \leq f_i(b)$ for any two points $a, b \in D$ such that $a \leq b$ and $a_i = b_i$. Then if $f$ is type K in $D$ and $x_0 < y_0 \in D$, $\Phi_t(x_0) < \Phi_t(y_0)$ and $f$ is monotone. The flow is said to be order preserving.

Remark 2.8.3 We can easily verify the type K condition by considering the signs of the off-diagonal elements of the Jacobian matrix of $f$. If

$$\frac{\partial f_i}{\partial x_j}(x) \geq 0, \quad i \neq j, \quad x \in D$$

then if $D$ is convex ($\mathbb{R}^2$ is convex since $tx + (1-t)y \in \mathbb{R}^2 \ \forall x, y \in \mathbb{R}^2$ and $\forall t \in [0,1]$) $f$ is type K and the system is monotone.

Restating equation (2.17) once more;

$$\frac{dI_c}{dt} = -\beta_c I_c^2 + \beta_c N_c I_c \left(1 - \frac{1}{R_c}\right) + I_b \xi_b (N_c - I_c),$$

$$\frac{dI_b}{dt} = -\beta_b I_b^2 + \beta_b N_b I_b \left(1 - \frac{1}{R_b}\right) + I_c \xi_c (N_b - I_b).$$

We have already shown that, in addition to an IFE at the origin, system (2.17) has a unique endemic equilibrium, $(I^*_c, I^*_b)$ for $R_c > 1$ and $R_b > 1$ and that these components satisfy

$I^*_c \geq N_c \left(1 - \frac{1}{R_c}\right)$ and $I^*_b \geq N_b \left(1 - \frac{1}{R_b}\right)$.

We consider the positive cone in $\mathbb{R}^2$, $(N_c \left(1 - \frac{1}{R_c}\right), \infty) \times (N_b \left(1 - \frac{1}{R_b}\right), \infty)$, and, in particular the set $\Omega$, previously defined as

$$\Omega = \left\{(N_c \left(1 - \frac{1}{R_c}\right), N_c) \times (N_b \left(1 - \frac{1}{R_b}\right), N_b)\right\}.$$ 

We will show that, as $t \to \infty$, $\lim_{t \to \infty} (I_c, I_b) \in \Omega$ provided that $R_c > 1$ and $R_b > 1$. The argument is the same for both species, so we show it only for $I_c$. We have already established that $0 \leq I_c \leq N_c$ and we can define $\dot{I}_c$ to be the solution of

$$\frac{dI_c}{dt} = -\beta_c I_c^2 + \beta_c N_c \dot{I}_c \left(1 - \frac{1}{R_c}\right),$$

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with \( \hat{I}_c(0) = I_c(0) > 0 \). We assume that at \( t = 0 \) we are at the IFE and that we introduce a small number of infected animals. Since \( I_c \leq N_c \) we must have

\[
\frac{dI_c}{dt} \geq -\beta_c I_c^2 + \beta_c N_c I_c \left( 1 - \frac{1}{R_c} \right).
\]

Therefore \( I_c(t) \geq \hat{I}_c(t) \). Consequently, on \( \Omega \) we must have, for \( R_c > 1 \)

\[
\liminf_{t \to \infty} I_c(t) \geq \lim_{t \to \infty} \hat{I}_c(t) = N_c \left( 1 - \frac{1}{R_c} \right).
\]

So \( \lim_{t \to \infty} I_c(t) \in (N_c(1 - \frac{1}{R_c}), N_c) \). Since \( I_c(t) \) is bounded from above by \( N_c \) (by the definition of \( N_c = S_c(t) + I_c(t) \) and the positivity of all the species) we can conclude that all solution trajectories of equation (2.17) are attracted to the set \( \Omega \).

Now we translate the coordinates of the system so that we remove the IFE from the cone \( \text{int}(\mathbb{R}^*_+ \times \mathbb{R}^*_+) \) and translate the origin to \( (N_c(1 - \frac{1}{R_c}), N_b(1 - \frac{1}{R_b})) \). Let us define

\[
\hat{I}_c := I_c - N_c \left( 1 - \frac{1}{R_c} \right) \quad \text{and} \quad \hat{I}_b := I_b - N_b \left( 1 - \frac{1}{R_b} \right).
\]

Then we can write

\[
\frac{d\hat{I}_c}{dt} = -\beta_c \left( I_c + N_c \left( 1 - \frac{1}{R_c} \right) \right)^2 + \beta_c N_c \left( \hat{I}_c + N_c \left( 1 - \frac{1}{R_c} \right) \right) \left( 1 - \frac{1}{R_c} \right)
\]

\[
-\xi_{bc} \left( \hat{I}_b + N_b \left( 1 - \frac{1}{R_b} \right) \right) \left( \hat{I}_c - \frac{N_c}{R_c} \right),
\]

\[
\frac{d\hat{I}_b}{dt} = -\beta_b \left( \hat{I}_b + N_b \left( 1 - \frac{1}{R_b} \right) \right)^2 + \beta_b N_b \left( \hat{I}_b + N_b \left( 1 - \frac{1}{R_b} \right) \right) \left( 1 - \frac{1}{R_b} \right)
\]

\[
-\xi_{cb} \left( \hat{I}_c + N_c \left( 1 - \frac{1}{R_c} \right) \right) \left( \hat{I}_b - \frac{N_b}{R_b} \right),
\]

for \( R_c > 1 \) and \( R_b > 1 \) we have \( \left. \frac{d\hat{I}_c}{dt} \right|_{I_c = 0} > 0 \) and \( \left. \frac{d\hat{I}_b}{dt} \right|_{I_b = 0} > 0 \). If we write

\[
\frac{d\hat{I}_c}{dt} = f_1(\hat{I}_c, \hat{I}_b), \quad \frac{d\hat{I}_b}{dt} = f_2(\hat{I}_c, \hat{I}_b),
\]

then

\[
\frac{\partial f_1}{\partial \hat{I}_b} = \xi_{bc} (N_c - \hat{I}_c R_c)
\]

and the equivalent holds for \( \frac{\partial f_2}{\partial \hat{I}_c} \). Hence

\[
\frac{\partial f_1}{\partial \hat{I}_b} > 0, \quad \frac{\partial f_2}{\partial \hat{I}_c} > 0,
\]

and thus the translated system with equation (2.23) is, as was the original system, cooperative.
Hence if $I = (I_c, I_b)$ and $\frac{dI}{dt} = (f_1(I_c, I_b), f_2(I_c, I_b))$, then $I \in \text{int}(\Omega)$, which is convex in $\mathbb{R}^2$ and thus is type $K$ on $\Omega$ and system (2.17) is monotone.

The flow $\Phi_t(I)$ which solves $\frac{dI}{dt} = f(I)$ is thus a monotone dynamical system and $\Phi_t(I)$ is defined $\forall t \geq 0$.

Consideration of the phase plane (the left hand chart in Figure 2.2) suggests that solution trajectories are forced into one or other of the regions $I \geq I^*$ or $I \leq I^*$, are attracted by the isoclines and then attracted to the equilibrium. We can thus conclude that there exists a unique globally stable equilibrium in $\Omega$. Since we have excluded all other equilibria from $\Omega$ than the endemic equilibrium, we can conclude that the endemic equilibrium is globally stable.

2.9 One-way cross infection only

For completeness we consider the case where, while there is intra-species infection in both cases, badgers can infect cattle but not vice versa. The non-dimensionalised two-dimensional model is now

$$\begin{align*}
\frac{dw}{dt} &= -w + R_c w(1 - w) + kU_c y(1 - w), \\
\frac{dy}{dt} &= -ky + kR_b y(1 - y).
\end{align*}$$

System (2.24) has an IFE which is stable if $\max(R_c, R_b) < 1$, while if $R_c > 1$ and $R_b < 1$ then there is a stable endemic equilibrium in cattle and an IFE in badgers, $\left(1 - \frac{1}{R_c}, 0\right)$. If $\min(R_c, R_b) > 1$ then there is an endemic equilibrium in both species

$$\begin{align*}
w^* &= \frac{1}{2R_c R_b} \left( kU_c (1 - R_b) - R_b (1 - R_c) \\
&+ \sqrt{(kU_c (1 - R_b) - R_b (1 - R_c))^2 + 4kR_b R_c U_c (R_b - 1)} \right), \\
y^* &= 1 - \frac{1}{R_b}.
\end{align*}$$

The eigenvalues of the linearisation of (2.24) about this endemic equilibrium are

$$\begin{align*}
\left\{ k(1 - R_b), -\frac{1}{R_b} \sqrt{(kU_c (1 - R_b) - R_b (1 - R_c))^2 + 4kR_b R_c U_c (R_b - 1)} \right\},
\end{align*}$$

so that the endemic state in both species is stable if it exists. We note that the stability of this equilibrium is independent of $U_c$ and $R_c$ although the size of the equilibrium population of infected cattle is an increasing function of $U_c$ and of $R_c$. Thus efforts to destabilise the equilibrium by dealing with the transmissibility among cattle or the cross infectivity from badgers to cattle will fail. The only remedy is to reduce $R_b$ to below unity.
2.10 Transients

The foregoing analysis has considered the existence and stability of equilibria. We have shown that the basic reproduction ratios and the analogous expressions for cross-infection dictate the size of the equilibrium population as well as the existence and stability of the endemic disease state and the IFE. The rate at which equilibria are approached or departed will also depend on these parameters.

However, the transient behaviour of the system is of great importance, since we need to understand the factors dictating the severity of the disease (how many animals actually become infected over a given time), the rapidity with which the system reaches a position arbitrarily close to an equilibrium and the anticipated rate of appearance of new infective cases in terms of the model parameters. We want to adopt an analytical approach to the problem, while being well aware of the difficulty involved and the paucity of any published research on the subject of transient behaviour.

2.10.1 Single species

Non-dimensionalising the single species model of equation (2.4) in the same way as was done for the two species system in equation (2.21) with

\[ v = \frac{S}{N^*}, \quad w = \frac{I}{N^*}, \quad m = \frac{N}{N^*}, \quad R_0 = \frac{\beta \lambda}{\mu (\mu + \gamma)}, \quad \alpha = \frac{\mu}{\mu + \gamma} \]

we obtain

\[ \frac{dv}{dt} = \alpha (1 - v) + w (1 - \alpha) - R_0 vw, \]

\[ \frac{dw}{dt} = -w + R_0 vw, \]

\[ m = w + v, \]

\[ w(0) = w_0, \quad v(0) = v_0, \quad m(0) = m_0. \]

Whole population

We can solve system (2.25) for \( m \):

\[ \frac{dm}{dt} = \alpha (1 - m), \quad m(0) = m_0 \]

which has the solution

\[ m(t) = 1 - (1 - m_0) e^{-\alpha t}. \]

Clearly \( m(t) \) has no extrema except for \( m = 1 \) which is the (stable) equilibrium. The solution thus allows us fully to understand the evolution of the population for \( t > 0 \).
Two classes

\[ \frac{dw}{dt} = 0 \text{ when } w = 0 \text{ (which is the IFE) or when } v = \frac{1}{R_0}, \text{ for which } w \text{ can take any positive value}. \]

Differentiating w.r.t \( t \) we can obtain some information about extrema of \( w \):

\[ \frac{d^2w}{dt^2} = -\frac{dw}{dt}(1 - R_0v) + \frac{dv}{dt}R_0w, \]

\[ \left. \frac{d^2w}{dt^2} \right|_{v = \frac{1}{R_0}} = R_0w \left( \alpha(1 - w) - \frac{\alpha}{R_0} \right). \]

Consequently if

- \( w < 1 - \frac{1}{R_0} \) then \( \left. \frac{d^2w}{dt^2} \right|_{v = \frac{1}{R_0}} > 0 \) so \( v = \frac{1}{R_0} \) is a minimum,

- \( w > 1 - \frac{1}{R_0} \) then \( \left. \frac{d^2w}{dt^2} \right|_{v = \frac{1}{R_0}} < 0 \) so \( v = \frac{1}{R_0} \) is a maximum.

The value taken by \( w \) when \( v = \frac{1}{R_0} \) will depend on the initial conditions and one can imagine that both a maximum or a minimum are possible. We can demonstrate this by numerically simulating either a maximum or a minimum for \( w(t) \) depending on the initial conditions we choose.

We can illustrate this by substituting \( v = m - w \) and using the expression for \( m \) in (2.26) into the second equation in (2.25) to obtain

\[ \frac{dw}{dt} = -w + R_0w \left( 1 - \left( 1 - m_0 \right)e^{-\alpha t} - w \right). \]

Thus \( \frac{dw}{dt} = 0 \) for \( w = 0 \) and \( w = \dot{w} = 1 - \frac{1}{R_0} - \left( 1 - m_0 \right)e^{-\alpha t} \). For \( R_0 > 1 \), as \( t \to \infty \), \( \dot{w} \to \dot{w} = 1 - \frac{1}{R_0} \). For \( R_0 < 1 \), \( \dot{w} \) does not exist and \( w = 0 \) is the only turning point. Taking the second derivative

\[ \left. \frac{d^2w}{dt^2} \right|_{w = \dot{w}} = \alpha R_0\dot{w}(1 - m_0)e^{-\alpha t}. \]

Thus \( \dot{w} \) is a maximum for \( m_0 > 1 \) and a minimum for \( m_0 < 1 \), hence either a maximum or a minimum can occur in progress to the endemic equilibrium depending on the initial conditions.

If \( t \) is large enough that \( m \approx 1 \) we can substitute for \( v \) in (2.25) and solve explicitly for \( w(t) \)

\[ \frac{dw}{dt} = -R_0w^2 + w(R_0 - 1) \]

\[ w(0) = w_0 \]

which has the solution

\[ w(t) = \frac{w_0(1 - R_0)}{(1 + R_0(w_0 - 1))e^{-(R_0-1)t} - w_0 R_0}. \]
If $R_o > 1$, this gives the characteristic S-shaped curve for the evolution of the size of the infective class, while the time derivative gives the bell shape of a sech$^2$ graph for the incidence of new cases.

2.10.2 Two species

Conjecture 2.10.1 The basic reproductive ratio, $R_{bc}$ or $\hat{R}_{bc}$ governs not only the existence and the stability of the IFE and the endemic disease state of the two animal system (2.1), but is also a key element in determining the size of the endemic infective populations, the rate at which equilibrium is approached and the total number of animals infected over a given period of time.

The transients of the two animal system are wholly intractable analytically. Conjecture (2.10.1) can thus only be demonstrated by numerical simulation (as we have already illustrated in Section 2.5).

2.11 Three species

As we noted in Chapter 1, it has been suggested that not only badgers, but also deer, may be involved in the transmission of bovine tuberculosis. We take precisely the same assumptions as we made for the two species SIS model and apply them to a three animal system where we consider each species able to infect both themselves and each other. Subscripts $b$, $c$ and $d$ notionally refer to badgers, cattle and deer.

The model system is now as follows, with the same assumptions and initial conditions as for the equations for system (2.1) extended pari passu to the additional classes.

\begin{align*}
\frac{dS_d}{dt} &= \Lambda_d - \mu_d S_d - \beta_d S_d I_d - \xi_d I_d I_b - \epsilon_{cd} S_d I_c + \gamma_d I_d, \\
\frac{dI_d}{dt} &= -\mu_d I_d + \beta_d S_d I_d + \xi_d I_d I_b + \epsilon_{cd} S_d I_c - \gamma_d I_d, \\
\frac{dS_c}{dt} &= \Lambda_c - \mu_c S_c - \beta_c S_c I_e - \xi_{ce} S_c I_b - \epsilon_{dc} S_c I_d + \gamma_c I_c, \\
\frac{dI_c}{dt} &= -\mu_c I_c + \beta_c S_c I_c + \xi_{ce} S_c I_b + \epsilon_{dc} S_c I_d - \gamma_c I_c, \\
\frac{dS_b}{dt} &= \Lambda_b - \mu_b S_b - \beta_b S_b I_b - \xi_{ab} S_b I_d - \epsilon_{db} S_b I_c + \gamma_b I_b, \\
\frac{dI_b}{dt} &= -\mu_b I_b + \beta_b S_b I_b + \xi_{ab} S_b I_d + \epsilon_{db} S_b I_c - \gamma_b I_b, \\
S_d + I_d &= N_d, \quad S_c + I_c = N_c, \quad S_b + I_b = N_b, \\
S_d > 0, \quad S_c > 0, \quad S_b > 0, \quad I_d \geq 0, \quad I_c \geq 0, \quad I_b \geq 0.
\end{align*}

(2.27)
By adding the first and second equations of system (2.27) we obtain

$$\frac{dN_d}{dt} = \Lambda_d - \mu_d N_d$$

and, as we showed for the two-animal system, equation (2.1), we have

$$\lim_{t \to \infty} N_d(t) = \frac{\Lambda_d}{\mu_d}.$$ 

The same argument applies equally to $N_c(t)$ and $N_b(t)$. Thus we are justified in assuming, in order to make progress, that $t$ is sufficiently large that we can take the total population of each animal species, $N_d, N_c$ and $N_b$ respectively, to be constant and thus we reduce the order of the system in equation (2.27) from six to three, by substituting for the susceptible class in each case. We thus obtain the following reduced system, recognising that we have not shown rigorously that the solutions of (2.27) approach those of this reduced system,

$$\frac{dI_d}{dt} = - (\mu_d + \gamma_d)I_d + (N_d - I_d)(\beta_d I_d + \xi_d b + \xi_d I_c),$$

$$\frac{dI_c}{dt} = - (\mu_c + \gamma_c)I_c + (N_c - I_c)(\beta_c I_c + \xi_c b + \xi_c I_d),$$

$$\frac{dI_b}{dt} = - (\mu_b + \gamma_b)I_b + (N_b - I_b)(\beta_b I_b + \xi_b I_d + \xi_b I_c).$$

Non-dimensionalisation

In order to simplify the analysis of system (2.28) we nondimensionalise with the following scheme

$$x = \frac{I_d}{N_d}, \quad y = \frac{I_c}{N_c}, \quad z = \frac{I_b}{N_b}, \quad R_d = \frac{\beta_d N_d}{\mu_d + \gamma_d}, \quad R_c = \frac{\beta_c N_c}{\mu_c + \gamma_c}, \quad R_b = \frac{\beta_b N_b}{\mu_b + \gamma_b},$$

$$U_{bc} = \frac{\xi_b c N_d}{\mu_b + \gamma_b}, \quad U_{cb} = \frac{\xi_c b N_b}{\mu_c + \gamma_c}, \quad U_{cd} = \frac{\xi_c d N_c}{\mu_c + \gamma_c}, \quad U_{bd} = \frac{\xi_b d N_b}{\mu_b + \gamma_b},$$

$$U_{dc} = \frac{\xi_d c N_d}{\mu_d + \gamma_d}, \quad U_{db} = \frac{\xi_d b N_b}{\mu_d + \gamma_d},$$

$$\beta = (\mu_c + \gamma_c)t, \quad k_1 = \frac{\mu_c + \gamma_c}{\mu_d + \gamma_d}, \quad k_2 = \frac{\mu_b + \gamma_b}{\mu_d + \gamma_d}.$$ 

We thus can write system (2.28) in the following simpler form, dropping the caret on $\hat{t}$

$$\frac{dx}{dt} = -x + (1 - x)(R_d x + k_2 U_{bd} z + k_1 U_{cd} y),$$

$$\frac{dy}{dt} = -k_1 y + (1 - y)(k_1 R_c y + k_2 U_{bc} z + U_{dc} x),$$

$$\frac{dz}{dt} = -k_2 z + (1 - z)(k_2 R_b z + k_1 U_{db} y + U_{db} x).$$

(2.29)
Infection free equilibrium

There is an infection free equilibrium, (0,0,0). If we linearise system (2.29) around the IFE, the Jacobian, $J$, is as follows

$$J = \begin{pmatrix} R_d - 1 & k_1 U_{cd} & k_2 U_{bd} \\ U_{dc} & k_1 (R_c - 1) & k_2 U_{bc} \\ U_{db} & k_1 U_{cb} & k_2 (R_b - 1) \end{pmatrix}.$$  

We investigate the local stability of the IFE as usual by applying the Routh Hurwitz conditions, discussed in the Introduction, for three dimensions. If the characteristic equation of $J$ is

$$\lambda^3 + b_1 \lambda^2 + b_2 \lambda + b_3 = 0,$$

then we require $b_1 > 0$, $b_1 b_2 - b_3 > 0$ and $b_3 > 0$ for the equilibrium to be locally asymptotically stable.

We can verify that the first and third of these conditions are met, but the second inequality is algebraically intractable. However, we can identify the conditions under which the IFE becomes unstable. $b_1 < 0$ requires that

$$R_d - 1 + k_1 (R_c - 1) + k_2 (R_b - 1) > 0.$$  

$R_d > 1$, $R_c > 1$ and $R_b > 1$ is a sufficient, but not necessary condition for this inequality to hold and thus for the IFE to be unstable.

$b_3 < 0$, on the other hand, requires that $\det(J) > 0$. After considerable algebraic manipulation we arrive at the necessary condition (given that $R_d > 1$, $R_c > 1$ and $R_b > 1$) that $\det(J) > 0$ and that the IFE is unstable as

$$R_{bdc} := \frac{U_{bc} U_{cb}}{(R_b - 1)(R_c - 1)} + \frac{U_{bd} U_{db}}{(R_b - 1)(R_d - 1)} + \frac{U_{db} U_{cd}}{(R_d - 1)(R_c - 1)} - \frac{U_{bc} U_{bd} U_{db} + U_{cb} U_{bd} U_{dc}}{(R_c - 1)(R_b - 1)(R_d - 1)} > 1.$$  

We see that the expression for $R_{bdc}$, the basic reproductive ratio for the system, contains the sum of the basic reproductive ratios for the three animal-pair systems (badgers/cattle, cattle/deer and deer/badgers), minus a fourth term, of opposite sign, which we conjecture represents the three-animal system specifically. (The expression is strikingly reminiscent of the expression for the union of a set of probabilities as being equal to their sum minus their intersection).

We have the same difficulty with this form for the basic reproduction ratio as for the two species model (not defined for any of $R_d = 1$, $R_c = 1$, $R_b = 1$), but are unable to find a more satisfactory version since, although we may easily compute the next generation matrix, $FV^{-1}$ (in the manner described in Section 2.4.1) as follows,

$$FV^{-1} = \begin{pmatrix} R_d & U_{cd} & U_{bd} \\ U_{dc} & R_c & U_{bc} \\ U_{db} & U_{cb} & R_b \end{pmatrix}$$  

we cannot express its eigenvalues in an algebraically comprehensible manner, since they are the solutions of a non-factorisable cubic equation.
Conjecture 2.11.1 Noting that system (2.28) is co-operative, we believe that there will be a unique endemic equilibrium if $R_{bcd} > 1$ which will be stable if it exists.

The work to prove this conjecture would follow the same lines as for the two species model, although the algebra would be much more complicated and potentially intractable.

2.12 $n$ species

We can extend the analysis to a system of $n$ species, with both inter- and intraspecies infectivity. We use the same SIS model as before, with no additional deaths due to disease and let $t$ be large enough that we can consider that the populations of each species to be constant. We can then describe the non-dimensionalised model (using the same scheme as in (2.11)) as a series of $n$ o.d.e.s for the infective classes of each species, where the $i$th equation is

$$\frac{dX_i}{dt} = -X_i + (1 - X_i)R_iX_i + (1 - X_i)\sum_{j=1}^{n} U_{ij}X_j. \quad (2.30)$$

We have made the assumption that in the non-dimensionalisation scheme we set all the $k_i = 1$ for simplicity (since $k_i$ does not in any event appear in the determinant of the Jacobian of the linearisation about the IFE). Here $R_i$ is the basic reproductive ratio for the $i$th species alone, while $U_{ij}$ is the analogue of the basic reproductive ratio for infection of the $i$th species by the $j$th species.

We can see immediately from equation (2.30) that the positive cone $R^+$ is invariant and that since all of the $X_i$ are non-negative, there can only be two equilibria, an IFE $X_i = 0, \ i = 1 \ldots n$ and an endemic equilibrium $X_i = X^*_i, \ i = 1 \ldots n$. We conjecture that the system exhibits a transcritical bifurcation and that the stable endemic equilibrium exists at the parameter set at which the determinant of the Jacobian of the linearisation about the IFE $J_n$ changes sign, where

$$J_n = \begin{pmatrix}
R_1 - 1 & U_{21} & U_{31} & U_{41} & \ldots & U_{n1} \\
U_{12} & R_2 - 1 & U_{32} & U_{42} & \ldots & U_{n2} \\
U_{13} & U_{23} & R_3 - 1 & U_{43} & \ldots & U_{n3} \\
\ldots & \ldots & \ldots & \ldots & \ldots & \ldots \\
U_{1n} & U_{2n} & U_{3n} & U_{4n} & \ldots & R_n - 1
\end{pmatrix}.$$

We can investigate the conditions under which the determinant of this matrix changes sign (from positive to negative for $n$ even and from negative to positive for $n$ odd) as the IFE becomes unstable. We obtain this in the form $\hat{R}_n = 1$ where

$$\hat{R}_n = \sum_{i,j=1}^{n} R_{ij} - \sum_{i,j,k=1}^{n} R_{ijk} + \sum_{i,j,k,m=1}^{n} R_{ijkm} - \sum_{i,j,k,m=1}^{n} R_{ijR_{km}} \ldots$$
Here we define

\[ R_{ij} = \frac{U_{ij}U_{ji}}{(R_i - 1)(R_j - 1)}, \]

\[ R_{ijk} = \frac{(U_{ij}U_{jk}U_{ki} + U_{ji}U_{ik}U_{kj})}{(R_i - 1)(R_j - 1)(R_k - 1)}, \]

\[ R_{ijkm} = \frac{(U_{ij}U_{jk}U_{km}U_{mi} + U_{ji}U_{im}U_{mk}U_{ki})}{(R_i - 1)(R_j - 1)(R_k - 1)(R_m - 1)}, \]

and so forth.

We conclude that, in an n-species environment, if any of the \( R_i > 1 \) then there will not be a stable IFE. \( \mathcal{J}_n \) is an M-matrix if all of its principal minors are positive, which will be true if

- all of the \( R_i < 1 \)
- and \( \frac{U_{12}U_{21}}{(R_1 - 1)(R_2 - 1)} < 1 \)

for the top left hand \((2 \times 2)\) minor
- and \( \frac{U_{12}U_{21}}{(R_1 - 1)(R_2 - 1)} + \frac{U_{13}U_{31}}{(R_1 - 1)(R_3 - 1)} + \frac{U_{23}U_{32}}{(R_2 - 1)(R_3 - 1)} - \frac{U_{12}U_{23}U_{31} + U_{21}U_{13}U_{32}}{(R_1 - 1)(R_2 - 1)(R_3 - 1)} < 1, \)

for the top left \((3 \times 3)\) minor and so forth, together with other similar inequalities for the other principal minors.

These inequalities represent conditions for a stable IFE in the various possible subsystems with 2, 3... \( n-1 \) species. Then

\[ (\mathcal{J}_n + MI)e_n = (\omega_0 + M)e_n \]

where \( e_n \) is a positive eigenvector and \( \omega_0 < 0 \) so that \( \mathcal{J}_n = \omega_0 e_n \).

Moreover, even if all of the \( R_i < 1 \), a stable endemic equilibrium might exist but only with all the \( n \) species present and disappear if a single species were removed - no matter that the individual contribution of that species to the overall level of infection is relatively small. In complex ecosystems, this may be an important factor in maintaining endemic disease.

### 2.13 Conclusions

We have seen that the two species system exhibits a transcritical bifurcation with parameter \( R_{bc} \). There is either a stable IFE and no endemic equilibrium
or an unstable IFE and a stable endemic equilibrium. The inter-species infection term means that where two species would have both been in an endemic equilibrium in the absence of the other, their mixing induces an endemic equilibrium with higher numbers of both of the infected classes.

More interestingly, where two species would otherwise have been infection-free, their mixing can produce an endemic infection, again if $R_{bc} > 1$. In the event where there is a population of cattle which is infection free, the introduction of a badger population is guaranteed to create an endemic infection once the density of susceptible badgers reaches the critical threshold level such that $R_{bc} > 1$, and infection is introduced, irrespective of whether, in isolation, the badgers would have had an endemic disease state or not. The three animal model would appear to demonstrate precisely the same behaviour, we might conjecture that the presence of a third species would amplify the effects of cross-infectivity from badgers to cattle.
Chapter 3

Culling strategies to eliminate endemic equilibria

3.1 Introduction

One of the approaches to the elimination of *M. bovis* in cattle has been the culling of badgers - either proactively or reactively (after a herd breakdown has taken place). We consider a number of culling strategies in this chapter, starting with the impact in a single species alone in the environment under different conditions and then looking at two species together. The model takes into account the population dynamics of the badger as well as the epidemiology of tuberculosis, but is clearly very general in its application.

A number of badger culling trials have been conducted and the impact of the culling on the incidence of tuberculosis in cattle has been observed. The results are somewhat inconclusive at this stage, [18], [52], [29]. It appears that complete eradication of badgers in an area does indeed reduce the level of incidence in new TB cases among cattle in that same area, but can result in an increase in incidence of TB in cattle in contiguous areas, possibly as a result of the migration of badgers avoiding the culling. On the other hand, partial removal of badgers appears to produce only a temporary reduction in the level of incidence of new cases of TB in cattle. It may well be that culling activities disrupt the social structure of badger groups and territories and cause different and perhaps increased dispersion patterns.

We use once more a deterministic, compartmental model with the following assumptions (where the assumptions have been commented upon in previous chapters we simply list them)

- animal densities are continuous.
- a logistic model (of the form $a_1 N(1-a_2 N)$ where $a_1$ and $a_2$ are constants and $N$ is the population density of animals) is used for the fecundity function, to take account of the experimental observation that the birth rate in badgers is population density-dependant. More complicated expressions have been used in the literature, such as $a_1 N(1-a_2 N^c)$ for some exponent $c$ (with $c \in [1,7]$ or $a_1 N e^{-a_2 N}$), these lead rapidly to much more intractable algebra than the logistic model. We assume that
both infectious and susceptible animals can produce offspring and that there are equal numbers of males and females and that all animals can reproduce (there is no maturity constraint).

- there is no latency period; animals become immediately infectious once infected.
- there is no vertical transmission of the disease.
- infection is through a mass action model.
- all the parameters are constant.
- there are no additional deaths due to the disease.
- the state variables are functions of time only, in particular there is no age or maturity structure.
- the populations are spatially homogeneous and isotropic and randomly mixed.

We consider in principle the introduction of an infinitesimally small number of infectious animals to a system initially in disease free equilibrium for the unculled model and that, in the culling models, the system is initially at the endemic equilibrium.

- The system is closed, there is no migration of animals into or out of the system. We shall see later in this chapter that allowing migration can have a profound effect on the dynamics of the system. In practice, our modelling will ultimately need to take account of the fact that badgers are largely territorial (with some inter-territorial spread) and a herd of cattle is primarily located within an individual farm (although cattle will move into the farm at the beginning and out of the farm at the end of their lives).

### 3.2 The basic model

We briefly review the population and epidemic dynamics of the basic model, without culling, since this model will behave somewhat differently from system (2.1). The model we use here is again developed from standard SIS models [45], [10]. The densities of susceptible and infectious animals are $S(t)$ and $I(t)$ respectively. The total population is $N(t) = S(t) + I(t)$. The raw birth rate is $s$, the death rate is $\mu$. The equilibrium population size will be $C(1 - \frac{\mu}{s})$ where $C$ is a carrying constant for the environment, while $\beta$ is the infection rate and $\gamma$ is the recovery rate. The model is

\[
\frac{dS}{dt} = s(S+I) \left(1 - \frac{S+I}{C}\right) - \mu S - \beta SI + \gamma I,
\]

\[
\frac{dI}{dt} = -\mu I + \beta SI - \gamma I,
\]

\[S(0) > 0, \quad I(0) \geq 0.\]
The dynamics of the overall population are governed by the following differential equation, obtained by adding the equations in (3.1)

\[
\frac{dN}{dt} = sN \left(1 - \frac{N}{C}\right) - \mu N, \quad N(0) > 0.
\]

Non-dimensionalisation

In order to simplify the analysis of system (3.1) we non-dimensionalise with the following quantities, in the same manner as in Chapter 2:

\[
x = \frac{S}{C}, \quad y = \frac{I}{C}, \quad m = \frac{N}{C}, \quad \hat{t} = (\mu + \gamma)t,
\]

\[
\alpha = \frac{\mu}{\mu + \gamma}, \quad \rho = \frac{s}{\mu + \gamma}, \quad R_b = \frac{\beta C}{\mu + \gamma}.
\]

Removing the carets we have

\[
\begin{align*}
\frac{dx}{dt} &= \rho(x + y)(1 - (x + y)) - \alpha x + (1 - \alpha)y - R_b xy, \\
\frac{dy}{dt} &= -y + R_b xy,
\end{align*}
\]

(3.2)

\[
x(0) \geq 0, \quad y(0) \geq 0.
\]

Preliminary remarks

Lemma 3.2.1 There are two equilibrium states for the total animal population, eradication and the carrying level population, the dynamics being governed by the bifurcation parameter \( \frac{p}{\alpha} \).

We have, from adding the equations of system (3.2), and letting \( m = x + y \)

\[
\frac{dm}{dt} = \rho m(1 - m) - \alpha m = f(m), \quad m(0) = m_0.
\]

(3.3)

A fecundity function must necessarily be non-negative for all \( m \).

The logistic form is the most obvious method of achieving a density-dependant fecundity function, although more strictly we should define it as, \( b(m) \) say, where

\[
b(m) = \begin{cases} 
\rho m (1 - m) & : 0 \leq m \leq 1 \\
0 & : \text{otherwise.}
\end{cases}
\]

This also ensures the non negativity of \( m(t) \). However, for simplicity throughout this thesis we use the form in equation (3.3) whenever we require a density dependant fecundity function, understanding it to be non-negative.

By setting \( f(m) = 0 \) we find that there are two possible equilibria for the total population, \( m = 0 \) (extinction) or \( m = m^* = 1 - \frac{2}{\rho} \) (population at carrying capacity). The second equilibrium can only exist if \( \rho > \alpha \), i.e. the raw birth rate exceeds the death rate. We will normally assume that \( \rho > \alpha \) so that, in the absence of culling, a stable population would result.
We can solve equation (3.3) directly to obtain

\[ m(t) = \frac{m_0 K}{(K - m_0)e^{-rt} + m_0}, \]

where \( K = 1 - \frac{\alpha}{\rho} \) and \( r = \rho - \alpha. \)

Thus \( K \) is the equilibrium population in the absence of culling and \( r \) the ratio of net birth rate \((s - \mu)\) to the mean length of time infective \((\mu + \gamma)\). We notice that if \( m_0 > 0 \) then \( m(t) > 0 \) for all \( t > 0 \). We will utilise this solution in the analysis of impulsive culling. We see in Figure 3.1 the behaviour of \( m(t) \) for two different initial conditions. (We have used the parameter values \( m_0 = 0.2, K = 1, r = 0.03. \))

![Figure 3.1: Evolution of the population with logistic fecundity](image)

**Positivity and boundedness**

**Proposition 3.2.2** If \( m(0) \geq 0 \) then \( m(t) \geq 0 \) for all \( t > 0 \) and is bounded from above.

The proof of this proposition is trivial and is omitted.

**Proposition 3.2.3** If \( x(0) \geq 0 \) and \( y(0) \geq 0 \) then \( x(t) \geq 0 \) for all \( t > 0 \) and \( y(t) \geq 0 \) for all \( t > 0 \) and both \( x(t) \) and \( y(t) \) are bounded from above.

Since \( m(t) = x(t) + y(t) \) and we have shown the positivity of \( m(t) \), if \( x(t) < 0 \) then \( y(t) > 0 \).

Moreover, since \( x(t) \) is a function of \( t \) only, we can write, whatever the sign of \( x(t) \)

\[ \frac{dy}{dt} = y(t)(R_bx(t) - 1), \]
so that

\[ y(t) = y(0)e^{\int_0^t (R_b x(\tau) - 1) d\tau} \geq 0 \quad \text{for} \quad y(0) \geq 0. \]

Thus we have proved the non-negativity of \( y(t) \). \( \square \)

Now let us consider \( x(t) \). Firstly we dispose of the case \( y(0) = 0 \), for then \( y(t) = 0 \) for all \( t \) and thus

\[ \frac{dx}{dt} = \rho x(1 - x) - \alpha x \]

and thus

\[ x \geq x(0)e^{\int_0^t \rho x(s)(1-x(s)) - \alpha x(s) ds} > 0. \]

Now let \( x(0) > 0 \) and \( y(0) > 0 \). For \( x(t) = 0 \) we have

\[ \frac{dx}{dt} = \rho y(1 - y) + (1 - \alpha)y. \]

Let us assume that at some time \( t_0, \ x(t_0) = 0 \) for the first time. But \( \frac{dx}{dt} |_{t_0} > 0 \) because, by definition of the fecundity function \( \rho y(1 - y) \geq 0 \) and, by definition, \( \alpha < 1 \). Hence, since \( x(t) \) and \( \dot{x}(t) \) are continuous, \( x(t) \) must have been negative for \( t < t_0 \) thus contradicting the assumption that \( t_0 \) was the first occasion that \( x(t) = 0 \).

Finally, if \( m(t) \) is bounded from above and \( x(t) \) and \( y(t) \) are positive, then \( x(t) \) and \( y(t) \) are also bounded from above. \( \square \)

Disease dynamics - equilibria

**Theorem 3.2.4** System (3.2) has three equilibria, namely \((0,0)\), eradication, \((1 - \frac{\alpha}{\rho}, 0)\) the infection-free equilibrium (IFE) and the endemic disease state, \((\frac{1}{R_b}, 1 - \frac{\alpha}{\rho} - \frac{1}{R_b})\). The system displays two transcritical bifurcations with parameters \( \frac{\alpha}{\rho} \) and \( R_b \left(1 - \frac{\alpha}{\rho}\right) \) respectively.

By setting the right hand sides of equations (3.2) equal to zero we find that there are three physically realistic solutions for \((x, y)\). We linearise around these equilibria and compute the eigenvalues of the Jacobian matrices for the linearisations to investigate local stability.

**Eradication**

At \((0,0)\) the eigenvalues \( \lambda_1, \lambda_2 \) of the linearisation of (3.2) are given by

\[ \lambda_1 = -1, \quad \lambda_2 = \rho - \alpha, \]

hence if \( \frac{\rho}{\alpha} < 1 \), the eradication equilibrium is an attractor.
The infection-free equilibrium

For the IFE to exist we must have $\frac{a}{\alpha} > 1$. At this equilibrium the eigenvalues of the Jacobian of the linearisation of (3.2) are given by

$$\lambda_1 = \alpha - \rho, \quad \lambda_2 = \frac{R_b}{1 - \frac{\alpha}{\rho}} - 1.$$

For local stability of the IFE we need $\frac{a}{\alpha} > 1$ and

$$R_b \left(1 - \frac{\alpha}{\rho}\right) < 1.$$

If $\frac{a}{\alpha} > 1$ then $R_b < 1$ is sufficient for the local stability of the IFE. The necessary condition on $R_b$ is that $R_b < 1 + \frac{\alpha}{\rho - \alpha}$. The critical value of the bifurcation parameter determining the stability of the IFE and the existence of the endemic disease equilibrium is $R_b = 1 + \frac{\alpha}{\rho - \alpha}$.

Remark 3.2.5 Had we chosen a non-dimensionalisation scheme which defined the basic reproductive ratio as $\hat{R}_b$ say where

$$\hat{R}_b = \frac{C\beta(1 - \frac{K}{x})}{\mu + \gamma} = \frac{\beta CK}{\mu + \gamma}$$

where $K$ is the equilibrium population, then $\hat{R}_b = 1$ would be the critical value. However, the non-dimensionalisation chosen has computational advantages and explicitly shows the impact of the parameters $\alpha$ and $\rho$.

Endemic disease state

At $(\frac{1}{\hat{R}_b}, 1 - \frac{\alpha}{\rho} - \frac{1}{\hat{R}_b})$ the eigenvalues of the Jacobian of the linearisation of (3.2) are

$$\lambda_1 = \alpha - \rho, \quad \lambda_2 = 1 - R_b \left(1 - \frac{\alpha}{\rho}\right).$$

Consequently the condition on $R_b$ both for the existence and the stability of the endemic equilibrium is the opposite to that for the IFE, $R_b > 1 + \frac{\alpha}{\rho - \alpha}$, while once again we must have $\frac{a}{\alpha} > 1$. If the endemic equilibrium exists it is locally stable.

The bifurcation diagram is shown in Figure 3.2.

The $(x, y)$ phase portrait

As $R_b$ decreases, the position of the endemic equilibrium, denoted $(x^*, y^*)$, moves to the right along the $\dot{x} = 0$ nullcline until it coincides with the IFE when $R_b = 1 + \frac{\alpha}{\rho - \alpha}$. As $R_b$ increases, the position of the endemic equilibrium moves to the left up the $\dot{x} = 0$ nullcline, increasing $y^*$ and decreasing $x^*$.

Global stability

The boundedness of $m = x + y$ implied by the solution to equation (3.3) together with the positivity of $x(t)$ and $y(t)$ show that $x(t)$ and $y(t)$ are bounded. As $t \to \infty$ there must therefore be either a stable equilibrium or a limit cycle.
We use the Dulac criterion to show the non-existence of periodic solutions. If we write system (3.2) in the form $\dot{x} = f(x, y), \dot{y} = g(x, y)$, with

$$f(x, y) = \rho(x + y)(1 - (x + y)) - ax + (1 - a)y - R_bxy,$$

$$g(x, y) = -y + R_bxy$$

and define $H(x, y) = \frac{1}{x+y}$ and $\Omega = (0, \infty) \times (0, \infty)$ then

$$\partial(H_f) = \frac{\rho(x + y)^2 + R_by^2 + y}{(x + y)^2}$$

$$\partial(H_g) = \frac{1 - R_bx}{(x + y)^2},$$

so that

$$\frac{\partial(H_f)}{\partial x} + \frac{\partial(H_g)}{\partial y} = -\frac{\rho(x + y) + R_by}{y(x + y)} < 0 \text{ for all } (x, y) \in \Omega.$$

We can thus conclude that there are no periodic solutions to system (3.2).

Choosing a suitable function to utilise Dulac's criterion

We found the function $H$ through systematic application of trial and improvement, making full use of Maple. The initial goal is to find a function which gives a sufficiently simple result when $\frac{\partial(H_f)}{\partial x} + \frac{\partial(H_g)}{\partial y}$ is computed to enable its sign to be easily seen. We started with simple reciprocals of the variables $x$ and $y$ to eliminate as many variable terms as possible in $Hf(x, y)$ and $Hg(x, y)$ and then added factors to eliminate as many sign changes as possible in the sum of the partial derivatives.

3.3 Recovery and reinfection

We may ask how the endemic population of susceptibles in an SIS model is made up, clearly there will be some individuals who are never infected, others
who are infected once only, others twice and so forth. Let us consider the system of equation (3.2) with the new assumption that a susceptible animal $x$, when infected for the first time passes into infected class $y_1$, recovers and passes into a recovered (and therefore once more susceptible) class, $r_1$, is then infected a second time and passes in this case into infective class $y_2$, then on recovery to recovered class $r_2$, infected class $y_3$ and finally into recovered class $r_3$. Subsequent reinfection passes the animal back to $y_3$ and thence to $r_3$ again. Thus the infected population is $y_1 + y_2 + y_3$ and the susceptible population is $x + r_1 + r_2 + r_3$.

Conjecture 3.3.1 The susceptible class at the endemic equilibrium, with $n$ recovered classes contains $\frac{1}{R_0}$ individuals in total, where the number infected $i$ times is $\frac{\psi^i(1-\psi)}{R_0}$ for $i \in [0,n-1]$ and $\frac{\psi^n}{R_0}$ is the number infected $n$ times, where $\psi$ is defined in (3.6).

The model equations are now

\[
\begin{align*}
\frac{dx}{dt} &= \rho (x + y_1 + y_2 + y_3 + r_1 + r_2 + r_3)(1 - (x + y_1 + y_2 + y_3 + r_1 + r_2 + r_3)) - \alpha x - R_b x (y_1 + y_2 + y_3), \\
\frac{dy_1}{dt} &= R_b x (y_1 + y_2 + y_3) - y_1, \\
\frac{dy_2}{dt} &= R_b r_1 (y_1 + y_2 + y_3) - y_2, \\
\frac{dy_3}{dt} &= R_b (r_2 + r_3) (y_1 + y_2 + y_3) - y_3, \\
\frac{dr_1}{dt} &= (1 - \alpha)y_1 - R_b r_1 (y_1 + y_2 + y_3) - r_1, \\
\frac{dr_2}{dt} &= (1 - \alpha)y_2 - R_b r_2 (y_1 + y_2 + y_3) - r_2, \\
\frac{dr_3}{dt} &= (1 - \alpha)y_3 - R_b r_3 (y_1 + y_2 + y_3) - r_3, \\
x(0) > 0, \quad y_i(0) = 0, \quad r_i(0) = 0 \quad \text{for} \quad i = 1, 2, 3,
\end{align*}
\]

(3.5)

with the usual initial conditions of the introduction of a single infected animal at $t = 0$. If we set the right hand sides of the equations of system (3.5) equal to zero and solve, we can find the values of the susceptible and recovered classes at equilibrium as follows.
\[
x + r_1 + r_2 + r_3 = \frac{1}{R_b}, \quad y_1 + y_2 + y_3 = 1 - \frac{\alpha}{\rho} - \frac{1}{R_b},
\]
\[
y_1 = R_b x \left(1 - \frac{\alpha}{\rho} - \frac{1}{R_b}\right),
\]
\[
r_1 = \frac{(1 - \alpha)y_1}{1 + R_b \left(1 - \frac{\alpha}{\rho} - \frac{1}{R_b}\right)} = \frac{(1 - \alpha)y_1}{R_b \left(1 - \frac{\alpha}{\rho}\right)} = \frac{x(1 - \alpha) \left(1 - \frac{\alpha}{\rho} - \frac{1}{R_b}\right)}{1 - \frac{\alpha}{\rho}},
\]
\[
y_2 = R_b r_1 \left(1 - \frac{\alpha}{\rho} - \frac{1}{R_b}\right) = \frac{(1 - \alpha) y_1}{1 - \frac{\alpha}{\rho}}
= \frac{(1 - \alpha - \frac{1}{R_b})^2 (1 - \alpha) R_b x}{1 - \frac{\alpha}{\rho}},
\]
\[
r_2 = \frac{(1 - \alpha)y_2}{1 + R_b \left(1 - \frac{\alpha}{\rho} - \frac{1}{R_b}\right)} = \frac{(1 - \alpha)y_2}{R_b \left(1 - \frac{\alpha}{\rho}\right)} = \frac{x(1 - \alpha)^2 \left(1 - \frac{\alpha}{\rho} - \frac{1}{R_b}\right)}{\left(1 - \frac{\alpha}{\rho}\right)^2},
\]
\[
y_3 = R_b \left(1 - \frac{\alpha}{\rho} - \frac{1}{R_b}\right) (r_2 + r_3),
\]
\[
r_3 = \frac{(1 - \alpha)y_3}{1 + R_b \left(1 - \frac{\alpha}{\rho} - \frac{1}{R_b}\right)}
= R_b \left(1 - \frac{\alpha}{\rho} - \frac{1}{R_b}\right) \left(1 - \frac{\alpha}{\rho} - \frac{1}{R_b}\right)
= \frac{(1 - \alpha) r_2 \left(1 - \frac{\alpha}{\rho} - \frac{1}{R_b}\right) + (1 - \alpha) r_3 \left(1 - \frac{\alpha}{\rho} - \frac{1}{R_b}\right)}{1 + R_b \left(1 - \frac{\alpha}{\rho} - \frac{1}{R_b}\right)}.
\]

If we now define
\[
\psi = \frac{(1 - \alpha) \left(1 - \frac{\alpha}{\rho} - \frac{1}{R_b}\right)}{1 - \frac{\alpha}{\rho}}, \quad (3.6)
\]
then, after some algebra we have
\[
\frac{1}{1 - \psi} = \frac{R_b \left(1 - \frac{\alpha}{\rho}\right)}{1 + \alpha R_b \left(1 - \frac{\alpha}{\rho} - \frac{1}{R_b}\right)}.
\]
Thus we have, after further algebra

\[ r_1 = \psi x, \quad r_2 = \psi^2 x, \quad r_3 = \frac{\psi^3 x}{1-\psi}, \]

and, since

\[ x \left( 1 + \psi + \psi^2 + \frac{\psi^3}{1-\psi} \right) = \frac{1}{R_b}, \quad x = \frac{1-\psi}{R_b}, \]

the susceptible classes are therefore

\[ x = \frac{1-\psi}{R_b}, \quad r_1 = \frac{\psi(1-\psi)}{R_b}, \quad r_2 = \frac{\psi^2(1-\psi)}{R_b}, \quad r_3 = \frac{\psi^3}{R_b}. \]

This suggests that the conjectured sequence is correct.

Biologically, the expression for the numbers of those never infected, \( \frac{\psi^3}{R_b} \), is intuitively reasonable, being inversely proportional to the infectivity and directly proportional to the death rate (since the shorter the life span the less chance to be infected).

### 3.4 Deaths due to disease

For simplicity we have hitherto considered that there were no deaths due to the disease itself. Relaxing this assumption we can amend the non-dimensionalised system of equation (3.2) as

\[
\begin{align*}
\frac{dx}{dt} & = \rho(x + y)(1-x-y) - \alpha x + (1-\alpha-\delta)y - R_b xy, \\
\frac{dy}{dt} & = -y + R_b xy, \quad x(0) > 0, \quad y(0) \geq 0,
\end{align*}
\]

(3.7)

where \( \delta \) is the scaled value of the death rate due to disease and the scaling is by a factor of \( \mu + \gamma + \delta \), so that the basic reproductive ratio is now

\[ R_b = \frac{N^* \beta}{\mu + \gamma + \delta}, \]

where \( N^* \) is the equilibrium total population at the infection free equilibrium and we have already defined the meaning of all the parameters.

**Lemma 3.4.1** System (3.7) exhibits two transcritical bifurcations with parameters \( R_b \) and \( \delta \) respectively. The linearisation of the system around the endemic equilibrium demonstrates oscillations increasing in amplitude and frequency with the rate of disease-related death \( \delta \).

### 3.4.1 Equilibria

There are three equilibria as we would anticipate; the IFE and the eradication equilibrium are identical to those of system (3.2), with the same stability criteria. More interesting is the endemic equilibrium, which is

\[ x^* = \frac{1}{R_b}, \]

\[ y^* = \frac{1}{2\rho R_b} \left( \frac{R_b(\beta - \alpha - \delta)}{2\rho + \sqrt{R_b^2(\beta - \alpha - \delta)^2 + 4\rho \delta R_b}} \right). \]
We note that the expression for \( x^* \) is the same as in system (3.2), but with the definition of \( R_b \) including \( \delta \). \( x^* \) is increasing \( y^* \) decreasing in \( \delta \). The condition that \( y^* > 0 \) is \( R_b > \frac{\rho}{\rho - \alpha} \) as in system (3.2).

### 3.4.2 Stability of the endemic state

**Proposition 3.4.2** The endemic state of system (3.7) is linearly stable, moreover for \( \delta > \delta_{\text{min}} \) (where \( \delta_{\text{min}} \) is defined in equation (3.8)) the endemic equilibrium is approached with an oscillating trajectory.

We study the local stability of the endemic state by considering the sign of the trace and the determinant of the Jacobian \( J \) of the linearisation of system (3.7), namely

\[
\text{det}(J) = \frac{B}{2\rho R_b} \left( B + R_b(\rho - \alpha - \delta) - 2\rho \right) > 0,
\]

\[
\text{trace}(J) = \frac{1}{2\rho R_b} \left( 2\rho R_b(1 + \delta) - R_b^2(\rho - \alpha - \delta) - B(2\rho + R_b) \right) < 0,
\]

where \( B = \sqrt{R_b^2(\rho - \alpha - \delta)^2 + 4\rho \delta R_b} \).

Thus the endemic equilibrium is stable whenever it exists and hence system (3.7) exhibits a transcritical bifurcation.

If the discriminant of the characteristic equation of the Jacobian of the linearisation around the endemic state is negative, then the eigenvalues will be complex and there will be an oscillatory approach to the equilibrium. We look for the onset of this behaviour where the discriminant is zero. The discriminant is \( \Delta \), where

\[
\Delta = \frac{B \left( R_b^2(\rho - \alpha - \delta) - 2\rho R_b(\rho - \alpha + 1) + 4\rho^2(1 - \delta) \right)}{2\rho^2 R_b} + \frac{R_b^3(\rho - \alpha - \delta)^2 - 2\rho R_b^2 ((\rho - \alpha)^2 + (\rho - \alpha)(1 - \delta) - 2\delta)}{2\rho^2 R_b} + \frac{2\rho^2 R_b ((\rho - \alpha - \delta)^2 + (1 - \delta)^2) + 8\rho^2 \delta}{2\rho^2 R_b}.
\]

We find that there is a minimum value of \( \delta(R_b) \), denoted by \( \delta_{\text{min}} \), above which the discriminant, \( \Delta \), is negative. We can obtain an explicit form of \( f \) where \( \delta_{\text{min}} = f(R_b) \) but the algebra is very complicated and unenlightening. However, substituting \( \rho = 1, \alpha = 0.2 \), biologically reasonable numerical values [2], we can express \( \delta_{\text{min}} \) as a function of \( R_b \) and thus establish the criteria for complex roots. It turns out that, with these parameter values

\[
\delta_{\text{min}} = \frac{88R_b^3 - 418R_b^2 + 531R_b - 90 + R_b(R_b^2 - 89R_b + 100)\sqrt{R_b(20R_b - 9)}}{10(16R_b^2 - 5R_b - 25)(R_b^2 + 4)}.
\]

(3.8)
We also note that, as $\delta$ increases, the frequency of the oscillations increases (the imaginary part of the eigenvalues increases), while the magnitude of the damping decreases (the absolute value of the real part of the eigenvalues decreases) so that the oscillation becomes more rapid and more transient. We do not have a biological explanation of this observation; further work is evidently required to consider the implications of this for the two species model.

If we consider $\delta$ to be small, we can express the endemic disease state in terms of a perturbation, $\delta$, of the endemic disease state with no deaths from disease. We obtain

$$y^* = \left(1 - \frac{a}{\rho} - \frac{1}{R_0}\right) \left(1 - \frac{\delta}{\rho - a} + \frac{\rho \delta^2}{R_0(\rho - a)^3} \cdots \right).$$

In effect, introducing deaths due to disease to an SIS model creates a removed class and thus the model properly becomes a Susceptible-Infective-Removed (SIR) model. SIR models are characterised by an oscillatory approach to the endemic equilibrium state.

### 3.5 Immigration

We have considered our systems to be closed up to this point. We now relax this condition and allow immigration of animals into the system. We first consider immigration of susceptibles only and then of a mix of susceptibles and infectives.

#### 3.5.1 Immigration of susceptibles

We can amend the model of system (3.2) to take account of an inflow of $m$, (scaled with the same nondimensionalisation scheme as system (3.2)) susceptibles in unit time as follows;

$$\frac{dx}{dt} = \rho(x + y)(1 - x - y) - ax + (1 - \alpha)y - R_0xy + m, \tag{3.9}$$

$$\frac{dy}{dt} = -y + R_0xy,$$

$x(0) > 0$ $y(0) > 0$.

Lemma 3.5.1 With the immigration of susceptibles into the model described by system (3.2) there is still a transcritical bifurcation, but with a smaller parameter, $\hat{R}_0$, than that in the original model, where $\hat{R}_0$ is defined in equation (3.10). For $\sqrt{(\rho - \alpha)^2 + 4pm} < 1$, the rate of increase in the size of the endemic infected population is greater than the rate of increase in immigration, i.e. $\frac{dn}{dm} > 1$, while the size of the endemic susceptible population is not dependent on the rate of immigration.

Once more we assume the introduction of an infected animal to the infection free equilibrium. We can solve the differential equation for $n(t) = x(t) + y(t)$ to demonstrate that, given the positivity of $x, y$, the problem is well-posed.
Eradication and IFE

There is no eradication equilibrium for any value of \( m_s \), as might be expected with an inflow of animals. There is an IFE with

\[
x = \frac{\rho - \alpha + \sqrt{(\rho - \alpha)^2 + 4 \rho m_s}}{2 \rho}.
\]

The eigenvalues of the Jacobian of the linearisation of system (3.9) around this equilibrium are

\[
\lambda_1 = -\sqrt{(\rho - \alpha)^2 + 4 \rho m_s}
\]

\[
\lambda_2 = \frac{1}{2 \rho} \left( -2\rho + R_b (\rho - \alpha) + \sqrt{(\rho - \alpha)^2 + 4 \rho m_s} \right).
\]

The IFE is locally stable provided that \( R_b < \tilde{R}_b \) where

\[
\tilde{R}_b = \frac{2 \rho}{\rho - \alpha + \sqrt{(\rho - \alpha)^2 + 4 \rho m_s}},
\]

(3.10)

where \( R_b \) is the basic reproductive ratio for the closed system.

The effect of the immigration is thus to reduce the size of the basic reproductive ratio by comparison with that required for the closed system by a factor of

\[
\frac{2}{1 + \sqrt{1 + \frac{4 \rho m_s}{(\rho - \alpha)^2}}}.
\]

This illustrates the need to deal with immigrating susceptible animals in order to control an epidemic, since the immigration in effect stabilises the endemic state.

Endemic equilibrium

The endemic equilibrium is at

\[
x^* = \frac{1}{R_b}, \quad y^* = \frac{R_b (\rho - \alpha) - 2 \rho + R_b \sqrt{(\rho - \alpha)^2 + 4 \rho m_s}}{2 \rho R_b}.
\]

We see immediately that \( y^* \) is increasing in \( m_s \), while \( x^* \) takes the same value as in the closed system. In fact

\[
\frac{dy^*}{dm_s} = \frac{1}{\sqrt{(\rho - \alpha)^2 + 4 \rho m_s}},
\]

so that for \( \sqrt{(\rho - \alpha)^2 + 4 \rho m_s} < 1 \), \( \frac{dy^*}{dm_s} > 1 \) the endemic infected population size increases faster than the rate at which immigration increases. Once more we find that the condition \( y^* > 0 \) is equivalent to \( R_b > \tilde{R}_b \). Finally, applying the Routh-Hurwitz conditions to the Jacobian, \( J \), of the linearisation around
the endemic equilibrium we have

\[
\text{trace}(J) = \frac{1}{2\rho} \left( (R_b(\rho - \alpha) - 2\rho) - (2\rho + R_b)\sqrt{(\rho - \alpha)^2 + 4\rho m_s} \right) < 0 \quad \forall \quad R_b,
\]

\[
\text{det}(J) = \frac{1}{2\rho} \sqrt{(\rho - \alpha)^2 + 4\rho m_s} \left( R_b(\rho - \alpha) - 2\rho, + \sqrt{(\rho - \alpha)^2 + 4\rho m_s} \right) > 0 \quad \forall \quad R_b > \bar{R}_0.
\]

Thus the endemic equilibrium, if it exists, is linearly stable. □

3.5.2 Immigration of both susceptibles and infectives

We modify the model described by system (3.9) as follows, with \( m_s \) susceptibles and \( m_i \) infectives immigrating in unit time (both scaled with the same non-dimensionalisation scheme as system (3.2));

\[
\begin{align*}
\frac{dx}{dt} &= \rho(x + y)(1 - x - y) - ax + (1 - \alpha)y - R_bxy + m_s, \\
\frac{dy}{dt} &= -y + R_bxy + m_i, \quad x(0) > 0, y(0) > 0.
\end{align*}
\]

(3.11)

Lemma 3.5.2 System (3.11) has a single equilibrium, the endemic disease state.

Conjecture 3.5.3 The equilibrium of (3.11) exists for all \( m_i > 0 \) and is locally stable.

The endemic equilibrium

There is an equilibrium for system (3.11), which is

\[
y^* = \theta, \quad x^* = \frac{\theta - m_i}{R_b}\theta,
\]

where \( \theta \) is a root of \( f(y) = 0 \) with,

\[
\begin{align*}
f(y) &= \rho R_b^2 y^4 + R_b(2\rho + R_b(\rho - \alpha))y^3 \\
&\quad - (R_b^2(m_s + m_i) + R_b(\rho - \alpha) - \rho + 2\rho m_i R_b)y^2 \quad (3.12) \\
&\quad + (R_b(\rho - \alpha) - 2\rho)m_i y + \rho m_i^2.
\end{align*}
\]

We evidently need to demonstrate the uniqueness and positivity of both \( x \) and \( y \) components of the equilibrium. Although solving this quartic equation \( f(y) = 0 \) is analytically possible in principle, we are able to find an explicit expression for \( y^* \) more straightforwardly in the following way.

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We can compute the total population at the equilibrium (by adding the two equations in (3.11)) to obtain

\[ z^* + y^* = \frac{\rho - \alpha + \sqrt{(\rho - \alpha)^2 + 4\rho (m_s + m_i)}}{2\rho}. \]

Setting this quantity equal to \( \theta + \frac{\theta - m_i}{R_b} \) and solving for \( \theta \) we obtain

\[ y^* = \frac{1}{4\rho R_b} \left( R_b (\rho - \alpha + G_1) - 2\rho + \sqrt{G_2} \right), \]

\[ G_1 = \sqrt{(\rho - \alpha)^2 + 4\rho (m_s + m_i)}, \]

\[ G_2 = R_b^2 \left( 2(\rho - \alpha)^2 + 4\rho (m_s + m_i) \right) - 4R_b (\rho - \alpha + 4\rho m_i) \]

\[ + 4\rho^2 + 2R_b G_1 (R_b (\rho - \alpha) - 2\rho). \]

**Proposition 3.5.4** The equation \( f(y) = 0 \), where \( f(y) \) is defined in (3.12), has a single real positive root \( \theta \) such that \( \theta > m_i \).

We prove the proposition as follows. We introduce \( z = y - m_i \) and define \( F(z) = f(z + m_i) \). Thus we need to show that there is a unique real positive root of \( F(z) \). Now \( \lim_{z \to +\infty} F(z) = +\infty \) while

\[ F(0) = m_i^2 R_b^2 \left( \rho m_i^2 - m_i (\rho - \alpha) - (m_i + m_s) \right). \]

Solving \( F(0) \) as a quadratic in \( m_i \), we find that \( F(0) < 0 \) for

\[ m_i < \frac{1}{2\rho} \left( \rho - \alpha + 1 + \sqrt{(\rho - \alpha + 1)^2 + 4m_s \rho} \right), \]

an unfeasibly large upper bound in the context of the total equilibrium population (with no immigration) being \( 1 - \frac{\alpha}{\rho} \). Thus, by continuity we must have either one or three real positive roots.

Differentiating with respect to \( z \) we have

\[ F'(0) = (4\rho m_i^4 + 3\alpha m_i^2 + 2\rho m_i^2) R_b^2 + \alpha m_i R_b \]

\[ - \left( (3\rho m_i^2 + 2m_s^2 + 2m_s m_i) R_b^2 + \rho m_i R_b \right). \]

Thus, since \( \rho > \alpha \), a sufficient condition for \( F'(0) < 0 \) is that

\[ 2\rho (2m_i + 1) + 3\alpha < 3\rho + 2 + \frac{m_s}{m_i}. \]

We have \( \rho >> \alpha, \rho \sim O(1) \) and if we consider the reasonable case where \( m_s \approx m_i \), then \( F'(0) < 0 \) for \( m_i < 1.25 \), an unrealistically large value. We thus conclude that \( F'(0) < 0 \). There are therefore two possible cases: (i) \( F(z) = 0 \) has a single positive root, with one minimum at positive \( z \), or (ii) \( F(z) = 0 \) has two local minima and one local maximum at positive \( z \) and either one positive root and two complex roots, two positive roots (one repeated) or three positive real roots. To distinguish between them we look at the number of positive roots for the cubic \( F'(z) = 0 \). In the first case \( F'(z) = 0 \) would have a unique positive root, in the second case more than one positive root.
We have already shown that $F'(0) < 0$. Since $F''(0) = -(R_b^2(m_s + m_i) + R_b(\rho - \alpha) + 2p m_i R_b) < 0$ it is clear that the maximum of $F(z)$ must be at negative $z$ and so $F'(z)$ must have a unique positive real root. We have thus proved that there is a unique positive equilibrium.

The expressions for the determinant and the trace of the Jacobian of the linearisation of system (3.11) about the endemic equilibrium are algebraically intractable. Numerical simulation with a wide range of parameters suggests that, for all $m_i > 0$ and for all $R_b > 0$ the endemic equilibrium exists and is asymptotically stable.

### 3.6 Continuous constant yield culling

In continuous constant yield culling a fixed number of animals, $A$, is culled in unit time. This might correspond in the physical world to a strategy of trapping a fixed number of animals each day or each week.

The culling process we envisage necessarily cannot distinguish between animals in different disease classes. Since we have assumed that the population is spatially homogeneous and randomly mixed, if one animal is culled we would anticipate that the probability that it was from the infectious class would be $\frac{x}{x + y}$ and from the susceptible class $\frac{y}{x + y}$. With the introduction of a total cull of a fixed number $A$ animals per unit time (scaled using the non-dimensionalisation scheme of system (3.2) - all of the culling parameters in our non-dimensionalised systems are scaled appropriately) we modify system (3.2) to give the following model, provided that at least $A$ animals are present.

\[
\frac{dx}{dt} = \rho(x + y)(1 - (x + y)) - \alpha x + (1 - \alpha)y - R_bxy - q_2\frac{Ax}{x + y},
\]

\[
\frac{dy}{dt} = -y + R_bxy - q_y\frac{Ay}{x + y},
\]

where

\[
q_x := \begin{cases} 
1 & : x > 0 \\
0 & : \text{otherwise} 
\end{cases}
\]

and

\[
q_y := \begin{cases} 
1 & : y > 0 \\
0 & : \text{otherwise,} 
\end{cases}
\]

to ensure positivity and to remove any potential singularity at the origin. Where we do not include $q$ in the subsequent analysis in this chapter we assume $q = 1$, i.e. we maintain the non-negativity of the state variables.

#### 3.6.1 Impact on the total population

**Lemma 3.6.1** If $A \geq A_{\text{crit}} = \frac{(\rho - \alpha)^2}{4\rho}$ then the population reaches zero in finite time. As $A$ decreases through $A_{\text{crit}}$ a pair of equilibria appears, one
stable and the other unstable. System (3.13) exhibits a saddle node bifurcation with parameter $\frac{(\rho - \alpha)^2}{4\rho}$.

Remark 3.6.2 The normal form of a saddle-node bifurcation is $\frac{dx}{dt} = \mu + x^3$, where $x$ is the state variable and $\mu$ is the bifurcation parameter. If $\mu < 0$ there are two fixed points, a stable fixed point at $-\sqrt{-\mu}$ and an unstable one at $+\sqrt{-\mu}$, if $\mu = 0$ (the bifurcation point) there a unique fixed point. If $\mu > 0$ there are no fixed points.

Remark 3.6.3 We note that, provided that $\rho > \alpha$, $A_{\text{crit}}$ is increasing in $\rho$ and decreasing in $\alpha$ as we should expect from biological considerations.

This behaviour for the system is shown in Figure 3.3. With $x + y = m$ we have

\[
\frac{dm}{dt} = \rho m(1 - m) - \alpha m - Aq = \phi(m),
\]

\[m(0) = m_0, \quad q = \begin{cases} 1 & : \ m > 0 \\ 0 & : \ otherwise. \end{cases} \]

Setting the right hand side of equation (3.14) equal to zero we have equilibria at

\[m_1 = \frac{1}{2} \left( 1 - \frac{\alpha}{\rho} \right) + \frac{1}{2\rho} \sqrt{(\rho - \alpha)^2 - 4\rho A}, \]

\[m_2 = \frac{1}{2} \left( 1 - \frac{\alpha}{\rho} \right) - \frac{1}{2\rho} \sqrt{(\rho - \alpha)^2 - 4\rho A} \]

provided that

\[A \leq A_{\text{crit}} = \frac{(\rho - \alpha)^2}{4\rho} \quad \text{and} \quad \frac{\rho}{\alpha} > 1. \]

Figure 3.3: Bifurcation diagram for system (3.13)
If \( A \) exceeds this critical level the total population crashes (reaches zero in finite time).

If \( A \leq A_{\text{crit}} \) then

\[
\phi'(m_1) = -\sqrt{(\rho - \alpha)^2 - 4\rho A} < 0, \quad \phi'(m_2) = \sqrt{(\rho - \alpha)^2 - 4\rho A} > 0
\]

so that \( m^* = m_1 \) is locally stable while \( m_2 \) is unstable.

**Proposition 3.6.4** If \( A \leq A_{\text{crit}} \), then

- if \( m(0) > m_2 \) then \( \lim_{t \to \infty} m(t) = m_1 \)
- if \( m(0) < m_2 \) then \( m(t) \) reaches zero in finite time

If we solve equation (3.14) we obtain, for \( A < A_{\text{crit}} \)

\[
m(t) = \frac{K}{2} + \frac{H}{2r} \tanh \left( \frac{Ht}{2K} - \tanh^{-1} \left( \frac{K - 2m_0}{r} \right) \right),
\]

where \( r = \rho - \alpha, \quad K = 1 - \frac{\alpha}{\rho} \) and \( H = \sqrt{rK(rK - 4A)} \).

As \( A \) is increased the size of the stable equilibrium population decreases until, for \( A = A_{\text{crit}} \)

\[
m_1 = m_2 = \frac{\rho - \alpha}{2\rho}.
\]

The minimum equilibrium population under a constant yield culling regime is half that of the population without culling. If \( A > A_{\text{crit}} \) there is no equilibrium and the population reaches zero in finite time.

For \( A > A_{\text{crit}} \) the solution of (3.14) is

\[
m(t) = \frac{K}{2} - \frac{\hat{H}}{2r} \tan \left( \frac{\hat{H}t}{2K} - \tan^{-1} \left( \frac{K - 2m_0}{r} \right) \right),
\]

We can thus find the time the population takes to crash, \( T \), as a function of \( A \)

\[
T(A) = \frac{2K}{\hat{H}} \left( \tan^{-1} \frac{r(K - 2m_0)}{\hat{H}} + \tan^{-1} \frac{rK}{\hat{H}} \right),
\]

where \( \hat{H} = \sqrt{rK(4A - rK)} \). The time to a population crash is decreasing in \( A \) for \( A > A_{\text{crit}} \).

### 3.6.2 Impact on individual disease classes

When culling is applied to a population of both susceptible and infective classes we can find constraints on the culling parameter such that the infective class only is eliminated, in contrast to the eradication of the entire population described in Section 3.6.1, provided that the basic reproductive ratio is below a given threshold.
Theorem 3.6.5 There are two physically feasible equilibria of system (3.13), the infection free equilibrium (IFE) and the endemic disease state, provided that \( A \leq A_{\text{crit}} \) as defined in equation (3.15) and \( \frac{\rho}{\alpha} > 1 \).

The criteria for existence and stability of these equilibria are the same as for equation (3.2). If \( R_b < \frac{\rho(\alpha-\rho+2)}{\rho-\alpha} \) the endemic equilibrium disappears if \( A > A^* \), where \( A^* := \frac{(\rho(\alpha-\rho+1))R_b(\rho-\alpha) - \rho}{(R_b+\rho)^2} \), so that for \( A^* \leq A < A_{\text{crit}} \), continuous fixed yield culling eradicates the disease.

If \( R_b > \frac{\rho(\alpha-\rho+2)}{\rho-\alpha} \) it is impossible to eliminate the endemic disease state without eradicating the total population.

Remark 3.6.6 Essentially, culling strategies designed to eliminate the infective class rather than eradicating the entire population are focused on reducing the basic reproductive ratio for the system below unity by increasing the death rate of both infectives and susceptibles. The population size resulting from this rate of culling is thus the minimum size below which no endemic disease is possible.

Remark 3.6.7 \( A^* \) is increasing in \( R_b \) for \( R_b < \rho \alpha \) in other words, as we would expect, it becomes more difficult to eradicate the infective population as the disease becomes more virulent. \( A^* \) is increasing in \( \rho \) and decreasing in \( \alpha \).

Setting the right hand sides of (3.13) equal to zero we find the following equilibria, provided that, in all cases, \( \rho > \alpha \).

Infection free equilibrium

The infection free equilibria of system (3.13) are

\[
\begin{align*}
y &= 0, \quad x_1 = \frac{1}{2}(1 - \frac{\alpha}{\rho}) + \frac{1}{2\rho}\sqrt{\frac{1}{\rho} - \frac{2}{\rho} \gamma - 4\rho A}, \\
y &= 0, \quad x_2 = \frac{1}{2}(1 - \frac{\alpha}{\rho}) - \frac{1}{2\rho}\sqrt{\frac{1}{\rho} - \frac{2}{\rho} \gamma - 4\rho A}.
\end{align*}
\]

provided that \( A \leq A_{\text{crit}} \) (defined in equation (3.15)). Linearising around this equilibrium we find that the eigenvalues of the Jacobian matrix are

* at \( (x_1, 0) \)

\[
\lambda_{1,1} = -1 + \frac{1}{2\rho}\left((R_b - \rho)(\rho - \alpha) + (R_b + \rho)\sqrt{(\rho - \alpha)^2 - 4\rho A}\right), \\
\lambda_{1,2} = -\sqrt{\frac{1}{\rho} - \frac{2}{\rho} \gamma - 4\rho A} < 0.
\]

We see that \( \lambda_{1,1} \) is monotone decreasing in \( A \). The condition that \( \lambda_{1,1} < 0 \) and thus that this equilibrium is locally stable, provided that \( A < A_{\text{crit}} \) is

\[
A > A^* = \frac{(\rho - \alpha + 1)(R_b(\rho - \alpha) - \rho)}{(R_b + \rho)^2}
\]

If \( 0 \leq A < A^* \) this equilibrium is a saddle. If \( A^* \leq A < A_{\text{crit}} \) it is a stable node.

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\[ \lambda_{2,1} = -1 + \frac{1}{2\rho} \left( (R_b - \rho)(\rho - \alpha) - (R_b + \rho)\sqrt{(\rho - \alpha)^2 - 4\rho} \right), \]
\[ \lambda_{2,2} = -\lambda_{1,2} > 0 \]

Since \( \lambda_{2,2} > 0 \) this equilibrium is always unstable.

Endemic equilibrium

There are two candidates for the endemic equilibrium values for the state variables, for \( A \leq A_{\text{crit}} \), we denote them \((x_1^*, y_1^*)\) and \((x_2^*, y_2^*)\), where
\[ x_1^* = \frac{1}{R_b} \left( \frac{r}{2} + 1 - \frac{\sqrt{r^2 - 4\rho A}}{2} \right), \]
\[ y_1^* = \frac{2A(R_b + \rho) - r(r + 1) + (r + 1)\sqrt{r^2 - 4\rho A}}{R_b(r - \sqrt{r^2 - 4\rho A})}, \]
\[ x_2^* = \frac{1}{R_b} \left( \frac{r}{2} + 1 + \frac{\sqrt{r^2 - 4\rho A}}{2} \right), \]
\[ y_2^* = \frac{2A(R_b + \rho) - r(r + 1) - (r + 1)\sqrt{r^2 - 4\rho A}}{R_b(r + \sqrt{r^2 - 4\rho A})}. \]

Here we have written \( r = \rho - \alpha \) for simplicity. Then
\[ x_1^*(A) + y_1^*(A) = m_1(A) \quad \text{and} \quad x_2^*(A) + y_2^*(A) = m_2(A) \]

where \( m_1 \) and \( m_2 \) are the stable and unstable total population equilibria respectively. As \( A \to 0 \), \( m_2 \to 0 \), \( x_1^* \to \frac{1}{R_b}(\rho - \alpha + 1) \), \( y_1^* \to -\frac{1}{R_b}(\rho - \alpha + 1) \). We thus select the physically realistic equilibrium as \((x_1^*, y_1^*)\). In fact, \( y_2^* < 0 \) for \( A < A^* \) so that \((x_2^*, y_2^*)\) is always unfeasible. It is clear that \( y_1^* > 0 \) provided that
\[ \frac{1}{R_b} < \frac{1}{R_b} \left( \frac{(\rho - \alpha)}{2} + \frac{1}{2}\sqrt{(\rho - \alpha)^2 - 4\rho A} \right) < \frac{1}{R_b} \left( \frac{1 + \sqrt{1 + 4AR_b}}{2R_b} \right), \]
which is true if
\[ \frac{1}{R_b} < \frac{1}{R_b} \left( \frac{(\rho - \alpha)}{2} + \frac{1}{2}\sqrt{(\rho - \alpha)^2 - 4\rho A} \right) < \frac{1}{R_b} \left( \frac{1 + \sqrt{1 + 4AR_b}}{2R_b} \right) \]

which we find, after some algebra, requires that \( 0 < A < A^* \), where \( A^* \) is given in equation (3.18).

While \( x_1^* \) is increasing in \( A \), \( m_1 \) is decreasing in \( A \). As \( A \) is increased we see that \( x_1^* = m_1 \), and thus \( y_1^* = 0 \), when
\[ \frac{1}{R_b} \left( \frac{(\rho - \alpha)}{2} + \frac{1}{2}\sqrt{(\rho - \alpha)^2 - 4\rho A} \right) = \frac{1}{2} \left( \frac{1 - \alpha}{\rho} \right) + \frac{1}{2\rho} \sqrt{(\rho - \alpha)^2 - 4\rho A}. \]

This requires that \( A = A^* \). Once \( A > A^* \) the endemic equilibrium disappears.
In order for the endemic equilibrium to disappear as $A$ is increased but while $A < A_{crit}$ we must have $x_1^*(A_{crit}) \geq m_1(A_{crit})$ which holds if $R_b < \frac{\ell(2+\rho-a)}{\rho-a}$.

We find that, for $R_b > \frac{\ell(2+\rho-a)}{\rho-a}$, $A^*$ is the value of $A$ at which the value of the unstable endemic infective class $y^*_2$, negative for $A < A^*$, is equal to zero.

Hence, we must have $R_b < \frac{\ell(2+\rho-a)}{\rho-a}$ if the endemic infective population is to be eliminated as $A$ increases without a population crash.

The value of $x^*_1$ at which the endemic equilibrium vanishes we will call $x_0$ and is given by the following expression

$$x_0 = \frac{1}{2\rho} \left( \rho - \alpha + \sqrt{\left( -\alpha R_b - 2\rho + \rho\alpha + R_b\rho - \rho^2 \right)^2 \over (R_b + \rho)^2} \right).$$

We can simplify this, provided once more that $R_b < \frac{\ell(2+\rho-a)}{\rho-a}$, to obtain

$$x_0 = \frac{1 + \rho - \alpha}{R_b + \rho}.$$

The minimum total population size for an endemic equilibrium to exist in the model system we are using is $x_0$.

Now, for an endemic disease equilibrium to exist in the unculled system we must have $R_b > \frac{\ell(2+\rho-a)}{\rho-a}$, so that $R_b(\rho - \alpha) > \rho$, in other words $\frac{\ell(2+\rho-a)}{R_b + \rho} > \frac{1}{R_b}$. Thus $x_0 > \frac{1}{R_b}$, i.e. the size of the susceptible population at the infection free equilibrium created as a result of culling is greater than the size of the healthy (susceptible) population at the endemic equilibrium.

The two equilibria, $y^*_1$ and $y^*_2$, represent the upper and lower halves of a parabola respectively. When $A^* < A_{crit}$ the saddle/node bifurcation is at a negative value of $y$. When $A^* > A_{crit}$ it is at a positive value of $y$ and when $A^* = A_{crit}$ it is at $y = 0$. Thus if $R_b > \frac{\ell(2+\rho-a)}{\rho-a}$, it is impossible to eliminate the infected class by constant yield culling without eradicating the entire population, thus, the more virulent the disease the more difficult it will be to eliminate it by a culling strategy which does not envisage the eradication of the entire animal population.

Local stability

Linearising around the endemic equilibrium of system (3.13), once more assuming that $R_b < \frac{\ell(2+\rho-a)}{\rho-a}$, the trace of the Jacobian matrix is $T$, where

$$T = \frac{2A(3\rho + R_b) + (2r + 1)\sqrt{r^2 - 4\rho - r(2r + 1)}}{\sqrt{r^2 - 4\rho - r}},$$

where once more $r = \rho - \alpha$. We find that $T = 0$ for $A = A_T$, where

$$A_T = \frac{\left( 1 + 2(\rho - \alpha) \right) (R_b + \rho(\rho - \alpha) - \rho)}{(R_b + 3\rho)^2}.$$
and, by simulation, that $T$ is monotone increasing in $A$. The condition that $A_T > A^*$ is that $R_b < \frac{\rho(2+p-a)}{q-\alpha}$. In other words, provided that the endemic equilibrium exists, the trace of the Jacobian is negative.

The determinant of the Jacobian is $D$ where

$$D = \frac{2\sqrt{r^2 - 4\rho A} (-A\rho(3r + 2) + r^2(r + 1) - R_b Ar)}{(\sqrt{r^2 - 4\rho A - r})^2} + \frac{2(r^2 - 4\rho A)(r(r + 1) - A(R_b + \rho))}{(\sqrt{r^2 - 4\rho A - r})^2}.$$ 

We find that the determinant is zero when $A = A_{crit}$ and $A = A^*$, moreover $\frac{dD}{dA} = 0$ for $A = A_D$, where

$$A_D = \frac{(R_b(\rho - \alpha) + \rho(3\rho - 3\alpha + 2))(3R_b(\rho - \alpha) + \rho(\rho - \alpha - 2))}{16\rho(R_b + \rho)^2}.$$ 

By simulation we find that $D$ is monotone decreasing in $A$ for $A < A_D$ and is monotone increasing for $A_{crit} > A > A_D$. This behaviour of the determinant and the trace of the Jacobian are illustrated in Figure 3.4, the points $p = A_D$ and $q = A_T$. The equation for the whole population shows a saddle-node bifurcation with parameter $\frac{(\rho - \alpha)^2}{4p}$. The system of equation (3.13) has, in addition, a transcritical bifurcation with parameter $\frac{A}{A^*}$ provided that $R_b < \frac{\rho(2+p-a)}{q-\alpha}$. If $R_b > \frac{\rho(2+p-a)}{q-\alpha}$ there is no such bifurcation as $A$ is increased, prior to the population crash. We see this behaviour in Figure 3.5, where only the positive branch of the curve representing $y_1^*$ is shown.

3.6.3 Global stability

We have already established that, provided $A < A_{crit}$ and $m(0) > m_2$, the total population reaches the stable equilibrium $m_1$. This, together with the positivity of $x(t)$ and $y(t)$, ensures that $x(t)$ and $y(t)$ are bounded, $x(t) + y(t) \to m_1$ as $t \to \infty$. Thus there must either be a stable equilibrium or a limit cycle.
for the components of system (3.13). For sufficiently large $t$ we can therefore substitute $x = m_1 - y$ in the second equation of (3.13) to obtain
\[ \frac{dy}{dt} = -y + R_b y(m_1 - y) - \frac{Ay}{m_1}, \]
which solves to give
\[ y(t) = \frac{y_0 \theta e^\theta}{\theta + R_b m_1 y_0 (e^\theta - 1)}, \]
where $\theta = R_b m_1^2 - m_1 - A > 0$

As $t \to \infty$, $y(t) \to \frac{\theta}{R_b m_1}$, and after some algebra we find $\frac{\theta}{R_b m_1} = y^*_1$. Thus we can exclude a periodic solution and conclude that the equilibria are globally stable.

**Phase Portrait**

The phase portrait is extremely complicated. Figure (3.6) illustrates the four possible behaviours of equation 3.13 depending upon the interval into which $A$ falls, providing that $R_b < \frac{\rho(2+\rho-\alpha)}{\rho-\alpha}$.

The nullclines of system (3.13) are
\[ x^2 + y^2 + \frac{Ax}{\rho(x+y)} - \frac{x(\rho - \alpha)}{\rho} - \frac{\rho + 1 - \alpha}{\rho} + xy \left( \frac{R_b}{\rho} + 2 \right) = 0, \]
\[ R_b x - 1 - \frac{A}{x+y} = 0, \quad y = 0. \]
(We have $q = 1$, noting that the origin is not an equilibrium for system (3.13) with $A > 0$ and that we consider the first quadrant only.) The nullclines $R_b x - 1 - \frac{A}{x+y} = 0$, $y = 0$ are shown with a hatched line. When $A = 0$

As $A$ is increased from zero, the $x$-axis remains one of the $y = 0$ nullclines, while the other $y = 0$ nullcline becomes a hyperbola, descending from an asymptote at $x = \frac{1}{b}$ to intersect the $x$-axis at $\frac{A}{(1 + \sqrt{1 + 4AR_b})}$. As $A$ increases this intersection moves in the direction of positive $x$.

The $\dot{z} = 0$ nullcline exhibits more complicated behaviour. In the first quadrant, for $A$ small and positive a branch of this nullcline intersects the $y$-axis at $\frac{\rho - 1}{\rho}$ (this point is fixed for all $A$) and the $x$-axis at $x_1 = \frac{1}{\rho} (\rho - \alpha) + \frac{1}{2\rho} (\rho - \alpha)^2 - 4\rho A$. The intersection of this branch with the $y = 0$ nullcline, $R_b x - 1 - \frac{A}{x+y} = 0$ is at $x^*, y^*$ and with the $y = 0$ nullcline, $y = 0$ at $(x_1, 0)$.

As $A$ increases, the intersection of this branch with the $x$-axis moves in the direction of negative $x$. Eventually, at $A = A^*$ we see that the endemic equilibrium and the IFE coincide so that for $A > A^*$ the intersection is no longer in the first quadrant and the endemic equilibrium disappears.
There is a second branch of the \( \dot{x} = 0 \) nullcline which intersects the x-axis at \( x_2 = \frac{1}{2p} (\rho - \alpha) - \frac{1}{2p} \sqrt{(\rho - \alpha)^2 - 4\rho A} \). As \( A \) increases \( x_2 \) moves in the direction of positive \( x \). At some value \( A^* < A < A_{\text{crit}} \) the two branches of the \( \dot{x} = 0 \) nullcline merge and, as \( A \) increases beyond \( A^* \), separate once more into two different branches, such that \( x_1 \) is now the intersection of this second branch with the x-axis. At \( A = A_{\text{crit}} \) we see that \( x_1 \) and \( x_2 \) coincide at \( x = \frac{\rho}{2\alpha} \). Finally, for \( A > A_{\text{crit}} \) the \( \dot{x} = 0 \) nullcline does not intersect the x-axis in the first quadrant.

**An alternative fixed yield culling strategy**

By definition it must take an infinite time to reach equilibrium with total population \( m = x_0 \). An alternative strategy would be to reduce the population to \( x_0 \) as rapidly as practical and then maintain the population at that level. For \( m(t) > A > A_{\text{crit}} \), the time to reach a population of size \( x_0 \), starting at \( m_0 \) at \( t = 0 \) is \( \theta_{x_0} \), where

\[
\theta_{x_0} = \frac{2}{\sqrt{4\rho A - (\rho - \alpha)^2}} \left( \tan^{-1} \frac{2\rho m_0 - \rho + \alpha}{\sqrt{4\rho A - (\rho - \alpha)^2}} + \tan^{-1} \frac{(R_b - \rho)(\rho - \alpha) - 2\rho}{(R_b + \rho)\sqrt{4\rho A - (\rho - \alpha)^2}} \right)
\]

which is decreasing in \( A \). The total number of animals culled to reach a population size of \( x_0 \) is evidently \( A\theta_{x_0} \), which we find (by Maple and confirmed by numerical simulation) also to be decreasing in \( A \). We also have

\[
\lim_{A \to \infty} A\theta_{x_0} = m_0 - \frac{\rho + 1 - \alpha}{R_b + \rho} = m_0 - x_0,
\]

as would be expected.

Thus the higher the culling rate, the fewer the total number of animals required to be culled to reach the population size at which an endemic equilibrium is unsustainable.

### 3.7 Impulsive constant yield culling

In this strategy, at some times \( t = nT, n \in \mathbb{Z}^+ \), the population is reduced instantaneously by a fixed number of animals \( B \). This might correspond in reality to a very short hunting season or to an annual cull where a fixed number of animals is culled. We consider that culling takes place separated by time intervals of constant duration \( T \).

#### 3.7.1 The whole population

The model to describe impulse culling for the whole population is as follows

\[
\frac{dm}{dt} = rm \left( 1 - \frac{m}{K} \right) \quad \text{for} \quad t \in \{(nT, (n+1)T) \quad n \in \mathbb{Z}^+ \},
\]

\[
m(nT^+) = m(nT^-) - B, \quad n \in \mathbb{Z}^+,
\]

\[
m(nT^+) = m_n,
\]

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which we derive from equation (3.3) by putting \( r = \rho - \alpha \) and \( K = 1 - \frac{p}{\rho} \) as before, for convenience. The culling is at a fixed amount \( B \) and is done with a constant frequency \( \frac{1}{n} \). In all that follows we take \( r > 0 \). Throughout this chapter we assume implicitly that \( m(nT^+) = \max\{m(nT^-) - B, 0\} \) to ensure that \( m_n \geq 0 \) and that this applies \textit{mutatis mutandis} to each individual state variable.

System (3.20) has no equilibria as such. However, a limit cycle exists such that the population immediately following a given cull is the same as that immediately following the preceding cull. We find that there are two positive values for the size of this population, one corresponding to a stable limit cycle and the other to an unstable limit cycle. Henceforth for simplicity we will refer to these as the equilibria of system (3.20).

Figure 3.7 shows the effect of impulsive constant yield culling in the form of a cobweb diagram for different initial populations, showing that the smaller equilibrium is unstable, leading to a population crash and the larger is stable.

![Figure 3.7: Cobweb plots for the population of system (3.20)](image)

**Theorem 3.7.1** If \( B > B_{\text{crit}} \), where

\[
B_{\text{crit}} = \frac{K \left( e^{\frac{rT}{4}} - 1 \right)}{e^{\frac{rT}{4}} + 1},
\]

the solution of system (3.20) reaches zero in finite time. If \( B < B_{\text{crit}} \) a stable limit cycle exists. System (3.20) exhibits a saddle-node bifurcation, with bifurcation parameter \( \frac{K}{B} \tanh \frac{rT}{4} \). If \( m(t) \) is below the value of the unstable bifurcation parameter \( \frac{K}{B} \tanh \frac{rT}{4} \), if \( m(t) \) is below the value of the unstable bifurcation parameter \( \frac{K}{B} \tanh \frac{rT}{4} \).

Solving equation (3.20) for \( t \in (nT, (n + 1)T) \) we have

\[
m(t) = \frac{Km_n}{(K - m_n)e^{-r(t-nT)} + m_n} = g(m_n, t),
\]

where \( m_n = m(nT^+) \).
By finding the extremum of \( g(m_n, t) \) we can see that the maximum population growth in any period of time \( T \) occurs when

\[
m_n = \frac{K}{1 + e^{\frac{rT}{K}}},
\]

and that the maximum population growth by the end of the period is

\[
g_{\text{max}} = \frac{K \left( e^{\frac{rT}{K}} - 1 \right)}{e^{\frac{rT}{K}} + 1}, \quad (3.21)
\]

while the time taken for the population to increase from \( m_n \) to \( m_n + B \) is

\[
T_B = \frac{1}{r} \ln \left( \frac{(K - m_n)(B + m_n)}{m_n(K - B - m_n)} \right). \quad (3.22)
\]

Thus, if the length of time between culls of size \( B \) is less than \( T_B \) the population will go to zero in finite time.

The behaviour of the population in the limit cycle is illustrated in Figure 3.8. We have used parameter values \( r = 0.9, K = 0.9, m_0 = 1, A = 0.15, T = 1 \). The bifurcation diagram for the whole population for different values of \( T \) is shown in Figure 3.9, the upper part of the curve represents the stable equilibrium, the lower the unstable. The broken straight line shows the relationship of the population immediately prior to extinction with \( T \).

**A discrete mapping**

We now consider the discrete map \( \Phi : (0, K) \to (0, K) \) where

\[
\Phi(m) = \frac{Km}{(K - m)e^{-rT} + m - B}, \quad (3.23)
\]
so that

\[ m_{n+1} = \Phi(m_n), \]

which describes the culling process. The population grows through the interval of length \( T \), at the end of which it is reduced by a constant amount \( B \).

We want to study the conditions in which a limit cycle can exist with period \( T \), such that the size of population after each cull is constant. This is the fixed point of the mapping \( \Phi \) defined by equation (3.23).

We are only considering \( m(t) \in (0, K) \) for, were \( m(\tilde{t}) > K \) for some time \( \tilde{t} \) then, since \( dm/dt < 0 \) for \( m(t) > K \), the population evolution (to an equilibrium value of \( K \) without culling), together with the application of culling, will ensure that \( m(t) < K \) for some \( t > \tilde{t} \).

We will designate equilibrium values of the variables in impulsive culling with carets to distinguish them from the equivalent quantities in the continuous model. We will demonstrate later that in the limit as \( T \to 0 \) the quantities are the same.

Fixed points
We find the fixed points of the map \( \Phi \) by solving

\[ \hat{m}^* = \Phi(\hat{m}^*) \] (3.24)
Equation (3.24) has two positive solutions

\[
\begin{align*}
\dot{m}_1 &= \frac{1}{2} (K - B) + \frac{1}{2} \sqrt{(K + B)^2 - \frac{4KB}{1 - e^{-rT}}}, \\
\dot{m}_2 &= \frac{1}{2} (K - B) - \frac{1}{2} \sqrt{(K + B)^2 - \frac{4KB}{1 - e^{-rT}}},
\end{align*}
\]

(3.25)

provided that

\[
B < B_{\text{crit}} = \frac{K \left(\frac{e^{rT}}{e^{rT} - 1}\right)}{e^{rT} + 1}
\]

which is necessary in order that the quantity under the square root is non-negative. Significantly \(B_{\text{crit}} = g_{\text{max}}\), (defined in equation (3.21)) thereby ensuring that the population remains non-negative.

Stability

The criterion for local stability of these fixed points is

\[
|g'(\dot{m}_i, T)| < 1, \quad i = 1, 2.
\]

We thus compute the derivative of \(g\) and substitute the appropriate values for \(\dot{m}\). Denoting \(\frac{dg}{dm}(\dot{m}_1) = \psi_1(B)\) and \(\frac{dg}{dm}(\dot{m}_2) = \psi_2(B)\) we find

\[
\begin{align*}
\psi_1(B) &= \frac{4K^2e^{-rT}}{\left(e^{-rT}(K + B) - B + K + (1 - e^{-rT})\sqrt{(K + B)^2 - \frac{4KB}{1 - e^{-rT}}})\right)^2}, \\
\psi_2(B) &= \frac{4K^2e^{-rT}}{\left(e^{-rT}(K + B) - B + K - (1 - e^{-rT})\sqrt{(K + B)^2 - \frac{4KB}{1 - e^{-rT}}})\right)^2}.
\end{align*}
\]

We see that, if \(B < \frac{K \left(\frac{e^{rT}}{e^{rT} - 1}\right)}{e^{rT} + 1}\) then \(|\psi_1(B)| < |\psi_2(B)|\) and we find that,

for \(B = \frac{K \left(\frac{e^{rT}}{e^{rT} - 1}\right)}{e^{rT} + 1}\), \(\psi_1(B) = \psi_2(B) = 1\).

Now, if we consider \(\Psi_1\) and \(\Psi_2\) as functions of \(B\) and differentiate w.r.t. \(B\), we obtain

\[
\psi_1'(B) = \frac{-8K^2e^{-rT}}{\left(e^{-rT}(K + B) - B + K + (1 - e^{-rT})\sqrt{(K + B)^2 - \frac{4KB}{1 - e^{-rT}}})\right)^3}
\]

\[
\times \left(\left(e^{-rT} - 1 + \frac{(1 - e^{-rT})\left(K + B - \frac{2K}{1 - e^{-rT}}\right)}{\sqrt{(K + B)^2 - \frac{4KB}{1 - e^{-rT}}}}\right)\right)^3,
\]

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\[
\psi_2'(B) = \frac{-8K^2e^{-rT}}{(e^{-rT}(K + B) - B - K - (1 - e^{-rT})\sqrt{(K + B)^2 - \frac{4KB}{1 - e^{-rT}}})^3} \times \left( e^{-rT} - 1 - \frac{(1 - e^{-rT})(K + B) - \frac{2K}{1 - e^{-rT}}}{\sqrt{(K + B)^2 - \frac{4KB}{1 - e^{-rT}}}} \right).
\]

After straightforward algebra we find that \( \psi'_1(B) > 0, \psi'_2(B) < 0 \) so that \( \psi_1(B) \) is increasing in \( B \) and thus, for

\[
B < \frac{K(e^{\frac{rT}{e}} - 1)}{e^{\frac{rT}{e}} + 1}, \quad \psi_1(B) < 1.
\]

By contrast, \( \psi_2(B) \) is decreasing in \( B \) and thus, for

\[
B < \frac{K(e^{\frac{rT}{e}} - 1)}{e^{\frac{rT}{e}} + 1}, \quad \psi_2(B) > 1.
\]

We can thus conclude that \( g'(_{\tilde{m}_1}) < 1 \) while \( g'(_{\tilde{m}_2}) > 1 \) for all \( B \) so that \( \tilde{m}_1 \) is stable while \( \tilde{m}_2 \) is unstable.

Equation (3.24) thus describes a saddle-node bifurcation with parameter \( \frac{B}{e^{-rT}} \tan \frac{T}{r} \). The greater \( T \), as we would expect, the larger the size of the cull can be before the population crashes.

As the value of \( B \) is increased, the smallest size of equilibrium population

\[
is \frac{K}{2} \left( 1 - \frac{1}{2} \tan \frac{T}{r} \right)
\]

for \( B = B_{crit} \). In order to allow the population sufficient time to recover a loss of \( B \) we must have \( T > T_B \) as defined in equation (3.22). Rearranging this inequality, the culling rate such that recovery takes place in an interval of length \( T \) is \( \tilde{B} \), where

\[
\tilde{B} = \frac{\tilde{m}^*(1 - e^{-rT})(K - \tilde{m}^*)}{(K - \tilde{m}^*)e^{-rT} + \tilde{m}^*},
\]

and we find \( \tilde{B} < B_{crit} \) for all \( T \).

If the population falls below \( \tilde{m}_2^* \) then, in finite time, \( m(t) \to 0 \). The cobweb diagram, together with the observation that, without culling, \( m(t) \to K \), demonstrates that the equilibrium \( m_1 \) is globally stable.

The equilibrium itself is a limit cycle of duration \( T \) which has the saw tooth shape as shown in Figure 3.8, which will be reached for any starting value of \( m(0) > \frac{K}{e^{\frac{rT}{e}} + 1} \). Now, if \( B \) were suitably chosen such that in finite time the system would be arbitrarily close to the limit cycle there would be no a priori reason to expect that the two disease classes would themselves reach an equilibrium at this same time. However, if we consider that the limit cycle for the
population is reached for $t$ very large, then it is reasonable to consider that, at this time, the two disease classes either both have reached a limit cycle or the infected class has reached zero.

### 3.7.2 The infected class

We can describe the effect of impulsive fixed yield culling on the two disease classes as follows

$$\frac{dx}{dt} = \rho(x + y)(1 - (x + y)) - \alpha x + (1 - \alpha)y - R_bxy,$$

$$\frac{dy}{dt} = -y + R_bxy,$$

for $t \in \{(nT, (n + 1)T) \in \mathbb{Z}^+\}$ in both cases, and

$$x(nT^+) = x(nT^-) - \frac{Bx(nT^-)}{x(nT^-) + y(nT^-)} = x_n,$$

$$y(nT^+) = y(nT^-) - \frac{By(nT^-)}{x(nT^-) + y(nT^-)} = y_n$$

Once again we have assumed that the cull consists of the removal of a fixed number of animals, having no regard to their disease status and thus that the probability of a given culled animal belonging to a given class is the proportion of that class to the total population. We simplify the computations in the rest of the section with the substitutions

$$r = \rho - \alpha, \quad K = 1 - \frac{\alpha}{\rho}$$

as we have previously used. In the analysis that follows we continue to assume that $\rho > \alpha$.

**Theorem 3.7.2** System (3.26) exhibits a stable limit cycle if $0 < B < B^*$, where

$$B^* = \frac{K \left(1 + e^{rT} - \left( e^{rT(K-1)} + e^{rT(1+K)} \right) \right)}{e^{rT} - 1}$$

with the size of the infected class smaller and the size of the susceptible class larger than the endemic equilibrium were there no culling.

If $R_b < \frac{d(\rho-\alpha+2)}{\rho-\alpha}$ then if $B^* < B < B_{\text{crit}}$ (defined in Theorem (3.7.1)) the infected class is eradicated and a stable infection free limit cycle results. If $R_b > \frac{d(\rho-\alpha+2)}{\rho-\alpha}$ then it is not possible to eliminate the infected class without eradicating the entire population.

If $B > B_{\text{crit}}$ then the entire population is eradicated in finite time.

Figure 3.10 shows the evolution of the state variables under this approach, with the parameter set $\{r = 0.9, K = 0.9, m_0 = 1, A = 0.15, T = 1, R_b = 2.17\}$. We have already solved equation (3.20) for $t \in \{(nT, (n + 1)T), n \in \mathbb{Z}^+\}$ to give

$$m(t) = \frac{Km_n}{(K - m_n)e^{-r(t-nT)} + m_n},$$
Figure 3.10: Evolution of the state variables of system (3.26)

substituting

\[ x(t) = m(t) - y(t) \quad \text{and} \quad m_n = x_n + y_n \]

the second equation of system (3.26) becomes

\[ \frac{dy}{dt} = -y + R_b y \left( \frac{K(x_n + y_n)}{(K - (x_n + y_n))e^{-r(t-nT)} + x_n + y_n} - y \right) \quad (3.27) \]

for \( t \in \{nT, (n + 1)T \} \ n \in \mathbb{Z}^+ \). We solve equation (3.27) on \( t \in \{nT, (n + 1)T \} \ n \in \mathbb{Z}^+ \) by making the substitution \( u = \frac{1}{y} \), and defining

\[ h(t) = \frac{KR_b(x_n + y_n)}{(K - (x_n + y_n))e^{-r(t-nT)} + x_n + y_n} - 1. \]

Then equation (3.27) is transformed into

\[ \frac{du}{dt} = R_b - uh(t). \]

This differential equation can be solved straightforwardly, using an integrating factor of \( e^{\int h(t)dt} \) to give

\[ u(t) = \frac{R_b \int_0^t e^{\int_0^s h(s)ds} ds + u(0)}{e^{\int_0^t h(s)ds}}. \]

Using the result that

\[ \int h(t)dt = \frac{R_b K}{r} \ln \left( (x_n + y_n)(e^{r(t-nT)} - 1) + K \right) - t, \]

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we have the solution for \( y(t) \) where \( t \in \{(nT, (n + 1)T) \quad n \in \mathbb{Z}^+\} \) as

\[
y(t) = \frac{y_n \left(1 + \left(\frac{x_n + y_n}{K}\right)(e^{(t-nT)} - 1)\right) R_b K}{y_n R_b \int_{nT}^{t} \left(1 + \left(\frac{x_n + y_n}{K}\right)(e^{(\tau-nT)} - 1)\right) \frac{R_b K}{r} e^{-(\tau-nT)} d\tau + 1}. \tag{3.28}
\]

Now, we see from system (3.26) that

\[
y_{n+1} = y((n + 1)T-) - \frac{By((n + 1)T-)}{x((n + 1)T+) + y((n + 1)T-)} = y((n + 1)T+)
\]

**Discrete mapping**

We can write the effect of the mapping \( \Phi \) described in equation (3.23) on \( y \) as the recurrence relation

\[
y_{n+1} = \frac{y_n \left(1 + \left(\frac{x_n + y_n}{K}\right)(e^{rT} - 1)\right) e^{-T} \left(1 - \frac{B}{x((n + 1)T+) + y((n + 1)T+) + B}\right)}{y_n R_b \int_{nT}^{(n+1)T} \left(1 + \left(\frac{x_n + y_n}{K}\right)(e^{(\tau-nT)} - 1)\right) \frac{R_b K}{r} e^{-(\tau-nT)} d\tau + 1}.
\]

For sufficiently large \( n \) either the population reaches a limit cycle or it crashes. On the assumption that the limit cycle is reached we can substitute

\[
\hat{m}^* = x((n + 1)T+) + y((n + 1)T+)
\]

and

\[
\theta = r - nT
\]

and simplify to obtain

\[
y_{n+1} = \frac{y_n \left(1 + \frac{\hat{m}^*}{K}(e^{rT} - 1)\right) e^{-T} \left(1 - \frac{B}{\hat{m}^* + B}\right)}{y_n R_b \int_{0}^{T} \left(1 + \frac{\hat{m}^*}{K}(e^{\theta} - 1)\right) \frac{R_b K}{r} e^{-\theta} d\theta + 1}. \tag{3.29}
\]

**Equilibria**

If we now further simplify the expression on the right hand side of equation (3.29) by writing

\[
\xi = \left(1 + \frac{\hat{m}^*}{K}(e^{rT} - 1)\right) e^{-T} e^{-T}, \quad \eta = 1 - \frac{B}{\hat{m}^* + B};
\]

\[
\zeta = R_b \int_{0}^{T} \left(1 + \frac{\hat{m}^*}{K}(e^{\theta} - 1)\right) \frac{R_b K}{r} e^{-\theta} d\theta,
\]

then the effect on the infected class of the application of the mapping \( \Phi \) is

\[
y_{n+1} = \frac{y_n \xi \eta}{\zeta y_n + 1}.
\]
This map has a fixed point \( y^* = \frac{\xi \eta - 1}{\xi} \), so that, for the equilibrium value of \( y(t) \) to be positive we need \( \xi \eta > 1 \). If \( \xi \eta < 1 \) then \( y_n \to 0 \) in finite time as \( n \) increases.

The condition for the elimination of the infective class, \( \xi \eta < 1 \), can be written in terms of the original quantities as

\[
\left( 1 + \frac{\hat{m}^* (e^{rT} - 1)}{K} \right) e^{-rT} \left( 1 - \frac{B}{\hat{m}^*} \right) < 1.
\]

(3.30)

If we now substitute \( \hat{m}^* = \hat{m}_1 \), where \( \hat{m}_1 \) is defined in equation (3.25), after more algebra, we find the value of \( B \) which solves inequality (3.30), which we term \( B^* \):

\[
B^* = \frac{K(1 + e^{rT}) - \left( K e^{rT(R_b K - 1)} + K e^{e^{rT(1+\gamma)}} \right)}{e^{rT} - 1}.
\]

(3.31)

\( B > B^* \) is thus the criterion for the elimination of the infective population.

3.7.3 Stability of the limit cycle

**Conjecture 3.7.3** The solution of system (3.26) is a limit cycle with no infectives, provided that \( B^* < B < B_{\text{crit}} \), where \( B_{\text{crit}} \) is defined in Theorem (3.7.1). This limit cycle is locally stable.

With the elimination of the infected class we have a limit cycle \( \hat{x}_T(t) \) of period \( T \) of where

\[
\hat{x}_T(t) = \begin{cases} 
\frac{K}{(\hat{x}^* - 1)} e^{-r(t-nT)} + 1 & : t \in (nT,(n+1)T), n \in \mathbb{Z}^+ \\
\hat{x}^* & : t = nT
\end{cases}
\]

with

\[
\hat{x}^* = \frac{1}{2} (K - B) + \frac{1}{2} \sqrt{(K + B)^2 - 4KB}.
\]

If we linearise system (3.26) around this limit cycle with the substitutions

\[
x = \hat{x} + \hat{x}_T(t), \quad y = \hat{y}
\]

and consider the infected class only then we have \( \frac{d\hat{y}}{dt} = \hat{y}(R_b \hat{x}_T(t) - 1) \) so that

\[
\hat{y}(t) = \hat{y}_0 e^{\int_0^t (R_b \hat{x}_T(s) - 1) ds}.
\]

If

\[
\int_0^T (R_b \hat{x}_T(s) - 1) ds < 0
\]

then we would expect that \( \hat{y} \to 0 \) as \( t \to \infty \). This condition can be written as

\[
\frac{1}{T} \int_0^T \hat{x}_T(s) ds < \frac{1}{R_b}.
\]

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Consequently we require that the culling yield $B$ be sufficiently large, greater than $B_0$ say, so that the mean value of $\bar{z}$ over the period of the limit cycle is less than $\frac{1}{K}$, the endemic disease equilibrium susceptible population in the absence of culling. Integrating, we obtain the required condition on $B$ as

$$B > B_0 = \frac{K \left( e^{rT} + 1 - e^{rT \frac{R_b K - 1}{R_b K + r}} - e^{rT \frac{1}{K}} \right)}{e^{rT} - 1},$$

while we have calculated in equation (3.31) that, for the elimination of the infective class, we must have

$$B > B^* = \frac{K \left( 1 + e^{rT} - \left( e^{rT \frac{R_b K - 1}{R_b K + r}} + e^{rT \frac{1}{K}} \right) \right)}{e^{rT} - 1}.$$

Then

$$B^* > B_0 \quad \text{if} \quad \frac{rT(R_b K - 1)}{R_b K + r} + e \frac{rT(1 + r)}{R_b K + r} < e \frac{rT(R_b K - 1)}{R_b K} + e \frac{rT}{R_b K}.$$

Although we can show that inequality (3.32) holds for all reasonable values of the parameters, an analytical proof is not straightforward for although

$$\frac{rT(R_b K - 1)}{R_b K + r} < \frac{rT(R_b K - 1)}{R_b K},$$

since $R_b K > 1$ if there is endemic disease, we have

$$\frac{rT(1 + r)}{R_b K + r} > \frac{rT}{R_b K}.$$

Expanding both sides of (3.32) in a Maclaurin series in $r$ to $O(r^3)$ suggests that the inequality holds for $\frac{1}{K} < R_b < \frac{2}{K}$ only. Expanding both sides of (3.32) in a Maclaurin series in $T$ to $O(T^3)$ suggests that the inequality holds for $\frac{1}{K} < R_b < \frac{1 + \sqrt{1 + r}}{K}$ only. These two approximations give results which agree quite well with numerical simulation on the original inequality (3.32). Indeed the upper limit $\frac{1 + \sqrt{1 + r}}{K}$ gives a result which agrees to 7 decimal places with the simulated result for a range of parameter values. The lower limit is of course the minimum value of $R_b$ for an endemic disease state to exist in the unculled system. Thus for at least

$$\frac{1}{K} < R_b < \frac{1 + \sqrt{1 + r}}{K}$$

the infection free equilibrium is locally stable for $B > B^*$. Thus the conjecture would appear to be reasonable.
3.8 Limiting behaviour of the impulsive fixed yield culling system

We want to be able to relate the results obtained with the impulsive fixed yield culling modelled by system (3.26) to those of the continuous culling modelled by system (3.13). To do this we consider the situation where the total number of animals impulse-culled remains constant over a given time interval, but \( T \to 0 \) and the culling ultimately becomes continuous; we want to show that

\[
A = \lim_{T \to 0} \frac{B(T)}{T},
\]

where \( A \) is the continuous culling rate and \( B \) the total number of animals removed at the end of each impulsive culling cycle.

**Theorem 3.8.1** As \( T \to 0 \) the equilibria and critical parameters in the solution to system (3.26) approach those arising from system (3.13). Specifically \( B^* \to A^*, \hat{x}^* \to x_0, B_{\text{crit}} \to A_{\text{crit}} \) and the populations immediately before a crash are equal in both models.

The size of cull necessary for the infective class to be eliminated

Using l'Hôpital’s rule twice on the expression for \( B^* \) given by equation (3.31) and substituting for \( r \) and \( K \) in terms of the original parameters \( p \) and \( a \) we obtain

\[
\lim_{T \to 0} \frac{B^* K r (R_b K - 1) (1 + r)}{K_b r K + r^2} = \frac{(\rho - \alpha + 1)(R_b (\rho - \alpha) - \rho)}{(R_b + \rho)^2} = A^*.
\]

Thus the limiting size of the fixed yield impulsive cull above which the infective class is eliminated is the same as the corresponding quantity for the continuous fixed yield cull.

The size of the susceptible class when the infected class is eliminated

If we substitute \( B = B^* \), which is defined in equation (3.31), into \( \hat{n}_1 = \frac{1}{2}(K - B) + \frac{1}{2} \sqrt{(K + B)^2 - \frac{4KB}{1 - e^{-rT}}} \) which we obtained in equation (3.25) we have the size of the susceptible class when the infective class is eliminated. If we then take the limit as \( T \to 0 \) we have

\[
\lim_{T \to 0} \hat{n}_1^* = \frac{1}{2} \left( \frac{2 + r - R_b K}{R_b K + r} \right) + \frac{K}{2} = \frac{\rho + 1 - \alpha}{R_b + \rho} = x_0,
\]

where \( x_0 \) is the size of population we obtained in equation (3.19), for continuous culling at which the disease is eradicated.

The size of cull at which the population crashes

The population crashes in system (3.20) if \( B > B_{\text{crit}} \) where

\[
B_{\text{crit}} = \frac{K \left( e^{\frac{r}{2}} - 1 \right)}{e^{\frac{r}{2}} + 1}.
\]

Once more using l'Hôpital’s rule.

\[
\lim_{T \to 0} \frac{B_{\text{crit}}}{T} = \frac{r K}{4} = \frac{(\rho - \alpha)^2}{4\rho} = A_{\text{crit}}.
\]
The population at \( B = B_{\text{crit}} \)

When \( B = B_{\text{crit}} \) the population in system (3.20) is \( \frac{K}{e^{t^2} + 1} \), and

\[
\lim_{t \to 0} \frac{K}{e^{t^2} + 1} = \frac{K}{2} = \frac{\rho - \alpha}{2\rho},
\]

which is the population when \( A = A_{\text{crit}} \) in the continuous culling model.

**Constraint on the basic reproductive ratio**

In system (3.13) we saw that we could not eliminate the infective population without eradicating the entire population if the basic reproductive ratio exceeded the threshold value

\[
R_b > \frac{\rho(2 + \rho - \alpha)}{\rho - \alpha}.
\]

In the system (3.20), to avoid a population crash, as \( B \) is increased, before the infected population is eliminated we must have \( B^* < B_{\text{crit}} \). We see that also this implies an upper bound on \( R_b \) if such a result is to be obtained. Considering \( B^* \) as a function of \( R_b \) we have

\[
B^*(R_b) = \left( K(1 + e^{rT}) - Ke^{r\frac{T(R_bK-1)}{K^\alpha + 1}} + Ke^{r\frac{T(1+r)}{K^\alpha + 1}} \right) e^{rT}.
\]

\[
\frac{dB^*}{dR_b} = -\frac{K^2Tr(1+r)}{(R_bK + r)^2(e^{rT} - 1)}.
\]

\[
\frac{dB^*}{dR_b} = 0 \quad \text{if} \quad R_b = \frac{2+r}{K}.
\]

\[
\frac{d^2B^*}{dR_b^2} \bigg|_{R_b=\frac{2+r}{K}} = -\frac{K^3Tr(1+r)}{8(1+r)^4(e^{rT} - 1)} < 0.
\]

If \( R_b = \frac{2+r}{K} \) then \( B^*(R_b) \) has a maximum. When we substitute for \( R_b = \frac{2+r}{K} \) we obtain the maximum permitted value of \( B^* \),

\[
B^*(R_b) = B_{\text{crit}}.
\]

Consequently as \( R_b \) increases beyond \( \frac{2+r}{K} \), we find the population on the unstable part of the curve, going to zero in finite time.

Finally, we recover the same threshold value for \( R_b \) as for system (3.13)

\[
\frac{2+r}{K} = \frac{\rho(\rho + 2 - \alpha)}{\rho - \alpha}.
\]

This completes the proof that the limit of impulsive fixed yield culling as \( T \to 0 \) is continuous fixed yield culling.
3.9 Continuous constant rate culling

In a continuous constant rate (also known as constant effort or constant proportion) culling strategy we remove animals at a fixed rate $P$ which is proportional to the size of the population concerned. Such a process in the physical world might correspond to setting a fixed number of traps each day, so that the size of the cull is proportional to the size of the population, hence the larger the population the greater the numbers culled. Thus a given proportion of the population, and the same proportion of each of the disease classes, would be removed in at rate $P$ in unit time. The model equations are as follows, with, as usual $\rho > \alpha$,

\[
\frac{dx}{dt} = \rho(x + y)(1 - (x + y)) - \alpha x - R_b x y + (1 - \alpha) y - P x,
\]

\[
\frac{dy}{dt} = R_b x y - y - P y, \tag{3.33}
\]

$x(0) > 0, \; y(0) > 0.$

For the whole population, $m = x + y$ we have

\[
\frac{dm}{dt} = \rho m(1 - m) - \alpha m - P m \quad m(0) = m_0 > 0, \tag{3.34}
\]

with equilibria at $m = 0$ and $m^* = 1 - \frac{\alpha + P}{\rho}$. Moreover, solving equation (3.34) we have

\[
m(t) = \frac{m_0 \theta}{\theta e^{-\theta t} + \rho m_0 (1 - e^{-\theta t})}, \tag{3.35}
\]

where $\theta = P - (\rho - \alpha)$. If $P < \rho - \alpha$ a positive equilibrium population is approached as $t \to \infty$, if $P > \rho - \alpha$ the population tends to zero as $t \to \infty$, thus there can be no population crash.

**Theorem 3.9.1** Continuously culling at a fixed rate $P$ eliminates the entire population in system (3.33) if $P \geq P_{\text{crit}}$ where

\[P_{\text{crit}} = \rho - \alpha,\]

but if $P^* < P < P_{\text{crit}}$, where

\[P^* = \frac{R_b(\rho - \alpha) - \rho}{R_b + \rho},\]

then the infected class is eliminated and a disease free equilibrium population results.

Setting the right hand sides of the equations of system (3.33) equal to zero and solving, we find three equilibria; eradication, the infection-free equilibrium and the endemic equilibrium.

**Eradication**

The eigenvalues of the Jacobian of system (3.33) linearised around the equilibrium $(0,0)$ are

\[\lambda_1 = -1 - P \quad \lambda_2 = \rho - \alpha - P,\]
hence if

$$P > P_{\text{crit}} = \rho - \alpha,$$

then the eradication equilibrium is an attractor and the population is eradicated. (Note that this is not a population crash, since the equilibrium will be reached in infinite time).

### The infection free equilibrium (IFE)

The IFE is $\left(1 - \frac{\alpha}{\rho} - \frac{P}{\rho}, 0\right)$. The IFE can only exist if $P < P_{\text{crit}} = \rho - \alpha$, otherwise the population is eradicated. The eigenvalues of the Jacobian of the linearisation around the IFE are

$$\lambda_1 = P - \rho + \alpha, \quad \lambda_2 = R_b \left(1 - \frac{\alpha}{\rho} - \frac{P}{\rho}\right) - P - 1.$$

The criterion for existence of the IFE ensures the negativity of $\lambda_1$. For $\lambda_2 < 0$ we require

$$P > P^* = \frac{R_b(\rho - \alpha) - \rho}{R_b + \rho}. \quad (3.37)$$

If $R_b < 1 + \frac{\alpha}{\rho - \alpha}$, which is the criterion for stability of the IFE in the unculled model, system (3.2), then $\lambda_2 < 0$ for all $P$ and the IFE is locally stable so long as $P < P_{\text{crit}}$. If, however, $R_b > 1 + \frac{\alpha}{\rho - \alpha}$, the unculled model IFE would now be unstable and so $P > P^*$ will ensure that the IFE becomes stable. Thus culling stabilises the IFE.

Another way to consider the stability of the IFE is to write the requirement as

$$R_b < \frac{\rho(P + 1)}{\rho - P - \alpha}.$$

The right hand side of this inequality is increasing in $P$ so that as $P$ increases the IFE becomes stable, a larger force of infection is needed to drive system (3.33) to an endemic disease state than in the unculled model.

**Definition 3.9.2** The force of infection at equilibrium is defined as the product of the infectivity $\beta$ (which here is a constant but need not be) and the size of the infective population at equilibrium. We shall use this term in subsequent chapters.

### The endemic equilibrium

The endemic disease equilibrium of system (3.33) is at

$$x^* = \frac{1}{R_b} + \frac{P}{R_b}, \quad y^* = 1 - \frac{\alpha}{\rho} - \frac{1}{R_b} - P \left(\frac{1}{\rho} + \frac{1}{R_b}\right).$$

The endemic equilibrium exists provided that $y^* > 0$ so that we need $P < P^* = \frac{R_b(\rho - \alpha) - \rho}{R_b + \rho}$. The eigenvalues of the Jacobian matrix of system (3.33) linearised around the endemic equilibrium are

$$\lambda_1 = P - \rho + \alpha, \quad \lambda_2 = \left(R_b \left(1 - \frac{\alpha}{\rho} - \frac{P}{\rho}\right) - P - 1\right).$$

Thus the criteria for stability of the endemic equilibrium are $P < \rho - \alpha$ (for $\lambda_1 < 0$) and $P < \frac{R_b(\rho - \alpha) - \rho}{R_b + \rho}$, (for $\lambda_2 < 0$). Since, for $\rho > \alpha$, $\frac{R_b(\rho - \alpha) - \rho}{R_b + \rho} < \rho - \alpha$, the endemic equilibrium is stable.
if the endemic equilibrium exists it is stable.

As $P$ increases from zero, $x^*$ increases (at the rate of $\frac{1}{R_b}$) and $y^*$ decreases (at a faster rate, $\frac{1}{\rho} + \frac{1}{R_b}$) so that the total population declines (at the rate of $\frac{1}{\rho}$).

At $P = P^* = \frac{R_b(\rho - \alpha) - \rho}{R_b + \rho}$ the endemic disease state disappears and the total population, now consisting solely of susceptibles, continues to decline with increasing $P$ at the same rate until eradication occurs when $P = P_{\text{crit}} = \rho - \alpha$. This is shown in Figure 3.11. The culling rate at which the infected population

![Figure 3.11: Bifurcation diagram for system (3.33)](image)

is eliminated, $P^* = \frac{R_b(\rho - \alpha) - \rho}{R_b + \rho}$ is increasing in $R_b$, so that the culling effort required to remove the infected population increases as $R_b$ grows.

However, if we consider the limit,

$$
\lim_{R_b \to \infty} P^* = P_{\text{crit}},
$$

so that it is always possible in principle to eliminate the infectious class without eradicating the population, however virulent the infection, in contrast to fixed yield culling where such a strategy is only feasible if $R_b$ is less than an upper bound (which we found in Section 3.6.2).

The significance of $x_0$

At $y^* = 0$ we find that the size of the susceptible population is

$$
x^* = x_0 = \frac{\rho + 1 - \alpha}{R_b + \rho}.
$$

This is the same value for $x_0$ as in fixed yield culling, defined in equation (3.19), the maximum size of population below which, with a given value of $R_b$, it is not possible to establish an endemic equilibrium state. To understand the
significance of $x_0$ we can consider continuous fixed rate culling as, in effect, increasing the death rate in the unculled model of system (2.1) from $\mu$ to $\mu + \theta$. The basic reproductive ratio for the resulting system will then be

$$R_b = \frac{\beta C(1 - \frac{\mu + \theta}{s})}{\mu + \gamma + \theta}$$

and we find that $R_b = 1$, the value below which an endemic disease state cannot exist, when

$$\theta = \frac{\beta C(s - \mu) - s(\mu + \gamma)}{\beta C + s}.$$ 

Thus we have

$$\frac{\theta}{\mu + \gamma} = \frac{R_b(\rho - \alpha) - \rho}{R_b + \rho} = \rho^*$$

The equilibrium population size for a culling rate of $\rho^*$ is $x_0$.

3.9.1 Global stability

We established the boundedness of $m(t)$ and the positivity of $x(t)$ and $y(t)$ in Section 3.2 and we can eliminate the possibility of a periodic solution to system (3.33) in the same way as for the equilibria of system (3.2) by using Dulac’s criterion.

We write system (3.33) in the form $\dot{x} = f_2(x, y)$, $\dot{y} = g_2(x, y)$ where

$$f_2(x, y) = \rho(x + y)(1 - (x + y)) - \alpha x + (1 - \alpha)y - R_byy - Px, $$

$$g_2(x, y) = -y + R_byy - Py.$$ 

We define

$$H(x, y) = \frac{1}{xy + y^2},$$

and $\Omega = (0, \infty) \times (0, \infty)$, then

$$\frac{\partial(Hf_2)}{\partial x} = -\frac{\rho(x + y)^2 - y(1 + P + R_by)}{y(x + y)^2}, \quad \frac{\partial(Hg_2)}{\partial y} = \frac{P + 1 - R_by}{(x + y)^2},$$

so that

$$\frac{\partial(Hf_2)}{\partial x} + \frac{\partial(Hg_2)}{\partial y} = -\frac{\rho(x + y) + R_by}{y(x + y)} < 0 \quad \text{for all} \quad (x, y) \in \Omega.$$ 

We can thus conclude that there are no periodic solutions to system (3.33) and that the equilibria obtained are globally stable.

An alternative fixed rate culling strategy

As with the case of fixed yield culling, an alternative strategy is to reduce the population as rapidly as practical to $x_0$ and maintain it at this level thereafter. While for $P_{crit} > P > P^*$ the equilibrium population size will be less than $x_0$ it will take an infinite time to reach it. However, if $P > P^*$ we can compute the time taken to reduce the population for $m_0$ at $t = 0$ to $x_0$, $T_{x_0}$ as

$$T_{x_0} = \frac{1}{(\rho + 1 - \alpha)} \ln \left( \frac{(P - \rho + \alpha + \rho m_0)(\rho - \alpha + 1)}{m_0(R_b(P - \rho + \alpha) + \rho(1 + P)))} \right),$$

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noting, *en passant*, that if \( P < \rho - \alpha \) the argument of the logarithm is less than unity so that \( T_{x_0} > 0 \) for all \( P > P^* \). As we would expect, \( T_{x_0} \) is decreasing in \( P \).

We can compute the total number of animals required to be culled in order to reduce the population from \( m_0 \) to \( x_0 \), \( N_{x_0} \) as

\[
N_{x_0} = \int_0^{T_{x_0}} Pm(t)dt = \frac{P}{\rho} \ln \left( \frac{(R_b + \rho)(P - \rho + \alpha + \rho m_0)}{R_b(P - \rho + \alpha) + \rho(1 + P)} \right).
\]

Once again we find numerically that \( N_{x_0} \) is decreasing in \( P \), thus the greater the culling rate the fewer total animals are required to be culled in order to reduce the population to the level at which no endemic disease is sustainable. In fact,

\[
\lim_{P \to \infty} N_{x_0} = m_0 - \frac{\rho + 1 - \alpha}{R_b + \rho} = m_0 - x_0
\]

as we should expect.

### 3.10 Impulsive constant rate culling

In this strategy, at some times \( t = \{nT, n \in \mathbb{Z}^+\} \), the population is reduced by a fixed proportion \( Q \). This could describe a policy of a fixed annual regular reduction of the population where the effort is proportional to the size of the population - where the more animals flushed from cover, the more are culled. We consider culling at intervals of constant length \( T \).

#### 3.10.1 The whole population

The model is derived from equation (3.3) by putting \( r = \rho - \alpha \) and \( K = 1 - \frac{\rho}{\rho} \) for convenience. The culling is at a fixed proportion \( Q \) and is done with a constant frequency \( \frac{1}{T} \). In all that follows we take \( r > 0 \) and we use carets to distinguish the impulsive model equilibria from the continuous model.

\[
\frac{dm}{dt} = rm(1 - m) \quad \text{for} \quad t \in \{(nT, (n+1)T) \quad n \in \mathbb{Z}^+\},
\]

\[
m(nT+) = m(nT-) - Qm(nT-) \quad n \in \mathbb{Z}^+ \quad Q \in [0, 1), \quad (3.38)
\]

\[
m(nT+) = m_n.
\]

We can solve equation (3.38) on \( t \in (nT, (n+1)T) \) as before, obtaining

\[
m(t) = \frac{K m_n}{(K - m_n)e^{-r(t-nT)} + m_n} = g(m_n, t). \quad (3.39)
\]

**Theorem 3.10.1** If \( Q > Q_{\text{crit}} \), where

\[
Q_{\text{crit}} = 1 - e^{-rT}
\]

then the total population \( m(t) \), defined by equation (3.39) tends to zero as \( t \to \infty \). If \( Q < Q_{\text{crit}} \) a stable limit cycle is established.
Discrete mapping
We prove this theorem as follows; the discrete mapping is now \( \Psi : (0, K) \to (0, K) \)
\[
m_{n+1} = \Psi(m_n)
\]
where
\[
m_{n+1} = g(m_n, T)(1 - Q),
\]
\[
m_{n+1} = \frac{Km_n(1 - Q)}{(K - m_n)e^{-rT} + m_n}.
\]

Fixed points
Solving equation (3.40) we find fixed points at \( m = 0 \) and
\[
m = \hat{m}^* = K \left(1 - \frac{Q}{1 - e^{-rT}}\right).
\]
Clearly if
\[
Q > Q_{\text{crit}} = 1 - e^{-rT}
\]
then the right hand side of equation (3.41) becomes negative and the population will go to zero in finite time.

Stability
The fixed point \( \hat{m}^* \) is locally stable if it exists, since
\[
|\Psi'(\hat{m}^*)| = \frac{e^{-rT}}{1 - Q} < 1.
\]
Moreover, by consideration of a cobweb diagram analogous to that shown for impulsive fixed yield culling in Figure 3.7, we can see that the fixed point, if it exists, is globally stable.

The time for the population to increase from \( m_n \) to \( \frac{m_m}{1 - Q} \) is \( T_Q \), where
\[
T_Q = \frac{1}{r} \ln \frac{K - m_n}{K(1 - Q) - m_n}.
\]
Hence we must have \( T > T_Q \) to establish a limit cycle. Taking \( K > m_n \) for reasons we have previously discussed, we must also have \( Q < 1 - \frac{m_m}{K} \). The culling proportion corresponding to the fixed point \( \hat{m}^* \) is
\[
Q = \left(1 - \frac{\hat{m}^*}{K}\right)(1 - e^{-rT}) < Q_{\text{crit}},
\]
so that a limit cycle is always possible no matter what the culling rate.

As for fixed yield impulse culling, the equilibrium of system (3.38) is a limit cycle of period \( T \) which again has a saw tooth shape. This will be reached for any starting value of \( m(0) > 0 \). Now, if \( Q \) were suitably chosen so that system (3.38) approached arbitrarily close to the limit cycle in finite time, there would be no \textit{a priori} reason to expect that the two disease classes themselves would reach an equilibrium at the same time. However, if we consider that the limit cycle for the population is reached for \( t \) very large then it is reasonable to consider that, at this time, the two disease classes either both have reached a limit cycle or the infected class has reached zero.
3.10.2 The infected class

The equations for the two state variables of system (3.38) are

\[
\frac{dx}{dt} = \rho(x + y)(1 - (x + y)) - ax + (1 - a)y - R_bxy,
\]

\[
\frac{dy}{dt} = -y + R_bxy,
\]

for \( t \in \{ (nT, (n+1)T) \ n \in Z^+ \} \) in both cases and

\[
x(nT+) = x(nT-)(1 - Q) = x_n \quad y(nT+) = y(nT-)(1 - Q) = y_n.
\]

Using the method for the solution of \( y(t) \) for \( t \in \{ (nT, (n+1)T) \ n \in Z^+ \} \) obtained in equation (3.28), we can obtain an expression for the size of the infected class as follows

\[
y(t) = \frac{y_n \left( 1 + \frac{x_n + y_n}{K} \right) \left( e^{r(t-nT) - 1} \right)}{y_n R_b \int_{nT}^{t} \left( 1 + \frac{x_n + y_n}{K} \right) \left( e^{r(r-nT) - 1} \right) e^{-(r-nT)} \, dr + 1}
\]

for \( t \in \{ (nT, (n+1)T) \ n \in Z^+ \} \ y(nT+) = y(nT-)(1 - Q) = y_n.

Theorem 3.10.2 If \( 0 < Q < Q^* \) where

\[
Q^* = 1 - e^{-\frac{r(R_b K - 1)T}{K + r}}
\]

a stable limit cycle exists for system (3.43) with both susceptible and infected classes present. If \( Q^* < Q < Q_{\text{crit}} = 1 - e^{-rT} \), then the infected class is eliminated and a stable infection free limit cycle exists.

We prove this theorem as follows;

Discrete mapping

The effect of the mapping \( \Psi \) described in equation (3.40) on \( y \) we write as the recurrence relation

\[
y_{n+1} = \frac{y_n \left( 1 + \frac{x_n + y_n}{K} \right) \left( e^{r(t-nT) - 1} \right)}{y_n R_b \int_{nT}^{(n+1)T} \left( 1 + \frac{x_n + y_n}{K} \right) \left( e^{r(r-nT) - 1} \right) e^{-(r-nT)} \, dr + 1}
\]

For sufficiently large \( n \) either the population reaches a limit cycle or it crashes. On the assumption that the limit cycle is reached, we can substitute

\[
\hat{y} = x((n+1)T+) + y((n+1)T+) = x_n + y_n
\]

and

\[
\theta = r - nT
\]
and simplify to obtain,

\[ y_{n+1} = \frac{y_n \left( 1 + \frac{n^*}{K}(e^{RbK} - 1) \right) \frac{RbK}{r} e^{-T(1 - Q)}}{y_n \int_0^T \left( 1 + \frac{n^*}{K}(e^{\theta} - 1) \right) \frac{RbK}{r} e^{-\theta} d\theta + 1} \]

Elimination of the infected class

Repeating the same analysis as in the case of fixed yield impulsive culling in Section 3.7, we obtain the condition that lim\(_{n \to \infty} y_n = 0\) as

\[ (1 + \frac{n^*}{K}(e^{RbK} - 1)) \frac{RbK}{r} e^{-T(1 - Q)} < 1. \]

If we now substitute the value of \(n^*\) from equation (3.41) we obtain a value for \(Q^*\), the culling rate at which the infective class is eliminated. If \((1 - Q) e^{(RbK-1)T} < e^{-(RbK-1)T}\) then \(Q > Q^* = 1 - e^{-\frac{RbK}{RbK+\tau}}\).

3.10.3 Stability of the limit cycle

Lemma 3.10.3 The limit cycle solution of system (3.38) with the infected class eliminated is stable provided that the culling rate is greater than \(Q_0\), where \(Q_0\) is defined in equation (3.44).

The limit cycle with no infective class is \((\dot{x}_T(t), 0)\) of period \(T\) is

\[ \dot{x}_T(t) = \begin{cases} \frac{K}{(\dot{x}^*-1)e^{-r(t-nT)}} + 1 & : t \in (nT,(n+1)T), n \in Z^+ \\ \dot{x}^* & : t = nT \end{cases} \]

with

\[ \dot{x}^* = K \left( 1 - \frac{Q}{1 - e^{-rT}} \right). \]

Carrying out the same analysis as in the case of impulsive fixed yield culling we require that

\[ \frac{1}{T} \int_0^T \dot{x}_T(s)ds < \frac{1}{Rb}. \]

if \(\dot{x}_T(t)\) is to be locally stable. This will be true if \(Q > Q_0\) say, where

\[ Q_0 = 1 - \frac{e^{\frac{T}{Rb}} (1 - e^{-rT})}{e^{rT} - 1}. \] (3.44)

Simulating with a range of parameters we find that \(Q^* < Q_0 < Q_{crit}\), so that while the limit cycle with no infectives is locally stable for \(Q > Q_0\), we have not shown it to be stable for all of the range of values of \(Q\) at which the infective class is eliminated.

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3.11 Limiting behaviour of the impulsive fixed rate culling system

Once again we want to be able to relate the results obtained with impulsive fixed rate culling modelled by system (3.38) to those of continuous culling modelled by system (3.33). To do this, we consider the situation where the total number of animals impulse culled remains constant, but $T \to 0$ and the culling ultimately becomes continuous. We want to show that

$$P = \lim_{T \to 0} \frac{Q(T)}{T},$$

where $P$ and $Q$ are the continuous and impulsive fixed culling rates respectively.

**Theorem 3.11.1** As $T \to 0$ the equilibria and critical parameters in the solution to system (3.38) approach those in system (3.33). Specifically $Q^* \to P^*$ and $\hat{x}_* \to x_0$, $Q_{\text{crit}} \to P_{\text{crit}}$.

The size of cull necessary for the infective class to be eliminated

If the total number of animals culled remains a constant proportion of the population, but $T \to 0$ so the culling becomes continuous, we show that

$$\lim_{T \to 0} \frac{Q^*}{T} = P^*.$$

Using l'Hôpital's rule we have

$$\lim_{T \to 0} \frac{Q^*}{T} = \frac{r(R_b K - 1)}{R_b K + r} = \frac{R_b (\rho - \alpha) - \rho}{R_b + \rho} = P^*,$$

which is the culling rate in the continuous model, system (3.33), at which the endemic equilibrium disappears and the infection free equilibrium becomes stable.

The size of the susceptible class when the infected class is eliminated

If we substitute $Q = Q^*$ in the expression for $\hat{n}^*$ in equation (3.41) and use l'Hôpital's rule we obtain

$$\hat{n}^* = K \left( \frac{e^{-\frac{r(R_b K - 1)T}{R_b K + r}} - e^{-rT}}{1 - e^{-rT}} \right),$$

$$\lim_{T \to 0} \hat{n}^* = \frac{K(r + 1)}{R_b K + r} \frac{\rho - \alpha + 1}{R_b + \rho} = x_0.$$

This is the population level, discussed in Section 3.9, at which the endemic disease equilibrium is not sustainable.
Culling rate at which the population is eradicated

In order not to eradicate the total population in impulsive fixed rate culling, system (3.41) we must have \( Q < Q_{\text{crit}} = 1 - e^{-rT} \). Once more,

\[
T \to 0, \quad \frac{Q_{\text{crit}}}{T} \to r = \rho - \alpha = P_{\text{crit}}.
\]

We have thus demonstrated that, in the case of fixed rate culling, the limiting case of impulse culling is continuous culling.

3.12 Culling the infective class only

We now consider culling only infected animals. This might be achieved by a strategy of, for example trapping, inspecting and releasing the uninfected animals (assuming that a sufficiently accurate test exists for this to be done). For fixed yield culling this would be on the basis of a fixed number of infected animals to be culled in unit time.

3.12.1 Fixed yield continuous culling of the infected class only

We work for the remainder of this section with the non-dimensionalised system of equation (3.2) and a culling yield of \( A \) animals per unit time.

\[
\begin{align*}
\frac{dx}{dt} &= \rho(x + y)(1 - (x + y)) - ax + (1 - a)y - R_bxy, \\
\frac{dy}{dt} &= -y + R_bxy - q_yA,
\end{align*}
\]

where

\[
x(0) > 0, \quad y(0) > 0,
\]

and

\[
q_y := \begin{cases} 
1 & : \ y > 0 \\
0 & : \ \text{otherwise.}
\end{cases}
\]

We assume that \( R_b > \frac{\rho}{\rho - \alpha} \) and \( \rho > \alpha \). We take \( q_y = 1 \).

**Lemma 3.12.1** As the culling rate, \( A \), is increased under a strategy of fixed yield continuous culling of the infective class only, the size of the equilibrium infective population decreases until, for \( A \geq A_0 \), where \( A_0 \) is defined in (3.48) it reaches zero in finite time.

We prove the lemma in this section.

We will term the critical value of \( A \) at which the infective population crashes as \( A_0 \). System (3.45) has equilibria which can be expressed as;

\[
x^* = \frac{\psi + A}{R_b\psi}, \quad y^* = \psi,
\]

where \( \psi \) is a positive root of the quartic equation \( f(z) = 0 \), where

\[
f(z) = \rho R_b^2 z^4 + R_b(2\rho - R_b(\rho - \alpha)) z^3 + (AR_b(R_b + 2\rho) + \rho - R_b(\rho - \alpha)) z^2 + (2A\rho - AR_b(\rho - \alpha)) z + \rho A^2.
\]

\[
(3.46)
\]
We note that when \( A = 0 \) equation (3.46) becomes;

\[
f_0(z) = \rho R_b^2 z^4 + R_b \left( 2\rho - R_b (\rho - \alpha) \right) z^3 + (\rho - R_b (\rho - \alpha)) z^2 = 0,
\]

which has roots \( \{0, 0, -\frac{1}{R_b}, 1 - \frac{\alpha}{\rho} - \frac{1}{R_b} \} \). The fourth value is the value of \( y^* \) in the unculled model so that we can be sure, by continuity, that \( f(z) \) has a positive root for small values of \( A \) at least.

**Conjecture 3.12.2** For values of \( A < A_0 \), where \( A_0 \) is defined in equation (3.48) below, \( f(z) = 0 \) has two real positive roots corresponding to two feasible endemic states for system (3.45), one of which (with the larger value of \( y^* \)) is stable, the other unstable.

We can illustrate the existence of two positive roots of \( f(z) = 0 \) for \( A < A_0 \), one stable and the other unstable by numerical simulation for a wide range of parameter values but we are not yet able to prove the conjecture analytically.

If \( A \) is small then by writing \( z(A) = z_0 + z_1 A \) we can approximate the largest real root in \([0,1]\) (where it exists) of \( f(z) \) as

\[
z = 1 - \frac{\alpha}{\rho} - \frac{1}{R_b} - \left( \frac{R_b (\rho - \alpha) + \rho (\rho - \alpha - 1)}{(R_b (\rho - \alpha) - \rho)(\rho - \alpha)} \right) A.
\]

The infective population will crash if \( f(z) = 0 \) has no real positive roots. To find the conditions for \( f(z) = 0 \) to have complex roots we need to study the discriminant, \( \Delta \) of \( f(z) \), as a function of \( A \), since a double root will exist whenever the discriminant is zero and we know that this therefore indicates the position of a complex pair of roots for an infinitesimal change in \( A \).

The discriminant of an \( n \)th order polynomial of the form

\[
a_n z^n + a_{n-1} z^{n-1} + \ldots + a_1 z + a_0 = 0
\]

can be expressed as the following product of the \( n \)th powers of the differences between pairs of roots \( r_i \) and \( r_j \)

\[
\Delta_n = a_n^{2n-2} \prod_{i>j} (r_i - r_j)^n.
\]

In the case of equation (3.45) we can compute the discriminant, using Maple, to be

\[
\Delta = R_b^6 A^2 ((\rho - \alpha)^2 - 4\rho A) g(A),
\]

where

\[
g(A) = R_b^2 (R_b + 4\rho)^2 A^2 - 2R_b (R_b^2 (2(\rho - \alpha)^2 + \rho - \alpha) - R_b\rho (4(\rho - \alpha) + 1) + 4\rho^2) A
\]

\[
+ (R_b (\rho - \alpha) - \rho)^2
\]

(3.47)
Finding the six roots of $\Delta$ (apart from the repeated zero root which is trivial) is achieved by finding the roots of $g(A) = 0$. There is a repeated real root $\frac{\rho - \alpha}{4\rho}$, which we recognise as $A_{\text{crit}}$ from Section 3.2.1, and two further roots

\begin{align*}
A_5 &= \frac{1}{R_b(4\rho + R_b)^2} \left( (2(\rho - \alpha)^2 + \rho - \alpha)R_b^2 - \rho(4(\rho - \alpha) + 1)R_b + 4\rho^2 \\
&\quad + 2|R_b(\rho - \alpha) - 2\rho| \sqrt{R_b(R_b(\rho - \alpha)^2 + R_b(\rho - \alpha) - \rho)} \right), \\
A_6 &= \frac{1}{R_b(4\rho + R_b)^2} \left( (2(\rho - \alpha)^2 + \rho - \alpha)R_b^2 - \rho(4(\rho - \alpha) + 1)R_b + 4\rho^2 \\
&\quad - 2|R_b(\rho - \alpha) - 2\rho| \sqrt{R_b(R_b(\rho - \alpha)^2 + R_b(\rho - \alpha) - \rho)} \right).
\end{align*}

In order that $A_5$ and $A_6$ are real we must have $R_b(\rho - \alpha)^2 + R_b(\rho - \alpha) - \rho \geq 0$, this requires that

$$R_b \geq \frac{\rho}{(\rho - \alpha)^2 + \rho - \alpha}.$$

Since the necessary and sufficient condition for the disease to be endemic is that $R_b > \frac{\rho}{\rho - \alpha}$, it follows that $A_5$ and $A_6$ are real whenever the disease is endemic. We expect to find that at least some of the values of $A_5$ and $A_6$ will represent the culling rates at which the infective population will crash.

Observation 3.12.3 $A_5 > 0$ and $A_6 > 0$ for $R_b > \frac{\rho}{\rho - \alpha}$.

Clearly $A_5 \geq A_6$. The two expressions are equal for $R_b = \frac{\rho}{\rho - \alpha}$. $A_6 = 0$ for $R_b = \frac{\rho}{\rho - \alpha}$ only and $\lim_{R_b \to \infty} A_6 = 0$. Hence we must have $A_6 > 0$ for conditions in which an endemic disease exists.

This is illustrated in Figure 3.12 which shows a plot of the level curves of $\Delta = 0$ for different values of $R_b$ with $\rho = 1, \alpha = 0.1$. The different zones on the graph represent areas where there are, as labelled, two real positive or negative roots and two complex roots, four complex roots or four real positive roots for (3.47). These results were obtained by repeatedly solving (3.47) for different values of $R_b$. A crash of the infective population will occur when there are no positive real roots. For $R_b \in \left(\frac{\rho}{\rho - \alpha}, \frac{2\rho}{\rho - \alpha}\right)$, culling at a rate greater than $A_5$ will cause an infected population crash as the roots of (3.47) are a complex conjugate pair and two real negative values. For $R_b > \frac{2\rho}{\rho - \alpha}$, culling at a rate greater than $A_6$ produces a crash since the roots are two complex conjugate pairs. As $R_b$ increases further, $A_0 = A_{\text{crit}}$ at $R_b = \hat{R}_b$ where

$$\hat{R}_b = \frac{2\rho}{\rho - \alpha} \left( \rho - \alpha + 1 + \sqrt{(\rho - \alpha)^2 + 2(\rho - \alpha)} \right).$$
We can summarise these results as follows, where $A_0$ is the culling rate at which the infected population reaches zero in finite time

$$A_0 = \begin{cases} 
A_5 & : \frac{\rho}{\rho - \alpha} < R_b < 2\frac{\rho}{\rho - \alpha} \\
: \\
A_6 & : \frac{2\rho}{\rho - \alpha} < R_b < \hat{R}_b \\
: \\
A_{\text{crit}} & : R_b > \hat{R}_b.
\end{cases} \quad (3.48)$$

**Endemic equilibria prior to a crash**

We can extract some values for the endemic equilibrium as $A$ is increased immediately up to the value at which the infective population crashes and the values of $A_0$, for some specific values of $R_b$. Thus, when $R_b = 2\frac{\rho}{\rho - \alpha}$ we have, substituting $A = A_5$, at the point in Figure 3.12 where $A_5 = A_6$

$$A_0 = \frac{(\rho - \alpha)^2}{4\rho(2(\rho - \alpha) + 1)},$$

$$x^* = \frac{\sqrt{2}(\rho - \alpha)(\alpha + \sqrt{2}(2(\rho - \alpha) + 1)(\rho - \alpha) - \rho)}{4\rho\sqrt{2(\rho - \alpha) + 1}(\rho - \alpha)},$$

$$y^* = \frac{\sqrt{2}(\rho - \alpha)\sqrt{(2(\rho - \alpha) + 1)(\rho - \alpha)}}{4\rho(2(\rho - \alpha) + 1)}.$$
while for $R_b = \hat{R}_b$

$$A_0 = \frac{(\rho - \alpha)^2}{4\rho},$$

$$y^* = \frac{(\rho - \alpha)\left(\rho - \alpha - \sqrt{(\rho - \alpha)^2 + 2(\rho - \alpha)}\right)}{4\rho\left(\rho - \alpha + 1 - \sqrt{(\rho - \alpha)^2 + 2(\rho - \alpha)}\right)}.$$

The expression for $x^*$ in this case cannot be readily simplified.

**Stability**

System (3.45) exhibits a saddle-node bifurcation with parameter $A_0$. As we have noted, there are in fact two pairs of equilibrium solutions. The lower half of the parabola which is the graph of $x^*(A)$ as a function of $A$ and the upper half of the parabola for $y^*(A)$ represent the stable solution and the opposite halves of each parabola the unstable solution respectively.

### 3.12.2 Continuous fixed rate culling of the infected class only

This strategy could be applied by trapping a fixed number of animals in unit time and culling whichever of them turned out to be infective, while releasing the others. It is of course tantamount to introducing deaths due to disease into the SIS model. The model equations are as follows;

$$\frac{dx}{dt} = \rho(x + y)(1 - (x + y)) - ax + (1 - a)y - R_bxy,$$

$$\frac{dy}{dt} = -y + R_bxy - Ay, \quad (3.49)$$

$$x(0) > 0, \quad y(0) > 0.$$ 

**Lemma 3.12.4** Culling the infective class only at a continuous fixed rate can eliminate the endemic equilibrium of system (3.49) for all $R_b$, with no risk of eliminating the entire population. The culling rate at which the endemic equilibrium is eliminated is $A^*$, given by

$$A^* = \frac{R_b(\rho - \alpha) - \rho}{\rho}. \quad (3.50)$$

**Lemma 3.12.5** The strategy of continuously culling only infectives requires more animals to be culled per unit time in order to destabilise the endemic equilibrium than when both the susceptible and infective classes are culled.

We prove these lemmas in this section.
Equilibria

As we expect, there are three equilibria for system (3.49): (0,0), the IFE and the endemic equilibrium. The latter is

\[ x^* = \frac{1 + A}{R_b}, \]

\[ y^* = \frac{1}{2\rho R_b} \left( R_b(\rho - \alpha - A) \right. \]
\[ \left. -2\rho(A + 1) + \sqrt{R_b^2(\rho - \alpha - A)^2 + 4\rho R_b A(1 + A)} \right). \] (3.51)

We take the positive square root to ensure that \( y^* \geq 0 \). Indeed \( y > 0 \) for

\[ A < A^* = \frac{R_b(\rho - \alpha) - \rho}{\rho} \] (3.52)

and at \( A = A^* \) we have \( x^* = 1 - \frac{\alpha}{\rho} \).

Efficiency of the culling operation

If we consider that the objective is to cull sufficient animals at a continuous fixed rate so that we destabilise the endemic equilibrium, we can compare the efficiency of the strategy of culling infectives only with that of culling all the animals. In Section 3.2 we found that the endemic equilibrium of system (3.49) with no culling is

\[ x^* = \frac{1}{R_b}, \quad y^* = 1 - \frac{\alpha}{\rho} - \frac{1}{R_b}, \quad m^* = 1 - \frac{\alpha}{\rho}. \]

If \( N_{\text{all}} \) is the total number of animals culled in unit time when all animals are culled, i.e. at a rate of \( P^* \) (defined in equation (3.37)) and \( N_{\text{infect}} \) the total when infectives only are culled at the rate of \( A^* \) defined in equation (3.52), (the culling rates that will lead to the elimination of the infective class) in each case starting at the endemic equilibrium, we have

\[ N_{\text{all}} = \frac{R_b(\rho - \alpha) - \rho}{R_b + \rho} \left( 1 - \frac{\alpha}{\rho} - \frac{1}{R_b} \right), \]

\[ N_{\text{infect}} = \left( \frac{R_b(\rho - \alpha) - \rho}{\rho} \right) \left( 1 - \frac{\alpha}{\rho} - \frac{1}{R_b} \right), \]

\[ \frac{N_{\text{infect}}}{N_{\text{all}}} = \frac{(R_b(\rho - \alpha))}{R_b(\rho - \alpha)}, \]

We see that \( \frac{N_{\text{infect}}}{N_{\text{all}}} > 1 \), i.e. animals are culled at a higher rate per unit time when only infectives are removed, if

\[ R_b > \frac{1 + \rho\sqrt{1 + 4(\rho - \alpha)}}{2(\rho - \alpha)}. \]
Since $\rho \sim O(1)$ and $\rho >> \alpha$ this gives a lower bound for $R_b$ of less than 2, a relatively modest level of basic reproductive ratio. Hence, for a virulent disease it would appear to be more effective to destabilise the endemic disease state by culling all animals than just the infective class.

We would, of course, need to take the analysis rather further by considering the total number of animals removed in some time interval under each strategy, since culling the infective class only must result at some point in a zero culling rate (at the IFE), whilst culling all the animals leads to a positive culling rate at the IFE. We are not able to solve the differential equations in system (3.49) explicitly, but we may estimate the total number of animals culled to eliminate the disease in the following manner.

The total number of animals removed when only the infective population is culled will be $Y = \int_0^\infty A y(t) dt$. Let us consider the expression for $y(t)$ which we can obtain by solving system (3.49) linearised around the IFE to obtain

$$y(t) = y(0)e^{-(\rho A - R_b(\rho - \alpha) + \rho)t},$$

where $y(0)$ must be non-zero else there is no disease and, provided that we start near to the IFE we may assume that $y(t)$ behaves approximately exponentially throughout the evolution and thus we can evaluate the integral

$$Y = \int_0^\infty A y(t) dt$$

to give us

$$Y = \frac{y(0)\rho A}{\rho A - R_b(\rho - \alpha) + \rho}.$$  

We now consider system (3.33), with a culling rate of $\theta$ and compute the total number of animals culled when both susceptibles and infectives are culled, and apply the same argument. The solutions for $x$ and $y$ obtained by solving (3.33) linearised about the IFE are

$$x(t) = -y(0)e^{-(\rho - \alpha - \theta - \frac{1}{\rho}(R_b(\rho - \alpha - \theta) + \rho(\rho - \alpha - 1 - 2\theta)))t} + (x(0) + y(0))e^{-(\rho - \alpha - \theta))t},$$

$$y(t) = y(0)e^{-\left(\frac{1}{2}(R_b(\theta - \rho + \alpha) + \rho(1 + \theta))t\right)}.$$  

Calculating the number of animals culled as $N$, where

$$N = \int_0^\infty \theta(x(t) + y(t)) dt$$

and taking $x(0) = 1 - \frac{\theta}{\rho}$ we have

$$N = \frac{y(0)\rho + \rho - \alpha}{\rho(\rho - \alpha - \theta)}.$$

We note that the expression for $N$ is independent of $R_b$, while $Y$ is increasing in $R_b$. Simulation suggests that the total number of animals culled to return to the IFE is greater when both susceptibles and infectives are culled - i.e. $N > Y$ provided that $y(0)$ is small. There is thus an interesting dichotomy between the rate of culling needed to destabilise the endemic disease state and the total number of animals eventually culled.
Local stability

The eigenvalues of the Jacobian, of the linearisation of system (3.49) around the equilibrium \((0,0)\) are

\[
\lambda_1 = \rho - \alpha, \quad \lambda_2 = -1 - \lambda,
\]

so it is always locally unstable for \(\rho > \alpha\). The linearisation about the IFE has eigenvalues

\[
\lambda_3 = \alpha - \rho, \quad \lambda_4 = -A + \frac{R_0(\rho - \alpha - \lambda)}{\rho}
\]

and becomes stable for \(A > A^*\), where \(A^*\) is defined in equation (3.50). Thus the entire population can never be eradicated, no matter what the value of \(A\).

At the endemic equilibrium, if the Jacobian of the linearisation is \(J\), it is more convenient to look at the determinant, \(\text{det}(J)\) and the trace \(\text{trace}(J)\). If the size of the infected class \(\hat{y}\) at the endemic equilibrium we have,

\[
\text{det}(J) = 2\hat{y}^2 R_0 \rho - (R_0(\rho - \alpha - A) - 2\rho(A + 1))\hat{y},
\]

so that

\[
\text{det}(J) > 0 \quad \text{for} \quad \hat{y} > \frac{1}{2\rho R_0} (R_0(\rho - \alpha - A) - 2\rho(A + 1)) < y^*.
\]

Hence, if the endemic equilibrium exists, \(\text{det}(J) > 0\). The trace of the Jacobian of system (3.49) is given by

\[
\text{trace}(J) = \rho(1 - x - y) - \alpha - R_0 y - \rho(x + y),
\]

\[
= -\frac{1}{x} \left( \rho y(1 - x - y) - (1 - \alpha)y + \rho(x + y) \right) < 0,
\]

using the equilibrium equations. The endemic equilibrium is thus locally asymptotically stable if it exists.

3.12.3 Impulsive culling of the infective class only

We are unable to make any progress analytically with an impulsive model, the recurrence relation obtained by applying the analysis of Section 3.2 in this case cannot be solved for fixed yield culling and neither can we obtain an explicit solution for the total population in the case of fixed rate culling.

3.13 Culling in systems with a latent class

We introduce a latent class, \(E\) to create a Susceptible Latent Infected Susceptible (SEIS) model, which we develop as the subject of Chapter 4. At this point we observe that diseases such as tuberculosis usually have a stage when the susceptible animal, although infected and incubating the disease, is not yet infectious and may well be asymptomatic. The simplest method of modelling this stage is to assume that the length of this latent period is exponentially distributed, with mean length \(\kappa\). We otherwise maintain the same assumptions as for equation (3.1).
3.13.1 Fixed yield continuous culling in the SEIS system

The model equations are as follows, for a culling rate \( A_1 \) animals per unit time.

\[
\frac{dS}{dt} = r(S + E + I) \left(1 - \frac{S + E + I}{C}\right) - \mu S - \beta SI + \gamma I - q_S \frac{A_1 S}{S + E + I},
\]

\[
\frac{dE}{dt} = \beta SI - (\kappa + \mu)E - q_E \frac{A_1 E}{S + E + I},
\]

\[
\frac{dI}{dt} = \kappa E - (\mu + \gamma)I - q_I \frac{A_1 I}{S + E + I},
\]

\[S + E + I = N, \quad S(0) > 0 \quad E(0) > 0 \quad I(0) > 0, \tag{3.53}\]

where we define

\[
q_S = \begin{cases} 
1 & S > 0 \\
0 & \text{otherwise}
\end{cases},
\]

\[
q_E = \begin{cases} 
1 & E > 0 \\
0 & \text{otherwise}
\end{cases},
\]

\[
q_I = \begin{cases} 
1 & I > 0 \\
0 & \text{otherwise}
\end{cases},
\]

to ensure positivity and to remove any potential singularity at the origin. We once more assume that \( r > \mu \).

**Lemma 3.13.1** For a culling rate satisfying \( A_1^* < A_1 < \frac{C(r - \mu)^2}{4\mu} \) (where \( A_1^* \) is defined in equation (3.54)) the endemic equilibrium of system (3.53) is eliminated and the equilibrium population is comprised solely of susceptibles, provided that the basic reproductive ratio \( r \) is below a threshold defined in equation (3.57). For \( A_1 > \frac{C(r - \mu)^2}{4\mu} \), the population crashes.

We prove this lemma in the sections which follow.

The whole population

Summing the three differential equations of system (3.53) we have, as for continuous fixed yield culling in the SIS model,

\[
\frac{dN}{dt} = rN \left(1 - \frac{N}{C}\right) - \mu N - A_1, \quad N(0) > 0,
\]

where \( N = S + E + I \), with precisely the same equilibria and stability criteria as in system (3.14). For \( A_1 > \frac{C(r - \mu)^2}{4\mu} \), the population reaches zero in finite time.

Disease classes

There are two feasible IFEs, by analogy with the SIS model we conjecture that one will be stable and the other unstable and that the stable equilibrium is \( S_0 \) where

\[
S_0 = \frac{C}{2r} (r - \mu) + \frac{C}{2r} \sqrt{(r - \mu)^2 - \frac{4A_1 r}{C}},
\]

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while in the unstable equilibrium the square root term has a negative sign.

The endemic equilibrium, \((S^*(A_1), E^*(A_1), I^*(A_1))\) cannot be obtained in an explicit form. Again, by analogy with the SIS model we might reasonably expect there to be two endemic equilibria, one positive and stable and the other containing negative components and unstable.

Simulation with a range of parameters suggests that this is indeed the case for both the IFE and the endemic equilibrium but we cannot prove this analytically.

If we obtain (with Maple) the equations, the roots of which are \(E^*\) and \(I^*\) and find the value of \(A_1\) for which one of these roots is zero (i.e. the constant terms in the equations are zero) we have \(I^*(A_1) = 0\) and \(E^*(A_1) = 0\) for \(A = A_1^*\) where

\[
A_1^* = \frac{C}{2r^3} \left( Z \sqrt{2rCk_\beta(k + 2r + \gamma) + \kappa^2(\beta^2C^2 + r^2) + r^2\gamma(\gamma - 2\kappa)} \right)
\]

\[
(\gamma + 2\mu + \kappa)r^3 + (\kappa^2 + \mu\gamma + 3Ck_\beta + \mu\kappa + \gamma^2)r^2
\]

\[
+ (2C\beta\kappa\gamma + 2C\kappa^2\beta + Ck_\beta\mu)r + \kappa^2\beta^2C^2 \right)
\]

where \(Z = Ck_\beta + r(k + \mu + \gamma + r)\). When \(A_1 > \frac{C(r-\mu)^2}{4r}\) the population will crash, when \(A_1 = \frac{C(r-\mu)^2}{4r}\), the expressions for the three disease classes constituting the endemic equilibrium are

\[
S^* = \frac{(\mu + r + 2\gamma)(\mu + r + 2\kappa)}{4C\kappa},
\]

\[
I^* = \frac{2C\kappa\beta(r - \mu) - r(\mu + r + 2\gamma)(\mu + r + 2\kappa)}{2r\beta(\mu + r + 2(\gamma + \kappa))},
\]

\[
E^* = \frac{2C\kappa\beta(r - \mu)(r + \mu + 2\gamma) - r(\mu + r + 2\gamma)^2(\mu + r + 2\kappa)}{4r\beta\kappa(\mu + r + 2(\gamma + \kappa))}.
\]

Clearly, the disease will be eliminated, as \(A_1\) increased, at some value of \(A_1 < \frac{C(r-\mu)^2}{4r}\) if \(I^* = 0\). Solving this inequality we obtain

\[
\frac{C\kappa\beta(r - \mu)}{r(\mu + \gamma)(\mu + \kappa)} < \frac{(\mu + r + 2\gamma)(\mu + r + 2\kappa)}{2(\mu + \kappa)(\mu + \gamma)}.
\]

The left hand side of the above inequality is the basic reproductive ratio \(R_0\) for system (3.53), discussed further in Chapter 4 and thus represents the maximum value of \(R_0\) for which fixed yield culling can eradicate the disease in this SEIS model.

Stability of equilibria

The criteria for the local stability of the equilibria in this model are directly analogous to those discussed in Section 3.3. The unculled model itself (i.e. with \(A = 0\)) is considered in Chapter 4.
3.13.2 Fixed rate continuous culling in the SEIS system

The model equations are as follows:

\[
\begin{align*}
\frac{dS}{dt} &= \tau(S + E + I) \left(1 - \frac{S + E + I}{C}\right) - \mu S - \beta SI + \gamma I - H_SS, \\
\frac{dE}{dt} &= \beta SI - (\kappa + \mu)E - H_E E, \\
\frac{dI}{dt} &= \kappa E - (\mu + \gamma)I - H_I I, \\
S + E + I &= N, \quad S(0) > 0 \quad E(0) > 0 \quad I(0) > 0.
\end{align*}
\] (3.55)

The culling rates are \(H_S\) for the susceptible, \(H_E\) for latent and \(H_I\) for infected classes. If \(H_S = 0\) then only the latent and susceptible classes are culled. If \(H_S = 0\) and \(H_E \neq 0\) only the infectives are culled. When not zero, we consider that we set \(H_S = H_E = H_I = H\).

**Lemma 3.13.2** Let the number of animals required to be culled in unit time to eliminate the endemic equilibrium in the SEIS model be \(N_{\text{all}}\) when all classes are culled, \(N_{\text{EI}}\) when latent and infected classes are culled and \(N_I\) when the infected class only is culled. Then, for all values of the basic reproductive ratio above unity, \(N_{\text{all}} < N_{\text{EI}} < N_I\).

We follow the same method as in Section 3.12 to prove the lemma. We calculate the value for the culling rates at which the endemic equilibrium is eliminated in each case to be as follows:

\[
\begin{align*}
H_{\text{all}}^* &= \frac{1}{2r} \left(-2r \theta + \sqrt{\theta^2 - 4r^2 \kappa C \beta + \gamma} \right), \\
H_{\text{EI}}^* &= \frac{1}{2r} \left(-r(2\kappa + \gamma) + \sqrt{r^2(\gamma - \kappa)^2 + 4r\kappa C \beta (r - \mu)} \right), \\
H_I^* &= \frac{1}{r(\mu + \kappa)} \left(\kappa C \beta (r - \mu) - r(\mu + \kappa)(\mu + \gamma) \right),
\end{align*}
\] (3.56)

where \(\theta = r(\gamma + \kappa) + Ck\beta\) and \(H_{\text{all}}, H_{\text{EI}}, H_I^*\) are the culling rates when all classes are culled, when latent and infected classes are culled and when the infected class only is culled respectively.

The endemic equilibrium for system 3.55 is calculated in Section 4.1 to be

\[
\begin{align*}
S^* &= \frac{(\kappa + \mu)(\mu + \gamma)}{\beta \kappa}, \\
I^* &= \frac{\kappa C \beta (r - \mu) - r(\kappa + \mu)(\mu + \gamma)}{r \beta (\mu + \kappa + \gamma)}, \\
E^* &= \frac{\mu + \gamma I^*}{\kappa}
\end{align*}
\]

If we now multiply \(H_{\text{all}}^*, H_{\text{EI}}^*, H_I^*\) by the appropriate disease class sizes at this endemic equilibrium we obtain expressions for \(N_{\text{all}}, N_{\text{EI}}\) and \(N_I\), the numbers
of animals culled per unit time, starting from the endemic equilibrium.

\[ N_{\text{all}} = \frac{C(r - \mu)}{2r^2} \left( -r(\kappa + 2\mu + \gamma) - C\kappa\beta + \sqrt{((\kappa - \gamma)^2 - 4C\kappa\beta)r^2 + 2C\kappa\beta(\gamma + \kappa)r + C^2\kappa^2\beta^2} \right), \]

\[ N_{EI} = \frac{1}{2C\kappa\beta r^2} \left( -r(\mu + \kappa + 2\gamma) + \sqrt{r^2(\gamma - \kappa)^2 + 4C\beta C(r - \mu)} \right) \times \left( \kappa\beta C(r - \mu) - r(\mu + \kappa)(\mu + \gamma) \right), \]

\[ N_I = \frac{(C\kappa\beta(r - \mu) - r(\mu + \gamma)(\mu + \kappa))^2}{r^2\beta(\mu + \gamma + \kappa)(\mu + \kappa)}. \]

We find, using Maple, that these three quantities are equal when the basic reproductive ratio for the model represented by system (3.55) with zero culling, \( R_0 = 1 \) where

\[ R_0 = \frac{C\kappa\beta(r - \mu)}{r(\mu + \gamma)(\mu + \kappa)}. \] (3.57)

Simulation suggests that, as \( R_0 \) increases above unity \( N_{\text{all}} > N_{EI} > N_I \) up to a larger value of \( R_0 \), beyond which the direction of the inequality is reversed, \( N_{\text{all}} < N_{EI} < N_I \). However, we are not able to obtain an explicit form for this larger value. Thus, the most efficient strategy to destabilise the endemic disease state by continuous culling of a population with an SEIS model will depend on the value of \( R_0 \), the virulence of the disease. For a virulent disease, culling all the animals is the most effective strategy.

Although this is true for the initial rate of culling, culling all the animals must by definition continue for all time and thus in principle would require culling of an infinite number of animals. In practice we would attempt to estimate the total number to be culled to reduce the infective class or total population to some arbitrary size.

3.13.3 Fixed latent period \( \tau \) with constant yield continuous culling

The fixed latent period model we use in this section is discussed in detail in Chapter 4. We consider culling \( A \) animals per unit time. The model equations then become, for the susceptible class;

\[ \frac{dS(t)}{dt} = r(S(t) + E(t) + I(t)) \left( 1 - \frac{(S(t) + E(t) + I(t))}{C} \right) - \mu S(t) + \gamma I(t), \]

\[ -\beta S(t)I(t) - q \frac{AS(t)}{S(t) + E(t) + I(t)}, \]

\[ S(0) > 0, \quad E(0) > 0, \quad I(0) > 0, \]

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where
\[
q := \begin{cases} 
1 & : \quad (S(t) + I(t) + E(t)) > 0 \\
0 & : \quad \text{otherwise.}
\end{cases}
\]
For brevity will we let \( q = 1 \) in the rest of this section, it being understood that the effect of \( q \) is to ensure that all population classes remain non-negative. We also have \( r > \mu \). For the latent class we have
\[
E(t) = \int_{t-r}^{t} \beta C S(\theta) I(\theta) \exp \left( -\int_{\theta}^{t} \mu + \frac{A}{S(t) + E(t) + I(t)} \, d\theta \right) \, d\theta,
\]
\[\tag{3.58}\]
\[E(0) > 0, \quad S(\theta) > 0, \quad I(\theta) > 0, \quad \theta \in [-\tau, 0].\]
The per capita rate of removal of the \( E(t) \) class by natural death or culling is
\[
\left( \mu + \frac{A}{S(t) + E(t) + I(t)} \right).
\]
If we differentiate the expression for \( E(t) \) with respect to \( t \) we obtain the delay differential equation for \( E(t) \);
\[
\frac{dE(t)}{dt} = \beta C S(t) I(t) \\
- \beta C S(t - \tau) I(t - \tau) \exp \left( -\int_{t-\tau}^{t} \mu + \frac{A}{S(t) + E(t) + I(t)} \, d\theta \right) \\
- \left( \mu + \frac{A}{S(t) + E(t) + I(t)} \right) E(t).
\]
\[\tag{3.59}\]
The delay differential equation for \( I(t) \) is then
\[
\frac{dI(t)}{dt} = \beta C S(t - \tau) I(t - \tau) \exp \left( -\int_{t-\tau}^{t} \mu + \frac{A}{S(t) + E(t) + I(t)} \, d\theta \right) \\
- \left( \mu + \gamma + \frac{A}{S(t) + E(t) + I(t)} \right) I(t)
\]
\[\tag{3.60}\]
\[I(0) > 0.\]

**Lemma 3.13.3** The population defined in the system of equations (3.58), (3.59) and (3.60) crashes for \( A > A_{\text{crit}} = \frac{(r - \mu)^2}{4r} \). For \( A_{\text{crit}} > A > A^* \), (where \( A^* \) is defined implicitly in (3.63)) the infective and latent classes are eliminated and the system tends to the infection free equilibrium.

Setting the right hand sides of (3.58), (3.59) and (3.60) equal to zero and solving for the state variables we obtain the equilibria for the model system.

**Linearisation about the IFE**

There are two infection free equilibria
\[
S = \frac{1}{2r} \left( (r - \mu) \pm \sqrt{(r - \mu)^2 - 4Ar} \right)
\]
provided that \( A < A_{\text{crit}} = \frac{(r - \mu)^2}{4r} \). We know from earlier in this chapter that the expression with the positive square root is stable, that with the negative
unstable. We linearise about the stable solution which we term \( S_0 \) with \( s = S - S_0, \ e = E \) and \( i = I \) to obtain the following linearised system;

\[
\frac{ds(t)}{dt} = r(s(t) + e(t) + i(t))(1 - 2S_0) - \mu s(t) + \gamma i(t) - \beta C i(t) S_0 - \frac{A s(t)}{S_0},
\]

\[
\frac{de(t)}{dt} = \beta C i(t) S_0 - \beta C i(t - \tau) S_0 \exp\left(-\left(\mu + \frac{A}{S_0}\right) \tau\right) - \mu e(t) - \frac{A e(t)}{S_0},
\]

\[
\frac{di(t)}{dt} = \beta C i(t - \tau) S_0 \exp\left(-\left(\mu + \frac{A}{S_0}\right) \tau\right) - (\mu + \gamma)i(t) - \frac{A i(t)}{S_0},
\]

where we reasonably assume that the exponential term \( e^{\frac{\mu(t)+\gamma(t)+\mu(t)}{S_0}} \approx 1 \) for small \( t \).

We now substitute \( s(t) = a_1 \exp(\lambda t), \ e(t) = a_2 \exp(\lambda t), \ i(t) = a_3 \exp(\lambda t) \), where \( a_1, a_2, a_3 \in \mathbb{R} \) and \( \lambda \in \mathbb{C} \) (in practice we take \( \lambda \in \mathbb{R} \) since we show in Chapter 4 that the real eigenvalue is dominant) to give us

\[
a_1\lambda = r(a_1 + a_2 + a_3)(1 - 2S_0) - \mu a_1 + \gamma a_3 - \beta C a_3 S_0 - \frac{A a_1}{S_0},
\]

\[
a_2\lambda = \beta C a_3 S_0 - \beta C a_3 S_0 \exp(-\lambda t) \exp\left(-\left(\mu + \frac{A}{S_0}\right) \tau\right) - \mu a_2 - \frac{A a_2}{S_0},
\]

\[
a_3\lambda = \beta C a_3 S_0 \exp(-\lambda t) \exp\left(-\left(\mu + \frac{A}{S_0}\right) \tau\right) - (\mu + \gamma) a_3 - \frac{A a_3}{S_0}.
\]

The condition that not all the \( a_i \) are zero is that

\[
\left(-\lambda + r(1 - 2S_0) - \mu - \frac{A}{S_0}\right)\left(-\lambda - \left(\mu + \frac{A}{S_0}\right)\right)\left(-\lambda + \beta C S_0 \exp(-\lambda t) \exp\left(-\left(\mu + \frac{A}{S_0}\right) \tau\right) - (\mu + \gamma) - \frac{A}{S_0}\right) = 0.
\]

The second term in the equation above gives us \( \lambda = -\left(\mu + \frac{A}{S_0}\right) < 0 \), while the first term gives us

\[
\lambda = r(1 - 2S_0) - \left(\mu + \frac{A}{S_0}\right).
\]

We have already established that the minimum value of \( S_0 \) (for \( A < A_{\text{crit}} \)) is \( \frac{(r-A)}{2r} \), so that \( r(1 - 2S_0) \leq \mu \) and thus this value of \( \lambda \) is also always negative.

The stability of the IFE is thus entirely determined by the properties of the third term of (3.62), which we call \( \phi(\lambda) \). The IFE is stable if there is a negative root and no positive root for \( \phi(\lambda) = 0 \), for which the condition is

\[
\beta C S_0 \exp\left(-\left(\mu + \frac{A}{S_0}\right)\right) \leq (\mu + \gamma) + \frac{A}{S_0}.
\]

and \( A = A^\ast \) is the value of \( A \) which solves this inequality. Since the left hand side of (3.63) is a transcendental function of \( A \) we cannot obtain an explicit
expression for $A^*$. 

For small $\tau$ we can expand the left hand side of the inequality in a Taylor series around $\tau = 0$ and solve for $A$ to give

$$
A^* \approx \frac{(r + \gamma)(\beta C(r - \mu) - r(\mu + \gamma))}{(\beta C + \tau)^2}
+ \left(\frac{\beta C(r - \gamma)(r + \gamma)(r((\mu + \gamma) + (r + \gamma)) - \beta C(r - \mu))}{(\beta C + \tau)^4}\right)\tau.
$$

The first term is the expression for $A^*$ in the SIS model discussed earlier in this chapter (in other words with $\tau = 0$).

### 3.13.4 Fixed latent period $\tau$ with constant rate continuous culling

In this case, with a constant culling rate $H$, our model is now

$$
\frac{dS(t)}{dt} = r(S(t) + E(t) + I(t)) (1 - (S(t) + E(t) + I(t)))
- (\mu + H)S(t) + \gamma I(t) + \beta C S(t) I(t),
$$

$$
\frac{dE(t)}{dt} = \beta C S(t) I(t) - \beta C S(t - \tau) I(t - \tau) \exp\left(-\left((\mu + H)\tau - (\mu + H)E(t)\right)\right),
$$

$$
\frac{dI(t)}{dt} = \beta C S(t - \tau) I(t - \tau) \exp\left(-((\mu + H)\tau - (\mu + \gamma + H)I(t)\right),
$$

$S(0) > 0$, $E(0) > 0$, $I(0) > 0$.

$$
(3.64)
$$

**Lemma 3.13.4** The population defined in system (3.64) tends to zero as $t \to \infty$ for $H > H_{\text{crit}} = r - \mu$. For a cull rate $H_{\text{crit}} > H > H^*$, (where $H^*$ is defined implicitly in (3.65)), the endemic equilibrium is eliminated and the system tends to the infection free equilibrium.

There is an IFE for system (3.64) at $(S_0, 0, 0)$ with $S_0 = 1 - \frac{\mu + H}{r}$ provided that $H < H_{\text{crit}} = r - \mu$. There is an endemic equilibrium $(S^*, E^*, I^*)$ such that $I^* = 0$ if

$$
\beta C \exp\left(-((\mu + H)\tau - (\mu + H))\right) = \frac{r(\mu + \gamma + H)}{r - (\mu + H)}.\tag{3.65}
$$

The value of $H$ that solves (3.65) is $H^*$, we find that $S^*(H^*) = S_0$.

We note that, if we assume that in the absence of culling the disease were endemic, we would have

$$
\frac{\beta C \exp(-\mu\tau)(r - \mu)}{r(\mu + \gamma)} = R_0 e^{-\mu\tau} > 1
$$

and so by geometric arguments we establish that $H^* < H_{\text{crit}}$ is the unique positive root of (3.65).
From (3.65) we must have
\[
\beta C \exp(-(\mu + H)\tau) \geq \frac{r(\mu + \gamma)}{r - \mu},
\]
which gives an upper bound of \( H^* \leq \frac{1}{r} \ln R_0 e^{-\mu\tau} \), but simulation shows that this is too large a bound to be useful. Expanding (3.65) in a Taylor series around \( \tau = 0 \) gives an explicit expression for \( H^* \) of
\[
H^* = \frac{\beta C(r - \mu) - r(\mu + \gamma)}{\beta C + r} - \frac{(\beta C - \gamma)(r + \gamma)\beta cr^2\tau}{(\beta C + r)^3},
\]
which gives results within 0.2\% of the numerical solution to (3.65) for \( \tau = 0.25 \), three months, which is a reasonable parameter value.

### 3.14 Culling and immigration

Thus far we have considered that our system is closed. In practice that is likely to be an unrealistic assumption, however, relaxing it has profound implications for the model. We use the SIS model of system (3.2) and consider the case of net immigration into the system. Clearly, net migration out of the system will simply ensure that the culling strategy reaches its objective more rapidly than in the closed system (although of course impacting significantly in the environment neighboring our system). We continue to assume that \( \rho > \alpha \).

#### 3.14.1 Fixed rate culling and immigration of susceptibles

We assume firstly that the immigrating animals are infection free and enter the susceptible class. The non-dimensionalised model with a scaled constant rate of migration of \( m > 0 \) animals per unit time and a scaled fixed culling rate of \( \theta \) is
\[
\frac{dx}{dt} = \rho(x + y)(1 - (x + y)) - \alpha x + (1 - \alpha)y - R_0 xy - \theta x + m, \tag{3.66}
\]
\[
\frac{dy}{dt} = -y + R_0 xy - \theta y,
\]
\[
x + y = n, \quad \frac{dn}{dt} = \rho n(1 - n) - \alpha n - \theta n + m,
\]
\[
x(0) > 0 \quad y(0) > 0.
\]

The whole population

The equilibrium population is
\[
n^* = \frac{\rho - \alpha - \theta + \sqrt{(\rho - \alpha - \theta)^2 + 4\rho m}}{2\rho}.
\]

It is clear from (3.66) that the population cannot reach zero for \( m > 0 \). If we solve (3.66) for \( n(t) \) we obtain
\[
n(t) = \frac{1}{2\rho} \left( \rho - \alpha - \theta + q \tanh^{-1} \left( q t - \tanh^{-1} \frac{2\rho n_0 - (\rho - \alpha - \theta)}{q} \right) \right),
\]
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where \( q = \sqrt{(\rho - \alpha - \theta)^2 + 4\rho m} \), from which we can calculate the time to reach a given population size as a function of \( \theta \).

**Disease classes**

There are two equilibria, the IFE, \((n^*, 0)\), and the endemic equilibrium \(x^* = \frac{1+\theta}{R_b}\), as in the closed system and

\[
y^* = \frac{1}{2\rho R_b} \left( R_b(\rho - \alpha - \theta) - 2\rho(1 + \theta) + R_b\sqrt{(\rho - \alpha - \theta)^2 + 4\rho m} \right).
\]

The Jacobian at \((x^*, y^*)\) is

\[
\left( \begin{array}{cc}
\rho(1 - 2(x^* + y^*)) - \alpha - R_b y^* - \theta & \rho(1 - 2(x^* + y^*)) + 1 - \alpha - R_b x^* \\
R_b y^* & -1 + R_b x^* - \theta
\end{array} \right).
\]

At the IFE the eigenvalues of the Jacobian are

\[
\lambda_1 = \rho(1 - 2n^*) - \alpha - \theta = -\rho n^* - \frac{m}{n^*} < 0
\]

\[
\lambda_2 = -1 - \theta + \frac{1}{2\rho} \left( R_b(\rho - \alpha - \theta) + \sqrt{(\rho - \alpha - \theta)^2 + 4\rho m} \right).
\]

\( \lambda_2 \) is monotone decreasing in \( \theta \). The condition for the stability of the IFE is \( \theta > \theta^* \) and for the existence of the endemic disease state is \( \theta < \theta^* \) where

\[
\theta^* = \frac{R_b(\rho - \alpha - 1) - 2\rho + R_b\sqrt{(\rho + 1 - \alpha)^2 + 4\rho m(R_b + \rho)}}{2(R_b + \rho)}. \tag{3.67}
\]

We see that \( \theta^* \) is increasing in \( m \), increasing as the square root of the immigration rate.

At the endemic equilibrium, \((x^*, y^*)\), noting that \(-1 + R_b x^* - \theta = 0\) from the equilibrium equations, the trace of the Jacobian is

\[
\rho(1 - 2(x^* + y^*)) - \alpha - R_b y^* - \theta = -\rho x^* - \frac{m}{x^*} = -\rho y^* \left( 1 - (x^* + y^*) \right) < 0.
\]

The determinant of the Jacobian is

\[-R_b y^* (\rho(1 - 2(x^* + y^*)) + 1 - \alpha - R_b x^*)\]

and we see that

\[
\rho(1 - 2(x^* + y^*)) + 1 - \alpha - R_b x^* = \frac{1}{y^*} \left( -m - x^*(\rho(1 - x^*) - \alpha - \theta) \right),
\]

\[
= \frac{1}{y^*} \left( -m + \frac{m x^*}{n^*} \right) = \frac{m}{n^*} < 0.
\]

Hence the determinant is always positive and the endemic equilibrium is always stable when it exists.

The population size at which \( y^* = 0 \) we term \( \tilde{z}_0 \) where

\[
\tilde{z}_0 = \frac{1}{2(R_b + \rho)} \left( \rho + 1 - \alpha + \sqrt{(\rho + 1 - \alpha)^2 + 4\rho m(R_b + \rho)} \right). \tag{3.68}
\]
and $\tilde{x}_0$ is increasing in $m$. We note that

$$\sqrt{(\rho + 1 - \alpha)^2 + 4m(R_b + \rho)} > \rho + 1 - \alpha,$$

so that $\tilde{x}_0 > \frac{\rho + 1 - \alpha}{R_b + \rho}$, the population size at which the endemic equilibrium is unsustainable in the closed model. In fact, if $x_0$ is this value for the closed model, then

$$\tilde{x}_0 = \frac{x_0}{2} + \frac{1}{2}\sqrt{\frac{x_0^2 + 4m}{R_b + \rho}}.$$

Immigration of susceptibles and infectives

If there is net immigration of both susceptibles and infectives, the IFE of system (3.66) disappears, since $y = 0$ is not a solution to (3.66) with any net immigration of infectives added to the second equation and hence there is no culling regime that will eliminate the disease entirely. Numerical simulation shows that the size of the infected equilibrium class, with a culling rate that would have reduced it to zero in the absence of immigration, increases faster than the rate of infective immigration at realistic parameter values.

3.14.2 Fixed yield culling and immigration of susceptibles

The model is as follows, with a culling rate of $\theta$ animals per unit time, net immigration of $m$ susceptibles:

$$\frac{dx}{dt} = \rho(x + y)(1 - (x + y)) - ax + (1 - \alpha)y - R_bxy - q_z \frac{\theta x}{x + y} + m,$$

$$\frac{dy}{dt} = -y + R_bxy - q_y \frac{\theta y}{x + y},$$

$x(0) > 0, \quad y(0) > 0$

where

$$q_z := \begin{cases} 1 & : x > 0 \\ 0 & : \text{otherwise} \end{cases}$$

and

$$q_y := \begin{cases} 1 & : y > 0 \\ 0 & : \text{otherwise} \end{cases}.$$

As far as the total population is concerned, the analysis is precisely the same as in the closed model with a culling rate of $\theta - m$. Thus the critical value of $\theta$ above which there is a population crash is

$$\theta_{\text{crit}} = \frac{(\rho - \alpha)^2}{4\rho} + m$$

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There are two IFEs, one stable and one unstable and one feasible (i.e. both components positive) endemic equilibrium \((x^*, y^*)\) where

\[
x^* = \frac{1}{2R_b(m - \theta)} \left( \theta(\alpha - \rho - 2) + 2m + \theta\sqrt{(\rho - \alpha)^2 - 4\rho(\theta - m)} \right),
\]

\[
y^* = \frac{1}{2R_b\rho(m - \theta)} \left( \theta (R_b(\rho - \alpha) + \rho(\rho - \alpha + 2)) + m(R_b(\rho - \alpha) - 2\rho) + (R_b(m - \theta) - \rho\theta) \sqrt{(\rho - \alpha)^2 + 4\rho(m - \theta)} \right).
\]

We find numerically that \(y^*\) is monotone decreasing in \(\theta\) and that \(y^* = 0\) for \(\theta = \theta^*\), where

\[
\theta^* = \frac{1}{2(R_b + \rho)^2} \left( 2mR_b(R_b + \rho) + (R_b(\rho - \alpha) - \rho)(\rho + 1 - \alpha) + (R_b(\rho - \alpha) - \rho)\sqrt{(\rho + 1 - \alpha)^2 + 4m(R_b + \rho)} \right).
\]

We are assuming that \(R_b > \frac{\rho}{\rho - \alpha}\), i.e. there would be endemic disease in the absence of culling.

The value of \(\theta\) at which the determinants of the linearisations of system (3.69) about the IFE and the endemic equilibrium are zero is \(\theta = \theta^*\). By simulation we are able to establish that the determinant at the IFE is positive for \(\theta > \theta^*\) and that at the endemic equilibrium positive for \(\theta < \theta^*\). In both cases the traces of the determinant are negative at \(\theta = \theta^*\).

While \(\theta_{\text{crit}}\) increases linearly as \(m\) increases, \(\frac{d\theta_{\text{crit}}}{dm} = 1\), \(\theta^*\) increases more rapidly since \(\frac{d\theta^*}{dm} > R_b\).

It is clearly a routine exercise to calculate the time taken for the population to crash or to reduce to the level at which no endemic disease is sustainable, \(x_0\) as defined in (3.68).

Once more, with net immigration of infectives, the IFE disappears and the endemic equilibrium cannot be removed by culling.

### Impulsive culling

It is relatively straightforward to apply impulsive culling regimes to the system with net immigration. We find analogous results to those obtained in the continuous case.

#### 3.15 Culling a single species with a fixed birth rate

We might conjecture that the particular results obtained in this chapter arise because of the choice of fecundity function. In this section we consider a model system with a constant birth rate and observe essentially similar results to those observed with a logistic fecundity function. We use \(A\) as the
culling parameter, $A_{\text{crit}}$, as the value of $A$ at which the population crashes or is eradicated and $A^*$ the value of $A$ at which the endemic equilibrium is eliminated. We assume that $A > 0$ only when the population being culled takes a strictly positive value.

### 3.15.1 The whole population

The model developed in Chapter 2 for the whole population was

$$\frac{dN}{dt} = \Lambda - \mu N, \quad N(0) = N_0 > 0. \quad (3.70)$$

Here $\Lambda$ is the birth rate and $\mu$ the per capita death rate. Equation (3.70) has a single, stable equilibrium at $N^* = \frac{\Lambda}{\mu}$. We can non-dimensionalise (3.70) in the usual way, $n'(t) = \alpha(1 - n(t))$, where $\alpha < 1$ and solve to obtain

$$n(t) = 1 + (n_0 - 1)e^{-\alpha t}, \quad (3.71)$$

where $n_0 = \frac{N_0}{N^*}$

**Continuous fixed yield culling**

The non-dimensionalised model is

$$\frac{dn}{dt} = \alpha(1 - n) - A, \quad n(0) = n_0 > 0. \quad (3.72)$$

We can solve (3.72) to give

$$n(t) = 1 - \frac{A}{\alpha} + \left(n_0 - 1 + \frac{A}{\alpha}\right)e^{-\alpha t},$$

which allows us to calculate that, for sufficiently large $A$ the population will reach zero in finite time, in fact this time is $\tau_0$ which is given by

$$\tau_0 = \frac{1}{\alpha} \ln \left(\frac{A + \alpha(n_0 - 1)}{A - \alpha}\right), \quad A > \alpha.$$  

The equilibrium population is now $n^*(A) = 1 - \frac{A}{\alpha}$, so that the critical culling rate for a population crash to occur will be $A_{\text{crit}} = \alpha$.

**Continuous fixed rate culling**

The model is

$$\frac{dn}{dt} = \alpha(1 - n) - An, \quad n(0) = n_0 > 0,$$

which has the solution

$$n(t) = \frac{\alpha}{\alpha + A} + \left(n_0 - \frac{\alpha}{\alpha + A}\right)e^{-(A+\alpha)t}.$$  

There is an equilibrium at $n^*(A) = \frac{\alpha}{\alpha + A}$, from which we can see that there is no finite $A_{\text{crit}}$.  

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Impulsive fixed yield culling

We model this as follows;

\[
\frac{dn}{dt} = \alpha(1 - n(t)) \quad \text{for} \quad t \in \{(mT, (m + 1)T), m \in \mathbb{N}\},
\]

\[n(mT^+) = n(mT^-) - A.\]

There is a fixed point for (3.73) at \(n_{\text{yield}}\) where

\[n_{\text{yield}} = 1 - \frac{A}{1 - e^{-\alpha T}} \quad \text{for} \quad A < 1 - e^{-\alpha T}.\]  

The population thus crashes for \(A > 1 - e^{-\alpha T}\).

Impulsive fixed rate culling

The model is as follows, with \(A < 1\),

\[
\frac{dn}{dt} = \alpha(1 - n(t)) \quad \text{for} \quad t \in \{(mT, (m + 1)T), m \in \mathbb{N}\},
\]

\[n(mT^+) = n(mT^-)(1 - A).\]

System (3.75) has a fixed point, \(n_{\text{rate}}\), where

\[n_{\text{rate}} = \frac{(1 - A)(1 - e^{-\alpha T})}{1 - e^{-\alpha T}(1 - A)} \quad \text{for} \quad A < 1.\]

3.15.2 The fixed birth rate SIS model with continuous fixed yield culling

The non-dimensionalised equations corresponding to (2.4) are

\[
\frac{dx}{dt} = \alpha(1 - x) + (1 - \alpha)y - R_0xy - \frac{Ax}{x + y},
\]

\[
\frac{dy}{dt} = -y + R_0xy - \frac{Ay}{x + y},
\]

\[x(0) > 0, \quad y(0) > 0.\]

There are two equilibria for system (3.76), the IFE \((1 - \frac{A}{\alpha}, 0)\) and the endemic equilibrium,

\[x^*(A) = \frac{A(\alpha - 1) + \alpha}{R_0(\alpha - A)}, \quad y^*(A) = \frac{R_0(\alpha - A)^2 - \alpha(\alpha - A + \alpha A)}{\alpha R_0(\alpha - A)}.\]

We see that \(y^*(A) \geq 0\) for

\[A \leq A^* = \frac{\alpha}{2R_0} \left(2R_0 + \alpha - 1 - \sqrt{(1 - \alpha)^2 + 4\alpha R_0}\right)\]

and that when \(y^*(A) = 0\) we have

\[x^*(A) = x_0 = \frac{1}{2R_0} \left(1 - \alpha + \sqrt{(1 - \alpha)^2 + 4\alpha R_0}\right).\]  

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Moreover we see that \( \lim_{R_0 \to \infty} A^* = \alpha = A_{\text{crit}} \) so that there is no restriction imposed by the size of \( R_0 \) on the elimination of the infected class by continuous fixed yield culling as there is in the case that a logistic recruitment function is used.

The eigenvalues of the Jacobian of the linearisation of (3.76) about the IFE are

\[
\lambda_1 = -\alpha, \quad \lambda_2 = -1 - \frac{\alpha A}{\alpha - A} + \frac{R_0(\alpha - A)}{\alpha}.
\]

Now,

\[
\frac{d\lambda_2}{dA} = -\left( \frac{\alpha^2 + R_0(\alpha - A)^2}{\alpha(\alpha - A)^2} \right) < 0,
\]

so that \( \lambda_2 \) is decreasing in \( A \) and is negative for \( A > A^* \). The IFE is locally stable for \( A_{\text{crit}} > A > A^* \).

The eigenvalues of the Jacobian of the linearisation about the endemic equilibrium are \( \lambda_1, -\lambda_2 \), so the endemic equilibrium is stable only if \( A < A^* \).

### 3.15.3 The fixed birth rate SIS model with continuous fixed rate culling

The non-dimensionalised model is

\[
\begin{aligned}
\frac{dx}{dt} &= \alpha(1 - x) + (1 - \alpha)y - R_0xy - Ax \\
\frac{dy}{dt} &= -y + R_0xy - Ay
\end{aligned}
\]  

(3.78)

System (3.78) has two equilibria, the IFE and the endemic equilibrium

\[
x^* = \frac{1 + A}{R_0}, \quad y^* = \frac{\alpha(R_0 - 1) - A(\alpha + A + 1)}{R_0(\alpha + A)}.
\]

The endemic equilibrium exists provided that

\[
A < A^* = \frac{1}{2} \left( -1 + \alpha + \sqrt{(1 - \alpha)^2 + 4\alpha R_0} \right).
\]

When \( y^*(A) = 0 \) once more \( x^*(A) = \bar{x}_0 \), where \( \bar{x}_0 \) is defined in (3.77) above.

The eigenvalues of the Jacobian of (3.78) linearised about the IFE are

\[
\mu_1 = -(\alpha + A), \quad \mu_2 = \frac{\alpha R_0}{\alpha + A} - 1 - A.
\]

Since

\[
\frac{d\mu_2}{dA} = -\frac{(\alpha + A)^2 + \alpha R_0}{(\alpha + A)^2} < 0
\]

\( \mu_2 \) is decreasing in \( A \) and \( \mu_2 < 0 \) for \( A > A^* \). The eigenvalues of the Jacobian of the linearisation about the endemic equilibrium are \( \mu_1, -\mu_2 \), so that we can conclude that the IFE is locally stable for \( A > A^* \), the endemic equilibrium for \( A < A^* \). If \( A > A^* \), then \( \lim_{t \to \infty} y(t) = 0 \).
The fixed birth rate SIS model with impulsive fixed yield culling

The impulsive fixed yield model is

\[
\frac{dx}{dt} = \alpha (1 - x) + (1 - \alpha)y - R_0xy,
\]
\[
\frac{dy}{dt} = -y + R_0xy \quad \text{for} \quad t \in \{(mT, (m + 1)T), m \in \mathbb{N}\},
\]
\[
x(mT+) = x(mT-) - \frac{Ax(mT-)}{n(mT-)}, \quad y(mT+) = y(mT-) - \frac{Ay(mT-)}{n(mT-)}.
\]

We have already found an expression for the total population in equation (3.71), substituting for \( x \) in (3.79) allows us to find an expression for \( y(t) \) between culls in the same manner as in Section 3.7.

\[
y(t) = \frac{y_m e^{((R_0-1)(t-mT) - \frac{1}{\alpha} R_0(1-n_o) e^{-\alpha(t-mT))}}}{R_0 y_m \int_{mT}^{t} e^{((R_0-1)(r-mT) - \frac{1}{\alpha} R_0(1-n_o) e^{-\alpha(r-mT))}} dr + e^{\frac{R_0(n_o-1)}{\alpha}}}
\]

The culling process is the map

\[
y_{m+1} = \frac{y_m e^{((R_0-1)T - \frac{1}{\alpha} R_0(1-n_m) e^{-\alpha T})}}{R_0 y_m \int_{mT}^{(m+1)T} e^{((R_0-1)(r-mT) - \frac{1}{\alpha} R_0(1-n_m) e^{-\alpha(r-mT))}} dr + e^{\frac{R_0(n_m-1)}{\alpha}}}
\]

where \( n_m \) is the total population at the start of the \( m \)th cull. For sufficiently large \( m \) either the whole population has a limit cycle or it crashes. Assuming that the population has reached the limit cycle, substituting the fixed point value already found for \( n_{\text{yield}} \) in (3.74) for \( n_m \) we can obtain an implicit expression for the value of \( A \) at which the fixed point for the infective class disappears:

\[
\frac{1 - A - e^{\alpha T}}{1 - e^{\alpha T}(1 + A)} \exp \left( (R_0 - 1)T - \frac{R_0 A(1 + e^{-\alpha T})}{\alpha(1 - e^{-\alpha T})} \right) = 1.
\]

If we call the left hand side of (3.81) \( g(A) \), then we see that \( g(0) = e^{T(R_0-1)} > 1 \) while \( g'(0) = -\frac{e^{T(R_0-1)}}{\alpha} g(T(R_0-1)) < 0 \) and we can calculate that \( \lim_{A \to \infty} g(A) = 0 \) Simulation suggests that \( g'(A) < 0 \) for all \( A > 0 \) so we can reasonably assume that there is a unique positive root for (3.81) which is \( A^* \).

The fixed birth rate SIS model with impulsive fixed rate culling

The fixed rate impulsive culling model is

\[
\frac{dx}{dt} = \alpha (1 - x) + (1 - \alpha)y - R_0xy,
\]
\[
\frac{dy}{dt} = -y + R_0xy \quad \text{for} \quad t \in \{(mT, (m + 1)T), m \in \mathbb{N}\}
\]
\[
x(mT+) = x(mT-) - Ax(mT-) \quad y(mT+) = y(mT-) - Ay(mT-).
\]

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The value of $y(t)$ between culls is given by (3.80) and the culling process is the map

$$y_{m+1} = \frac{y_m e^{((R_0-1)T-\frac{T}{\alpha} R_0(1-n_m) e^{-\alpha T})(1-A)}{R_0 y_m \int_{mT}^{(m+1)T} e^{((R_0-1)(r-mT)-\frac{T}{\alpha} R_0(1-n_m) e^{-\alpha (r-mT)})} dr + e^{-R_0 n_m}}$$

where $n_m$ is the total population at the start of the $m$th cull. For sufficiently large $m$ either the whole population has a limit cycle or it crashes. Assuming that the population has reached the limit cycle, substituting the fixed point value already found for $n_{rate}$ in (3.75) for $n_m$ we can obtain an implicit expression for the value of $A$ at which the fixed point of the infective class disappears.

$$(1 - A) \exp \left( T(R_0 - 1) - \frac{A R_0 (1 + e^{-\alpha T})}{\alpha (1 - e^{-\alpha T}(1 - A))} \right) = 1. \quad (3.83)$$

If we call the left hand side of (3.83) $h(A)$ then then we see that $h(0) = e^{T(R_0-1)} > 1$ while $h'(0) = -\frac{A}{\alpha} e^{T(R_0-1)} < 0$ and we can calculate that $\lim_{A \to \infty} h(A) = -\infty$. Simulation suggests that $h'(A) < 0$ for all $A > 0$ so we can reasonably assume that there is a unique positive root for (3.83) which is $A^*$. 

Comparison with the model with logistic population dynamics

The only qualitative difference between the fixed birth rate and logistical models is that in the former case there is no upper bound on $R_0$, above which it is impossible to eliminate the endemic equilibrium by fixed yield culling without crashing the population.

3.16 Culling in the two species SIS model

We now apply the analysis we have just used to study the single animal system to the two animal system (2.14). We make only two different assumptions from system (2.14), namely that the numbers of cattle are constant for all time (in practice this replicates a farmer's replacement of any stock which die with another susceptible animal), and that we apply a logistic fecundity function to the badger population as in the rest of this chapter. We also assume that, in the absence of infective badgers, cattle would be infection free. All the parameters are as defined in Section 2.4.1. and the total cattle population is normalised to unity.
3.16.1 Continuous fixed yield culling - two species

The system is as follows, $v(t)$ are infective cattle, $x(t)$ susceptible badgers and $y(t)$ infective badgers and the culling rate is $G$ badgers per unit time;

$$\frac{dv}{dt} = -v + R_c v(1 - v) + \kappa U_c y(1 - v),$$

$$\frac{dx}{dt} = \kappa \rho (x + y)(1 - x - y) - \kappa ax + \kappa (1 - \alpha) y - \kappa R_b x y - U_b x v - \frac{\kappa G x}{x + y},$$

$$\frac{dy}{dt} = -\kappa y + \kappa R_b x y + U_b x v - \frac{\kappa G y}{x + y},$$

$v(0) > 0$, $x(0) > 0$, $y(0) > 0$, (3.84)

where

$$q_x = \begin{cases} 1 & \text{if } x > 0 \\ 0 & \text{otherwise} \end{cases}$$

and

$$q_y = \begin{cases} 1 & \text{if } y > 0 \\ 0 & \text{otherwise} \end{cases}$$

to ensure positivity and to remove any potential singularity at the origin.

Theorem 3.16.1 If the culling rate $G > G_{\text{crit}}$ where

$$G_{\text{crit}} = \frac{(\rho - \alpha)^2}{4\rho},$$

(3.85)

the population of badgers will crash. If $G$ is bounded by $G_{\text{crit}} > G > G^*$, where $G^*$ is defined in equation (3.86), then the infective badgers will be eradicated and system (3.84) will display an infection free equilibrium in both species, provided that the basic reproductive ratio for infection badgers, $R_b < \hat{R}_b$, where $\hat{R}_b$ is defined in equation (3.87).

We prove this theorem in this section by finding the eigenvalues of the Jacobian of the linearisation around the IFE and the condition on $G$ that they are all negative. We then show that this same condition on $G$ ensures the non-positivity of the endemic equilibrium population of infected badgers.

Infection free equilibrium and stability

The IFE is $(0, \frac{1}{2\rho} ((\rho - \alpha) + \sqrt{(\rho - \alpha)^2 - 4G\rho}), 0)$, precisely the same for badgers as in the single species case. The eigenvalues of the Jacobian of the linearisation around the IFE are $\lambda_1 = -\kappa \sqrt{(\rho - \alpha)^2 - 4G\rho}$, which is always negative (for $G < G_{\text{crit}}$) and two extremely complicated expressions for eigenvalues $\lambda_2$ and $\lambda_3$, both of which are zero for $G = G^*$, where

$$G^* = \frac{(\rho + 1 - \alpha)(1 - R_c)(R_c R_b + R_b (\rho - \alpha) - \rho - (\rho - \alpha)(R_b R_c - U_b U_c))}{((R_c - 1)(R_b + \rho) - U_b U_c)^2}.$$

(3.86)

We consider the situation where $R_c < 1$, so that in the absence of infective badgers there would be no endemic disease in cattle. If $R_c > 1$ it will not be
possible to eliminate the disease by culling badgers only (simulation suggests that for $R_c > 1, G^* < 0$)

By numerical simulation we can demonstrate that both of these two eigenvalues are strictly decreasing in $G$ but we cannot prove this analytically. Thus if $G > G^*$ then the IFE is stable, provided that $G^* < G_{\text{crit}}$. We can show, again numerically, that the determinant of the Jacobian of the linearisation around the IFE is positive for $G < G^*$ (unstable equilibrium), negative for $G > G^*$ (stable equilibrium) and, after reaching a minimum, is not defined for $G > G_{\text{crit}}$. We note, en passant, that $G^* > 0$ is always true if there is endemic disease, for we require

$$U_b U_c (\rho - \alpha) - (R_b (\rho - \alpha) - \rho)(1 - R_c) > 0,$$

which is the same as

$$\frac{U_b U_c (\rho - \alpha)}{(1 - R_c)(R_b (\rho - \alpha) - \rho)} = R_{bc} > 1.$$

Here $R_{bc}$ is the threshold parameter for the unculled two animal system. We found in Chapter 2 that, when one species alone has a basic reproductive ratio greater than unity and the other species a basic reproductive ratio less than unity - the position we assume here, $R_{bc} < 0$. The IFE is only stable for $0 < R_{bc} < 1$

The maximum value of $R_b$ for which $G^* < G_{\text{crit}}$, say $\hat{R}_b$, is found by solving the latter inequality to obtain

$$\hat{R}_b = \frac{\rho(1 - R_c)(\rho + 2 - \alpha) - U_b U_c (\rho - \alpha)}{(\rho - \alpha)(1 - R_c)} .$$

(3.87)

The size of the susceptible badger population for $G = G^*$ is $\hat{x}_0$, (obtained by substituting $G = G^*$ in the expression for the susceptible equilibrium population and noting, in the next section that the infective species reaches zero at $G = G^*$) where

$$\hat{x}_0 = \frac{(1 - R_c)(\rho + 1 - \alpha)}{(1 - R_c)(R_b + \rho) + U_b U_c} .$$

(3.88)

We see that $\hat{x}_0$ is decreasing in $U_b U_c$ and, we also see that

$$\frac{d \hat{x}_0}{d R_c} = -\frac{U_b U_c (\rho + 1 - \alpha)}{((1 - R_c)(R_b + \rho) + U_b U_c)^2} < 0.$$

Thus $\hat{x}_0$ is decreasing in $R_c$, the basic reproductive ratio for the epidemic among cattle. Thus the more infective the disease among cattle, or the greater the cross infectivity, the larger the numbers of badgers that will need to be culled to eliminate the disease.

Endemic disease state

We cannot obtain explicit expressions for the endemic equilibrium of system (3.84). However, if once more we take $t$ large enough that we can consider the
population of badgers to be constant (as discussed in the Introduction), then we can substitute

\[ x = \frac{\rho - \alpha + \sqrt{(\rho - \alpha)^2 - 4\rho G}}{2\rho} - y \]

and reduce the order of system (3.84) from three to two.

With a repetition of the analysis in sections 2.5 to 2.7 we examine the geometry of the \((v, y)\) phase plane and the condition that the \(v\) and the \(y\) nullclines, which always intersect at the origin, also intersect again in the first quadrant. We find this condition to be \(G^* < G < G_{\text{crit}}\), with \(G^*\) defined by equation (3.86) and \(G_{\text{crit}}\) by equation (3.85). When \(G = G^*\), \(v = 0\), \(y = 0\) as required.

Finally, if we compute the spectral radius \((\Pi(G))\) of the next generation matrix we find that \(G^*\) is the root of \(\Pi(G) - 1 = 0\).

### 3.16.2 Continuous fixed rate culling-two species

The model equations are as follows, for culling proportion \(H\) of badgers per unit time, with the same variables and parameters as in the previous section and assuming that, in the absence of culling, the system would tend to the endemic equilibrium.

\[
\begin{align*}
\frac{dv}{dt} &= -v + R_c v(1 - v) + \kappa U_c y(1 - v), \\
\frac{dx}{dt} &= \kappa p(x + y)(1 - x - y) - \kappa \alpha x + \kappa (1 - \alpha) y - \kappa R_b x y - U_b x v - \kappa H x, \\
\frac{dy}{dt} &= -\kappa y + \kappa R_b x y + U_b x v - \kappa H y,
\end{align*}
\]

\[ v(0) > 0, \quad x(0) > 0, \quad y(0) > 0. \quad (3.89) \]

**Theorem 3.16.2** If \(H_{\text{crit}} < H < H^*\), where

\[ H_{\text{crit}} = \rho - \alpha \]

and

\[ H^* = \frac{U_b U_c (\rho - \alpha) + (1 - R_c)(R_b (\rho - \alpha) - \rho)}{(1 - R_c)(R_b + \rho) + U_b U_c}, \quad (3.90) \]

then system (3.89) displays a stable infection free equilibrium and the endemic equilibrium does not exist, no matter what the value of the system parameters. If \(H > H_{\text{crit}}\), the population goes to zero as \(t \to \infty\).

**Equilibria**

There are, as usual, three equilibria for system (3.89); eradication, \((0, 0, 0)\), the infection free equilibrium \(\left(0, 1 - \frac{\alpha + H}{\rho}, 0\right)\) and the endemic equilibrium.
Existence and stability of equilibria

The eradication equilibrium is an attractor if $H > H_{\text{crit}} = (\rho - \alpha)$, while the IFE is locally asymptotically stable if

$$H_{\text{crit}} > H > H^* = \frac{U_b U_c (\rho - \alpha) + (1 - R_c)(R_b (\rho - \alpha) - \rho)}{(1 - R_c)(R_b + \rho) + U_b U_c}.$$ 

We also obtain the same value for $H^*$ from computing the spectral radius ($\Pi(H)$) of the next generation matrix; we find that $H^*$ is the root of $\Pi(H) - 1 = 0$. When $H = H^*$, substituting in the expression for the susceptible population at the IFE we have the same susceptible population size as in fixed yield continuous culling, defined in (3.88).

$$x = x_0 = \frac{(1 - R_c)(\rho + 1 - \alpha)}{(1 - R_c)(R_b + \rho) + U_b U_c},$$

Although we cannot compute the endemic equilibrium explicitly we can express it as

$$x^* = \psi, \quad y^* = (1 - \psi - \frac{\alpha + H}{\rho}), \quad v^* = \frac{\kappa (R_b \psi - H - 1)(H + \alpha + \rho (\psi - 1))}{\rho U_b \psi},$$

where $\psi$ is a positive root of $f(x) = 0$ where

$$f(z) = z^3 \kappa \rho MR_b + \left( \rho U_b R_b - \kappa \rho U_b U_c (1 + H) - (\kappa R_b P - \rho (U_b + 2 \kappa (1 + H))) M \right) z^2 \quad (1 + H) \left( 2 \kappa MP + \kappa \rho (1 + H) + \rho U_b R_b + 2 \kappa PU_b U_c - \rho U_b \right) z$$

$$- P \kappa R_c (1 + H)^2$$

and where $P = \rho - \alpha - H$ and $M = R_b R_c - U_b U_c$.

If we, reasonably, assume that the coefficient of $z^3$ is positive, i.e. that inter-species infectivity is greater than intra-species infectivity, the constant term being negative we can be sure that there is at least one positive real root, but we cannot verify analytically the sign of the coefficient of $z^2$. If this coefficient is positive we have a sufficient (but not necessary) condition that the positive root is unique. (We conjecture, supported by numerical simulation, that it is.) We find (using Maple) that when $H = H^*$ both $v = 0$ and $y = 0$ and that this is moreover the value of $H$ at which $x^* = \frac{1 - \alpha + H}{\rho} = \tilde{x}$.

We can reduce the dimension of system (3.89) by taking $t$ to be large enough that we can consider the population of badgers to be constant and substitute for the susceptible class, $x$. Repeating the analysis in Sections 2.5 to 2.7 we find the condition that the $\dot{v}$ and the $\dot{y}$ nullclines, which always intersect at the origin, also intersect again in the first quadrant, is $H^* < H < H_{\text{crit}}$.

3.16.3 Impulsive culling in the two species model

We are not at this stage able to make any substantive progress algebraically with impulsive culling of badgers in the two species model.
3.17 Conclusions

We have shown that both fixed rate culling and fixed yield culling can, provided that the culling rates are within bounds we have established, eliminate the endemic disease equilibrium in a variety of models. Fixed yield culling can only eliminate the endemic equilibrium, however, in a model with a logistic fecundity function without the population crashing if the basic reproductive ratio for the system is relatively low, while there are no such constraints on fixed rate culling. Fixed yield culling can also lead to a population crash if the rate of culling exceeds a critical upper bound. Fixed rate culling, on the other hand, leads to eradication only as $t \to \infty$. We have shown that impulse culling in the one animal SIS model can be analysed in the same way as continuous culling and lead to analogous conclusions. The limit of impulsive culling as the frequency of culls goes to infinity is continuous culling. We hypothesise that this will prove to be true for the other models examined in this chapter. Finally we have shown that culling the infected class only may not be an efficient way to destabilise an endemic equilibrium.
Chapter 4

Models with a latent class

Hitherto, we have essentially been concerned with SIS models, where animals, once infected, become immediately infectious. In practice however, we need to consider a latent period when modelling a disease such as tuberculosis in badgers; research suggests that this period averages three to five months. There are essentially two ways to model a latent compartment; we may specify that the length of the latency period is a continuous random variable with a given distribution, or that it is constant. In this chapter we consider SEIS models (where we traditionally use $E$ (for Exposed) as the symbol for the latent compartment) using both approaches.

4.1 Exponentially distributed latency period

We continue to use the same assumptions as we made when considering the SIS model of system (2.1), except that we now introduce a latency period, when the animal, although infected, shows no symptoms and is not infectious. We consider the length of the latent period to be exponentially distributed with mean $\frac{1}{\lambda}$. (See Section 2.1 for a description of the exponential distribution.) While a more accurate model would consider explicitly the "disease age", the time since first infected, the exponential distribution is a widely used method of modelling a latency period and has the merit of simplicity.

4.1.1 The SEIS model

We use the following model, based on the models described in, for example, [8], [30], [11] and [21], where $S$, $E$ and $I$ are susceptible, latent and infectious classes respectively, $\mu$ is the death rate, $\gamma$ the recovery rate, $r$ the raw birth rate and $C$ the carrying constant for the environment;

\[
\frac{dS}{dt} = r(S + E + I) \left(1 - \frac{S + E + I}{C}\right) - \mu S - \beta SI + \gamma I,
\]

\[
\frac{dE}{dt} = \beta SI - (\kappa + \mu)E, \quad \frac{dI}{dt} = \kappa E - (\mu + \gamma)I, \tag{4.1}
\]

\[S(0) > 0, \quad E(0) \geq 0, \quad I(0) \geq 0 \quad S + E + I = N.\]

We assume, as usual, that the system is initially at an infection free equilibrium and that at $t = 0$ an infective is introduced to the system. There
are no additional deaths due to disease in this model. All the other model assumptions are as already discussed in Chapter 3.

4.1.2 Positivity

Lemma 4.1.1 $S(t), E(t)$ and $I(t)$ are non negative for all $t \geq 0$.

We prove this lemma by contradiction; let us assume that $S(0) > 0, E(0) > 0, I(0) > 0$ and that one or more of $S(t), E(t)$ or $I(t)$ become negative for some $t > 0$.

Suppose that the first of the three state variables to reach zero is $S$ and this happens when $t = t^* > 0$. Then

$$\frac{dS}{dt}(t^*) = r(E + I) \left(1 - \frac{E + I}{C}\right) + \gamma I > 0$$

by assumption. (As explained in Section 3.1, we define the fecundity function to be always non-negative.) Thus, by continuity of $S(t)$, $S(t^*) < 0$ for some $t < t^*$. Hence we contradict the assertion that $t^*$ was the first time that $S(t) = 0$, so we must have $S(t) > 0$ for all $t > 0$. The same argument evidently applies to the other two state variables mutatis mutandis. Thus none of the three variables can be the first to go negative.

We are still left with the need to exclude the possibility that two or more of the state variables go to zero simultaneously. Let us assume that $S(t), E(t)$ and $I(t)$ all reach zero for the first time at $t = t^* > 0$. Let $\hat{t} = t^* - t$ and let us shift the origin and introduce a new function $\hat{S}(\hat{t})$, defined by

$$S(t) = S(t^* - \hat{t}) = \hat{S}(\hat{t}),$$

and likewise for $E(t)$ and $I(t)$. Then

$$\frac{d\hat{S}}{d\hat{t}} = \frac{dS}{dt} \frac{dt}{d\hat{t}} = -\frac{dS}{dt},$$

and, once more, likewise for $E(t)$ and $I(t)$. We can thus write system (4.1) in terms of the new variables as

$$\frac{d\hat{S}}{d\hat{t}} = - \left[ r(\hat{S} + \hat{E} + \hat{I}) \left(1 - \frac{\hat{S} + \hat{E} + \hat{I}}{C}\right) - \mu \hat{S} - \beta \hat{S} \hat{I} + \gamma \hat{I} \right],$$

$$\frac{d\hat{E}}{d\hat{t}} = - \left[ \beta \hat{S} \hat{I} - (\kappa + \mu) \hat{E} \right], \quad \frac{d\hat{I}}{d\hat{t}} = - \left[ \kappa \hat{E} - (\mu + \gamma) \hat{I} \right],$$

$\hat{S}(0) = 0, \quad \hat{E}(0) = 0, \quad \hat{I}(0) = 0, \quad$ since $S(t^*) = 0, \quad E(t^*) = 0$ and $I(t^*) = 0$.

The unique solution of this system is

$$\hat{S}(\hat{t}) \equiv 0, \quad \hat{E}(\hat{t}) \equiv 0, \quad \hat{I}(\hat{t}) \equiv 0, \quad \hat{t} > 0.$$ 

However, $S(t), E(t)$ and $I(t)$ should all be strictly positive for $t < t^*$ and therefore we should have

$$\hat{S}(\hat{t}) > 0, \quad \hat{E}(\hat{t}) > 0, \quad \hat{I}(\hat{t}) > 0 \quad \text{for} \quad \hat{t} > 0.$$

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This contradicts the uniqueness of solutions of an o.d.e. Thus all three state
variables cannot reach zero simultaneously.

To show that \( E(t) \) and \( I(t) \) cannot both reach zero simultaneously, we deploy
the same argument applied just to these two variables to obtain a contradic-
tion.

If \( S(t) \) and \( E(t) \) were both to reach zero for the first time simultaneously
at \( t = t^* \) we would have

\[
\frac{dS}{dt} \bigg|_{t=t^*} = rI \left( 1 - \frac{I}{C} \right) + \gamma I > 0,
\]

which leads to the same contradiction as we found at the beginning of this
section. This argument can also be deployed to show that \( S(t) \) and \( I(t) \) can-
not both go to zero simultaneously.

Thus we have shown that the state variables are positive for all \( t > 0 \). \( \square \)

**Boundedness**

Our solving directly the differential equation for \( N = S + I + E \) in Section
4.1.3 and the positivity of the state variables proves that \( S(t), E(t) \) and \( I(t) \)
are all bounded from above and system (4.1) is well posed.

**Theorem 4.1.2** System (4.1) has three equilibria; eradication, an infection
free equilibrium and an endemic equilibrium. The eradication equilibrium is
unstable if \( r > \mu \). If \( R_0 < 1 \), where

\[
R_0 = \frac{\kappa C \beta (r - \mu)}{r (\mu + \gamma)(\mu + \kappa)}, \tag{4.2}
\]

the infection free equilibrium is globally stable. If \( R_0 > 1 \) the endemic equilib-
rium exists; whenever the endemic equilibrium exists it is locally stable. Thus
system (4.1) has two transcritical bifurcations.

The following two sections contain the proof of this theorem.

**4.1.3 Eradication equilibrium**

At \((0,0,0)\) the eigenvalues of the Jacobian of the linearisation are

\[
\lambda_{1,1} = r - \mu, \quad \lambda_{1,2} = -(\mu + \kappa), \quad \lambda_{1,3} = -(\mu + \gamma).
\]

If \( \mu > r \) then the eradication equilibrium is globally attracting. We can see
this by solving

\[
\frac{dN}{dt} = rN \left( 1 - \frac{N}{C} \right) - \mu N, \quad N(0) = N_0,
\]

to obtain

\[
N(t) = \frac{N_0 C (r - \mu)}{r N_0 + e^{-(r-\mu)t} C (r - \mu) - r N_0}.
\]

If \( \mu > r \) then as \( t \to \infty \) \( N(t) \to 0 \), while if \( \mu < r \) then as \( t \to \infty \)
\( N(t) \to \frac{C (r - \mu)}{r} \), which is the size of the infection-free susceptible population.
4.1.4 The infection free equilibrium

This equilibrium exists, provided that $r > \mu$, at $(N^*, 0, 0)$ where we define $N^* = \frac{C(r - \mu)}{r}$. Linearising system (4.1) around this equilibrium we find the eigenvalues of the Jacobian to be

$$
\begin{align*}
\lambda_{2,1} &= -\lambda_{1,1} \\
\lambda_{2,2} &= \frac{1}{2r} \left(-r(\mu + \gamma) - r(\mu + \kappa) + \sqrt{r^2(\gamma - \kappa)^2 + 4C\beta\kappa r(r - \mu)}\right) \\
\lambda_{2,3} &= \frac{1}{2r} \left(-r(\mu + \gamma) - r(\mu + \kappa) - \sqrt{r^2(\gamma - \kappa)^2 + 4C\beta\kappa r(r - \mu)}\right).
\end{align*}
$$

Clearly $\lambda_{2,1}$ and $\lambda_{2,3}$ are both negative. The condition that $\lambda_{2,2} < 0$ is that

$$
R_0 = \frac{\kappa C \beta (r - \mu)}{r(\mu + \gamma)(\mu + \kappa)} = \frac{\beta N^* \kappa}{(\mu + \gamma)(\mu + \kappa)} < 1.
$$

Thus the infection free equilibrium is locally asymptotically stable if $R_0 < 1$.

Global stability of the infection free equilibrium if $R_0 < 1$

Theorem 4.1.3 The infection free equilibrium of system (4.1) is globally stable if $R_0 < 1$, where $R_0$ is defined in (4.2).

We make use of the well-known Fluctuation Lemma, which we state without proof (see [5] for example).

Lemma 4.1.4 If $f : \mathbb{R} \to \mathbb{R}$ is differentiable and if

$$
\bar{f} = \liminf_{t \to \infty} f(t) < \limsup_{t \to \infty} f(t) = \tilde{f}
$$

then there are sequences $\{s_i\}_{i=1}^\infty$ and $\{t_i\}_{i=1}^\infty$, such that, for all $i$,

$$
f'(s_i) = f'(t_i) = 0
$$

and

$$
\lim_{i \to \infty} f(s_i) = \bar{f}, \quad \lim_{i \to \infty} f(t_i) = \tilde{f}.
$$

Remark 4.1.5 We recall the definition of limsup and liminf. The limit inferior of a sequence $\{x_n\}_{n=1}^\infty$ is defined as

$$
\liminf_{n \to \infty} x_n = \sup_{n \geq 0} \inf_{m \geq n} x_m = \sup\{\inf\{x_m : m \geq n\} : n \geq 0\}
$$

while the limit superior of $\{x_n\}_{n=1}^\infty$ is defined as

$$
\limsup_{n \to \infty} x_n = \inf_{n \geq 0} \sup_{m \geq n} x_m = \inf\{\sup\{x_m : m \geq n\} : n \geq 0\}.
$$

Thus $\liminf_{n \to \infty} x_n \leq \limsup_{n \to \infty} x_n$, with equality only if $\lim_{n \to \infty} \{x_n\}_{n=1}^\infty$ exists.

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In the following proof we denote \( \limsup_{t \to \infty} S(t) = \bar{S} \) with equivalent definitions for \( \bar{E} \) and \( \liminf_{t \to \infty} I(t) = \bar{I} \) and equivalently for \( E \). We recall that we have already proved that \( N, S, E \) and \( I \) are non-negative and bounded from above. Using the above lemma, we can find a sequence \( \{s_i\}_{i=1}^{\infty} \) such that \( \lim_{i \to \infty} I(s_i) = \bar{I} \) and \( I'(s_i) = 0 \) and write, from the third equation of system (4.1),
\[
\kappa E(s_i) - (\mu + \gamma)I(s_i) = 0.
\]
Let \( \epsilon > 0 \) be chosen arbitrarily. Then there is some \( t_\epsilon \) such that \( E(t) \leq \bar{E} + \epsilon \) for all \( t > t_\epsilon \). Moreover there is some \( i_0 > 0 \) such that \( i > i_0 \implies s_i > t_\epsilon \). Thus for any \( i > i_0 \) we have
\[
\kappa (\bar{E} + \epsilon) - (\mu + \gamma)I(s_i) \geq \kappa E(s_i) - (\mu + \gamma)I(s_i) = 0.
\]
If we let \( \epsilon \to 0 \) then
\[
\kappa \bar{E} - (\mu + \gamma)\bar{I} \geq 0
\]
and if we now let \( \epsilon \to 0 \) then
\[
\kappa \bar{E} - (\mu + \gamma)\bar{I} \geq 0, \quad \text{so} \quad \bar{I} \leq \frac{\kappa \bar{E}}{\mu + \gamma}.
\]
(4.3)
We can also find a sequence \( \{s_i\}_{i=1}^{\infty} \) such that \( \lim_{i \to \infty} E(s_i) = \bar{E} \) and \( E'(s_i) = 0 \) and write, from the second equation of system (4.1),
\[
\beta S(s_i)I(s_i) - (\mu + \kappa)E(s_i) = 0.
\]
Let \( \epsilon > 0 \) be chosen arbitrarily. Then there is some \( t_\epsilon \) such that \( I(t) \leq \bar{I} + \epsilon \) for all \( t > t_\epsilon \). Moreover there is some \( i_0 > 0 \) such that \( i > i_0 \implies s_i > t_\epsilon \). Thus for any \( i > i_0 \) we have
\[
\beta S(s_i)(\bar{I} + \epsilon) - (\mu + \kappa)E(s_i) \geq \beta S(s_i)I(s_i) - (\mu + \kappa)E(s_i) = 0
\]
and therefore, since \( N(t) = S(t) + E(t) + I(t) \) and the state variables are all non-negative,
\[
\beta N(s_i)(\bar{I} + \epsilon) - (\mu + \kappa)E(s_i) \geq 0.
\]
Our having solved the o.d.e. for \( N(t) \), with \( \lim_{t \to \infty} N(t) = N^\ast \) allows us to state that, as \( i \to \infty \)
\[
\beta N^\ast(\bar{I} + \epsilon) - (\mu + \kappa)\bar{E} \geq 0.
\]
If we now let \( \epsilon \to 0 \) then
\[
\beta N^\ast\bar{I} - (\mu + \kappa)\bar{E} \geq 0.
\]
We can combine (4.3) with the the above inequality to obtain
\[
\bar{E} \left( \frac{\beta N^\ast\kappa}{\mu + \gamma} - (\mu + \kappa) \right) \geq 0
\]
which is the same as
\[
\bar{E}(R_0 - 1) \geq 0,
\]
where \( R_0 \) was defined in equation (4.2). Since our assumption is that \( R_0 < 1 \) then \( \bar{E} \leq 0 \).
However, we have shown that $E(t) \geq 0$ for all $t \geq 0$ so that $E \geq 0$. Since by definition $E \leq \bar{E}$ we must have $E = \bar{E} = 0$ for $R_0 < 1$. If $\bar{E} = 0$ then we see immediately that $\bar{I} \leq 0$ from inequality (4.3) and the same argument leads us to $\bar{I} = \bar{I} = 0$.

Finally, by definition of $N^*$ we must have $S = \bar{S} = N^*$. Thus we have proved the global stability of the infection free equilibrium for $R_0 < 1$. □

4.1.5 Endemic equilibrium

System (4.1) has an endemic equilibrium with

$$S^* = \frac{(\kappa + \mu)(\mu + \gamma)}{\beta \kappa}, \quad E^* = \frac{\mu + \gamma}{\kappa} I^*, \quad I^* = \frac{\kappa C \beta (r - \mu) - r (\kappa + \mu)(\mu + \gamma)}{r \beta (\mu + \kappa + \gamma)}.$$

(4.4)

We see immediately that the condition for $I^* > 0$ is $R_0 > 1$, where $R_0$ was defined in equation (4.2).

The eigenvalues of the Jacobian of the linearisation of (4.1) about the endemic equilibrium are

$$\lambda_1 = \mu - r,$n

$$\lambda_2 = -\frac{1}{2} \left( \kappa + 2\mu + \gamma + \beta I^* + \sqrt{(\kappa - \gamma)^2 - \beta I^*(2\gamma + 2\kappa - \beta I^*) + 4\beta S^* \kappa} \right),$$

$$\lambda_3 = -\frac{1}{2} \left( \kappa + 2\mu + \gamma + \beta I^* - \sqrt{(\kappa - \gamma)^2 - \beta I^*(2\gamma + 2\kappa - \beta I^*) + 4\beta S^* \kappa} \right).$$

Clearly $\lambda_1 < 0$ and $\lambda_2 < 0$. The condition that $\lambda_3 < 0$ is that

$$I^* > \frac{\beta S \kappa - (\mu + \gamma)(\mu + \kappa)}{\beta (\mu + \mu + \gamma)}.$$

Substituting the value for $S^*$ calculated in (4.4), the above inequality reduces to $I^* > 0$. Thus we have shown that the endemic state is asymptotically stable whenever it exists. □

4.2 Fixed length of latency period

In this section we change a key assumption in the model we used in the last section, we now have a fixed length latency period, $\tau$ such that, for an animal infected at $t = 0$, the probability of being in the latent class at time $t$, $P_t(E)$, is

$$P_t(E) = \begin{cases} 1 & : t \leq \tau \\ 0 & : \text{otherwise}. \end{cases}$$

We assume from now on that $\tau > \mu$, so that the eradication equilibrium is a repeller.
The delay model

We can thus amend (4.1) as follows to produce the following system

\[
\frac{dS(t)}{dt} = r(S(t) + E(t) + I(t)) \left( 1 - \frac{S(t) + E(t) + I(t)}{C} \right) - \mu S(t) - \beta S(t)I(t) + \gamma I(t),
\]

\[
\frac{dI(t)}{dt} = e^{-\mu\tau} \beta S(t - \tau)I(t - \tau) - (\mu + \gamma)I(t),
\]

(4.5)

\[
E(t) = \int_{t-\tau}^{t} \beta S(\theta)I(\theta)e^{-\mu(t-\theta)}d\theta,
\]

\[
S(\theta) > 0, I(\theta) \geq 0, E(\theta) \geq 0 \quad \text{for} \quad \theta \in [-\tau, 0],
\]

\[
S(0) > 0 \quad E(0) \geq 0, \quad I(0) \geq 0.
\]

The death of susceptibles who become infected but die before they reach the end of the latent period is represented by the factor \(e^{-\mu\tau}\) in the second equation in system (4.5). The expression for \(E(t)\) equals the total number of individuals that acquired the infection at a time between \(t - \tau\) and \(t\) and are still alive at time \(t\). If we differentiate \(E(t)\) with respect to \(t\) we obtain a third delay differential equation;

\[
\frac{dE(t)}{dt} = \beta S(t)I(t) - e^{-\mu\tau} \beta S(t-\tau)I(t-\tau) - \mu E(t).
\]

For convenience we normalise the system with

\[
s(t) = \frac{S(t)}{C}, \quad \epsilon(t) = \frac{E(t)}{C}, \quad i(t) = \frac{I(t)}{C}, \quad n(t) = \frac{N(t)}{C}, \quad \hat{\beta} = \beta C,
\]

to give us, removing the caret from \(\hat{\beta}\)

\[
\frac{ds(t)}{dt} = r(s(t) + \epsilon(t) + i(t)) \left( 1 - (s(t) + \epsilon(t) + i(t)) \right)
\]

\[
-\mu s(t) - \beta s(t)i(t) + \gamma i(t),
\]

\[
\frac{de(t)}{dt} = \beta s(t)i(t) - e^{-\mu\tau} \beta s(t - \tau)i(t - \tau) - \mu \epsilon(t),
\]

\[
\frac{di(t)}{dt} = e^{-\mu\tau} \beta s(t - \tau)i(t - \tau) - (\mu + \gamma)i(t),
\]

(4.6)

\[
s(\theta) > 0, \quad \epsilon(\theta) \geq 0, \quad i(\theta) \geq 0 \quad \text{for} \quad \theta \in [-\tau, 0],
\]

\[
s(0) > 0 \quad \epsilon(0) \geq 0, \quad i(0) \geq 0.
\]

4.2.1 Positivity and boundedness

Proposition 4.2.1 All the state variables of system (4.5) are non-negative, subject to the initial conditions of equation (4.5).
We develop the proof of the proposition here; the results apply to all the delay models we use for the remainder of this chapter.

The fecundity term in the differential equation for \( S(t) \) contains \( E(t) \), but we have defined this term to be non-negative for all values of the state variables. Thus we can consider the first two equations of system (4.5) only and prove the positivity of \( S(t) \) and \( I(t) \) by applying Theorem 5.2.1 on p 81 of Smith, [49]. In the first equation of (4.5) if \( S(0) = 0 \) and \( I > 0 \) then \( S' > 0 \), while in the second, if \( I(0) = 0 \), given that \( S(-\tau) \geq 0 \) and \( I(\tau) \geq 0 \) we have \( I' > 0 \) and thus we can conclude that \( S(t) \geq 0 \) and \( I(t) \geq 0 \) for all \( t > 0 \). The positivity of \( E(t) \) follows immediately from the form of the expression in the third equation of (4.5), the integral of a positive function.

**Theorem 4.2.2** System (4.6) has an infection free equilibrium which is globally stable if \( R_0 e^{-\mu\tau} < 1 \), where \( R_0 \) is defined as

\[
R_0 = \frac{\beta n^*}{\mu + \gamma}
\]  

and \( n^* \) is the equilibrium total population. If \( R_0 e^{-\mu\tau} > 1 \) a stable endemic equilibrium exists and the IFE is unstable. System (4.6) displays a transcritical bifurcation with parameter \( R_0 e^{-\mu\tau} \). The endemic equilibrium is eliminated and the IFE becomes stable for \( \tau > \frac{1}{\mu} \ln R_0 \).

### 4.2.2 The infection free equilibrium

System (4.6) has an infection free equilibrium \( (1 - \frac{\mu}{4}, 0, 0) \) if \( \mu < r \). If we put

\[
x(t) = s(t) - \left(1 - \frac{\mu}{4}\right), \quad y(t) = \epsilon(t), \quad z(t) = i(t)
\]

and substitute in system (4.6) we obtain, after simplification and ignoring non-linear terms, the linearised system

\[
\frac{dx(t)}{dt} = (2\mu - r) (x(t) + y(t) + z(t)) - \mu x(t) - \frac{\beta(r - \mu)z(t)}{\tau} + \gamma z(t)
\]

\[
\frac{dy(t)}{dt} = \beta \left(1 - \frac{\mu}{r}\right) (z(t) - e^{-\mu\tau} z(t - \tau)) - \mu y(t)
\]

\[
\frac{dz(t)}{dt} = \beta (t - \tau) e^{-\mu\tau} z(t - \tau) - \mu + \gamma) z(t),
\]

where \( x(t) \) may be positive or negative but \( y(t) > 0 \) and \( z(t) > 0 \) to correspond with physical reality.

**Lemma 4.2.3** The infection free equilibrium of (4.6) is globally stable if \( R_0 e^{-\mu\tau} < 1 \), where \( R_0 \) is defined in (4.7).

The third equation of (4.8) is decoupled, we now use a theorem from Kuang, [41] which we state as follows:

**Theorem 4.2.4** If \( \dot{u} = au(t - \tau) - bu(t) \), where \( a, b \) are constants with \( b > a > 0 \) and \( u(t) > 0 \), then \( u(t) \to 0 \) as \( t \to \infty \).
Remark 4.2.5 To illustrate this theorem we linearise \( \dot{u} = au(t - \tau) - bu(t) \) around the equilibrium \( u = 0 \) and look for solutions of the form \( u(t) = u_0 e^{r t} \), obtaining the characteristic equation
\[
\lambda + b = ae^{-\lambda \tau}.
\]

It is straightforward to show that if \( b > a > 0 \) then no solutions can exist for \( \text{Re}(\lambda) > 0 \).

In the case of the third equation of (4.8) we can apply this theorem to state that if
\[
\beta \left( \frac{r - \mu}{r} \right) e^{-\mu \tau} < \mu + \gamma,
\]
i.e. \( R_0 e^{-\mu \tau} < 1 \), then \( \lim_{t \to \infty} z(t) = 0 \). In this case we must also have \( y(t) \to 0 \) from the second equation of (4.8) and, provided that \( \mu < r \), we have \( x \to 0 \) from the first equation.

We now consider the sign of the roots of the characteristic equation arising from system (4.8), which is
\[
(\lambda + r - \mu)(\lambda + \mu)(\lambda - n^* \beta e^{-(\mu + \lambda) \tau}) + \mu + \gamma = 0. \tag{4.9}
\]
The necessary and sufficient condition for stability is that \( \text{Re}(\lambda) < 0 \). The first two factors of (4.9) give negative roots, so the stability of the IFE thus depends entirely on the behaviour of
\[
p(\lambda) = \frac{\lambda}{\mu + \gamma} + 1 - R_0 e^{-(\mu + \lambda) \tau}. \tag{4.10}
\]
As a function of a real number \( \lambda \), it is clear that \( p(\lambda) \) is increasing. Also note that \( p(\lambda) > 0 \) for \( \lambda \) real, large and positive, while \( p(\lambda) < 0 \) for \( \lambda \) real, large and negative. Therefore the equation \( p(\lambda) = 0 \) has a unique real root \( r_0 \). It also has complex roots, but we prove that the real root \( r_0 \) is dominant.

Let \( \lambda = x + iy \) be a complex root so that \( p(x + iy) = 0 \). Taking the real part of (4.10) with \( \lambda = x + iy \) gives
\[
0 = \frac{x}{\mu + \gamma} + 1 - R_0 e^{-(\mu + x) \tau} \cos y \tau
\]
\[
\geq \frac{x}{\mu + \gamma} + 1 - R_0 e^{-(\mu + x) \tau} = p(x).
\]
Also, \( p(r_0) = 0 \) therefore \( p(x) \leq p(r_0) \). Since \( p \) is monotone increasing it follows that \( x \leq r_0 \) so that the real root \( r_0 \) is dominant as claimed. We therefore consider only real roots of (4.10).

**Proposition 4.2.6** If \( R_0 e^{-\mu \tau} \), where \( R_0 \) is defined in equation (4.7) is less than unity then there is a unique negative real root of \( p(\lambda) = 0 \), where \( p(\lambda) \) is given by equation (4.10), while if \( R_0 e^{-\mu \tau} > 1 \) there is a unique positive root.

We have shown that there is a unique real root of (4.10). We have \( p(0) = 1 - R_0 e^{-\mu \tau} \), Thus the root will be negative providing that \( R_0 e^{-\mu \tau} < 1 \) while, conversely, if \( R_0 e^{-\mu \tau} > 1 \), the root is positive. \( \square \)
Finally we note that a unique positive real root can only exist if $R_0e^{-\mu\tau} > 1$, equivalently $\tau < \frac{1}{\mu}\ln R_0$. Thus, if the latent period is very long, the IFE will be stable no matter how virulent the disease. In practice, since $\frac{1}{\mu}$ is the average life expectancy of the animal this inequality would only be meaningful if $R_0$ were close to unity. Thus if $R_0 = 1.5$, then the latent period could be as much as 40% of the animal’s average lifespan without the positive real root disappearing.

Global stability of the IFE

Proposition 4.2.7 If $R_0e^{-\mu\tau} < 1$, where $R_0$ is defined in equation (4.7), the infection free equilibrium of system (4.6) is globally stable.

Since $s(t)$ is bounded from above by $\max(s(0), n^*)$ we must have

$$\lim_{t \to \infty} \sup_{t \to \infty} s(t) \leq n^*.$$ 

Given $\epsilon > 0$ there exists $t_\epsilon > 0$ such that $s(t) \leq n^* + \epsilon$ for $t > t_\epsilon$.

We have shown that $i(t) > 0$ for $i(0) > 0$. The third equation of (4.6) is

$$\frac{di(t)}{dt} = e^{-\mu\tau}\beta s(t-\tau)i(t-\tau) - (\mu + \gamma)i(t).$$

We choose $\epsilon > 0$ sufficiently small that

$$e^{-\mu\tau}\beta(n^* + \epsilon) < \mu + \gamma,$$

which is possible because we assume that $\frac{\delta n^*e^{-\mu\tau}}{\mu + \gamma} < 1$, the condition that the endemic equilibrium does not exist. For this $\epsilon$ there exists a $t_\epsilon > 0$ such that $s(t) \leq n^* + \epsilon$ for all $t \geq t_\epsilon$.

Thus it follows that for $t > t_\epsilon + \tau$ we must have

$$\frac{di}{dt} \leq e^{-\mu\tau}\beta(n^* + \epsilon)i(t-\tau) - (\mu + \gamma)i(t).$$

Since the delay term has a positive coefficient, a non-negative function $i(t)$ satisfying the above inequality will be bounded from above by $\hat{i}(t)$, where $\hat{i}(t)$ satisfies the following equation

$$\frac{d\hat{i}}{dt} = e^{-\mu\tau}\beta(n^* + \epsilon)\hat{i}(t-\tau) - (\mu + \gamma)\hat{i}(t)$$

and $\hat{i}(t)$ satisfies the same initial conditions as $i(t)$.

Equation (4.11) is now in a form which allows us once more to apply Theorem 4.2.4. Since $e^{-\mu\tau}\beta(n^* + \epsilon) < \mu + \gamma$, it follows that $\hat{i}(t) \to 0$ as $t \to \infty$. Hence it also follows that $i(t) \to 0$ as $t \to \infty$. Thus we have proved that the infection free equilibrium is globally stable if $R_0e^{-\mu\tau} < 1$. 

□
4.2.3 The endemic equilibrium

Proposition 4.2.8 If \( R_0 e^{-\mu t} > 1 \), where \( R_0 \) is given by (4.7) a stable endemic equilibrium exists for system (4.6).

There is an endemic equilibrium for system (4.6), \((s^*, e^*, i^*)\), at

\[
s^* = \frac{\mu + \gamma}{\beta e^{-\mu t}}
\]

\[
e^* = \frac{\left(\beta e^{-\mu t}(r - \mu) - \mu r + \gamma\right)(1 - e^{-\mu t})(\mu + \gamma)}{\beta r(\gamma(1 - e^{-\mu t}) + \mu)}
\]

\[
i^* = \frac{\mu \left(\beta e^{-\mu t}(r - \mu) - \mu r + \gamma\right)}{\beta r(\gamma(1 - e^{-\mu t}) + \mu)}.
\]

For \( i^* \) and \( e^* \) to exist we must have,

\[
\frac{\beta(r - \mu)e^{-\mu t}}{r(\mu + \gamma)} = \frac{\beta n^*e^{-\mu t}}{\mu + \gamma} = R_0 e^{-\mu t} > 1.
\]

Thus we have proved that \( R_0 e^{-\mu t} > 1 \) is a necessary and sufficient condition for the existence of an endemic equilibrium. \( \square \)

Linearising system (4.6) around the endemic equilibrium leads to intractable algebra. As discussed in the Introduction, we can reduce the order of system (4.6) by taking \( t \) large enough so that the total population is constant and thus substitute for the latent class in terms of the others.

We thus obtain, for sufficiently large \( t \),

\[
\frac{ds(t)}{dt} = \mu \left(1 - \frac{\mu}{r}\right) - \mu s(t) - \beta s(t)i(t) + \gamma i(t)
\]

\[
\frac{di(t)}{dt} = e^{-\mu t} \beta s(t) - \tau i(t) - (\mu + \gamma) i(t).
\]

We now substitute \( x = s - s^* \) and \( y = i - i^* \) into these equations, substitute the known quantities for \( s^*, i^* \) from equation (4.12), linearise and then look for solutions of the form \( x(t) = a_1 e^{\lambda t}, y = a_2 e^{\lambda t} \). Simplifying and finding the conditions for a non trivial solution for \( a_1, a_2 \) we obtain the characteristic equation for the linearisation at the endemic equilibrium, namely

\[
f(\lambda) = \lambda^2 + A(\lambda)\lambda + B(\lambda) = 0,
\]

where we define \( A \) and \( B \) as the following functions of \( \lambda \);

\[
A(\lambda) = (\mu + \gamma) \left(1 - e^{-\lambda t} + \frac{\mu}{\gamma(1 - e^{-\mu t}) + \mu} \left(R_0 e^{-\mu t} - 1\right)\right) + \mu,
\]

\[
B(\lambda) = \mu(\mu + \gamma)(1 - e^{-\lambda t}) + \frac{\mu(\mu + \gamma(1 - e^{-(\mu + \lambda) t})\left(\mu + \gamma\right)(R_0 e^{-\mu t} - 1)}{r(\gamma(1 - e^{-\mu t}) + \mu)}.
\]

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Proposition 4.2.9 If $R_0e^{-\mu r} > 1$ equation (4.13) has no positive real roots and we conjecture that (4.13) has at least one negative real root.

We prove this proposition in the following manner, assuming that the real root of $f(\lambda) = 0$ will be dominant. Now $\lim_{\lambda \to +\infty} f(\lambda) = +\infty$ and $f(0) = B(0) = \frac{\mu}{T} (\mu + \gamma)(R_0e^{-\mu r} - 1)$, which is positive for $R_0e^{-\mu r} > 1$. We consider $\text{sgn}(f'(\lambda))$ for $\lambda > 0$;

$$f'(\lambda) = 2\lambda + \lambda A'(\lambda) + A(\lambda) + B'(\lambda).$$

If $f'(\lambda) > 0$ for $\lambda > 0$ we can exclude the possibility of positive roots for $R_0e^{-\mu r} > 1$. By inspection $A(\lambda) > 0$ for $\lambda > 0$ whatever the value of $R_0 > 0$. $A'(\lambda) = \tau e^{\lambda r}(\mu + \gamma) > 0$. Finally

$$B'(\lambda) = \tau e^{-\lambda r}(\mu + \gamma) + \frac{\mu \gamma e^{-(\mu + \lambda)r}(\mu + \gamma)(R_0e^{-\mu r} - 1)}{\tau(\gamma(1 - e^{-\mu r}) + \mu)}$$

and we see immediately that $R_0e^{-\mu r} > 1$ is a sufficient condition for $B'(\lambda) > 0$. Thus we have shown that $f'(\lambda) > 0$ for all $\lambda > 0$, hence excluding the possibility of positive roots. Conversely, if $R_0e^{-\mu r} < 1$ then the endemic equilibrium does not exist.

We cannot prove analytically that there is at least one negative root for (4.13) for $R_0e^{-\mu r} > 1$, although simulation suggests that there is. Thus if $R_0e^{-\mu r} > 1$ the endemic equilibrium exists and is locally stable.

4.3 Criss-cross infection with fixed delay

As a preliminary to our considering the two animal system with inter- and intra-species infectivity, we analyse the simpler system with criss-cross infection only. We simplify matters further by utilising the simple recruitment function of Chapter 2 rather than the logistic fecundity function. Finally we ignore the latent classes since, with this simple recruitment function, we can decouple the differential equation for these classes from the rest of the system. We thus have the following model, with all of the variables, parameters and all other assumptions as for system (2.1), except for the fixed latency periods $\tau_c$ and $\tau_b$ for cattle and badgers respectively,

$$\frac{dS_c(t)}{dt} = \Lambda_c - \mu_c S_c(t) - \xi_{bc} S_c(t) I_b(t) + \gamma_c I_c(t),$$

$$\frac{dI_c(t)}{dt} = e^{-\mu_c \tau_c} \xi_{bc} S_c(t - \tau_c) I_b(t - \tau_c) - (\gamma_c + \mu_c) I_c(t),$$

$$\frac{dS_b(t)}{dt} = \Lambda_b - \mu_b S_b(t) - \xi_{cb} S_b(t) I_c(t) + \gamma_b I_b(t),$$

$$\frac{dI_b(t)}{dt} = e^{-\mu_b \tau_b} \xi_{cb} S_b(t - \tau_b) I_c(t - \tau_b) - (\gamma_b + \mu_b) I_b(t),$$

$$S_c(0) > 0, I_c(0) > 0, S_b(0) > 0, I_b(0) > 0 \quad \theta \in [-\max\{\tau_b, \tau_c\}, 0].$$
The mass action terms express the fact that a cow which is exposed to an infective badger at time $t_0$ will itself become infective at time $t_0 + \tau_c$ while a badger exposed to an infective cow at time $t_0$ will itself become infective at time $t_0 + \tau_b$. We find that there are two equilibria, the infection free equilibrium and the endemic state.

**Theorem 4.3.1** The infection free equilibrium of system (4.14), which is \( \left( \frac{\Delta \xi}{\mu_c}, \frac{\Delta \lambda}{\mu_b}, 0 \right) \), is locally stable if \( R_0e^{-(\mu_c\tau_c+\mu_b\tau_b)} < 1 \) where

\[
R_0 = \frac{\xi_{bc}\xi_{cb}\lambda_c\lambda_b}{\mu_b\mu_c(\mu_c + \gamma_c)(\mu_b + \gamma_b)}.
\] (4.15)

If \( R_0e^{-(\mu_c\tau_c+\mu_b\tau_b)} > 1 \) then a locally stable endemic equilibrium exists and the IFE is unstable.

We prove this theorem in the following two sections.

**4.3.1 Infection free equilibrium**

There is an IFE of system (4.14) at \( \left( \frac{\Delta \xi}{\mu_c}, \frac{\Delta \lambda}{\mu_b}, 0 \right) \). If we make the substitution

\[
u(t) = I_c(t), \quad x(t) = S_b(t) - \frac{\Delta \lambda}{\mu_b}, \quad y(t) = I_b(t),
\]

in system (4.14), simplify and ignore any terms higher than first order, we obtain the linearisation of system (4.14) around the infection free equilibrium as

\[
\begin{align*}
\frac{du(t)}{dt} &= -\mu_c u(t) - K_c \xi_{bc} y(t) + \gamma_c v(t), \\
\frac{dv(t)}{dt} &= K_c \xi_{bc} y(t - \tau_c)e^{-\mu_c \tau_c} - (\mu_c + \gamma_c) v(t), \\
\frac{dx(t)}{dt} &= -\mu_b x(t) - K_b \xi_{cb} v(t) + \gamma_b y(t), \\
\frac{dy(t)}{dt} &= K_b \xi_{cb} v(t - \tau_b)e^{-\mu_b \tau_b} - (\mu_b + \gamma_b) y(t),
\end{align*}
\] (4.16)

where \( K_c = \frac{\Delta \xi}{\mu_c}, K_b = \frac{\Delta \lambda}{\mu_b} \). We now look for an Ansatz of the form

\[
u(t) = c_1e^{\lambda t}, \quad v(t) = c_2e^{\lambda t}, \quad x(t) = c_3e^{\lambda t}, \quad y(t) = c_4e^{\lambda t}.
\]

Making this substitution, we write the linearisation in the form \( Mc = 0 \), where \( c = (c_1, c_2, c_3, c_4)^T \) and

\[
M = \begin{pmatrix}
-\mu_c - \lambda & \gamma_c & 0 & -K_c \xi_{bc} \\
0 & -(\mu_c + \gamma_c) - \lambda & 0 & K_c \xi_{bc} e^{-(\mu_c + \lambda) \tau_c} \\
0 & -K_b \xi_{cb} & -\mu_b - \lambda & \gamma_b \\
0 & K_b \xi_{cb} e^{(\mu_b + \lambda) \tau_b} & 0 & -(\mu_b + \gamma_b) - \lambda
\end{pmatrix}.
\]

The condition on \( \lambda \) such that \( c \) is not identically zero, is that \( det(M) = 0 \). This gives us the characteristic equation of (4.16), \( \phi(\lambda) = 0 \), where

\[
\phi(\lambda) = (\lambda + \mu_c)(\lambda + \mu_b)(\lambda^2 + A\lambda + B(\lambda))
\] (4.17)
and where

\[ A = \mu_c + \gamma_c + \mu_b + \gamma_b, \]
\[ B = (\mu_c + \gamma_c)(\mu_b + \gamma_b) - K_cK_b\xi_{cb}\xi_{bc}e^{-(\mu_c\tau_c + \mu_b\tau_b)}e^{-(\tau_c + \tau_b)\lambda}. \]

The are two real negative roots, \( \lambda = -\mu_c \) and \( \lambda = -\mu_b \) for (4.17). The interesting behaviour of \( \phi \) results from the properties of the third factor of \( \phi(\lambda) \).

**Proposition 4.3.2** If \( R_0e^{-(\mu_c\tau_c + \mu_b\tau_b)} < 1 \) (where \( R_0 \) is defined in (4.15)) equation (4.17) has no real positive roots and at least one real negative root.

We see that \( A > 0 \), while \( B > 0 \) for \( \lambda \geq 0 \) and

\[ \frac{K_cK_b\xi_{cb}\xi_{bc}}{(\mu_c + \gamma_c)(\mu_b + \gamma_b)} < 1. \]

We recognise the above expression as \( R_0 \) for the criss-cross SIS model in Chapter 2 which was defined in equation (2.8). Thus for \( R_0 < 1 \), \( \phi(0) > 0 \) and

\[ \lim_{\lambda \to +\infty} \phi(\lambda) = +\infty, \quad \lim_{\lambda \to -\infty} \phi(\lambda) = -\infty. \]

Moreover,

\[ \frac{d\phi}{d\lambda} > 0 \quad \forall \lambda > 0, \]

since all the individual terms of the derivative are positive. There must thus be a unique negative root for \( R_0 < 1 \). In fact this is a sufficient condition only, the necessary and sufficient condition being that

\[ 0 < \hat{R}_0 = \frac{K_cK_b\xi_{cb}\xi_{bc}e^{-(\mu_c\tau_c + \mu_b\tau_b)}}{(\mu_c + \mu_b)(\gamma_c + \gamma_b)} < 1. \quad (4.18) \]

Conversely, if \( \hat{R}_0 > 1 \), \( \phi(0) < 0 \) and there is a unique positive root.

Moreover, we observe that the second and fourth equations of system (4.16) are decoupled from the first and the third. If we are able to demonstrate that, under certain conditions, \( v(t) \) and \( y(t) \) → 0 as \( t \to \infty \) then it must follow from the form of the first and third equations that \( u(t) \) and \( x(t) \) → 0 as \( t \to \infty \) and the IFE is linearly stable. The reduced system is

\[ \frac{dv(t)}{dt} = K_c\xi_{bc}v(t - \tau_c)e^{-\mu_c\tau_c} - (\mu_c + \gamma_c)v(t), \quad (4.19) \]

\[ \frac{dy(t)}{dt} = K_b\xi_{cb}v(t - \tau_b)e^{-\mu_b\tau_b} - (\mu_b + \gamma_b)y(t), \]

which is clearly cooperative and thus we may use Theorem 5.5.1 of Smith [49] which allows us to conclude that the principal eigenvalue of (4.19) is real. The characteristic equation associated with this system is \( \lambda^2 + A(\lambda)\lambda + B(\lambda) = 0 \), the third factor on the right hand side of equation (4.17), which we have already analysed in this section, shows that for \( R_0 > 1 \), \( v(t) \to 0 \) and \( y(t) \to 0 \) as \( t \to \infty \).

Thus, \( \hat{R}_0 \), defined in (4.18) determines the local stability of the IFE. This proves the proposition. \( \Box \)
4.3.2 Endemic equilibrium

There is an endemic equilibrium for system (4.14) with

\[ S_b^* = \frac{\Lambda_b + \gamma_b I_b^*}{\mu_b + \xi_{cb} I_c^*}, \quad S_c^* = \frac{\Lambda_c + \gamma_c I_c^*}{\mu_c + \xi_{cb} I_b^*} \]

\[ I_b^* = \frac{1}{\xi_{bc}} \times \frac{\xi_{bc} \xi_{cd} \Lambda_c \lambda_b e^{-(\mu_c \tau_c + \mu_b \tau_b)} - \mu_b \mu_b (\mu_b + \gamma_b)(\mu_c + \gamma_c)}{(\mu_b (\mu_b + \gamma_b)(\mu_c + \gamma_c) - \xi_{cd} \Lambda_c \lambda_b e^{-(\mu_c \tau_c + \mu_b \tau_b)} - \mu_c \mu_c (\mu_c + \gamma_c)(\mu_b + \gamma_b)(\mu_c \gamma_c - \xi_{cb} \Lambda_c))}, \]

\[ I_c^* = \frac{1}{\xi_{cb}} \times \frac{\xi_{cd} \xi_{bc} \Lambda_b \lambda_c e^{-(\mu_b \tau_b + \mu_c \tau_c)} - \mu_c \mu_c (\mu_c + \gamma_c)(\mu_b + \gamma_b)}{(\mu_c (\mu_c + \gamma_c)(\mu_b + \gamma_b) - \xi_{cb} \Lambda_b \lambda_c e^{-(\mu_b \tau_b + \mu_c \tau_c)} - \mu_b \mu_c (\mu_c + \gamma_c)(\mu_b \gamma_b - \xi_{bc} \Lambda_b))}. \]

We see immediately that \( I_c \) and \( I_b \) are only positive for \( R_0 e^{-(\mu_c \tau_c + \mu_b \tau_b)} > 1 \), so this is the necessary and sufficient condition for the existence of the endemic state.

Conjecture 4.3.3 The endemic equilibrium state of system (4.14) is stable if it exists; if the endemic equilibrium exists the IFE is unstable.

We have already demonstrated that the IFE is unstable for \( R_0 e^{-(\mu_c \tau_c + \mu_b \tau_b)} > 1 \), where \( R_0 \) is defined in equation (4.15), which is the condition that the endemic equilibrium exists. It remains to be shown analytically that the endemic equilibrium is stable whenever it exists, numerical simulation suggests that it is.

4.4 Two species with inter- and intra-species infectivity and fixed delay

The model equations are as follows with \( S, E \) and \( I \) susceptible, latent and infective classes for cattle (subscript c) and for badgers (subscript b) and all the parameters have already been defined in this chapter. We continue to use
a constant recruitment function for simplicity.

\[ \frac{dS_c(t)}{dt} = \Lambda_c - \mu_c S_c(t) - \beta_c S_c(t) I_c(t) - \xi_{bc} S_c(t) I_b(t) + \gamma_c I_c, \]

\[ \frac{dE_c(t)}{dt} = \beta_c S_c(t) I_c(t) + \xi_{bc} S_c(t) I_b(t) - e^{-\mu_c \tau_c} \xi_{bc} S_c(t - \tau_c) I_b(t - \tau_c), \]

\[ e^{-\mu_c \tau_c} \beta_c S_c(t - \tau_c) I_c(t - \tau_c) - \mu_c E_c(t), \]

\[ \frac{dI_c(t)}{dt} = e^{-\mu_c \tau_c} \xi_{bc} S_c(t - \tau_c) I_b(t - \tau_c) + e^{-\mu_c \tau_c} \beta_c S_c(t - \tau_c) I_c(t - \tau_c) \]

\[-(\gamma_c + \mu_c) I_c(t), \]

\[ \frac{dS_b(t)}{dt} = \Lambda_b - \mu_b S_b(t) - \beta_b S_b(t) I_b(t) - \xi_{cb} S_b(t) I_c(t) + \gamma_b I_b, \]

\[ \frac{dE_b(t)}{dt} = \beta_b S_b(t) I_b(t) + \xi_{cb} S_b(t) I_c(t) - e^{-\mu_b \tau_b} \xi_{cb} S_b(t - \tau_b) I_c(t - \tau_b), \]

\[ e^{-\mu_b \tau_b} \beta_b S_b(t - \tau_b) I_b(t - \tau_b) - \mu_b E_b(t), \]

\[ \frac{dI_b(t)}{dt} = e^{-\mu_b \tau_b} \xi_{cb} S_b(t - \tau_b) I_c(t - \tau_b) + e^{-\mu_b \tau_b} \beta_b S_b(t - \tau_b) I_b(t - \tau_b) \]

\[-(\mu_b + \gamma_b) I_b, \]

\[ N_c(t) = S_c(t) + E_c(t) + I_c(t), \quad N_b(t) = S_b(t) + E_b(t) + I_b(t), \]

\[ S_c(\theta) > 0, E_c(\theta) > 0, I_c(\theta) > 0, \quad S_b(\theta) > 0, E_b(\theta) > 0, I_b(\theta) > 0, \quad \theta \in [-\tau, 0]. \]

\[ (4.20) \]

**Proposition 4.4.1** A sufficient condition for the infection free equilibrium of system (4.20) to be linearly stable is that \( R_b < 1, R_c < 1 \) and \( R_2 < 1 \), where \( R_2 \) is defined in equation (4.26).

**Conjecture 4.4.2** A necessary and sufficient condition for the infection free equilibrium of system (4.20) to be linearly stable is that \( \mu_2 < 1 \), where \( \mu_2 \) is defined in equation (4.25).

**Positivity and boundedness**

We utilise Theorem 5.2.1 on p 81 of Smith, [49] to verify that each of the six state variables in system (4.20) is non-negative for all time, provided that it starts non-negative. This, together with the definition of \( N_c(t) = S_c(t) + E_c(t) + I_c(t) \) and \( N_b(t) = S_b(t) + E_b(t) + I_b(t) \), which gives us differential equations

\[ \frac{dN_c(t)}{dt} = \Lambda_c - \mu_c N_c(t) \quad \text{and} \quad \frac{dN_b(t)}{dt} = \Lambda_b - \mu_b N_b(t), \]

which we solved in Chapter 2 to show that

\[ \lim_{t \to \infty} N_c(t) = \frac{\Lambda_c}{\mu_c}, \quad \text{and} \quad \lim_{t \to \infty} N_b(t) = \frac{\Lambda_b}{\mu_b}, \]

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ensures that each of the state variables is bounded from above.

Non-dimensionalisation and linearisation

To simplify the analysis we can ignore the differential equations for $E_c(t)$ and $E_b(t)$, since they can be obtained from the other two differential equations for each species of equations (4.20) and (4.21). We non-dimensionalise system (4.20) with the following scheme, where $N_c^*$ and $N_b^*$ are the equilibrium populations of cattle and badgers respectively.

\[
\begin{align*}
    v &= \frac{S_c}{N_c^*}, \quad w = \frac{I_c}{N_c^*}, \quad x = \frac{S_b}{N_b^*}, \quad y = \frac{I_b}{N_b^*}, \\
    \alpha_c &= \frac{\mu_c}{\mu_c + \gamma_c}, \quad \alpha_b = \frac{\mu_b}{\mu_b + \gamma_b}, \quad k = \frac{\mu_b + \gamma_b}{\mu_c + \gamma_c}, \\
    U_b &= \frac{N_b^* \xi_b}{\mu_c + \gamma_c}, \quad U_c = \frac{N_c^* \xi_c}{\mu_b + \gamma_b}, \quad R_c = \frac{N_c^* \beta_c}{\mu_c + \gamma_c}, \quad R_b = \frac{N_b^* \beta_b}{\mu_b + \gamma_b}, \\
    \dot{t} &= (\mu_c + \gamma_c) t, \quad \dot{\tau}_b = (\mu_c + \gamma_c) \tau_b, \quad \dot{\tau}_c = (\mu_c + \gamma_c) \tau_c,
\end{align*}
\]

to give us, once we remove the carets, the model equations:

\[
\begin{align*}
    \frac{dv(t)}{dt} &= \alpha_c (1 - v(t)) + w(t) (1 - \alpha_c) - R_c v(t) w(t) - k U_c v(t) y(t), \\
    \frac{dw(t)}{dt} &= -w + e^{-\alpha_c \tau_c} R_c v(t - \tau_c) w(t - \tau_c) + k e^{-\alpha_c \tau_c} U_c v(t - \tau_c) y(t - \tau_c), \\
    \frac{dx(t)}{dt} &= k \alpha_b (1 - x(t)) + k y(t) (1 - \alpha_b) - k R_b x(t) y(t) - U_b x(t) w(t), \\
    \frac{dy(t)}{dt} &= -k y(t) + k e^{-k \alpha_b \tau_b} R_b x(t - \tau_b) y(t - \tau_b) + e^{-k \alpha_b \tau_b} U_b x(t - \tau_b) w(t - \tau_b),
\end{align*}
\]

\[v(\theta) > 0, \quad w(\theta) > 0, \quad x(\theta) > 0, \quad y(\theta) > 0, \quad \theta \in [-\max\{\tau_b, \tau_c\}, 0],
\]

\[v(0) > 0, \quad w(0) \geq 0, \quad x(0) > 0, \quad y(0) \geq 0. \quad (4.22)
\]

If we make the substitution

\[
p(t) = v(t) - v^*, \quad q(t) = w(t) - w^*, \quad r(t) = x(t) - x^*, \quad s(t) = y(t) - y^*,
\]

where $(v^*, w^*, x^*, y^*)$ is any equilibrium solution of system (4.22), simplify and consider only first order terms, we obtain the linearisation of system (4.22)
around a general equilibrium;

\[
\frac{dp(t)}{dt} = -\alpha_c p(t) + q(t)(1 - \alpha_c) - R_c(v^*q(t) + w^*p(t)) - U_c k(v^*s(t) + y^*p(t)),
\]

\[
\frac{dq(t)}{dt} = -q(t) + e^{-\alpha_c\tau_c} R_c(v^*q(t - \tau_c) + w^*p(t - \tau_c)) + ke^{-\alpha_c\tau_c} U_c k(v^*s(t - \tau_c) + y^*p(t - \tau_c)),
\]

\[
\frac{dr(t)}{dt} = -k\alpha_b r(t) + k s(t)(1 - \alpha_b) - kR_b(x^*s(t) + y^*r(t)) - U_b (x^*q(t) + w^*r(t)),
\]

\[
\frac{ds(t)}{dt} = -kq s(t) + e^{-k\alpha_b\tau_b} R_b (x^*s(t - \tau_b) + y^*r(t - \tau_b)),
\]

\[
+ e^{-k\alpha_b\tau_b} U_b (x^*q(t - \tau_b) + w^*r(t - \tau_b)).
\]

Now we assume an Ansatz of the form

\[
p(t) = c_1 e^{\lambda t}, \quad q(t) = c_2 e^{\lambda t}, \quad r(t) = c_3 e^{\lambda t}, \quad s(t) = c_4 e^{\lambda t}
\]

and substitute into the linearised system (4.23).

The infection free equilibrium

If we consider the IFE, which in non-dimensionalised terms is \((v, w, x, y) = (1, 0, 1, 0)\), then the condition that there is a solution to the linearised system (4.23) which is not identically zero can be written in matrix form as \(Mc = 0\), where \(c = (c_1, c_2, c_3, c_4)^T\) and \(M\) is given by

\[
\begin{pmatrix}
-\alpha_c - \lambda & 1 - \alpha_c - R_c & 0 & -kU_c \\
0 & -1 + e^{-(\alpha_c + \lambda)\tau_c} R_c - \lambda & 0 & ke^{-(\alpha_c + \lambda)\tau_c} U_c \\
0 & -U_b & -k\alpha_b - \lambda & k(1 - \alpha_b - R_b) \\
0 & e^{-(k\alpha_b + \lambda)\tau_b} U_b & 0 & -k + ke^{-(k\alpha_b + \lambda)\tau_b} R_b - \lambda
\end{pmatrix}.
\]

(4.24)

We compute the next generation matrix in the same way as in the Introduction and can hence define the basic reproductive ratio for this two-animal SEIS system as \(R_2\) where

\[
R_2 = \frac{1}{2} \left( R_c e^{-\alpha_c\tau_c} + R_b e^{-k\alpha_b\tau_b} \right)
\]

\[
+ \frac{1}{2} \sqrt{\left( R_c e^{-\alpha_c\tau_c} - R_b e^{-k\alpha_b\tau_b} \right)^2 + 4 U_c U_b e^{-\alpha_c\tau_c} e^{-k\alpha_b\tau_b}},
\]

which bears an evident resemblance to \(R_{bc}\) defined in equation (2.16): each of the basic reproductive ratios for the infection processes is multiplied by a factor representing the death of infected animals while still in the latent compartment.
We can also manipulate the expression for $\hat{R}_2$ in the same manner as was done in Chapter 2 Section 4 to deduce that if $\hat{R}_2 < 1$ then

$$R_2 = \frac{U_b U_c e^{-(\mu_b \gamma_b + \mu_c \gamma_c)}}{(1 - R_b e^{-\mu_b \gamma_b})(1 - R_c e^{-\mu_c \gamma_c})} < 1,$$

(4.26)

which is important in our analysis of the characteristic equation of the linearisation about the IFE. The characteristic equation of $M$ is

$$(\lambda + \alpha_c)(\lambda + \alpha_b) (\lambda^2 + A(\lambda)\lambda + B(\lambda)) = 0,$$

(4.27)

where

$$A = -\left(k(R_b e^{-(k\alpha_b + \lambda)\gamma_b} - 1) + R_c e^{-(\alpha_c + \lambda)\gamma_c} - 1\right),$$

$$B = (R_b R_c - U_b U_c) e^{-(k\alpha_b + \lambda)\gamma_b} - (\alpha_c + \lambda)\gamma_c$$

$$+ k (1 - R_b e^{-(k\alpha_b + \lambda)\gamma_b} - R_c e^{-(\alpha_c + \lambda)\gamma_c})$$

We denote the third term of equation (4.27) $O(\lambda)$. We assume that equation (4.27) has a unique, dominant real root. We therefore focus only on real solutions of $\phi(\lambda) = 0$.

If $R_c < 1$, $R_b < 1$ and $R_2 < 1$, assumed conditions for the non-existence of the endemic state, then $B(0) > 0$ while $A(\lambda) > 0$ so $\lim_{\lambda \to +\infty} \phi(\lambda) = +\infty$ and $\lim_{\lambda \to +\infty} \phi(\lambda) = +\infty$.

$\frac{dA}{d\lambda} > 0$ and $\frac{dB}{d\lambda} > 0$ for $\lambda > 0$ so that there can be no positive roots in this case. We cannot prove analytically the conditions for the existence of negative roots, although simulation suggests that this is the case.

**Conclusion**

We have shown that incorporating a latent class into the SIS disease model does not significantly alter the disease dynamics, whether the length of the latent period is modelled by an exponential distribution or by a fixed period. This is true both for a single species and for two mutually infective species.
Chapter 5

Spatially heterogeneous systems

5.1 Introduction

We now consider more realistic models, in which we do not assume spatial homogeneity. We choose to model spatial heterogeneity using diffusion models, where animals move away from a source through a terrain. We consider a number of different diffusion models - one and two species SIS and SEIS, with both an exponentially distributed and fixed length of latency period. We also consider spatially non homogeneous culling models.

5.2 One species SIS, one-dimensional diffusion

We start with the single animal species with a very simple system to gain a basic understanding of the dynamics of the model. We take the SIS model of Section 3.4, with additional deaths from disease, and consider diffusion of both state variables along one spatial dimension only.

Derivation of the model equations

Let us consider an animal species with population density $n(x, t)$ per unit length, diffusing in one dimension across an interval $(x, x + \delta x)$ in time interval $(t, t + \delta t)$ with a flux $q(x, t)$ passing the point $x$ in unit time. Then

- the number of animals in the interval $(x, x + \delta x)$ at time $t$ is $n(x, t)\delta x$ and at time $t + \delta t$ is $n(x, t + \delta t)\delta x$.

- the net numbers entering the interval $(x, x + \delta x)$ during time interval of duration $\delta t$ is $q(x, t)\delta t$, while the numbers leaving will be $q(x + \delta x, t)\delta t$.

Let the change in animal numbers in the interval resulting from births, deaths and other processes be $f(n)\delta x\delta t$. The change in the numbers of animals in the interval between time $t$ and time $t + \delta t$ is then equal to the net inflow of animals plus $f(n)\delta x\delta t$.

$$n(x, t + \delta t)\delta x - n(x, t)\delta x = -q(x + \delta x, t)\delta t + q(x, t)\delta t + f(n)\delta x\delta t. \quad (5.1)$$
We can expand both sides of (5.1) using Taylor's Theorem
\[ n(x, t + \delta t) = n(x, t) + \frac{\partial n}{\partial t} \delta t + O(\delta t^2), \]
\[ q(x + \delta x, t) = q(x, t) + \frac{\partial q}{\partial x} \delta x + O(\delta x^2). \]
Substituting these expansions into equation (5.1), ignoring quadratic and higher terms and letting \( \delta x \to 0 \) and \( \delta t \to 0 \) we have
\[ \frac{\partial n}{\partial t} = -\frac{\partial q}{\partial x} + f(n). \]
We use the empirical result known as Fick's Law, that animals in a population will tend to flow away from high population density, to model the flux as
\[ q = -D \frac{\partial n}{\partial x}, \]
where \( D \) is the diffusion constant. Thus we obtain the so-called reaction-diffusion equation, which is
\[ \frac{\partial n}{\partial t} = D \frac{\partial^2 n}{\partial x^2} + f(n). \]

Alternative derivation of the reaction-diffusion equation

Let us assume that a population moves, in one dimension only, a distance of \( \delta x \) in time \( \delta t \), that the movement is equally probable in either direction and none of the population remains stationary. Then if \( n(x, t) \) is the population at time \( t \) in the interval \((x, x+\delta x)\), we can express the population in the interval at time \( t+\delta t \) as
\[ n(x, t + \delta t) = \frac{1}{2} n(x - \delta x, t) + \frac{1}{2} n(x + \delta x, t) + f(x, t)\delta t, \]
where \( f(x, t) \) is the rate of creation of new (or destruction of old) members of the population at \( x \) at time \( t \). With a Taylor expansion of the two sides of this equation we have
\[ n(x, t) + \delta tn_t + \frac{1}{2}(\delta t)^2 n_{tt} + O(\delta t^3) = \frac{1}{2} \left( n(x, t) - \delta x n_x + \frac{1}{2}(\delta x)^2 n_{xx} \right) + \frac{1}{2} \left( n(x, t) + \delta x n_x + \frac{1}{2}(\delta x)^2 n_{xx} \right) + O(\delta x^3) + f(x, t)\delta t. \]
If we now simplify and ignore \( O((\delta x)^3) \) and \( O((\delta t)^3) \)
\[ n_t + \frac{1}{2} \delta t n_{tt} = \frac{(\delta x)^2}{2\delta t} n_{xx} + f(x, t). \]
If the scaling is such that \( \frac{(\delta x)^2}{2\delta t} = D \) where \( D \) is the diffusivity (which may be constant or a function of \( x \) and/or of \( t \)), and we let \( \delta t \to 0 \) and \( \delta x \to 0 \), we obtain
\[ \frac{\partial n}{\partial t} = D \frac{\partial^2 n}{\partial x^2} + f(x, t), \]
as in the previous subsection.

If \( f(n) \) is linear, the reaction-diffusion equation may, in certain circumstances, be solved explicitly (depending on the initial conditions). We are interested in systems where \( f(n) \) is non-linear in general and, in particular, in the circumstance when we may obtain a travelling wave solution.
5.2.1 SIS model with diffusion

We modify the static model equations (3.1) by applying a reaction-diffusion term to both state variables, assuming that they each diffuse with the same diffusion constant, \( \hat{D} \), i.e. there is no impact of the disease on the animals' diffusion rates. Thus we can write the spatially heterogeneous model equations as

\[
\frac{\partial S}{\partial t} = \hat{D} \frac{\partial^2 S}{\partial z^2} + r(S + I) \left(1 - \frac{S + I}{C}\right) - \mu S - \beta SI + \gamma I, \\
\frac{\partial I}{\partial t} = \hat{D} \frac{\partial^2 I}{\partial z^2} - \mu I + \beta SI - \gamma I - dI,
\]

With \( S, I \) are densities of susceptibles and infectives respectively, diffusing along the z axis from the origin, with raw birth rate \( r \), carrying constant \( C \), natural death rate \( \mu \), death rate from disease \( d \), infectivity \( \beta \) and recovery rate \( \gamma \), with the introduction of one infected animal an infinitesimal time after \( t = 0 \) at \( z = 0 \). Throughout this chapter we assume that \( r > \mu \), so that the trivial equilibrium is always a repeller.

Lemma 5.2.1 System (5.2) has three equilibria - the eradication equilibrium, the infection free equilibrium and the endemic equilibrium. Each equilibrium can be connected to any other equilibrium by a travelling wave solution to the partial differential equations (5.2). Moreover, any travelling wave solution moves with a minimum speed of \( c_{\text{min}} \), where

\[
c_{\text{min}} = \max \left\{ 2\sqrt{D(\rho - \alpha)}, \frac{2}{\sqrt{\rho}} \sqrt{D(R_b(\rho - \alpha) - \rho)} \right\}
\]

and the quantities \( D, \rho, \alpha \) and \( R_b \) are defined in (5.3) below.

We use the following non-dimensionalisation scheme which retains the parameters whose impact on the behaviour of system (5.2) we want to study

\[
x = \frac{S}{C}, \quad y = \frac{I}{C}, \quad m = \frac{N}{C}, \quad \hat{t} = (\mu + d + \gamma)t, \\
\alpha = \frac{\mu}{\mu + \gamma + d}, \quad \rho = \frac{r}{\mu + \gamma + d}, \quad R_b = \frac{\beta C}{\mu + \gamma + d}, \quad \delta = \frac{d}{\mu + \gamma + d}, \quad D = \frac{\hat{D}}{\mu + \gamma + d},
\]

to give us, dropping the caret, the non-dimensionalised system

\[
\frac{\partial x}{\partial t} = D \frac{\partial^2 x}{\partial z^2} + \rho(x + y)(1 - x - y) - \alpha x + (1 - \alpha - \delta)y - R_b xy, \\
\frac{\partial y}{\partial t} = D \frac{\partial^2 y}{\partial z^2} - y + R_b xy,
\]

\[
x(z,0) = x_0(z) > 0 \quad y(z,0) \geq 0.
\]
General considerations

If we consider a general system of reaction diffusion equations of the form

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + f(u) + g(u), \quad (5.5)$$

where

- $x \in \mathbb{R}$ is the space variable
- $u = (u_1, u_2, u_3 \ldots)$ are the state variables
- $f = (f_1, f_2, f_3 \ldots)$ is a non-linear population dynamics function
- $g = (g_1, g_2, g_3 \ldots)$ is a non-linear disease dynamics function
- $D$ is a non-negative diagonal matrix of diffusion coefficients.

Equation (5.5) may possess a trivial equilibrium, $u = 0$, an infection free equilibrium, $u_0$ and an endemic equilibrium $u^*$ at which $f(u) + g(u) = 0$. To study the spatial spread of the disease we look for travelling wave solutions which connect the IFE and the endemic equilibrium.

**Definition 5.2.2** A planar travelling wave solution is a solution which travels without change of shape at a constant velocity and depends on space only in the direction of travel.

Writing $z = x + ct$ transforms the one-dimensional version of equation (5.5) into an ordinary differential equation

$$-c \frac{du}{dz} + D \frac{d^2 u}{dz^2} + f(u) + g(u) = 0$$

where solutions $u(z)$ move from right to left. The boundary conditions are those which are required for the solution to connect the two equilibrium states;

$$\lim_{z \to +\infty} f(z) = u^* \quad \lim_{z \to -\infty} u(z) = u_0 > 0.$$ 

Applying this approach to system (5.4), with $\psi = z + ct$, we have

$$c \frac{dx}{d\psi} = D \frac{d^2 x}{d\psi^2} + \rho(x + y)(1 - x - y) - ax + (1 - \alpha - \delta)y - R_b xy, \quad (5.6)$$

$$c \frac{dy}{d\psi} = D \frac{d^2 y}{d\psi^2} - y + R_b xy.$$ 

In order to solve system (5.6), we reduce it to four first-order ordinary differential equations as follows:

$$\frac{dx}{d\psi} = u, \quad \frac{du}{d\psi} = \frac{1}{D} (cu - \rho(x + y)(1 - x - y) + ax - (1 - \alpha - \delta)y + R_b xy),$$

$$\frac{dy}{d\psi} = w, \quad \frac{dw}{d\psi} = \frac{1}{D} (cw + y - R_b xy). \quad (5.7)$$

We have already found the equilibria for system (5.7) by solving the spatially homogeneous model in Section 3.4: they are the trivial solution, $(0,0,0,0)$, the IFE, $\left(1 - \frac{\rho}{\alpha}, 0, 0, 0\right)$ and the endemic equilibrium,

$$\left(\frac{1}{R_b}, 0, \frac{1}{2\rho R_b} \left(R_b(\rho - \alpha - \delta) + \sqrt{(R_b(\rho - \alpha - \delta))^2 + 4\rho\delta R_b}\right), 0\right).$$
The trivial solution

In order to consider the circumstances in which a travelling wave could realistically connect the second and third of these stationary solutions to the trivial solution, we consider first the constraint on \( c \). Linearising system (5.7) about the trivial solution, we obtain the eigenvalues of the Jacobian as follows (we take \( \rho > \alpha \) so that the trivial solution (eradication) is a repeller):

\[
\begin{align*}
\lambda_1 &= \frac{c + \sqrt{c^2 + 4D}}{2D}, \\
\lambda_2 &= \frac{c - \sqrt{c^2 + 4D}}{2D}, \\
\lambda_3 &= \frac{c + \sqrt{c^2 - 4D(\rho - \alpha)}}{2D}, \\
\lambda_4 &= \frac{c - \sqrt{c^2 - 4D(\rho - \alpha)}}{2D}
\end{align*}
\]

and we see that there are always three positive eigenvalues (or eigenvalues with positive real part). If \( |c| < 2\sqrt{D(\rho - \alpha)} \), we will have a conjugate pair of complex eigenvalues, indicating oscillations as trajectories leave the trivial solution. Since neither \( x \) nor \( y \) may be negative, for a travelling wave connecting the trivial solution to any other equilibrium to be biologically feasible we must have

\[ |c| \geq |c_{\text{crit}}| = 2\sqrt{D(\rho - \alpha)}. \tag{5.8} \]

The eigenvectors associated with these eigenvalues are as follows, the four components are associated in each case with \( x, \dot{x}, y, \dot{y} \) respectively

\[
\begin{pmatrix}
\frac{\delta - \theta}{\theta} \\
\lambda_1 \frac{\delta - \theta}{\theta} \\
1 \\
\lambda_1
\end{pmatrix}
= 
\begin{pmatrix}
\frac{\delta - \theta}{\theta} \\
\lambda_2 \frac{\delta - \theta}{\theta} \\
1 \\
\lambda_2
\end{pmatrix}
= 
\begin{pmatrix}
1 \\
\lambda_3 \\
0 \\
0
\end{pmatrix}
= 
\begin{pmatrix}
1 \\
\lambda_4 \\
0 \\
0
\end{pmatrix},
\]

where we have defined \( \theta = \rho + 1 - \alpha \). The sign pattern of these eigenvectors is as follows, assuming reasonably that \( \delta - \theta < 0 \):

\[
\begin{pmatrix}
- \\
- \\
+ \\
+
\end{pmatrix}
= 
\begin{pmatrix}
+ \\
+ \\
0 \\
0
\end{pmatrix}
= 
\begin{pmatrix}
+ \\
0 \\
0 \\
0
\end{pmatrix}.
\]

For trajectories leaving the trivial solution we need \( x > 0, y \geq 0, \dot{x} > 0 \) and \( \dot{y} \geq 0 \). The third and fourth eigenvectors have the appropriate sign pattern so that a trajectory connecting the trivial solution to the endemic equilibrium is at least plausible.
The infection free equilibrium

The eigenvalues of the Jacobian of the linearisation about the IFE, which is \( (1 - \frac{\alpha}{\rho}, 0, 0, 0) \), are

\[
\mu_1 = \frac{c + \sqrt{c^2 + 4D(\rho - \alpha)}}{2D}, \quad \mu_2 = \frac{c - \sqrt{c^2 + 4D(\rho - \alpha)}}{2D},
\]

\[
\mu_3 = \frac{cp + \sqrt{c^2p^2 - 4pD(Rb(p - \alpha) - \rho)}}{2pD},
\]

\[
\mu_4 = \frac{cp - \sqrt{c^2p^2 - 4pD(Rb(p - \alpha) - \rho)}}{2pD}.
\]

Recalling that \( R_b > \frac{\rho - \alpha}{\rho - \alpha} \) for the existence of an endemic disease state and the instability of the IFE (as we showed in Chapter 3), we see that the linearisation about the IFE gives rise to positive eigenvalues (or eigenvalues with positive real part), \( \mu_1 \) and \( \mu_3 \), \( \mu_2 \) is negative while the sign of \( \mu_4 \) (for \( \mu_4 \) real) depends on the magnitude of \( R_b \). If \( R_b \leq \frac{\rho - \alpha}{\rho - \alpha} \) then \( \mu_4 < 0 \). If \( R_b > \frac{\rho - \alpha}{\rho - \alpha} \) then \( \mu_4 > 0 \). Since \( x \) and \( y \) are now perturbations from the IFE, while there is no reason \( x \) may not be negative, \( y \) must be non-negative. If \( R_b \leq \frac{\rho - \alpha}{\rho - \alpha} \) this condition is met. However, if \( R_b > \frac{\rho - \alpha}{\rho - \alpha} \) the constraint on \( c \) to ensure that there are no oscillations is

\[
|c| > |c_{\text{min}}| = \frac{2}{\sqrt{\rho}} \sqrt{D(R_b(p - \alpha) - \rho)}.
\]

(5.9)

\( |c_{\text{min}}| \) may be larger than \( |c_{\text{crit}}| \), since

\[
\frac{2}{\sqrt{\rho}} \sqrt{D(R_b(p - \alpha) - \rho)} > 2\sqrt{D(\rho - \alpha)}
\]

if \( R_b > \rho + \frac{\rho - \alpha}{\rho - \alpha} \).

The right hand side of the second inequality above is thus \( \rho \) greater than the critical value for \( R_b \) for an endemic equilibrium, so that for quite modestly infectious disease \( c_{\text{min}} > c_{\text{crit}} \). This minimum wavespeed is increasing in \( R_b \), demonstrating that the more infectious the disease, the faster it spreads. The minimum wavespeed is also increasing in \( \rho \), the birth rate and \( D \) the diffusion rate, while decreasing in \( \alpha \), the death rate. All of these relationships appear to be biologically plausible.

We find that the eigenvectors associated with these eigenvalues are as follows;

\[
\begin{pmatrix}
1 \\
\mu_1 \\
0 \\
0
\end{pmatrix}, \quad
\begin{pmatrix}
1 \\
\mu_2 \\
0 \\
0
\end{pmatrix}, \quad
\begin{pmatrix}
\frac{-\phi + \delta \rho}{\phi} \\
-\mu_3 \frac{-\phi + \delta \rho}{\phi} \\
\mu_3 \\
\mu_3
\end{pmatrix}, \quad
\begin{pmatrix}
\frac{-\phi + \delta \rho}{\phi} \\
-\mu_4 \frac{-\phi + \delta \rho}{\phi} \\
\mu_4 \\
\mu_4
\end{pmatrix}
\]

(5.10)
where \( \phi = (R_b + \rho)(\rho - \alpha) - \rho > 0 \) for \( R_b > \frac{\rho}{\rho - \alpha} \). The eigenvectors have the following sign patterns, (found by algebra and by numerical simulation where necessary);

\[
\begin{pmatrix}
+ \\
0 \\
0
\end{pmatrix}
\begin{pmatrix}
- \\
0 \\
0
\end{pmatrix}
\begin{pmatrix}
- \\
+ \\
+
\end{pmatrix}
\begin{pmatrix}
- \\
+ \\
+
\end{pmatrix}.
\]

The last pair of eigenvectors have the right sign pattern for a travelling wave from the IFE to the endemic equilibrium to be at least feasible - pointing in the direction of negative \( x \) and positive \( y \).

**The endemic equilibrium**

The eigenvalues of the Jacobian of the linearisation around the endemic equilibrium are not tractable algebraically, numerical simulation suggests that they are always complex (as we have already found from the solution of a spatially homogeneous SIS model with death of infectives). We are thus forced to rely on numerical simulation to find the sign pattern of the real parts of the eigenvectors. They are as follows

\[
\begin{pmatrix}
+ \\
- \\
-
\end{pmatrix}
\begin{pmatrix}
- \\
+ \\
-
\end{pmatrix}
\begin{pmatrix}
- \\
+ \\
-
\end{pmatrix}
\begin{pmatrix}
- \\
+ \\
-
\end{pmatrix}.
\]

The second and third of these eigenvectors are orientated towards positive \( y \) and negative \( x \), which is consistent with trajectories approaching the endemic equilibrium. It is thus reasonable to conclude that a travelling wave from the infection free equilibrium to the endemic equilibrium is at least plausible.

5.3 Two species SIS model with one-dimensional diffusion

We now consider a two species model. We assume that cattle are modelled by a static, spatially homogeneous system, moreover with constant population, while badgers diffuse through them along a single spatial dimension from right to left. For simplicity we ignore deaths from disease (we have already shown that, while the inclusion of deaths due to disease results in an oscillatory solution to the linearisation around the endemic equilibrium, the properties of the model are broadly similar to those when there are no additional deaths.
due to disease) and there is no latent period. The model equations are

\[ \frac{\partial I_c}{\partial t} = \beta_c I_c (N_c - I_c) + \xi_{bc} (N_c - I_c) I_b - (\mu_c + \gamma_c) I_c, \]

\[ \frac{\partial S_b}{\partial t} = D_s \frac{\partial^2 S_b}{\partial x^2} + r_b (S_b + I_b) \left( 1 - \frac{S_b + I_b}{C_b} \right) - \mu_b S_b + \gamma_b I_b - \beta_b S_b I_b - \xi_{cb} S_b I_c, \]

\[ \frac{\partial I_b}{\partial t} = D_I \frac{\partial^2 I_b}{\partial x^2} - (\mu_b + \gamma_b) I_b + \beta_b S_b I_b + \xi_{cb} S_b I_c, \]

\[ S_b(x, 0) = S_0(x) > 0, \quad I_b(x, 0) = 0, \quad I_c(x, 0) = 0. \]

with the introduction of an infected badger some time after \( t = 0 \) at \( x = 0 \).

The subscripts \( c \) and \( b \) refer to cattle and badgers respectively, \( S \) is the susceptible class, \( I \) the infectious class and \( N \) the total population of a species. \( N_c = N_c^* \) is the equilibrium population of cattle, \( \mu \) is death rate, \( r \) raw birth rate and \( C_b \) the badger carrying constant for the environment, \( \beta \) is the intra-specific infectivity and \( \xi \) the interspecies infectivity in the direction of the subscripts, \( \gamma \) is the recovery rate. We assume that the diffusion coefficients, are the same for both susceptible and infective badgers so that \( D_s = D_I \).

We use the an analogous non-dimensionalisation scheme to that in sub-section 2.14, namely

\[ v = \frac{I_c}{N_c}, \quad u = \frac{S_b}{C_b}, \quad y = \frac{I_b}{C_b}, \quad n = \frac{N_b}{C_b}, \quad \dot{t} = (\mu_c + \gamma_c) t, \]

\[ R_c = \frac{N_c \beta_c}{\mu_c + \gamma_c}, \quad R_b = \frac{C_b \beta_b}{\mu_b + \gamma_b}, \quad U_c = \frac{N_b \xi_{bc}}{\mu_c + \gamma_c}, \quad U_b = \frac{N_c \xi_{cb}}{\mu_c + \gamma_c}, \]

\[ \alpha = \frac{\mu_c}{\mu_b + \gamma_b}, \quad \rho = \frac{r_b}{\mu_b + \gamma_b}, \quad k = \frac{\mu_b + \gamma_b}{\mu_c + \gamma_c}, \quad D = \frac{\dot{D}}{\mu_b + \gamma_b}. \]

This gives us, after removing the carets, the following non-dimensionalised model:

\[ \frac{\partial v}{\partial t} = R_c v (1 - v) + kU_c y (1 - v) - v, \]

\[ \frac{\partial u}{\partial t} = kD \frac{\partial^2 u}{\partial x^2} + k\rho(u + y)(1 - u - y) - k\alpha u + k(1 - \alpha) y - kR_b uy - U_b uv, \]

\[ \frac{\partial y}{\partial t} = kD \frac{\partial^2 y}{\partial x^2} - ky + kR_b uy + U_b uv, \]

\[ v(x, 0) = 0 \quad u(x, 0) = n^* = 1 - \frac{\alpha}{\rho}, \]

\[ u(0, t) = n^*, \quad u_x(x, 0) = 0, \quad y(x, 0) = 0. \]
Remark 5.3.1 Since \( u + y = n \), we can write the equation for the whole badger population as

\[
\frac{\partial n}{\partial t} = kD \frac{\partial^2 n}{\partial x^2} + kpn(1 - n) - k\alpha n,
\]

which is the very famous equation ascribed to Fisher.

There are two steady states for (5.13), \( n = 0 \) and \( n = n^* = 1 - \frac{\alpha}{\rho} \). If we linearise (5.13) about \( n^* \) with \( n = \bar{n} + n^* \) we obtain, to first order

\[
\frac{\partial \bar{n}}{\partial t} = kD \frac{\partial^2 \bar{n}}{\partial x^2} - k\rho n^* \bar{n}.
\]

We now put \( \bar{n} = e^{\lambda t} e^{\omega x} \) as a trial solution and substitute in the equation above;

\[
\lambda = -kD\omega^2 - k\rho n^* < 0 \quad \text{for all} \quad \omega \in \mathbb{R}.
\]

We thus conclude that the equilibrium \( n^* \) is locally stable.

5.3.1 Travelling waves

We have already established in Chapter 3 that system (5.12) has three equilibria - the trivial equilibrium \((0, 0, 0)\), the infection free equilibrium, \((0, n^*, 0)\) and the endemic equilibrium (which cannot be obtained explicitly but which we denote \((v^*, x^*, y^*)\)). We consider the possibility of a travelling wave connecting the infection free equilibrium and the endemic equilibrium. In order to make progress we note that \( n \) is determined by (5.13), which has \( n = n^* = 1 - \frac{\alpha}{\rho} \) as a steady state. We assume that \( n(x, t) \) has reached this steady state everywhere in the domain and therefore we can replace \( u \) by \( n^* - y \) to reduce the dimension of the system to two.

\[
\frac{\partial v}{\partial t} = R_c v (1 - v) + kU_c y (1 - v) - v,
\]

\[
\frac{\partial y}{\partial t} = kD \frac{\partial^2 y}{\partial x^2} - ky + kR_b y (n^* - y) + U_b v (n^* - y),
\]

where at least one of \( v_0(x) \) and \( y_0(x) \) is not identically zero. We can also write (5.14) as

\[
(v, y) = D (v, y)_{xx} + f(v, y).
\]

Here we define \( f = (f_1, f_2)^T \), \( D = \begin{pmatrix} 0 & 0 \\ 0 & kD \end{pmatrix} \) and

\[
\begin{pmatrix} f_1 \\ f_2 \end{pmatrix} = \begin{pmatrix} R_c v (1 - v) + kU_c y (1 - v) - v \\ -ky + kR_b y (n^* - y) + U_b v (n^* - y) \end{pmatrix}.
\]

A travelling wave solution with speed \( c \) has the form \((v(x + ct), y(x + ct))\) and connects the IFE with the endemic equilibrium, i.e.

\[
\lim_{x + ct \to +\infty} (v, y) = (v^*, y^*) \quad \text{and} \quad \lim_{x + ct \to -\infty} (v, y) = (0, 0).
\]
The solution satisfies

\[ c \begin{pmatrix} \frac{dv}{dz} \\ \frac{dy}{dz} \end{pmatrix} = D \begin{pmatrix} \frac{d^2v}{dz^2} \\ \frac{d^2y}{dz^2} \end{pmatrix} + f \begin{pmatrix} v \\ y \end{pmatrix}, \]

(5.15)

\[ v(-\infty) = 0, \quad y(-\infty) = 0, \quad v(\infty) = v^*, \quad y(\infty) = y^* \]

where \( v^* \) and \( y^* \) are the endemic equilibrium values and \( z = x + ct \). We now employ the following theorem based on the work of Li et al [44].

**Theorem 5.3.2** There exists a minimal \( c_0 \) such that, for every \( c > c_0 \), system (5.15) has a non-decreasing travelling wave solution \((v(x + ct), y(x + ct))\) with speed \( c \), provided that conditions 1 to 5 below are satisfied. If \( c < c_0 \) no travelling wave solutions can exist.

1. \( f = 0 \) has two solutions, the IFE, \((0,0)\) and the endemic equilibrium, \((v^*, y^*)\)
2. \( f \) is co-operative i.e. \( \frac{\partial f_1}{\partial y} > 0 \) and \( \frac{\partial f_2}{\partial v} > 0 \)
3. \( f \) does not depend explicitly on either \( x \) or \( t \)
4. \( f \) is continuous, has uniformly bounded continuous first partial derivatives for \((0,0) \leq (v, y) \leq (v^*, y^*)\). The Jacobian matrix of the linearisation about \((0,0)\) has non-negative off-diagonal entries and a positive eigenvalue with an eigenvector which has positive components.
5. \( D \) is a diagonal matrix with positive entries.

System (5.14) satisfies the first four of these requirements. However \( D \) has non-negative as opposed to positive entries, we make the assumption that in this case Theorem 5.3.2 applies nonetheless based upon the following argument.

Let us assume that \((v_\epsilon, y_\epsilon)\) is the solution of (5.15) with \( D \) replaced with

\[ D_\epsilon = \begin{pmatrix} \epsilon & 0 \\ 0 & kD \end{pmatrix}, \]

where \( \epsilon > 0 \). By Theorem 5.3.2 this solution must exist and satisfy \( v_\epsilon(-\infty) = 0, y_\epsilon(-\infty) = 0 \) for each \( \epsilon > 0 \). Then, by continuity with respect to the parameters, for each fixed \( z \) we must have \((v_\epsilon(z), y_\epsilon(z)) \rightarrow (v(z), y(z)) \) as \( \epsilon \rightarrow 0 \), where \((v(z), y(z))\) satisfies (5.14). Also, for each fixed \( \epsilon, (v_\epsilon(z), y_\epsilon(z)) \rightarrow 0 \) as \( z \rightarrow -\infty \).

The potential problem is that it does not immediately follow from the previous paragraph that \( v(z), y(z) \rightarrow 0 \) as \( z \rightarrow -\infty \) because in principle \( v \) could behave like \( v(z) \sim e^{cz} \) as \( z \rightarrow -\infty \). The pointwise limit of this function as \( \epsilon \rightarrow 0 \) is 1. However, \((v(-\infty), y(-\infty))\) and \((v_\epsilon(-\infty), y_\epsilon(-\infty))\) must both satisfy the equilibrium equations derived from (5.14) by setting all the derivatives
to zero and hence \((v(-\infty), y(-\infty)) = (0, 0)\).

Thus the Jacobian, \(J(v, y)\), is

\[
J(v, y) = \begin{pmatrix} R_c(1 - 2v) - kU_c y - 1 & kU_c(1 - v) \\ U_b(n^* - y) & kR_b(n^* - 2y) - U_bv - k \end{pmatrix}
\]

and by inspection we see that all the entries are uniformly bounded and continuous. About the IFE the Jacobian is

\[
J(0,0) = \begin{pmatrix} R_c - 1 & kU_c \\ U_b n^* & k(R_b n^* - 1) \end{pmatrix}
\]

The eigenvalues are;

\[
\lambda_1 = \frac{1}{2} \left( R_c - 1 + k(R_b n^* - 1) + \sqrt{\left( (R_c - 1) - k(R_b n^* - 1) \right)^2 + 4U_bU_c n^* k} \right)
\]

\[
\lambda_2 = \frac{1}{2} \left( R_c - 1 + k(R_b n^* - 1) - \sqrt{\left( (R_c - 1) - k(R_b n^* - 1) \right)^2 + 4U_bU_c n^* k} \right)
\]

with eigenvectors

\[
\left\{ \left( 1, \frac{1 - R_c + \lambda_1}{kU_c} \right)^T, \left( 1, \frac{1 - R_c + \lambda_2}{kU_c} \right)^T \right\}
\]

If we write \(\lambda_1\) in the form

\[
\lambda_1 = \frac{1}{2} \left( (R_c - 1) + k(R_b n^* - 1) 
\right.
\]

\[
+ \sqrt{\left( (R_c - 1) + k(R_b n^* - 1) \right)^2 - 4k(R_c - 1)(R_b n^* - 1) + 4U_bU_c n^* k}, \right)
\]

we see that if \(R_c > 1\) and \(R_b n^* > 1\), the condition for endemic disease in each species alone, then \(\lambda_1 > 0\). If \(R_c < 1\) and \(R_b n^* < 1\), then \(\lambda_1 > 0\) provided

\[
\frac{U_bU_c n^*}{(1 - R_c)(1 - n^*R_b)} > 1,
\]

which we recognise as the basic reproductive ratio for the two animal system (5.11), analogous to \(R_{bc}\) defined in (2.11). Hence, if the condition for the existence of an endemic equilibrium is satisfied, then \(\lambda_1 > 0\).

The second component of the eigenvector associated with \(\lambda_1\) is evidently positive if \(R_c < 1\). If \(R_c > 1\) then by writing the numerator as

\[
\frac{1}{2} \left( (1 - R_c) + (k(R_b n^* - 1)) + \sqrt{((1 - R_c) - (k(R_b n^* - 1)))^2 + 4U_bU_c n^* k} \right)
\]

we see that it is positive in this case too.

The conditions of Theorem (5.3.2) are thus satisfied and hence we may conclude that travelling waves exist for system (5.14), for all speeds greater than \(c_0\).
5.3.2 Calculating the spread rate

The minimal speed, \( c_0 \) described in Theorem 5.3.2, is equal to \( c^* \), the spread rate for system (5.14). The following is taken from Li [44];

Definition 5.3.3 The spread rate for the non linear system (5.5) with initial conditions not equal to \( u_0 \) is a number \( c^* \) such that, for \( u_0 \neq u^* \) and \( 0 < \epsilon \ll 1 \)

\[
\lim_{t \to \infty} \left\{ \sup_{x \leq (c^*-\epsilon)t} \| u(x, t) - u_0 \| \right\} = 0,
\]

\[
\lim_{t \to \infty} \left\{ \sup_{x \geq (c^*+\epsilon)t} \| u(x, t) - u^* \| \right\} = 0.
\]

This definition expresses the statement that for all wavespeeds greater than the spread rate, the system tends to the endemic equilibrium, while for wavespeeds below the spread rate the system tends to the IFE.

Definition 5.3.4 System (5.14), linearised about an equilibrium can be written

\[
\frac{\partial Z}{\partial t} = D \frac{\partial^2 Z}{\partial x^2} + JZ
\]

where \( Z = (v, y)^T \) and \( J \) is the Jacobian of the linearisation about that equilibrium. The spread rate for the linearised system (5.16) is a number \( \bar{c} \) for which

\[
\lim_{t \to \infty} \left\{ \sup_{x \leq (\bar{c}-\epsilon)t} \| Z(x, t) \| \right\} = 0,
\]

\[
\lim_{t \to \infty} \left\{ \sup_{x \geq (\bar{c}+\epsilon)t} \| Z(x, t) \| \right\} > 0.
\]

If \( c^* = \bar{c} \) then the spread rate for the non-linear system is the same as that of the linear system and the non-linear system is said to be linearly determinate.

We are interested in the circumstances in which system (5.14) is linearly determinate, since this allows us to study the much easier linear system. The following theorem is taken from [42]:

Theorem 5.3.5 If conditions 1 to 4 of Theorem 5.3.2 are satisfied and if we assume \( D \) having non-negative entries is sufficient and that if in addition the Jacobian of the linearisation of system (5.14) about the IFE, \( J(0,0) \), is irreducible and if a subtangential condition,

\[
f \left( p \begin{pmatrix} v \\ y \end{pmatrix} \right) \leq pJ(0,0) \begin{pmatrix} v \\ y \end{pmatrix}
\]

for all \( p > 0 \), is satisfied, then the spread rate \( c^* \) is linearly determinate. Moreover the spread rate, \( \bar{c} \) for the linearised system is

\[
\bar{c} = \inf_{\lambda > 0} \sigma_\lambda,
\]

(5.17)

where \( \sigma_\lambda \) is the largest eigenvalue of the matrix

\[
B_\lambda = \frac{J(0,0) + \lambda^2 D}{\lambda}.
\]

(5.18)
Remark 5.3.6 A square $n \times n$ matrix $A = a_{ij}$ is called reducible if the indices $1, 2, \ldots, n$ can be divided into two disjoint nonempty sets $\{i_1, i_2, \ldots, i_\mu\}$ and $\{j_1, j_2, \ldots, j_\nu\}$ (with $\mu + \nu = n$) such that $a_{i_\alpha j_\beta} = 0$ for $\alpha = 1, 2, \ldots, \mu$ and $\beta = 1, 2, \ldots, \nu$. An irreducible matrix is one which is not reducible. The Jacobian of the linearisation of a system where one or more components are decoupled would be a reducible matrix.

Remark 5.3.7 For a scalar o.d.e. $\dot{u} = f(u)$, we can visualise the subtangential condition, which is $uf'(0) > f(u)$ for $u \geq 0$, as ensuring that solutions are bounded from above.

We can illustrate Theorem 5.3.5 by considering its application to Fisher's equation in one dimension,

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + f(u).$$

Then

$$B_\lambda = \frac{f'(0) + D\lambda^2}{\lambda}$$

and thus, $\sigma_\lambda$ is simply the value of the right hand side, so

$$\bar{c} = \inf_{\lambda > 0} \sigma_\lambda = \min_{\lambda > 0} \left( \frac{f'(0)}{\lambda} + D\lambda \right).$$

Differentiating the expression w.r.t. $\lambda$, we find that the minimum value of $\sigma_\lambda$ occurs for $\lambda = \sqrt{\frac{f'(0)}{D}}$. Substituting we obtain the well-known value for $\bar{c}$ for Fisher's equation (see also [45]), namely

$$\bar{c} = 2\sqrt{Df'(0)}.$$

For system (5.14), the subtangential condition is

$$PJ(0,0) \begin{pmatrix} v \\ y \end{pmatrix} = \begin{pmatrix} p((R_c - 1)v + kUcy) \\ p(U_bvn^* + ky(R_bn^* - 1)) \end{pmatrix} \geq p \begin{pmatrix} R_cv(1 - pv) + kUcy(1 - pv) - v \\ -ky + kR_by(n^* - py) + U_by(n^* - py) \end{pmatrix} \quad (5.19)$$

for $p \geq 0$ and $v, y \geq 0$. Now

$$(R_c - 1)v + kUcy \geq R_cv(1 - pv) + kUcy(1 - pv) - v$$

is the same as

$$-pR_c v - kUcy \leq 0,$$

so that the first element of inequality (5.19) is always true. As for the second,

$$U_bvn^* + ky(R_bn^* - 1) \geq -ky + kR_by(n^* - py)y + U_by(n^* - py),$$

reduces to

$$-pkR_by - U_bvn^* \leq 0$$

which is also always true. Thus the subtangential condition is met for system (5.14).
If we now compute the matrix $B_\lambda$, defined in equation (5.18), we obtain

$$B_\lambda = \begin{pmatrix}
\frac{R_c - 1}{\lambda} & \frac{kU_c}{\lambda} \\
U_b n^* & kD\lambda + \frac{k(R_b n^* - 1)}{\lambda}
\end{pmatrix}$$

with the following characteristic equation determining its two eigenvalues $\sigma_\pm$

$$f(\sigma, \lambda) = \lambda^2 \sigma^2 - (kD\lambda^3 + \lambda T)\sigma + \Delta + (R_c - 1)kD\lambda^2 = 0 \quad (5.20)$$

where

$$T = \text{trace}(J(0, 0)) = k(R_b n^* - 1) + R_c - 1 > 0$$

and

$$\Delta = \det(J(0, 0)) = k(R_b n^* - 1)(R_c - 1) - k n^* U_b U_c < 0.$$ 

Since for the endemic state to exist we know that we must have

$$U_b U_c n^* (R_b n^* - 1) (R_c - 1)$$

and we assume that $R_b > \frac{1}{n^*}$ and $R_c > 1$. The IFE is thus unstable so we can be sure that at least one of $\sigma(\lambda)_\pm > 0$ and thus that the determinant is negative.

To find $\xi$, defined in (5.17) we need to find an extremum of $\sigma(\lambda)$, i.e. where $\sigma'(\lambda) = 0$. We have $f(\sigma(\lambda), \lambda) = 0$ and thus

$$\frac{\partial f(\sigma(\lambda), \lambda)}{\partial \sigma} \cdot \frac{d\sigma(\lambda)}{d\lambda} + \frac{\partial f(\sigma(\lambda), \lambda)}{\partial \lambda} = 0$$

so that when $d\sigma(\lambda)/d\lambda = 0$ we must have $\frac{\partial f(\sigma(\lambda), \lambda)}{\partial \lambda} = 0$.

Thus, the condition that $\sigma(\lambda)$ has an extremum is that $\frac{\partial f(\sigma(\lambda), \lambda)}{\partial \lambda} = 0$.

If both $\frac{\partial f(\sigma(\lambda), \lambda)}{\partial \lambda} = 0$ and $f(\sigma(\lambda), \lambda) = 0$, then the value of $\lambda$ at which both equations are satisfied will necessarily be a double root of (5.20), considered as a cubic equation in $\lambda$. At this double root, the discriminant of (5.20) in $\lambda$, $g(\sigma)$, a cubic in $\sigma^2$, is zero and the resulting equation, $g(\sigma) = 0$, will have $\xi$ as one of its roots. The equation is

$$g(\sigma) = (T^2 - 4\Delta)\sigma^6 + 2kD \left( (R_c - 1)(T^2 - 6\Delta) + T(9\Delta - 2T^2) \right) \sigma^4 + k^2D^2 \left( (R_c - 1)(T^2(R_c - 1) + 6\Delta(3T + 2(1 - R_c)) - 27\Delta^2) \right) \sigma^2 - 4\Delta(R_c - 1)^3k^3D^3 = 0. \quad (5.21)$$
We cannot extract a useful explicit expression for $\sigma$ from (5.21). However we may obtain some qualitative information from it. If we write equation (5.21) in the form $p\omega^3 + q\omega^2 + r\omega + s = 0$, where $\omega = \sigma^2$, we see immediately that $p > 0$ and $s < 0$ so that there must be at least one positive real root. To establish the uniqueness of this root requires us to establish $\text{sgn}(q)$ and $\text{sgn}(r)$, which we can not do analytically. Simulation suggest that there is a unique positive root.

Interestingly, given that $D$ is small, if we neglect $O(D^2)$, then we can solve $g(\sigma) = 0$ directly to give a quadruple root of zero and

$$|\sigma| = \sqrt{\frac{2Dk}{T^2 - 4\Delta}} \left( (2T^2 - 9\Delta) - (R_c - 1)(T^2 - 6\Delta) \right),$$

(5.22)

provided that

$$T(2T^2 - 9\Delta) > (R_c - 1)(T^2 - 6\Delta).$$

If this condition is satisfied then the positive root is unique.

The foregoing analysis applies equally to either the larger or the smaller roots of $f(\sigma, \lambda) = 0$. We must be sure to take the larger root. The simplest approach is the direct solution of equation (5.20) to give

$$\sigma = \frac{\lambda^2 Dk + T}{2\lambda} + \frac{1}{2\lambda} \sqrt{(T + kD\lambda^3)^2 - 4(\Delta - \lambda^2 Dk(1 - R_c))}.$$  

(5.23)

Finding the minimum of the expression on the right hand of the above equation results in our having to solve a sixth order polynomial in $\lambda$. Once more, however, we utilise the fact that $D$ is small to expand the right hand side in a Taylor series around $D = 0$. Ignoring $O(D^2)$ allows us to find the minimum value of $\sigma$ to be when

$$\lambda = \sqrt{\frac{W}{DV}},$$

where

$$V = k(\sqrt{T^2 - 4\Delta} + T + 2(1 - R_c)),$$

$$W = T\sqrt{T^2 - 4\Delta} + T^2 - 4\Delta.$$

Thus our approximation for $\bar{\sigma}$ is

$$\bar{\sigma} = \inf_{\lambda > 0} |\sigma| \approx \sqrt{\frac{D}{4WV}} \left( kW + VT + \sqrt{(kW + VT)^2 - 4DV + 4kWV(1 - R_c)} \right).$$

Numerical simulation with the parameter set $\{D = 0.1, R_c = 0.8, R_b = 2.5, k = 0.9, U_b = 1, U_c = 2\}$ gives the following results for $\bar{\sigma}$ to three d.p.s:

- from the approximation in (5.22), $\bar{\sigma} = 0.649$
- from the zero of $g(\sigma)$, $\bar{\sigma} = 0.754$
- from the approximation to the minimum of (5.23), $\bar{\sigma} = 0.707$
- the exact minimum value of the exact solution of equation (5.20), $\bar{\sigma} = 0.754$
The linearisation of system (5.12)

An alternative method of explicitly calculating $\bar{e}$ for system (5.11) involves transforming system (5.12) into ordinary differential equations with the substitution $z = x + ct$ and finding the conditions for feasible travelling wave solutions. The transformed system is

$$
\frac{c}{dt} = R_v(1 - v) + kUcY(1 - v) - v,
$$

$$
\frac{dU}{dz} = Dk\frac{d^2U}{dz^2} + k\rho(u + y)(1 - u - y) - k\alpha u + k(1 - \alpha)y - kRbuy - Ubv,
$$

$$
\frac{dy}{dz} = Dk\frac{d^2y}{dz^2} - ky + kRbuy + Uby,
$$

$$
\frac{d\rho}{dz} = Dk\frac{d^2\rho}{dz^2} + k\rho(1 - n) - k\alpha n,
$$

$v(-\infty) = 0$, $u(-\infty) = 0$, $y(-\infty) = 0$,

$v(\infty) = v^*$, $u(\infty) = u^*$, $y(\infty) = y^*$.

We investigate the stationary solutions for (5.24) for the whole badger population by writing

$$
\frac{dn}{dz} = m, \quad \frac{dm}{dz} = \frac{1}{kD}(\rho n - \rho n(1 - n) + \alpha n).
$$

There are two equilibria for (5.25), the trivial solution and the carrying population equilibrium. At the trivial solution, $(0, 0)$ the characteristic equation of the Jacobian of the linearisation is

$$
\lambda^2 - \lambda\frac{c}{Dk} + \frac{\rho - \alpha}{Dk} = 0,
$$

and the discriminant of this equation is $\frac{c^2}{Dk^2} - 4\left(\frac{\rho - \alpha}{Dk}\right)$. To exclude the possibility of complex eigenvalues, thus ensuring the non-negativity of the state variables, this discriminant must be positive and thus, $|c| > |c_{\min}| = 2\sqrt{k(\rho - \alpha)D}$. With the same analysis as in Section 5.2, we conclude that a travelling wave from the trivial state to either the IFE or the endemic state will be plausible.

Approximating a solution

While we cannot solve the equations of system (5.12) analytically, we may hope to learn more about the system by approximating a solution of the system linearised around the leading edge of the travelling wave connecting the trivial equilibrium to the IFE. Let $n_0(z)$ be the travelling wave solution for $n(z)$, then $u(z) + y(z) = n_0(z)$ and we can reduce the problem to

$$
\frac{dv}{dz} = R_v(1 - v) + kUcY(1 - v) - v,
$$

$$
\frac{dy}{dz} = kD\frac{d^2y}{dz^2} - ky + kRb(y(n_0 - y) + Uby(n_0 - y),
$$

$n(-\infty) = 0 = v(-\infty) = 0$, $y(-\infty) = 0$. 

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We assume that there would be no endemic equilibrium in cattle in the absence of badgers so that \( R_c < 1 \). We linearise around \((0,0)\), close to \( z = -\infty \), when \( n_0(-\infty) = 0 \)

\[
\frac{dv}{dz} = -v + R_cv + kU_cv,
\]

(5.27)

\[
\frac{dy}{dz} = kD_2\frac{dy}{dz} - ky.
\]

The second of these equations is not coupled and we can solve it directly to give

\[
y(z) = A_1e^{\lambda_1z} + B_1e^{\lambda_2z},
\]

where \( A_1 \) and \( B_1 \) are constants and

\[
\lambda_1 = \frac{1}{2Dk} \left( c + \sqrt{c^2 + 4Dk^2} \right), \quad \lambda_2 = \frac{1}{2Dk} \left( c - \sqrt{c^2 + 4Dk^2} \right).
\]

Since \( y(-\infty) = 0 \), \( B_1 = 0 \), so

\[
y(z) = A_1e^{\lambda_1z}.
\]

We can now substitute our solution for \( y(z) \) into the first equation of (5.27) and obtain a differential equation in \( v \) only, which is straightforwardly solved by the integrating factor method to give

\[
v(z) = \frac{kU_cvA_1e^{\lambda_1z}}{c\lambda_1 + 1 - R_c} + A_3e^{1-R_c}z,
\]

where \( A_3 \) is a constant. As \( z \to -\infty \), \( v \to 0 \) by the boundary conditions (5.26), so \( A_3 = 0 \).

Finally, we can now substitute for \( v \) and \( y \) in the linearised equation for \( u \), with \( r = \rho - \alpha \)

\[
kD_2\frac{du}{dz^2} - c\frac{du}{dz} + kurt = -kA_1(r + 1)e^{\lambda_1z}.
\]

The characteristic equation for the homogeneous problem is the same as that arising from equation (5.25) with the same constraint on \( c \) for a travelling wave solution. We can solve for \( u(z) \) to obtain

\[
u(z) = C_1e^{\omega_1z} + C_2e^{\omega_2z} - \frac{k}{kD\lambda_1^2 - c\lambda_1 + k(\rho - \alpha)}(\rho - \alpha + 1)e^{\lambda_1z},
\]

where \( C_1, C_2 \) are constants and

\[
\omega_1 = \frac{1}{2Dk} \left( c + \sqrt{c^2 - 4(\rho - \alpha)Dk^2} \right), \quad \omega_2 = \frac{1}{2Dk} \left( c - \sqrt{c^2 - 4(\rho - \alpha)Dk^2} \right).
\]

Thus

\[
u(z) = C_1e^{\frac{1}{2Dk}(c+\sqrt{c^2-4(\rho-\alpha)Dk^2})z} + C_2e^{\frac{1}{2Dk}(c-\sqrt{c^2-4(\rho-\alpha)Dk^2})z} - \frac{k}{kD\lambda_1^2 - c\lambda_1 + k(\rho - \alpha)}(\rho - \alpha + 1)e^{\lambda_1z}.
\]

The criterion for \( c > |c_{\text{min}}| \) for a travelling wave clearly arises from the population dynamics term, not the infectivity term.
5.3.3 Equilibria and the feasibility of a travelling wave solution

Lemma 5.3.8 System (5.11) has three equilibria - the eradication equilibrium, the infection free equilibrium and the endemic equilibrium.

Conjecture 5.3.9 Any one of these equilibria can be connected to any other by a travelling wave solution to the partial differential equations (5.11).

We have rewritten (5.11) in the form of an o.d.e. system in (5.24). We can reduce the order of system (5.24) from two to one as follows;

\[
\begin{align*}
\frac{dv}{dz} &= R_c v(1 - v) - v + kU_c y(1 - v), \\
\frac{du}{dz} &= w, \\
kD \frac{dw}{dz} &= c w - k\rho (u + y)(1 - u - y) + k\alpha u - k(1 - \alpha) y + kR_b y y + U_b w, \\
\frac{dy}{dz} &= q, \\
kD \frac{dq}{dz} &= c q + ky - kR_b y y - U_b w,
\end{align*}
\]

(5.28)

with boundary conditions \(v(-\infty), u(-\infty), w(-\infty), y(-\infty), q(-\infty) = 0\) and \(v(\infty) = v^*, u(\infty) = u^*, w(\infty) = 0, y(\infty) = y^*, q(\infty) = 0\).

The trivial solution

At \((0, 0, 0, 0, 0)\) the five eigenvalues of the linearisation of (5.28) are as follows,

\[
\lambda_1 = \frac{1}{c} (R_c - 1),
\]

\[
\lambda_2 = \frac{c + \sqrt{c^2 - 4k^2 D(\rho - \alpha)}}{2kD}, \\
\lambda_3 = \frac{c - \sqrt{c^2 - 4k^2 D(\rho - \alpha)}}{2kD}, \\
\lambda_4 = \frac{c + \sqrt{c^2 + 4k^2 D}}{2kD}, \\
\lambda_5 = \frac{c - \sqrt{c^2 + 4k^2 D}}{2kD}.
\]

For \(R_c < 1\) we have \(\lambda_1 < 0\), while \(\lambda_2, \lambda_3, \lambda_4 > 0\) and \(\lambda_5 < 0\) for all parameter values. In order to ensure that the state variables remain non-negative we thus have the constraint on \(c\) as before to ensure all the eigenvalues are real:

\[
|c| > |c_{crit}| = 2k\sqrt{D(\rho - \alpha)}. 
\]

(5.29)

The five eigenvectors are

\[
\begin{pmatrix}
1 \\
0 \\
0 \\
0 \\
0
\end{pmatrix}, \quad \begin{pmatrix}
0 \\
1 \\
\lambda_2 \\
\lambda_3 \\
0
\end{pmatrix}, \quad \begin{pmatrix}
0 \\
1 \\
0 \\
0
\end{pmatrix}, \quad \begin{pmatrix}
-c\lambda_4 + R_c - 1 \\
\lambda_4(-c\lambda_4 + R_c - 1) \\
-c\lambda_4 + R_c - 1 \\
\lambda_4(-c\lambda_4 + R_c - 1)
\end{pmatrix}, \quad \begin{pmatrix}
1 \\
\frac{-c\lambda_5 + R_c - 1}{kU_c} \\
\frac{-c\lambda_5 + R_c - 1}{kU_c} \\
\frac{-c\lambda_5 + R_c - 1}{kU_c}
\end{pmatrix}
\]

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These eigenvectors have the following sign pattern, taking $R_c < 1$ - no disease in cattle in the absence of badgers, where necessary we use simulation, with the parameter set \{c = 1, D = 0.1, R_c = 0.8, R_b = 2.5, k = 0.9, U_b = 1, U_c = 2, \rho = 1, \alpha = 0.1}\}

\[
\begin{pmatrix}
+ \\
0 \\
0 \\
0 \\
\end{pmatrix}
\begin{pmatrix}
0 \\
+ \\
0 \\
0 \\
\end{pmatrix}
\begin{pmatrix}
0 \\
+ \\
0 \\
0 \\
\end{pmatrix}
\begin{pmatrix}
+ \\
- \\
+ \\
- \\
\end{pmatrix}
\begin{pmatrix}
+
\end{pmatrix}
\begin{pmatrix}
+
\end{pmatrix}
\begin{pmatrix}
+
\end{pmatrix}
\begin{pmatrix}
+
\end{pmatrix}
\begin{pmatrix}
+
\end{pmatrix}
\begin{pmatrix}
+
\end{pmatrix}
\]

Plausibility of travelling wave solutions

In this chapter and also in Chapter 7 we investigate whether the sign patterns of the eigenvalues and the associated eigenvectors of the linearised systems are consistent with the conditions for a travelling wave leaving the equilibrium we are studying and connecting with another equilibrium. While the behaviour of the eigenvectors close to the equilibrium cannot ensure that a travelling wave solution actually will exist, we can identify the properties of these eigenvectors such that a travelling wave is not plausible. Such analysis thus does not in any way constitute a proof of the existence of travelling wave solutions, merely reasonable evidence for their plausibility.

We are only concerned with the sign pattern of eigenvectors associated with positive eigenvalues or eigenvalues with positive real part, since they are the only ones which can escape from the equilibrium. For all of the models we will be considering, if $x_j$ are the deviations from the equilibrium of the susceptible classes and $y_k$ of the infective and exposed classes then we need the following sign patterns for a trajectory leaving the equilibrium if a travelling wave solution is to be plausible:

- from the trivial equilibrium (towards the infection free equilibrium) 
  \[ x_j > 0, \quad \dot{x}_j > 0, \quad y_k = 0, \quad \dot{y}_k = 0 \]

- from the infection free equilibrium (towards the endemic equilibrium) 
  \[ x_j < 0, \quad \dot{x}_k < 0, \quad y_k > 0, \quad \dot{y}_j > 0 \]

- from the endemic equilibrium (towards the infection free equilibrium) 
  \[ x_j > 0, \quad \dot{x}_j > 0, \quad y_k < 0, \quad \dot{y}_k < 0 \]

We apply these conditions at each of the equilibria we consider. Trajectories leaving the trivial equilibrium must have $u > 0$ and $\dot{u} > 0$, while all of the other quantities must be non-negative. The second, third and fourth eigenvectors are associated with positive eigenvalues and are candidates for a travelling wave solution. The second and third eigenvectors above have the appropriate sign pattern for a plausible travelling wave solution, while the fourth does not.

The infection free equilibrium

The five eigenvalues of the Jacobian for the linearisation around the infection free equilibrium of (5.28) are \[
\frac{c \pm \sqrt{c^2 + 4k^2D(\rho - \alpha)}}{2kD},
\]

together with the three
roots of a cubic equation, \( f(\lambda) = 0 \), where

\[
f(\lambda) = c \rho k D \lambda^3 - (c^2 \rho + k D \rho (R_c - 1)) \lambda^2 + (c \rho (R_c - 1) + c k (R_b (\rho - \alpha) - \rho)) \lambda - k (\rho - \alpha) (R_b R_c - U_b U_c) + k (R_b (\rho - \alpha) - k \rho (1 - R_c)).
\]

In order to find a constraint on \( c \) which ensures that \( v \) and \( y \) remain non-negative, we examine the conditions such that the discriminant of \( f(\lambda) \) is zero, since this will indicate the onset of a pair of complex roots. We apply the same criteria as earlier in Section 5.3.1 to \( f(\lambda) \) to find the constraints on \( c \) such that \( \lambda \) is positive and real.

Solving \( f'(\lambda) = 0 \) we have two roots;

\[
\lambda_{\pm} = \frac{1}{3c \rho k D} \left( \rho \lambda^2 + \rho k D (R_c - 1) \pm \sqrt{H_1} \right)
\]

where

\[
H_1 = \rho^2 \rho^4 - k \rho D \left( \rho (R_c - 1) + 3k (R_b (\rho - \alpha) - \rho) \right) \rho^2 + k^2 D^2 \rho^2 (R_c - 1)^2.
\]

For a real value for \( \lambda \) we must have \( H_1 \geq 0 \). This condition is attained when

\[
|c| \geq |c_{\text{min}}| = \sqrt{\frac{k D}{2 \rho} \left( \rho (R_c - 1) + 3k (R_b (\rho - \alpha) - \rho) + \sqrt{H_2} \right)}.
\]

where

\[
H_2 = 9k^2 (R_b (\rho - \alpha) - \rho)^2 + 6k \rho (R_c - 1)(R_b (\rho - \alpha) - \rho) - 3\rho^2 (R_c - 1)^2.
\]

Numerical simulation, however, suggests that this value for \( |c_{\text{min}}| \) is smaller than \( c_{\text{crit}} \), defined in (5.29).

The sign pattern of the eigenvectors associated with these eigenvalues using the same parameter set as in Section 5.3.2 is as follows, where the sign of the eigenvalue appears above the eigenvector

\[
\begin{pmatrix}
+ & - & + & + & - \\
- & + & - & + & + \\
+ & + & - & 0 & 0 \\
+ & - & - & 0 & 0 \\
+ & + & + & 0 & 0
\end{pmatrix}.
\]

A vector pointing in an appropriate direction for a trajectory leaving the IFE in the direction of the endemic state requires \( v > 0, u < 0, \dot{u} < 0, y > 0, \dot{y} > 0 \), the sign pattern of the first eigenvector, which is associated with a positive eigenvalue. Thus a travelling wave solution is again plausible. We might consider that the fourth eigenvector had a suitable sign pattern if we admitted the possibility of a vector with \( v \geq 0, u < 0, \dot{u} < 0, y \geq 0, \dot{y} \geq 0 \), connecting to the endemic equilibrium.
By the stable manifold theorem (see for example [25] p 84) there exists a one dimensional manifold tangent to this fourth vector, which is invariant for the flow of (5.24), i.e. one of the solution trajectories lies along this manifold. But \((v, y, q) = (0, 0, 0)\) satisfy the first, fourth and fifth equations of (5.28) identically, so the subset \(\{(v, y, q) = (0, 0, 0)\}\) of \(\mathbb{R}^5\) is invariant. By the uniqueness of the unstable manifold, the solution referred to above must remain for all \(z\) in the subset \(\{(v, y, q) = (0, 0, 0)\}\) of \(\mathbb{R}^5\). Such a solution clearly does not have the possibility of connecting to the endemic equilibrium.

The endemic equilibrium
At this equilibrium we are obliged to rely entirely on numerical simulation, using the same parameter set as Section 5.3.2 to arrive at the sign pattern for the eigenvalues and associated eigenvectors of the Jacobian of the linearised system as follows with sign of the eigenvalue above the eigenvector

\[
\begin{pmatrix}
- & + & - & - & + \\
+ & + & - & + & + \\
- & + & + & - & + \\
+ & - & + & - & - \\
\end{pmatrix}
\]

The second and fifth eigenvalues are positive, the associated eigenvector both have the appropriate sign pattern for a solution trajectory leaving the endemic equilibrium, namely \(v < 0, u > 0, \dot{u} > 0, y < 0, \dot{y} < 0\). Thus a travelling wave solution connecting the endemic equilibrium and the infection free equilibrium is plausible.

5.4 One species with an exponentially distributed latency period
We consider the SEIS model already analysed (system 4.1), with additional deaths due to disease and with the latency period, \(1/\epsilon\), exponentially distributed, and we introduce motion by assuming that the animals are diffusing along a single spatial dimension. The transformation \(\varphi = x + ct\) converts the equations from p.d.e.s to o.d.e.s as before. The non-dimensionalised model is as follows, where \(x, y, z\) are the non-dimensionalised susceptible, latent and infected classes respectively, \(R_0\) is the basic reproductive ratio from the SIS.
system (3.1) and all the other symbols have their usual meaning.

\[
\frac{dx}{d\varphi} = \frac{D}{D\varphi^2} + \rho(x + y + z)(1 - (x + y + z)) - \alpha x + (1 - \alpha - \delta)z - R_bxz,
\]

\[
\frac{dy}{d\varphi} = \frac{D}{D\varphi^2} + R_bxz - (\epsilon + \alpha)y,
\]

\[
\frac{dz}{d\varphi} = \frac{D}{D\varphi^2} + cy - z,
\]

\[
x(-\infty) = 0, \quad y(-\infty) = 0, \quad z(-\infty) = 0,
\]

\[
x(\infty) = x^*, \quad y(\infty) = y^* \quad z(\infty) = z^*.
\]

(5.30)

Lemma 5.4.1 System (5.30) has three equilibria - the eradication equilibrium, the infection free equilibrium and the endemic equilibrium.

Conjecture 5.4.2 Each equilibrium can be connected to any other equilibrium by a travelling wave solution of system (5.30).

We can reduce system (5.30) to six first order equations as follows

\[
\frac{dx}{d\varphi} = u,
\]

\[
\frac{du}{d\varphi} = \frac{1}{D} \left( cu - \rho(x + y + z)(1 - (x + y + z)) + \alpha x - (1 - \alpha - \delta)z + R_bxz \right),
\]

\[
\frac{dy}{d\varphi} = q, \quad \frac{dw}{d\varphi} = \frac{1}{D} \left( cq - R_bxz + (\epsilon + \alpha)y \right),
\]

\[
\frac{dz}{d\varphi} = w, \quad \frac{dw}{d\varphi} = \frac{1}{D} \left( cw + z - cy \right).
\]

(5.31)

Setting the right hand sides of (5.31) equal to zero we can find three stationary solutions for system (5.31). We investigate the eigenvectors of the Jacobian of the linearisations around these equilibria to establish the feasibility of travelling wave solutions. We first consider the trivial solution.

5.4.1 The trivial equilibrium

The eigenvalues of the linearisation about the trivial equilibrium of (5.31) are as follows,

\[
\lambda_1 = \frac{c + \sqrt{c^2 - 4D(\rho - \alpha)}}{2D}, \quad \lambda_2 = \frac{c - \sqrt{c^2 - 4D(\rho - \alpha)}}{2D},
\]

\[
\lambda_3 = \frac{c + \sqrt{c^2 + 4D}}{2D}, \quad \lambda_4 = \frac{c - \sqrt{c^2 + 4D}}{2D},
\]

\[
\lambda_5 = \frac{c + \sqrt{c^2 + 4D(\epsilon + \alpha)}}{2D}, \quad \lambda_6 = \frac{c - \sqrt{c^2 + 4D(\epsilon + \alpha)}}{2D}.
\]

(5.32)
\( \lambda_2, \lambda_6 < 0 \), the remainder are positive for all parameter values. For \(|c| < |c_{\text{crit}}| = 2\sqrt{D(p - \alpha)}\), \( \lambda_1, \lambda_2 \) are a complex pair, we thus require that \(|c| > 2\sqrt{D(p - \alpha)}\). The signs of the associated eigenvectors are as follows (arrived at algebraically wherever possible and numerically, with the parameter set \( \{ R_b = 2.17, \rho = 1, \alpha = 0.1, D = 0.1, \epsilon = 0.4, \delta = 0.6, c = 0.8 \} \), where the algebra is intractable), the sign of the eigenvalue is shown above the eigenvector:

\[
\begin{pmatrix}
+ \\ + \\ 0 \\ 0 \\ - \\
- \\ + \\ 0 \\ 0 \\ + \\
+ \\ - \\ 0 \\ 0 \\ - \\
- \\ + \\ 0 \\ 0 \\ + \\
+ \\ - \\ 0 \\ 0 \\ - \\
\end{pmatrix}
\]

A trajectory from the trivial equilibrium to the infection free equilibrium must point to positive \( x \), and positive \( \dot{x} \). The first eigenvector above meets this criterion and the eigenvalue is positive, so a travelling wave solution is plausible.

5.4.2 The infection free equilibrium

The eigenvalues of the Jacobian of the linearisation at this equilibrium are

\[
\lambda_{1,2} = \frac{c \pm \sqrt{c^2 + 4D(p - \alpha)}}{2D}
\]

\[
\lambda_{3,4,5,6} = \frac{1}{2D \rho} \left( \rho c \pm \sqrt{\rho^2(c^2 + 2D(1 + \epsilon + \alpha)) \pm 2\rho D \sqrt{\rho^2(\alpha - 1 + \epsilon)^2 + 4\rho \epsilon R_b(p - \alpha)}} \right).
\]

We note that, in order to avoid the possibility of complex eigenvalues (which would require that \( y \) and \( z \) go negative and thus do not represent biological reality) we must have the quantities under the square root signs non-negative. This requires that

\[
|c| \geq |c_{\text{min}}| = \frac{1}{\rho} \sqrt{2\rho D \left( -\rho(\epsilon + \alpha + 1) + \sqrt{4R_b \rho \epsilon(\rho - \alpha) + \rho^2(\epsilon + \alpha - 1)^2} \right)}.
\]

This threshold can only exist if the quantity under the first square root sign is positive, which in turn requires that

\[
\epsilon > \frac{\alpha \rho}{R_b(\rho - \alpha) - \rho}.
\]

However, \(|c_{\text{min}}| \ll |c_{\text{crit}}| \) (conclusion reached from numerical simulation).

Trajectories originating from the IFE to reach the endemic equilibrium would need the following sign pattern;

\[
x < 0, \quad y > 0, \quad z > 0, \quad \frac{dx}{d\varphi} < 0, \quad \frac{dy}{d\varphi} > 0, \quad \frac{dz}{d\varphi} > 0.
\]
The sign pattern of the eigenvectors and eigenvalues is suggested by numerical simulation with the same parameter set as in 5.4.1 to be

\[ \begin{pmatrix} + & - & + & - & + & - \\ + & 0 & - & + & 0 & - \\ 0 & 0 & 0 & + & 0 & + \\ 0 & 0 & 0 & + & 0 & + \end{pmatrix} \]

We see immediately that the fifth eigenvector is associated with a positive eigenvalue and provides the requisite sign pattern. We can conclude that a travelling wave can feasibly connect the trivial solution and the infection free equilibrium.

5.4.3 The endemic equilibrium

The endemic equilibrium is at

\[ x^* = \frac{\epsilon + \alpha}{\epsilon R_b}, \quad y^* = \frac{\theta}{\epsilon R_b}, \quad z^* = \frac{\theta}{R_b} \]

where \( \theta \) is the root of \( f(z) = 0 \), where

\[ f(z) = \rho(1 + \epsilon)^2 z^2 + \left( R_b \epsilon^2 (\delta - \rho + \alpha) - \epsilon R_b (\rho - \alpha) + 2 \rho (1 + \epsilon)(\epsilon + \alpha) \right) z \]

\[ + (\epsilon + \alpha)(\rho(\epsilon + \alpha) - \epsilon R_b(\rho - \alpha)) = 0. \]

The sign pattern of the trajectories originating from the endemic equilibrium must be as follows

\[ x > 0, \quad y < 0, \quad z < 0, \quad \frac{dx}{d\rho} > 0, \quad \frac{dy}{d\rho} < 0, \quad \frac{dz}{d\rho} < 0. \]

The characteristic equation of the Jacobian of the linearisation around the endemic equilibrium is algebraically intractable. However, numerical simulation with the same parameter set as in 5.4.1 suggests that the sign pattern of the eigenvalues and eigenvectors is as follows.

\[ \begin{pmatrix} - & - & + & + & - & - \\ + & - & - & - & + & + \\ - & + & + & + & + & - \\ + & - & + & + & + & - \end{pmatrix} \]

The sixth eigenvector is associated with a positive eigenvalue and has a satisfactory sign pattern and we thus conclude that a travelling wave from the IFE to the endemic equilibrium is feasible.

We thus consider it reasonable that travelling wave solutions can exist to connect each of the three equilibria of system (5.31). □
5.5 Two species SEIS model

We continue with the SEIS model for badgers analysed in the previous section and our previous assumption that cattle have a constant population, are static and spatially homogeneous and we can represent their disease by an SIS model. With the same analysis as before in this chapter, we have the following non-dimensionalised system, transformed into o.d.e.s. \( v \) represents infected cattle, \( x, y, z \) are susceptible, latent and infective badgers respectively. All the parameters are as previously defined in this chapter.

\[
\begin{align*}
\frac{dv}{d\phi} & = -v + R_c v(1 - v) + kU_c z(1 - v), \\
\frac{dx}{d\phi} & = kD \frac{d^2x}{d\phi^2} + k\rho(x + y + z)(1 - (x + y + z)) - k\alpha x + k(1 - \alpha - \delta)z - kR_b xz - U_b x v, \\
\frac{dy}{d\phi} & = kD \frac{d^2y}{d\phi^2} + kR_b x z + U_b x v - k(\epsilon + \alpha) y, \\
\frac{dz}{d\phi} & = kD \frac{d^2z}{d\phi^2} + k\epsilon y - kz,
\end{align*}
\]

\((5.33)\)

\[v(-\infty) = 0, x(-\infty) = 0, \quad y(-\infty) = 0, \quad z(-\infty) = 0,\]

\[v(\infty) = v^*, x(\infty) = x^*, \quad y(\infty) = y^* \quad z(\infty) = z^*.\]

We transform this into the following first order system.

\[
\begin{align*}
\frac{dv}{d\phi} & = \frac{1}{c} \left( -v + R_c v(1 - v) + kU_c z(1 - v) \right), \quad \frac{dx}{d\phi} = u, \\
\frac{du}{d\phi} & = \frac{1}{kD} \left( cu - k\rho(x + y + z)(1 - (x + y + z)) + k\alpha x \\
& \quad - k(1 - \alpha - \delta)z + kR_b x z + U_b x v \right), \\
\frac{dy}{d\phi} & = q, \quad \frac{dq}{d\phi} = \frac{1}{kD} \left( cq - kR_b x z - U_b x v + k(\epsilon + \alpha) y \right), \\
\frac{dz}{d\phi} & = w, \quad \frac{dw}{d\phi} = \frac{1}{kD} \left( cw - k\epsilon y + kz \right).
\end{align*}
\]

There are three physically feasible equilibria: the trivial equilibrium, the infection free equilibrium and the endemic state.

**Conjecture 5.5.1** Travelling wave solutions can exist to connect each of the three equilibria of system (5.33) to the other two.

The trivial equilibrium

There are the same constraints on \( c \) as in the previous section to ensure that there are no complex eigenvalues of the Jacobian of the linearisation around
this equilibrium. The seven eigenvalues are the same as the six in (5.32) together with \( \frac{1}{e}(R_e - 1) \). Numerical simulation with the parameter set \( \{k = 1, R_b = 2.17, \rho = 1, \alpha = 0.1, R_e = 0.8, U_b = 1, U_c = 2, D = 0.1, \epsilon = 0.4, \delta = 0.6, \phi = 0.81\} \) suggests that the eigenvalues and eigenvectors have the following sign pattern:

\[
\begin{pmatrix}
0 & + & + & + & 0 & + & + \\
0 & - & - & + & + & - & + \\
0 & 0 & 0 & 0 & 0 & + & + \\
0 & + & - & 0 & 0 & + & 0 \\
0 & + & + & 0 & 0 & - & 0 \\
0 & + & + & 0 & 0 & 0 & + \\
0 & + & - & 0 & 0 & 0 & 0 \\
\end{pmatrix}
\]

Trajectories originating from the trivial equilibrium would need to have the following sign pattern

\[
v \geq 0, \quad x > 0, \quad y \geq 0, \quad z \geq 0, \quad \frac{dx}{d\phi} > 0, \quad \frac{dy}{d\phi} \geq 0, \quad \frac{dz}{d\phi} \geq 0.
\]

The fourth and fifth eigenvectors above are associated with positive eigenvectors and have this sign pattern, so we conclude that such trajectories are feasible.

The Infection free equilibrium

The characteristic equation of the Jacobian of the linearisation around this equilibrium factorises into a quadratic factor and a quintic factor. The quintic gives rise to real or complex roots depending on the relationship between the parameters, but the behaviour is extremely complicated and does not have any obvious biological interpretation.

The sign pattern of the real parts of the eigenvectors and eigenvalues of this Jacobian, suggested from numerical simulation with the same parameter set as in the previous section, is as follows

\[
\begin{pmatrix}
0 & + & + & + & 0 & + & + \\
0 & - & - & + & + & - & + \\
0 & 0 & 0 & 0 & 0 & + & + \\
0 & + & - & 0 & 0 & + & 0 \\
0 & + & + & 0 & 0 & - & 0 \\
0 & + & + & 0 & 0 & 0 & + \\
0 & + & - & 0 & 0 & 0 & 0 \\
\end{pmatrix}
\]

The sign pattern of trajectories originating at the IFE must be

\[
v \geq 0, \quad x < 0, \quad y > 0, \quad z > 0, \quad \frac{dx}{d\phi} < 0, \quad \frac{dy}{d\phi} > 0, \quad \frac{dz}{d\phi} > 0.
\]

The second eigenvector has the correct sign pattern to be a candidate for a trajectory leaving the IFE and is associated with a positive eigenvalue.
The endemic equilibrium

The sign pattern of trajectories from the endemic equilibrium must be

\[ v < 0, \quad x > 0, \quad y < 0, \quad z < 0, \quad \frac{dx}{d\varphi} > 0, \quad \frac{dy}{d\varphi} < 0, \quad \frac{dz}{d\varphi} < 0. \]

By numerical simulation with the same parameter set as in the previous section we find the sign pattern of the the eigenvalues and the eigenvectors (or their real parts where they are complex) of the Jacobian of the linearisation around this equilibrium to be as follows

\[
\begin{pmatrix}
+ & - & - & - & + & - & - & - \\
+ & + & + & + & + & + & + & - \\
- & - & - & - & + & - & + & + \\
- & - & - & + & + & - & - & - \\
+ & + & + & + & + & + & + & + \\
+ & + & + & + & + & + & + & + \\
+ & + & + & + & + & + & + & + \\
+ & + & + & + & + & + & + & + \\
\end{pmatrix}
\]

The sign patterns of the first and seventh eigenvectors correspond to the pattern needed for a trajectory leaving the endemic equilibrium and each is associated with a positive eigenvalue.

### 5.6 One species - diffusion with a fixed latent period

The model equations, with all the variables and parameters as previously defined in this chapter and with a fixed latent period of \( \tau \) are as follows:

\[
\frac{\partial S(x,t)}{\partial t} = D \frac{\partial^2 S(x,t)}{\partial x^2}
\]

\[
+r(S(x,t) + E(x,t) + I(x,t)) \left( 1 - \frac{1}{C} (S(x,t) + E(x,t) + I(x,t)) \right)
\]

\[-\mu S(x,t) - \beta S(x,t)I(x,t) + \gamma I(x,t),
\]

\[
\frac{\partial E(x,t)}{\partial t} = D \frac{\partial^2 E(x,t)}{\partial x^2}
\]

\[
+ \beta S(x,t)I(x,t) - e^{-\mu \tau} \beta S(x,t-\tau)I(x,t-\tau) - \mu E(x,t),
\]

\[
\frac{\partial I(x,t)}{\partial t} = D \frac{\partial^2 I(x,t)}{\partial x^2} + e^{-\mu \tau} \beta S(x,t-\tau)I(x,t-\tau) - (\mu + \delta + \gamma) I(x,t),
\]

\[ S(x,\theta), E(x,\theta), I(x,\theta) > 0, \quad \theta \in [-\tau, 0] \quad x \in (-\infty, \infty), \]

\[ S(x,0) = S_0(x), \quad E(x,0) = E_0(x), \quad I(x,0) = I_0(x). \] (5.34)
With the substitution $z = x + ct$ (and thus $x + c(t - \tau) = z - ct$) we have

$$c \frac{dS(z)}{dz} = D \frac{d^2 S(z)}{dz^2} + rS(z) + E(z) + I(z)) \left(1 - \frac{1}{C}(S(z) + E(z) + I(z))\right)$$

$$-\mu S(z) - \beta S(z)I(z) + \gamma I(z),$$

$$c \frac{dE(z)}{dz} = D \frac{d^2 E(z)}{dz^2} + \beta S(z)I(z) - e^{-\mu r}\beta S(z - ct)I(z - ct) - \mu E(z),$$

$$c \frac{dI(z)}{dz} = D \frac{d^2 I(z)}{dz^2} + e^{-\mu r}\beta S(z - ct)I(z - ct) - (\mu + \delta + \gamma)I(z).$$

(5.35)

System (5.35) has three equilibria, the trivial equilibrium, the infection free equilibrium and the endemic equilibrium. The latter is at $I^* = 0$ where $0$ is the root of $f(z) = 0$, where

$$f(z) = \frac{\mu + \gamma + \delta}{\beta e^{-\mu r}}$$

and $I^* > 0$ for $R_0e^{-\mu r} > 1$, where

$$R_0 = \frac{N^* \beta}{\mu + \gamma + \delta}$$

(5.36)

and where $N^* = C \left(1 - \frac{\mu}{r}\right)$ is the total population at the infection free equilibrium.

The infection free equilibrium

If we linearise around the IFE, $(N^*, 0, 0)$ and look for an Ansatz of the form

$$\tilde{S} = a_1e^{\lambda z}, \quad \tilde{E} = a_2e^{\lambda z}, \quad \tilde{I} = a_3e^{\lambda z}$$

where $\tilde{S}, \tilde{E}, \tilde{I}$ are the rescaled variables, we obtain the characteristic equation of the linearisation of system (5.34) about the IFE in the form

$$\begin{pmatrix}
\lambda c - \lambda^2 D - \mu + r & -2\mu + r & -2\mu + r + N^* \beta - \gamma \\
0 & \lambda c - \lambda^2 D + \mu & -N^* \beta (1 - e^{-(\mu+c)\tau}) \\
0 & 0 & \lambda c - \lambda^2 D + (\mu + \delta + \gamma) - N^* \beta e^{-(\mu+c)\tau}
\end{pmatrix}
\begin{pmatrix}
a_1 \\
a_2 \\
a_3
\end{pmatrix} = 0.$$
For non-trivial solutions the constraint on \( \lambda \) is given by 
\[
f(\lambda) = (\lambda c - \lambda^2 D - \mu + \tau)(\lambda c - \lambda^2 D + \mu)
\]
\[
(\lambda c - \lambda^2 D + (\mu + \delta + \gamma) - N^* \beta e^{-(\mu + \omega_A)\tau})
\]
The third factor contains the interesting part of this transcendental equation, since the first two factors routinely solve as follows, where the first eigenvalue of each pair has the positive square root term,
\[
\lambda_{1,2} = \frac{1}{2D}(c \pm \sqrt{c^2 - 4D(r - \mu)}), \quad \lambda_{3,4} = \frac{1}{2D}(c \pm \sqrt{c^2 + 4D\mu}).
\]
If we set the third factor equal to zero we obtain an equation of the form
\[
-\lambda^2 D + \lambda c + A - Be^{-\lambda \tau} = 0, \quad (5.37)
\]
where \( A = \mu + \gamma + \delta \) and \( B = N^* \beta e^{-\mu \tau} \). If \( B < A \), i.e. \( R_0 > 1 \), where \( R_0 \) is defined in (5.36), there will be one positive and one negative real root. If \( B > A \) there will be either two positive real roots, a double root or no real roots. We find the critical value of \( \lambda \) at which the real roots disappear by differentiating equation (5.37) with respect to \( \lambda \) and solving the resulting equation and (5.37) itself simultaneously. We thus have
\[
\lambda_{\text{crit}} = \frac{1}{2D\tau c} \left( \tau c^2 - 2D + \sqrt{\tau^2 c^4 + 4D^2 + 4\tau^2 c^2 D(\mu + \gamma + \delta)} \right). \quad (5.38)
\]
We take the positive square root since we can see by geometry that \( \lambda_{\text{crit}} > 0 \). If we now substitute for \( \lambda \) into equation (5.37) we obtain the corresponding value of \( c_{\text{min}} \) at the IFE, defined as the root of the following equation in \( c \).
\[
2D - \sqrt{\tau^2 c^4 + 4D^2 + 4\tau^2 c^2 D(\mu + \gamma + 4)}
\]
\[
= -N^* \beta e^{2\tau^2} e^{-\mu \tau} e^{-\psi} \left( \frac{-2D + \sqrt{\tau^2 c^4 + 4D^2 + 4\tau^2 c^2 D(\mu + \gamma + 4)}}{2D} \right). \quad (5.39)
\]
We assume that in practice \( \tau \) is small enough that we may approximate by expanding both sides of this equation with a Taylor expansion in powers of \( \tau \), ignoring terms \( O(\tau^4) \), and solve for \( c \). The approximation is
\[
|c_{\text{min}}| = 2 \left. \frac{D(R_0(1 - \mu \tau) - 1)}{2R_0 \tau + \mu + \delta + \gamma} \right|^{\frac{1}{2}}.
\]
|\( c_{\text{min}} \)| is, as would be expected from biological considerations, increasing in \( R_0 \) for \( \tau < \frac{1}{D} \) and \( R_0 > \frac{1}{1 - \mu \tau} \). However, the approximation is only within 8% of the exact value found by simulation.

With numerical simulation with the parameter set \( \{ r = 0.6, \mu = 0.4, \gamma = 0.2, \tau = 0.4, D = 0.1, \beta = 1, c = 0.6, N^* = 2.33, R_0 = 2.48 \} \), we obtain the following sign pattern for the eigenvectors of the Jacobian of the linearisation around the infection free equilibrium. The six elements in the
eigenvectors correspond to \( \left( \frac{d\hat{S}}{dt}, \frac{d\hat{E}}{dt}, \frac{d\hat{I}}{dt} \right) \) respectively.

\[
\begin{pmatrix}
+ & + & - & - & - & + \\
- & - & 0 & 0 & 0 & - \\
0 & 0 & 0 & 0 & 0 & - \\
0 & 0 & 0 & 0 & 0 & - \\
\end{pmatrix}
\]

For trajectories leaving the IFE in the direction of the endemic equilibrium we would expect the sign pattern to be

\[
\dot{S} < 0, \quad \frac{d\hat{S}}{dz} < 0, \quad \hat{E} > 0, \quad \frac{d\hat{E}}{dz} > 0, \quad \hat{I} > 0, \quad \frac{d\hat{I}}{dz} > 0,
\]

which is the case for the sixth eigenvector above (multiplied by a negative constant). We also see that the third eigenvector points in the direction of the trivial solution.

The trivial solution

Linearising (5.35) about the trivial solution and finding the condition that there are non-trivial solutions to the Ansatz as above we find the constraint on \( c \) such that all the variables remain positive to be \( |c| > 2\sqrt{D(r - \mu)} \), which is equivalent, because of scaling to \( 2\sqrt{D(\rho - a)} \) as for system (5.2). Thus we can conclude that the minimum wavespeed for system (5.34) will be the maximum of \( 2\sqrt{D(\rho - a)} \) and the root of equation (5.39). The eigenvectors of the Jacobian of the linearisation about the trivial solution of (5.34) are the same as those for the Jacobian of the linearisation about the trivial solution of (5.30), which we have already shown to have a sign pattern allowing a plausible travelling wave solution between the IFE and the trivial state.

5.7 Culling in a spatially heterogeneous environment

We now turn to the effect of culling in an environment where one species, badgers, is distributed heterogeneously in one-dimension with spatial co-ordinate \( \xi \).

5.7.1 Travelling waves and fixed yield culling

We amend the diffusion model of system (5.4) by adding a culling term as described in model (3.13). As the animals diffuse they are culled at a fixed
number \( A \) per unit time and space. The model for a single species is

\[
\frac{\partial x}{\partial t} = D \frac{\partial^2 x}{\partial \xi^2} + \rho(x + y)(1 - x - y) - \alpha x + (1 - \alpha) y - R_0 xy - qA \frac{x}{x + y},
\]

\[
\frac{\partial y}{\partial t} = D \frac{\partial^2 y}{\partial \xi^2} - y + R_0 xy - qA \frac{y}{x + y},
\]

\[x(\xi, 0) = x_0(\xi) > 0 \quad y(\xi, 0) = y_0(\xi) \geq 0. \tag{5.40}\]

We define

\[q := \begin{cases} 1 & : \quad x + y > 0 \\ 0 & : \quad \text{otherwise} \end{cases}\]

to ensure positivity and to remove any potential singularity at the origin. On the understanding that \( A > 0 \) only for \( x + y > 0 \) we will henceforth put \( q = 1 \).

**Proposition 5.7.1** Provided that \( A < A^* \), where

\[A^* = \frac{(\rho - \alpha + 1)(R_0(\rho - \alpha) - \rho)}{(R_0 + \rho)^2},\]

a travelling wave solution connecting the two equilibria of system (5.40) is feasible, with minimum wavespeed \( c_{\text{min}} \), defined in (5.42).

We know from Chapter 3 that system (5.40) has no trivial equilibrium, that the population crashes for \( A > A_{\text{crit}} = \frac{(\rho - \alpha)^2}{4 \rho} \) and that there are two physically feasible stable spatially homogeneous equilibria, the larger of the two IFEs and the endemic equilibrium with positive components. We also know that we must have \( R_0 < \frac{\rho(\rho - \alpha + 2)}{\rho - \alpha} \) if culling is to eliminate the infective class without a population crash, so we make this assumption in the following analysis. To study the possibility of travelling wave solutions connecting these two equilibria, as for the unculled model, we put \( z = \xi + ct, \frac{dx}{dz} = u \) and \( \frac{dy}{dz} = w \) and thus transform (5.40) into a system of first order o.d.e.s.

\[
\frac{dx}{dz} = u, \quad \frac{du}{dz} = \frac{1}{D} \left( cu - \rho(x + y)(1 - x - y) + \alpha x - (1 - \alpha) y + R_0 xy + A \frac{x}{x + y} \right),
\]

\[
\frac{dy}{dz} = w, \quad \frac{dw}{dz} = \frac{1}{D} \left( cw + y - R_0 xy + A \frac{y}{x + y} \right). \tag{5.41}\]

At the IFE \( \left( \frac{\rho - \alpha}{2 \rho} + \frac{1}{2 \rho} \sqrt{(\rho - \alpha)^2 - 4 \rho A}, 0, 0, 0 \right) \), provided that \( A < A_{\text{crit}} \).

The eigenvalues of the Jacobian are

\[\mu_1 = \frac{1}{2D} \left( c + \sqrt{c^2 + 4D \sqrt{(\rho - \alpha)^2 - 4 \rho A}} \right),\]

\[\mu_2 = \frac{1}{2D} \left( c - \sqrt{c^2 + 4D \sqrt{(\rho - \alpha)^2 - 4 \rho A}} \right),\]

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where $\mu_1 > 0, \mu_2 < 0$ and

$$\mu_3 = \frac{1}{2D\rho} \left( c_{\rho+} \right) \sqrt{c^2 \rho^2 - 2D\rho \left( R_0(\rho - \alpha) - 2\rho(\rho - \alpha + 2) + (R_0 + \rho)\sqrt{(\rho - \alpha)^2 - 4\rho A} \right)},$$

$$\mu_4 = \frac{1}{2D\rho} \left( c_{\rho-} \right) \sqrt{c^2 \rho^2 - 2D\rho \left( R_0(\rho - \alpha) - 2\rho(\rho - \alpha + 2) + (R_0 + \rho)\sqrt{(\rho - \alpha)^2 - 4\rho A} \right)}.$$

We have $\mu_3 > 0, \mu_4 < 0$ for $A < A^*$ and $\mu_3 > 0, \mu_4 > 0$ for $A > A^*$. Hence, from positivity considerations we must have $|c| > |c_{\text{min}}|$, where

$$|c_{\text{min}}| = \frac{1}{\rho} \sqrt{2\rho D (R_0 + \rho)\sqrt{(\rho - \alpha)^2 - 4\rho A} + R_0(\rho - \alpha) - 2\rho(\rho - \alpha + 2)} \tag{5.42}$$

We note that if $A = A^* = \frac{(\rho-\alpha+1)(R_0(\rho-\alpha)-\rho)}{(R_0+\rho)^2}$ (the threshold value of $A$ above which the endemic equilibrium disappears) then $c_{\text{min}} = 0$, commensurate with the fact that this value of $A$ is the parameter in the transcritical bifurcation of the (spatially homogeneous) system. $c_{\text{min}}$ is decreasing in $A$, the greater the culling yield the slower the speed with which the disease spreads.

We can obtain the sign pattern of the eigenvectors at the IFE and also at the endemic equilibrium (the latter being algebraically intractable) by simulation, for $A < A^*$, to give the following result;

<table>
<thead>
<tr>
<th>Infection free equilibrium</th>
<th>Endemic equilibrium</th>
</tr>
</thead>
<tbody>
<tr>
<td>$1$</td>
<td>$+$</td>
</tr>
<tr>
<td>$1$</td>
<td>$+$</td>
</tr>
<tr>
<td>$0$</td>
<td>$-$</td>
</tr>
<tr>
<td>$0$</td>
<td>$-$</td>
</tr>
<tr>
<td>$0$</td>
<td>$+$</td>
</tr>
<tr>
<td>$0$</td>
<td>$-$</td>
</tr>
<tr>
<td>$0$</td>
<td>$+$</td>
</tr>
</tbody>
</table>

Leaving the IFE requires $x < 0, u < 0, y > 0, w > 0$ the sign pattern of the third eigenvector (multiplied by a negative constant). Leaving the endemic equilibrium requires $x > 0, u > 0, y < 0, w < 0$, a pattern satisfied by the second and fourth eigenvectors.

We can therefore conclude that a travelling wave connecting these two equilibria is at least feasible. \qed
5.7.2 Travelling waves and fixed rate culling

The equivalent model to that of system (5.41) where the culling is at a constant proportion $B$ of the population per unit space and time is as follows

\[
\frac{dx}{dz} = u, \quad \frac{du}{dz} = \frac{1}{D} \left( cu - \rho(x+y)(1-x-y) + \alpha x - (1-\alpha)y + \rho_0 xy + Bz \right),
\]

\[
\frac{dy}{dz} = w, \quad \frac{dw}{dz} = \frac{1}{D} \left( cw + y - \rho_0 xy + By \right).
\]

(5.43)

We have three possible equilibria, extinction, the IFE and the endemic equilibrium, thus we can consider the possibility of travelling waves connecting any two of them.

Proposition 5.7.2

1. Provided that $B < B^*$, where

\[
B^* = \frac{\rho_0(\rho - \alpha) - \rho}{\rho_0 + \rho},
\]

travelling wave solutions are plausible connecting the extinction equilibrium and the infection free equilibrium of system (5.43) with minimum wavespeed given by

\[
|c_0| = \max \left\{ 2\sqrt{D(\rho - \alpha - B)}, \quad \frac{2}{\rho} \sqrt{D\rho (\rho_0(\rho - \alpha) - \rho - B(\rho_0 + \rho))} \right\}.
\]

2. For $B > B^*$ travelling wave solutions are plausible connecting the extinction equilibrium and the infection free equilibrium of system (5.43) with minimum wavespeed given by

\[
|c_0| = 2\sqrt{D(\rho - \alpha - B)}.
\]

3. For $B > B^*$ travelling wave solutions are also plausible connecting the trivial equilibrium to the endemic equilibrium of system (5.43).

Extinction

The eigenvalues at the extinction equilibrium are

\[
\lambda_1 = \frac{1}{2D} \left( c + \sqrt{c^2 + 4D(1+B)} \right), \quad \lambda_2 = \frac{1}{2D} \left( c - \sqrt{c^2 + 4D(1+B)} \right),
\]

where $\lambda_1 > 0, \lambda_2 < 0$, and

\[
\lambda_3 = \frac{1}{2D} \left( c + \sqrt{c^2 - 4D(\rho - \alpha - B)} \right),
\]

\[
\lambda_4 = \frac{1}{2D} \left( c - \sqrt{c^2 - 4D(\rho - \alpha - B)} \right).
\]
whence we require $c > c_{\text{min}} = 2\sqrt{D(p - \alpha - B)}$ from positivity considerations. We have $\lambda_3 > 0$, $\lambda_4 > 0$. As $B \to B_{\text{crit}}$, where $B_{\text{crit}} = p - \alpha$, we have $c_{\text{min}} \to 0$. The eigenvectors at the trivial solution and their sign pattern are

$$
\begin{pmatrix}
-1 \\
-\lambda_1 \\
1 \\
\lambda_1
\end{pmatrix} - \begin{pmatrix}
-1 \\
-\lambda_2 \\
1 \\
\lambda_2
\end{pmatrix} + \begin{pmatrix}
1 + \\
\lambda_3 \\
0 \\
0
\end{pmatrix} + \begin{pmatrix}
1 + \\
\lambda_4 \\
0 \\
0
\end{pmatrix}
$$

The pattern of eigenvectors for a solution trajectory moving from the trivial state to the IFE needs to be consistent with $x > 0, u > 0, y = 0, w = 0$ for which the third or fourth eigenvalues (corresponding to positive eigenvalues) will do. Thus a travelling wave from the trivial state to the IFE is feasible. The eigenvector pattern for a solution trajectory from the trivial state to the endemic equilibrium, consistent with $x > 0, u > 0, y \geq 0, w \geq 0$ would also be satisfied by the third and fourth eigenvectors.

**Infection free equilibrium**

At the IFE, $\left(1 - \frac{\alpha + B}{\rho}, 0, 0, 0\right)$ the eigenvalues are

$$
\lambda_5 = \frac{1}{2D} \left(c + \sqrt{c^2 + 4D(p - \alpha - B)}\right),
$$

$$
\lambda_6 = \frac{1}{2D} \left(c - \sqrt{c^2 + 4D(p - \alpha - B)}\right),
$$

$$
\lambda_7 = \frac{c}{2D} + \frac{1}{2D} \sqrt{c^2 \rho^2 - 4D \rho (R_0 (p - \alpha) - \rho - B(R_0 + \rho))},
$$

$$
\lambda_8 = \frac{c}{2D} - \frac{1}{2D} \sqrt{c^2 \rho^2 - 4D \rho (R_0 (p - \alpha) - \rho - B(R_0 + \rho))}.
$$

In the case of $\lambda_7, \lambda_8$ to ensure that the quantity under the square root is positive we need to have $|c| > |c_1|$, where

$$
c_1 = \frac{2}{\rho} \sqrt{D \rho (R_0 (p - \alpha) - \rho - B(R_0 + \rho))}.
$$

(5.44)

$c_1$ only exists for $B < B^*$. For $B > B^*$ there is no constraint on $c$.

$\lambda_5 > 0, \lambda_6 < 0, \lambda_7 > 0, \lambda_8 > 0$ if $B < B^*$(the value of $B$ at which the endemic equilibrium becomes unstable) and $\lambda_5 > 0, \lambda_6 < 0, \lambda_7 > 0, \lambda_8 < 0$ if $B > B^*$. Once again we note that both $c_1$ and $c_{\text{min}}$ are decreasing in $B$. As the culling rate increases the spread rate decreases.

We observe that $c_1 > c_{\text{min}}$ for

$$
B < \frac{1}{R_0} ((R_0 - \rho)(p - \alpha) - \rho) < B_{\text{crit}} \ \forall \ R_0.
$$
and that $|c_1|$ is increasing in $R_0$. The eigenvectors at the IFE and their sign pattern for $B > B^*$ are

$$
\begin{pmatrix}
1 \\
\lambda_5 \\
0
\end{pmatrix} + 
\begin{pmatrix}
1 \\
\lambda_6 \\
0
\end{pmatrix} + 
\begin{pmatrix}
-1 \\
-\lambda_7 \\
0
\end{pmatrix} + 
\begin{pmatrix}
-1 \\
-\lambda_8 \\
0
\end{pmatrix}.
$$

The pattern of eigenvectors for a trajectory moving from the IFE to the trivial solution must be consistent with $x < 0, u < 0, y = 0, w = 0$ and so the third eigenvector will do. For a trajectory moving from the IFE to the endemic equilibrium the pattern must be consistent with $x < 0, u < 0, y > 0, w > 0$, in which case the third eigenvector also has the right sign pattern for all values of $B$.

**Endemic equilibrium**

At the endemic equilibrium $\left(\frac{1+B}{R_0}, 0, 1 - \frac{\alpha + B}{\rho} - \frac{1+B}{R_0}, 0\right)$, the eigenvalues are $\lambda_5, \lambda_6$ as above, and $\lambda_9, \lambda_{10}$ where

$$\lambda_9 = \frac{c}{2D} + \frac{1}{2\rho D} \sqrt{c^2 \rho^2 + 4D \rho (R_0 (\alpha - \alpha) - \rho - B (R_0 + \rho))},$$

$$\lambda_{10} = \frac{c}{2D} - \frac{1}{2\rho D} \sqrt{c^2 \rho^2 + 4D \rho (R_0 (\alpha - \alpha) - \rho - B (R_0 + \rho))}.$$

The eigenvectors and their sign patterns are as follows, where two possible signs are shown for a component, the former is for $B < B^*$, the latter for $B > B^*$

$$
\begin{pmatrix}
1 \\
\lambda_5 \\
\psi
\end{pmatrix} + 
\begin{pmatrix}
1 \\
\lambda_6 \\
\psi
\end{pmatrix} + 
\begin{pmatrix}
-1 \\
-\lambda_9 \\
1
\end{pmatrix} + 
\begin{pmatrix}
-1 \\
-\lambda_{10} \\
1
\end{pmatrix} + 
\begin{pmatrix}
0 \\
\lambda_9 \\
0
\end{pmatrix} + 
\begin{pmatrix}
0 \\
\lambda_{10} \\
0
\end{pmatrix}.
$$

where $\psi = - \left(\frac{R_0 (\alpha - \alpha) - \rho - B (R_0 + \rho)}{\rho (\rho - \alpha - B)}\right)$. We see that the third eigenvector sign pattern is consistent with $x < 0, u < 0, y > 0, w > 0$ but that no pattern appears to be consistent with $x < 0, u < 0, y < 0, w < 0$ for a trajectory connecting the endemic equilibrium and the trivial state except in the case that $B > B^*$ in which case the first eigenvector will do.

### 5.8 Culling on a finite interval

As a more realistic model than considering culling in an infinite space, we might consider animals contained in a finite interval scaled to $(0, 1)$ and study
a model system of the form
\[
\frac{\partial x}{\partial t} = D \frac{\partial^2 x}{\partial \xi^2} + \rho(x + y)(1 - x - y) - \alpha x + (1 - \alpha)y - R_0 xy - f(x, \xi, t),
\]
\[
\frac{\partial y}{\partial t} = D \frac{\partial^2 y}{\partial \xi^2} - y + R_0 xy - f(y, \xi, t),
\]
\[
x(\xi, 0) = x_0(\xi) > 0, \quad y(\xi, 0) = y_0(\xi) \geq 0, \quad \xi \in (0, 1),
\]
where the parameters and variables have the meanings defined in the previous section with either Dirichlet boundary conditions (lethal boundary)
\[
x(0, t) = x(1, t) = 0, \quad y(0, t) = y(1, t) = 0
\]
or Neumann boundary conditions (no flux, i.e. a closed system or possibly one with equal movement of animals in and out of the system at each boundary)
\[
x_\xi(0, t) = x_\xi(1, t) = 0, \quad y_\xi(0, t) = y_\xi(1, t) = 0.
\]
In practice Neumann boundary conditions are a more realistic approximation of the real world (e.g. a closed boundary) than Dirichlet conditions (e.g. animals being killed on the boundary). The choice of boundary conditions has a significant impact on the resulting dynamics. The function \(f(-, \xi, t)\) represents a general non-homogeneous culling function which we take to be at least piecewise continuous in all three variables and non-negative.

We note that since we define \(x + y = n\) and provided that \(f\) is linear in the first variable, so that \(f(x, \xi, t) + f(y, \xi, t) = f(n, \xi, t)\) (e.g. \(f = An\) as in fixed rate culling), we can simplify the problem to
\[
\frac{\partial n}{\partial t} = D \frac{\partial^2 n}{\partial \xi^2} + \rho n(1 - n) - \alpha n - f(n, \xi, t),
\]
\[
\frac{\partial y}{\partial t} = D \frac{\partial^2 y}{\partial \xi^2} - y + R_0(n - y)y - f(y, \xi, t),
\]
\[
n(\xi, 0) = n_0(\xi) > 0, \quad y(\xi, 0) = y_0(\xi) \geq 0,
\]
with appropriate boundary conditions, where the first equation is decoupled from the second.

5.8.1 Non-homogeneous equilibria with fixed rate culling

For simplicity we first consider \(f(n, \xi, t) = An\), replicating one of the models used in the previous section. We look for spatially non-homogeneous equilibrium solutions, using some of the ideas of [46]. We can see that in this case there are three possible equilibria for system (5.46), the trivial solution \((0, 0)\), the IFE \((n^*(\xi), 0)\) and the endemic equilibrium \((n^*(\xi), y^*(\xi))\).

Remark 5.8.1 We note that the existence of \(\xi\)-dependent equilibria is not guaranteed. Constant values of \(n^*\) and \(y^*\) will satisfy the Neumann problem. The only constant solution to the Dirichlet problem however is \(n^* = 0\).
For the Dirichlet problem, \( n^*(\xi) \), is a non-homogeneous steady state, (if it exists, i.e. if there is some \( \xi \in (0,1) \) such that \( \xi \) maximises \( n^*(\xi) \)) satisfying

\[
D \frac{d^2 n^*}{d\xi^2} + \rho n^*(1 - n^*) - \alpha n^* - A n^* = 0, \quad n^*(0) = n^*(1) = 0.
\]

We can find an upper bound on \( n^*(\xi) \). Let there be \( \xi_0 \) such that

\[
\max_{\xi \in [0,1]} n^*(\xi),
\]

then \( \frac{d^2 n^*}{d\xi^2}(\xi_0) \leq 0 \) so that

\[
\rho n^*(\xi_0)(1 - n^*(\xi_0)) - \alpha n^*(\xi_0) - A n^*(\xi_0) \geq 0
\]

and hence

\[
n^*(\xi) \leq 1 - \frac{A + \alpha}{\rho}.
\]

This bound is the same value as the equilibrium population density of spatially homogeneous fixed rate culling found in Chapter 3.

5.8.2 The trivial equilibrium

Linearising the first equation of system (5.46) with homogeneous Dirichlet boundary conditions about the trivial equilibrium we obtain

\[
\frac{\partial n}{\partial t} = D \frac{\partial^2 n}{\partial \xi^2} + (\rho - \alpha - A)n.
\]

We try the Ansatz \( n(\xi, t) = u(\xi)e^{\lambda t} \) and substitute into the equation above to obtain the eigenvalue problem;

\[
-\frac{d^2 u}{d\xi^2} = \theta^2 u, \quad u(0) = u(1) = 0
\]

where \( \theta = \sqrt{\frac{1}{D}(\rho - \alpha - A - \lambda)} \).

This gives us solutions of the form \( u_j = B_j \sin j\pi \xi \), where \( B_j \) is the \( j \)th coefficient of the Fourier sine series expansion of \( n_0(\xi) \), thus the \( j \)th eigenvalue is \( \lambda_j = -Dj^2\pi^2 + \rho - \alpha - A \). We can thus write an expression for \( n \) as

\[
n(\xi, t) = e^{(\rho - \alpha - A)t} \sum_{j=1}^{\infty} e^{-Dj^2\pi^2t} B_j \sin j\pi \xi.
\]

Evidently, \( n(\xi, t) \to 0 \) as \( t \to \infty \) if \( A > \rho - \alpha - D\pi^2 \). Thus we have a definition of \( A_{\text{crit}} \) for system (5.46) as

\[
A_{\text{crit}} = \rho - \alpha - D\pi^2,
\]

which is reduced by \( D\pi^2 \) from the spatially homogeneous model - the faster the animals diffuse the lower the culling rate at which they are eradicated.
Had we linearised system (5.46) with homogeneous Neumann boundary conditions about the trivial equilibrium we would have obtained an expression for $n$ as

$$n(\xi, t) = e^{(\rho - \alpha - A)t} \sum_{j=0}^{\infty} e^{-Dj^2\pi^2t} C_j \cos j\pi \xi,$$

where $C_j$ is the $j$th coefficient of the Fourier cosine series expansion of $n_0(\xi)$. The first term, $C_0 e^{(\rho - \alpha - A)t}$, is dominant and is not $\xi$-dependent.

5.8.3 The IFE and the endemic equilibrium

Linearising (5.46) about a non-trivial equilibrium $(n^*(\xi), y^*(\xi))$, with

$$u(\xi, t) = n(\xi, t) - n^*(\xi), \quad i(\xi, t) = y(\xi, t) - y^*(\xi),$$

we obtain

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial \xi^2} - u(A - \rho + \alpha + 2\rho n^*),$$

$$\frac{\partial i}{\partial t} = D \frac{\partial^2 i}{\partial \xi^2} - i(1 + A) + R_0 y^*(u - i) + R_0 i(n^* - y^*).$$

(5.47)

At the infection free equilibrium, $(n^*(\xi), 0)$, we can write the eigenvalue problem for $i$ as

$$\frac{\partial i}{\partial t} = D \frac{\partial^2 i}{\partial \xi^2} - i(1 + A) + R_0 i n^*$$

and consider both Dirichlet and Neumann boundary conditions in turn.

* If $n^*$ is a non zero constant on $(0, 1)$

We know that this is only possible for Neumann boundary conditions. Let $i(\xi, t) = e^{\lambda_j t} \phi_j(\xi)$, where $\phi_j(\xi)$ is the eigenfunction corresponding the $j$th eigenvalue ($\lambda_j$) of the Laplacian operator with Neumann conditions (as in the preceding subsection). Then, substituting in the second equation of (5.47) we obtain

$$\lambda_j = -Dj^2\pi^2 - (1 + A - R_0 n^*).$$

We have already established in Chapter 3 that in this case $n^* = 1 - \frac{A + \alpha}{\rho}$, so that for stability of the IFE, $\lambda_j < 0$, for $j = 0, 1, 2, \ldots$, we must have $A > A^*$ where

$$A^* = \frac{R_0 (\rho - \alpha) - \rho}{R_0 + \rho},$$

which is the same result as we obtained in Chapter 3 for the spatially homogeneous system.

* If $n^*$ is not constant on $(0, 1)$

We assume homogeneous Dirichlet boundary conditions. Let $i = e^{\eta t} \psi(\xi)$,
where $\psi$ is some suitable function. Substituting in the second equation of (5.47) and multiplying through by $\psi$ we obtain

$$\sigma \psi(\xi)^2 = D \frac{d^2 \psi(\xi)}{d\xi^2} \psi(\xi) - \psi(\xi)^2(1 + A) + R_0 \psi(\xi)^2 n^*(\xi).$$

Integrating with respect to $\xi$ between 0 and 1 and using $\psi(0) = \psi(1) = 0$ we have

$$\sigma \int_0^1 \psi(\xi)^2 d\xi = -D \int_0^1 \left( \frac{d\psi(\xi)}{d\xi} \right)^2 d\xi - (1 + A) \int_0^1 \psi(\xi)^2 d\xi + R_0 \int_0^1 \psi(\xi)^2 n^*(\xi) d\xi.$$

Then the IFE will be stable provided $\sigma < 0$, hence if $A > \bar{A}_D$ where

$$\bar{A}_D = \sup_{\psi \in W_0^{1,2}(0,1)} \frac{\int_0^1 (R_0 n^*(\xi) - 1) \psi(\xi)^2 d\xi - D \int_0^1 \left( \frac{d\psi(\xi)}{d\xi} \right)^2 d\xi}{\int_0^1 \psi(\xi)^2 d\xi},$$

where $W_0^{1,2}(0,1)$ is a subset of $W^{1,2}(0,1)$, the Sobolev space of functions $\eta$ such that $\eta$ is square-integrable on $(0,1)$, at least once differentiable on $(0,1)$ and zero at the boundary.

If we apply Neumann boundary conditions we obtain an equivalent result, using this time $\frac{d\psi}{d\xi}(0) = \frac{d\psi}{d\xi}(1) = 0$, but the supremum is taken over a different function space, thus we require that $A > \bar{A}_N$, where

$$\bar{A}_N = \sup_{\psi \in W_1^{1,2}(0,1)} \frac{\int_0^1 (R_0 n^*(\xi) - 1) \psi(\xi)^2 d\xi - D \int_0^1 \left( \frac{d\psi(\xi)}{d\xi} \right)^2 d\xi}{\int_0^1 \psi(\xi)^2 d\xi},$$

where $W_1^{1,2}(0,1)$ is a subset of $W^{1,2}(0,1)$, the Sobolev space of functions $\eta$ such that $\eta$ is square-integrable on $(0,1)$, at least once differentiable on $(0,1)$ and with the first derivative zero at the boundary.

Which is the larger, $\bar{A}_D$ or $\bar{A}_N$ is not obvious simply from considering the function space over which the suprema are taken. However the Dirichlet problem implies a steady reduction in the population due to the lethal boundary, so we might expect that $\bar{A}_D < \bar{A}_N$.

### 5.9 Fixed yield culling on a finite interval

This section is based on the ideas in [13]. We can amend model (5.46) for spatially non-homogeneous fixed yield culling with homogeneous Dirichlet bound-
ary conditions as follows

\[ \frac{\partial n}{\partial t} = D \frac{\partial^2 n}{\partial \xi^2} + \rho n(1 - n) - an - Af(\xi), \]

\[ \frac{\partial y}{\partial t} = D \frac{\partial^2 y}{\partial \xi^2} - y + R_0(n - y)y - Af(\xi) \frac{y}{n}, \]  

\( n(\xi, 0) = n_0(\xi) > 0, \quad y(\xi, 0) = y_0(\xi) \geq 0, \)

\( n(0, t) = n(1, t) = 0, \quad y(0, t) = y(1, t) = 0. \)

The number of animals culled is a function of the location of the culling and we specify the properties of \( f \) as

\[ f(\xi) \geq 0, \quad \xi \in (0, 1), \quad f(\xi) = 0 \quad \text{for} \quad n = 0, \]

\[ \int_0^1 f(\xi) d\xi = 1, \]

\[ \max f(\xi) \bigg|_{\xi \in (0, 1)} = M < \infty. \]

If we consider the total population, then irrespective of the disease status, the non-homogeneous equilibrium solution, \( n(\xi) \) of (5.48), if it exists, must satisfy

\[ -D \frac{\partial^2 n}{\partial \xi^2} = \rho n(1 - n) - an - Af(\xi). \]  

The problem \( \theta_{\xi\xi} + \lambda^2 \theta = 0 \) with homogeneous Dirichlet boundary conditions has a principal eigenfunction \( \theta(\xi) = \beta \sin \pi \xi \), where \( \beta \) is a constant, which is positive on \((0, 1)\) and \( \theta_{\xi\xi} = -\pi^2 \theta \). Multiplying (5.49) through by \( \theta \) and integrating w.r.t. \( \xi \) between 0 and 1 we obtain

\[ -\int_0^1 \left( D \frac{\partial^2 n}{\partial \xi^2} \theta(\xi) + (\rho - \alpha)n(\xi)\theta(\xi) \right) d\xi \]

\[ = -\rho \int_0^1 n(\xi)^2 \theta(\xi) d\xi - A \int_0^1 f(\xi) \theta(\xi) d\xi. \]  

The right hand side of (5.50) is non-positive for \( n \geq 0 \) so that the left hand side must also be non-positive. Integrating the first term of the left hand side of (5.50) by parts twice, using \( \theta(0) = \theta(1) = 0 \) and \( n(0) = n(1) = 0 \) and substituting for \( \theta_{\xi\xi} \) we obtain

\[ (D\pi^2 - (\rho - \alpha)) \int_0^1 n(\xi)\theta(\xi) d\xi \leq 0, \]

thus we must have \( \rho - \alpha > \pi^2 D \) if we are to observe a positive non-homogeneous solution, \( n(\xi) \), to (5.49).

Observation 5.9.1 If \( n(\xi) = 0 \) for \( \xi = 0 \) and \( \xi = 1 \) and \( \frac{\partial^2 n}{\partial \xi^2} > 0 \) for \( \xi \in (0, 1) \) then the Maximum Principle (see for example [150] p 41) assures us that \( n(\xi) \leq 0 \) for \( \xi \in (0, 1) \).
Equation (5.49) implies that at the boundaries $\frac{d^2n}{d\xi^2} \geq 0$. This suggests that the general shape of $n^*(\xi)$ is as in Figure 5.1 if we are to observe positive non-homogeneous solutions. Let us now assume that a positive non-homogeneous steady state $n(\xi)$ exists, such that for some $\xi_0 \in [0,1]$ we have

$$n(\xi_0) = \max_{\xi \in [0,1]} n(\xi).$$

Then $\frac{d^2n}{d\xi^2}(\xi_0) \leq 0$, which implies that we must have

$$n(\xi) \leq n(\xi_0) \leq \frac{1}{2\rho} \left( \rho - \alpha + \sqrt{(\rho - \alpha)^2 - 4\rho Af(\xi_0)} \right),$$

and in particular

$$Af(\xi_0) \leq \frac{(\rho - \alpha)^2}{4\rho} \quad \text{and so} \quad M \leq \frac{(\rho - \alpha)^2}{4\rho A}.$$

### 5.9.1 Non-homogeneous equilibria with fixed yield culling

If we let $f(\xi) = 1$, so that culling takes place at the same rate throughout the interval, then the non-homogeneous equilibrium $n^*(\xi)$ satisfies the equation

$$-D \frac{d^2n}{d\xi^2} = h(n, A) = r n \left( 1 - \frac{n}{K} \right) - A,$$

with homogeneous Dirichlet boundary conditions for $\xi \in [0,1]$. Here we have put $r = \rho - \alpha$ and $K = 1 - \frac{\alpha}{\rho}$ for simplicity.
We have already shown that if a positive non-homogeneous equilibrium \( n^* \) exists then there is a local maximum \( n^*(\xi_0) = p \), say. We define

\[
H(n, A) = \int_0^n h(\nu, A) d\nu. \tag{5.52}
\]

If \( n(\xi) \) is a positive solution to (5.51) then both \( n(\xi_0 - \xi) \) and \( n(\xi_0 + \xi) \) are solutions to

\[
-D \frac{\partial^2 z}{\partial \xi^2} = h(z, A), \quad z(0) = n(\xi_0), \quad \frac{dz}{d\xi} \bigg|_{\xi=0} = 0.
\]

By uniqueness we must have \( n(\xi_0 - \xi) = n(\xi_0 + \xi) \), so \( n \) is symmetric about \( \xi_0 \). Thus since \( n(0) = n(1) = 0 \) it follows that \( \xi_0 = \frac{1}{2} \).

Multiplying (5.51) through by \( \frac{dn}{d\xi} \),

\[
-D \frac{dn}{d\xi} \frac{d^2n}{d\xi^2} = \frac{dn}{d\xi} H'(n, A)
\]

and integrating

\[
\frac{D}{2} \left( \frac{dn}{d\xi} \right)^2 \bigg|_{\xi}^{\xi_0} = \int_{n(\xi)}^{n(\xi_0)=p} H'(n, A) dn,
\]

whence

\[
\frac{dn}{d\xi} = \sqrt{\frac{2}{D} (H(p, A) - H(n, A))}.
\]

Rearranging and integrating

\[
\int_0^p \frac{ds}{\sqrt{H(p, A) - H(s, A)}} = \int_0^{\xi_0} \sqrt{\frac{2}{D}} d\xi = \frac{1}{\sqrt{2D}} \quad \text{since} \quad \xi_0 = \frac{1}{2}.
\]

If \( n(\xi) \) is a solution to (5.51) then we have that \( p = \max_{\xi \in (0,1)} n(\xi) \) satisfies

\[
\int_0^p \frac{ds}{\sqrt{H(p, A) - H(s, A)}} = F(p, A) = \frac{1}{\sqrt{2D}}.
\]

\( p \) is thus a root of the equation

\[
\tilde{F}(p, A) = F(p, A) - \frac{1}{\sqrt{2D}} = 0, \tag{5.53}
\]

which gives us an exact, albeit implicit upper bound for \( n^* \).

There are clearly constraints on the permissable values of \( p \) in (5.53), we must have \( p \in \Omega \), where

\[
\Omega = \{p; H(p, A) > H(s, A), \quad s \in [0, p]\}.
\]

Note that, with the choice for \( h(n, A) \) in (5.51),

\[
H(n, A) = \frac{rn^2}{2} - \frac{rn^3}{3K} - An.
\]

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We require that $H(n, A)$ be monotone increasing, i.e. that $a_1 < n < a_2$ where

$$a_1 = \frac{K}{2} - \frac{K}{2r} \sqrt{r^2 - \frac{4Ar}{K}}, \quad a_2 = \frac{K}{2} + \frac{K}{2r} \sqrt{r^2 - \frac{4Ar}{K}}. $$

We note that the roots of $H(n, A) = 0$, are $0, b_1$ and $b_2$ where

$$b_1 = \frac{3K}{4} - \frac{1}{4} \sqrt{9K^2 - \frac{48KA}{r}}, \quad b_2 = \frac{3K}{4} + \frac{1}{4} \sqrt{9K^2 - \frac{48KA}{r}}. $$

Figure 5.2 illustrates $H(n, A)$ and $h(n, A)$. Hence we must have $a_1 < p < a_2$.

![Figure 5.2: Constraints on p in equation (5.53)](image)

if positive equilibrium solutions are to exist.

**Two positive equilibria**

In the static model with fixed yield continuous rate culling we found that there were two positive equilibria, the larger stable and the smaller unstable. We now look for the conditions that two or more positive equilibrium solutions exist in the non-homogeneous case. We first establish the constraint on $r$ for there to be any positive equilibrium solutions.

**Lemma 5.9.2** *Positive equilibrium solutions to (5.51) are possible only if $r > D\pi^2$.*
We prove this by finding and evaluating a lower bound for \( \tilde{F}(p, A) \).

\[
\tilde{F}(p, A) = \int_0^p \frac{ds}{\sqrt{\left( \frac{tp^2}{2} - \frac{tp^3}{3K} - Ap \right) - \left( \frac{rs^2}{2} - \frac{rs^3}{3K} - As \right)}} - \frac{1}{\sqrt{2D}}
\]

\[
= \int_0^p \frac{ds}{\sqrt{\frac{r}{2} (p^2 - s^2) - \frac{r}{3K} (p^3 - s^3) - A(p - s)}} - \frac{1}{\sqrt{2D}}
\]

\[
= \int_0^p \frac{ds}{\sqrt{\left( \frac{r}{2} (p + s) - \frac{r}{3K} (p^2 + ps + s^2) - A \right)}} - \frac{1}{\sqrt{2D}}
\]

\[
> \sqrt{\left( \frac{2}{r} \right)} \int_0^p \frac{ds}{\sqrt{\left( p^2 - s^2 \right)}} - \frac{1}{\sqrt{2D}}
\]

\[
= \sqrt{\left( \frac{2}{r} \right)} \sin^{-1} \left( \frac{s}{p} \right) \bigg|_0^p - \frac{1}{\sqrt{2D}} = \frac{\pi}{\sqrt{2r}} - \frac{1}{\sqrt{2D}}.
\]

Thus if \( r < D\pi^2 \), then \( \tilde{F}(p, A) > 0 \) and there can be no positive solution to (5.51). \( \square \)

If the population net birth rate \( \rho - \alpha < D\pi^2 \), fixed yield culling will not produce a spatially non-homogeneous equilibrium - i.e. the population will be eliminated.

**Lemma 5.9.3** If \( r > 3D\pi^2 \) and

\[
A < \min \left\{ \frac{3K(r - D\pi^2)^2}{8r}, \frac{3KD\pi^2(r - 3D\pi^2)}{2r}, \frac{3K(r - D\pi^2)(5r + 3D\pi^2)}{64r} \right\}
\]

then a minimum of two distinct roots \( p \) exist for the equation \( \tilde{F}(p, A) = 0 \).

**Remark 5.9.4** The two (or more) values of \( p \) would correspond either to the different extrema of a solution with more than one extremum in \((0, 1)\) or to the different extrema associated with various coexisting solutions of equation (5.51).

We define below certain functions \( U(p, A) \) and \( L(p, A) \) such that

\[
U(p, A) \geq \tilde{F}(p, A) \geq L(p, A).
\]

and find the conditions that they both have two zeros in \( \Omega \), thus ensuring that \( \tilde{F}(p, A) \) has at least two roots in \( \Omega \). The situation is illustrated in Figure 5.3. Since \( p^2 + ps < p^2 + ps + s^2 \) and \( \frac{p + s}{2p} < 1 \) for \( s \in [0, p) \) we have
Figure 5.3: Roots of $U(p, A)$ and $L(p, A)$

\[
L(p, A) = \int_0^p \frac{ds}{\sqrt{(p-s)^2 \left(\frac{r}{2} (p+s) - \frac{rp}{3K} (p+s) - \frac{A(p+s)}{2p}\right)}} - \frac{1}{\sqrt{2D}}
\]

\[
= \int_0^p \frac{ds}{\sqrt{(p^2 - s^2) \left(\frac{r}{2} - \frac{rp}{3K} - \frac{A}{2p}\right)}} - \frac{1}{\sqrt{2D}}
\]

\[
= \frac{\pi}{2} \left(\frac{r}{2} - \frac{rp}{3K} - \frac{A}{2p}\right) - \frac{1}{\sqrt{2D}}
\]

while since $(p+s)^2 > p^2 + ps + s^2$ and $\frac{p+s}{p} > 1$ we use a similar calculation to obtain

\[
U(p, A) = \int_0^p \frac{ds}{\sqrt{(p^2 - s^2) \left(\frac{r}{2} - \frac{2rp}{3K} - \frac{A}{p}\right)}} - \frac{1}{\sqrt{2D}} =
\]

\[
= \frac{\pi}{2} \left(\frac{r}{2} - \frac{2rp}{3K} - \frac{A}{p}\right) - \frac{1}{\sqrt{2D}}
\]

$L$ exists provided that $A < \frac{rp}{2} - \frac{2rp^2}{3K}$, while $U$ exists provided that

$A < \frac{rp}{2} - \frac{2rp^2}{3K}$.
The roots of \( U = 0 \) are \( c_1 \) and \( c_2 \) where
\[
c_1 = \frac{K}{8r} \left( 3(r - D\pi^2) - \sqrt{9(r - D\pi^2)^2 - \frac{96rA}{K}} \right),
\]
\[
c_2 = \frac{K}{8r} \left( 3(r - D\pi^2) + \sqrt{9(r - D\pi^2)^2 - \frac{96rA}{K}} \right),
\]
provided that \( A < \frac{3K(r - D\pi^2)^2}{32r} \), while the roots of \( L = 0 \) are \( d_1, d_2 \) where
\[
d_1 = \frac{K}{4r} \left( 3(r - D\pi^2) - \sqrt{9(r - D\pi^2)^2 - \frac{24rA}{K}} \right),
\]
\[
d_2 = \frac{K}{4r} \left( 3(r - D\pi^2) + \sqrt{9(r - D\pi^2)^2 - \frac{24rA}{K}} \right),
\]
provided that \( A < \frac{3K(r - D\pi^2)^2}{8r} \).

Thus the necessary and sufficient conditions for the two roots of \( U \) and \( L \) to lie in \( \Omega \) are
\[
d_1 > a_1, \quad d_2 < a_2, \quad c_1 > a_1 \quad \text{and} \quad c_2 < a_2.
\]
The first two inequalities ensure that the roots of \( L(p, A) \) lie in \( \Omega \), the second two ensure that the minimum of \( U(p, A) \), which is negative because of the geometry of \( U(p, A) \), lies in \( \Omega \). The constraints on \( A \) and \( r \) such that the above inequalities hold are

- \( d_1 > a_1 \) and \( d_2 < a_2 \) provided that \( A < \frac{3KD\pi^2(r - 3D\pi^2)}{2r} \) and \( r > 3D\pi^2 \),
- \( c_1 > a_1 \) and \( c_2 < a_2 \) provided that \( A < \frac{3K(r - D\pi^2)(5r + 3D\pi^2)}{64r} \).

Which of the constraints yield the lowest bound will depend thus on \( r = \rho - \alpha \) and \( D \), as we should expect from biological considerations.

**Conjecture 5.9.5** In the same way as for the static model, we conjecture that if there are two non-homogeneous equilibrium solutions to (5.51) then the smaller equilibrium will be unstable and the larger stable.

### 5.10 Conclusions

We have demonstrated that plausible travelling wave solutions for the models used, on an infinite domain, with specified minimum wavespeeds can connect each equilibrium to each of the other equilibria. The minimum wavespeed is generally increasing in the basic reproductive ratio for the model system concerned - the more contagious the disease the greater the spread speed. Culling decreases the minimum wavespeed.

Finally, on a finite domain, we find constraints on the culling rate which permit spatially non-homogeneous equilibrium solutions.
Chapter 6

Age structured models

6.1 Introduction

We have hitherto ignored age structure in our models in the interests of simplicity. However, animal population and disease dynamics are essentially age-dependent and we now consider how to model populations with an age structure.

We define $n(a, t)$ as the density of animals of age $a$ at time $t$; thus $n(a, t)$ is a distribution function and the number of animals aged between ages $a_1$ and $a_2$ will be $\int_{a_1}^{a_2} n(a, t) \, da$. We use lower case symbols to denote density and upper case symbols for numbers of animals.

We consider a general fecundity function rather than the specific functions we have used hitherto. The density of animals of age zero at time $t$ is $n(0, t)$: this is thus the birth rate. The number of animals born between time $t_1$ and $t_2$ will be $\int_{t_1}^{t_2} n(0, t) \, dt$.

There are essentially two approaches to modelling the age structure of a population: renewal integral equations and delay differential equations.

6.2 Deriving an age structured population model

If the density function of animals aged $a$ at time $t$ is $n(a, t)$ then, if $\mu(a)$ is the age-related death rate function, we can express the change in density over an interval $\delta t$ as

$$n(a + \delta t, t + \delta t) = n(a, t) - \mu(a)n(a, t)\delta t. \quad (6.1)$$

We consider $\mu$ as a variable at this stage, later we will take it to be constant for simplicity. The probability that an individual, alive at time $t_1$, is still alive at time $t_2$ is $e^{-\int_{t_1}^{t_2} \mu(a) \, da}$. We require that $\mu(a)$ is positive, bounded and at least piecewise continuous. If we expand the left hand side of equation (6.1) in a Taylor series we obtain,

$$n(a, t) + n_a \delta t + n_t \delta t + O(\delta t^2) = n(a, t) - \mu(a)n(a, t)\delta t.$$

Dividing through by $\delta t$ and taking the limit as $t \to \infty$ we have

$$\frac{\partial n}{\partial a} + \frac{\partial n}{\partial t} = -\mu(a)n(a, t), \quad (6.2)$$
with initial conditions \( n(a, 0) = n_0(a) \), which is the initial age distribution and \( n(0, t) = B(t) \), where \( B(t) \) is the fecundity function. Thus deaths are explicitly included in equation (6.2), while births appear as a boundary condition. Equation (6.2) is known as the McKendrick-von Foerster equation.

6.3 The renewal integral equation

We can solve equation (6.2) using the method of characteristics to give us the following expression for \( n(a, t) \);

\[
n(a, t) = \begin{cases} 
B(t - a)e^{-\int_0^t \mu(\theta)d\theta} & : t > a \\
n_0(a - t)e^{-\int_t^0 \mu(\theta)d\theta} & : t < a
\end{cases}
\]  

(6.3)

where \( n_0(a) \) is the age distribution at time \( t = 0 \) and \( B(t) \) is the birth rate at time \( t \). We do not specify, or may not even know, the form of \( B \). However we may write

\[
B(t) = \int_0^\infty f(a)n(a, t)da,
\]

(6.4)

where \( f(a) \geq 0 \) is some age-dependant maternity function (and \( \lim_{a \to \infty} f(a) = 0 \)).

Deriving the renewal equation

Substituting the expression for \( n(a, t) \) in equation (6.3) into (6.4) we obtain

\[
B(t) = \int_0^t f(a)B(t - a)e^{-\int_0^a \mu(\theta)d\theta} da + \int_0^\infty f(a)n_0(a - t)e^{-\int_t^0 \mu(\theta)d\theta} da.
\]

With a change of variable, \( \xi = a - t \) we can write the second of the integrals as

\[
g(t) = \int_0^\infty f(\xi + t)n_0(\xi)e^{-\int_0^\xi \mu(\theta)d\theta} d\xi
\]

and if we put \( h(a) = e^{-\int_0^a \mu(\theta)d\theta} \), then we arrive at the following renewal equation, ascribed to Euler:

\[
B(t) = \int_0^t f(a)h(a)B(t - a)da + g(t).
\]

(6.5)

The first term represents the births due to those born at time \( t - a \), the second to those already born at \( t = 0 \). Thus we can study the evolution of the birth rate and hence the size of the population over time. Evidently, as \( t \to \infty \), \( g(t) \to 0 \), so that we can express equation (6.5) for large \( t \) as

\[
B(t) = \int_0^\infty k(a)B(t - a)da
\]

(6.6)
where \( k(a) = f(a)h(a) \) for simplicity. The integrand in the above equation shows the number of births to individuals aged \( a \), evidently therefore born at time \( t - a \) and surviving until age \( a \). If we substitute \( B = B_0e^{rt} \) in equation (6.6), we obtain the characteristic equation;

\[
\int_0^\infty e^{-ar}k(a)da - 1 = 0. \tag{6.7}
\]

Now if \( r \in \mathbb{R} \) and \( \phi(r) = \int_0^\infty e^{-ar}k(a)da \) then \( \phi \) is monotone decreasing in \( r \), since

\[
\phi'(r) = -\int_0^\infty ae^{-ar}h(a)da < 0 \quad \forall \quad r
\]

while \( \lim_{r \to -\infty} \phi(r) = +\infty \) and \( \lim_{r \to +\infty} \phi(r) = 0 \). There is thus a unique positive root, \( r_0 \), to equation (6.7) if \( \phi(0) > 1 \) and hence the birthrate increases with time in this case. Therefore \( n(a, t) \) also increases with time if \( t > a \), by equation (6.3). We can see that \( \phi(0) \) is a basic reproductive ratio for the population, it expresses the number of offspring an adult will produce in its lifetime.

If \( r \in \mathbb{C} \) we can write \( r = u + iv \). If \( u < 0 \) any complex solution will oscillate to zero as \( a \) increases and can be ignored. Let us assume therefore that \( u \geq 0 \). We write equation (6.7) as

\[
\int_0^\infty e^{-au}(\cos av - i \sin av)k(a)da = 1.
\]

Taking the real part

\[
\int_0^\infty e^{-au}(\cos av)k(a)da = 1.
\]

Hence,

\[
\phi(u) = \int_0^\infty e^{-au}k(a)da \geq 1 = \phi(r_0),
\]

so that, since \( \phi \) is strictly decreasing, \( r_0 \geq u \) and the real, positive root is dominant. The dynamics of the renewal equation (6.5) are thus driven by the unique real root.

### 6.4 Delay differential equations

The alternative modelling approach to renewal integral equations is to formulate a system of delay differential equations for the total number of immature (juvenile) and mature (adult) individuals. We adopt this approach in the following sections. We consider that only mature adults can reproduce; let the age at maturity be a constant \( \tau \), then the number of juveniles, \( N_J(t) \) and the number of adults, \( N_A(t) \) will be given by

\[
N_J(t) = \int_0^{\tau} n(a, t)da, \quad N_A(t) = \int_{\tau}^\infty n(a, t)da.
\]

For adults we have, assuming that \( \mu \), the death rate from natural causes, is constant and that \( n(\infty, t) = 0 \), by integrating equation (6.2) with respect to \( a \)

\[
\frac{dN_A}{dt} = n(\tau, t) - \mu N_A(t). \tag{6.8}
\]
In order to obtain \( n(\tau, t) \), the rate at which animals are reaching maturity, we solve equation (6.2) by the method of characteristics and obtain, for \( \tau < t \)

\[
n(\tau, t) = n(0, t - \tau)e^{-\mu\tau} = B(N_A(t - \tau))e^{-\mu\tau}.
\] (6.9)

The boundary condition is now expressed as \( n(0, t) = B(N_A(t)) \), which is a function of \( N_A(t) \), in contrast to \( n(0, t) = B(t) \), which is a function of time as we used in the previous section. In this case \( B(N_A) \) is a prescribed function of \( N_A \) with properties described below.

**Properties of \( B(N_A) \)**

In order to serve as a realistic birth rate function we require the following properties for \( B(N_A) \).

- \( B(N_A) \) is a continuous and differentiable function of \( N_A \), with a continuous second derivative.

- \( B(N_A) \) is bounded
  
  \[
  \sup_{N_A > 0} B(N_A) = \bar{B} < \infty.
  \]

- \( B(0) = 0 \) so that there are no births if there is no adult population. \( B(N_A) \geq 0 \) for \( N_A \geq 0 \).

- If the population is not to go extinct we need \( B'(0) > \bar{\mu}(0) \) where \( \bar{\mu}(t) \) is the mean per capita death rate,

\[
\bar{\mu}(t) = \frac{\int_0^\infty \mu(a)n(a, t)da}{\int_0^\infty n(a, t)da},
\]

- \( \lim_{N_A \to \infty} B(N_A) = 0 \). The density dependency of the birth rate function is exhibited by its increasing monotonically as the population increases from zero, to a maximum \( \bar{B} \) after which it decreases monotonically with \( N_A \) to zero. We will have \( B(N_A) = 0 \) when the total population reaches the carrying level for the environment.

If we combine equations (6.8) and (6.9) we obtain a delay differential equation for \( N_A \)

\[
\frac{dN_A}{dt} = B(N_A(t - \tau))e^{-\mu\tau} - \mu N_A(t).
\] (6.10)

In a similar manner we obtain a delay differential equation for \( N_J \):

\[
\frac{dN_J}{dt} = B(N_A(t)) - B(N_A(t - \tau))e^{-\mu\tau} - \mu N_J(t).
\] (6.11)

### 6.5 An age-structured SIS model

We first briefly recap the analysis of the simple SIS epidemic model without age structure which we introduced in Chapter 2. Animals are born susceptible, become infected through a mass-action process, are immediately infectious and subsequently recover to become once more susceptible. Our objective is now
to study the age-structured SIS model of a single animal species. $S$ and $I$ are susceptible and infective spatial densities respectively, $\beta$ the infection rate, $\mu$ the natural per capita death rate, $d$ the per capita death rate from disease and $\gamma$ the per capita recovery rate. All the latter parameters are taken to be constant. We define the adult and juvenile populations as

$$S(t) = S_I(t) + S_A(t), \quad I(t) = I_J(t) + I_A(t), \quad N(t) = N_I(t) + N_A(t),$$

so that $N_A = S_A + I_A$.

$$\frac{dS}{dt} = B(N_A(t)) - \beta SI + \gamma I - \mu S,$$

$$\frac{dI}{dt} = \beta SI - (\mu + d + \gamma) I,$$

$$S(0) = S_0 > 0, \quad I(0) = I_0 > 0.$$

We find that there are two equilibria apart from extinction; the IFE, $(\frac{B(N_A)}{\mu}, 0)$ (where $N_A^*$ is the equilibrium population in the absence of infection) and the endemic equilibrium:

$$S^* = \frac{\mu + d + \gamma}{\beta}, \quad I^* = \frac{\beta B(N_A^*) - \mu(\mu + d + \gamma)}{\beta(\mu + d)},$$

where $N_A^*$ is the equilibrium population with endemic infection. When $I^* = 0$, we have $N_A^* = \hat{N}_A^*$, the equilibrium adult population for an infection-free equilibrium. System (6.12) displays a bifurcation with parameter $R_0$, where we define

$$R_0 = \frac{\beta B(\hat{N}_A^*)}{\mu(\mu + d + \gamma)}. \quad (6.13)$$

From the second equation of system (6.12) we can deduce that $I(t) > 0$ for $I_0 > 0$ since

$$I(t) = I_0 \exp \left( \int_0^t (\beta S(s) - (\mu + d + \gamma)) ds \right) \geq 0.$$

Given that $S(0) > 0$, if we assume that $S(t) = 0$ for the first time when $t = \hat{t}$, then, from the first equation of system (6.12) we must have

$$\left[ \frac{dS}{dt} \right]_{t=\hat{t}} = B(N_A(\hat{t})) + \gamma I(\hat{t}) > 0,$$

since we assume that $I(0)$ cannot be zero else we only have the trivial solution. By continuity this implies that $S(t) < 0$ for some $t < \hat{t}$ so that $\hat{t}$ cannot have been the first time that $S(t) = 0$. We thus have a contradiction of our original assumption of $S(t)$ becoming zero for the first time. We can conclude that $S(t) > 0$ for all $t > 0$.

Finally, for the total population $N(t)$ in the absence of infection we have

$$\frac{dN}{dt} = B(N_A(t)) - \mu N - dI \leq B(N_A(t)) - \mu N \leq \bar{B} - \mu N.$$
so that
\[
\limsup_{t \to \infty} N(t) \leq \frac{\bar{B}}{\mu}.
\]
Since \( \bar{B} \) is bounded by definition, \( N(t) \) is bounded from above. Therefore \( \mathcal{S}(t) \) and \( I(t) \) are both bounded from above.

We can write the general age-structured SIS model as follows, for \( a \geq 0, t \geq 0 \)
\[
\begin{align*}
\frac{\partial s(a, t)}{\partial a} + \frac{\partial s(a, t)}{\partial t} &= -\lambda(a, t)s(a, t) - \mu(a)s(a, t) + \gamma(a)i(a, t), \\
\frac{\partial i(a, t)}{\partial a} + \frac{\partial i(a, t)}{\partial t} &= \lambda(a, t)s(a, t) - (\mu(a) + d(a))i(a, t) - \gamma(a)i(a, t),
\end{align*}
\]
with the following definitions and boundary conditions;
\[
\begin{align*}
\lambda(a, t) &= \int_0^\infty \beta(a, \alpha)i(\alpha, t)d\alpha, \\
s(0, t) &= B(N_A(t)) \quad N_A(t) = S_A(t) + I_A(t), \\
s(a, 0) &= s_0(a), \quad i(0, t) = 0 \quad i(a, 0) = i_0(a),
\end{align*}
\]
where \( s(a, t) \) and \( i(a, t) \) are the age distributions of susceptible and infective animals respectively, \( \mu(a) \) is the natural death rate, \( d(a) \) is the death rate from disease, \( \gamma(a) \) the rate of recovery from the disease, \( \beta(a, \alpha) \) the probability of transmission of disease from an animal aged \( \alpha \) to one of age \( a \). We consider that reproduction takes place only after maturity is reached and that the new born are always initially susceptible, there being no vertical transmission. Both juveniles and adults may be susceptible or infectious.

Let the age at maturity be a constant \( \tau \), then, if the subscripts \( J \) and \( A \)
refer to juveniles and adults respectively,
\[
\begin{align*}
n(a, t) &= n_A(a, t) + n_J(a, t) \\
s(a, t) &= s_A(a, t) + s_J(a, t) \\
i(a, t) &= i_A(a, t) + i_J(a, t).
\end{align*}
\]
We define
\[
\begin{align*}
\mathcal{S}(t) &= \int_\tau^\infty s(a, t)da, \quad \mathcal{S}_J(t) = \int_0^\tau s(a, t)da, \\
N_A(t) &= \int_\tau^\infty (s(a, t) + i(a, t))da,
\end{align*}
\]
with equivalent definitions for \( I_A \) and \( I_J \). The fecundity function \( B(N_A) \) is
described in the previous section and we assume that all members of the adult class can reproduce.

We note that, by definition
\[
\begin{align*}
\mathcal{S}(t) &= \int_0^\infty s(a, t)da, \quad I(t) = \int_0^\infty i(a, t)da,
\end{align*}
\]
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where \( S \) and \( I \) are the total numbers of susceptibles and infectives respectively. We observe in passing that, if all the parameters are assumed to be independent of \( a \) and \( \alpha \), then \( \lambda(a, t) = \beta I(t) \) and we can integrate both sides of the two equations in system (6.14) with respect to \( a \) to retrieve the age-independent equations of equation (6.12).

6.5.1 Steady state solutions

In order to derive some explicit results, we consider \( \beta, \mu \) and \( d \) to be constant, \( \gamma = 0 \) (for simplicity, so that in effect we now have an SI model) and \( t \) large enough that we may assume that the system has reached equilibrium, then we can solve (6.14) to obtain the following expressions for the equilibrium distributions of the state variables:

\[
s^*(a) = B(N_A^*)e^{-(\lambda^*+\mu)a},
\]

\[
i^*(a) = \frac{\lambda^* B(N_A^*)}{\lambda^* - d} \left( e^{-(\mu+d)a} - e^{-(\mu+\lambda^*)a} \right),
\]

where \( B(N_A^*) \) is the birth rate at equilibrium and \( \lambda^* \) is the equilibrium force of infection. Equation (6.16) does not give explicit expressions for \( s^*(a) \) and \( i^*(a) \) since we have

\[
0 = B(N_A^*) = B\left( \int_0^\infty (s^*(a) + i^*(a))\,da \right) = B(S_A^* + I_A^*)
\]

\[
\lambda^* = \beta \int_0^\infty i^*(a)\,da = \beta(I_A^* + I_d^*).
\]

With a general form of \( B(\cdot) \) such as we use here, we cannot hope to find explicit expressions for \( s^*(a) \) and \( i^*(a) \). We can however integrate the second equation of (6.16) to obtain an expression for \( I^* \), the endemic infective population and the condition that this is a positive quantity gives us an expression for the basic reproductive ratio, \( R_0 \),

\[
I^* = \frac{\lambda^* B(N_A^*)}{\lambda^* - d} \left( \frac{1}{\mu + d} - \frac{1}{\mu + \lambda^*} \right).
\]

Substituting \( \lambda^* = \beta I^* \) we obtain, after simplifying

\[
I^* = \frac{\beta B(N_A^*) - \mu(\mu + d)}{\beta(\mu + d)}
\]

and so \( I^* > 0 \) provided that

\[
R_0 = \frac{\beta B(N_A^*)}{\mu(\mu + d)} > 1.
\]

Moreover, since we are also able to compute \( R_0 \) without recourse to \( B \) (as described in the next section), we can legitimately express the endemic equilibrium quantities in terms of \( R_0 \), (which is necessarily greater than unity in this case) using the substitutions

\[
B(N_A^*) = \frac{\mu(\mu + d)}{\beta} R_0 \quad \text{and} \quad \beta I^* = \mu(R_0 - 1).
\]
Thus we can write, at the endemic equilibrium
\[ s^*(a) = \frac{\mu(\mu + d)}{\beta} R_0 e^{-\mu R_0 a}, \]
\[ i^*(a) = \frac{R_0 \mu^2(\mu + d)(R_0 - 1)}{\beta(\mu(R_0 - 1) - d)} \left( e^{-(\mu+d)a} - e^{-\mu R_0 a} \right). \]

We can verify that \( i^*(a) > 0 \); if \( \mu(R_0 - 1) > d \) then \( \mu R_0 > \mu + d \) and so \( e^{-\mu R_0} < e^{-(\mu+d)} \). Conversely, if \( \mu(R_0 - 1) < d \) then \( \mu R_0 < \mu + d \) and \( e^{-\mu R_0} > e^{-(\mu+d)} \). Clearly \( s^*(a) > 0 \). While \( s^*(a) \) is monotone decreasing in \( a \), \( i^*(a) \) is monotone increasing in \( a \) to a maximum and monotone decreasing to zero thereafter - as age increases, the proportion of the population at that age which becomes infected increases (since the longer the exposure the higher the chance of infection), while this is balanced by the increasing effect of natural and disease related deaths.

The age at which the density of infectives reaches a maximum is found by solving \( \frac{di^*}{da} = 0 \) for \( a \) to obtain
\[ a_{max} = \frac{1}{\mu(R_0 - 1) - d} \ln \left( \frac{\mu R_0}{\mu + d} \right). \]

Clearly \( a_{max} > 0 \).

We can examine the relationship between \( a_{max} \) and the parameters \( d \) and \( R_0 \). Thus differentiating,
\[ \frac{da_{max}}{dd} = \frac{(\mu + d) \left( 1 + \ln \left( \frac{\mu R_0}{\mu + d} \right) \right) - \mu R_0}{(\mu + d)(\mu(R_0 - 1) - d)^2}, \]
and since \( 1 + \ln \left( \frac{\mu R_0}{\mu + d} \right) \leq \frac{\mu R_0}{\mu + d} \), we have \( \frac{da_{max}}{dd} \leq 0 \), so that the greater the death rate from infection the lower the age of maximum infection.

\[ \frac{da_{max}}{dR_0} = \frac{\mu R_0 \left( 1 - \ln \left( \frac{\mu R_0}{\mu + d} \right) \right) - (\mu + d)}{R_0(\mu(R_0 - 1) - d)^2}, \]
so that \( \frac{da_{max}}{dR_0} < 0 \), thus the greater the basic reproductive ratio the lower the age of maximum infection. Both of these results accord with biological expectations.

Equilibrium values for the adult and juvenile populations

By applying the definitions in equation (6.15) and integrating \( s(a) \) and \( i(a) \) with respect to \( a \) with the appropriate limits, we can obtain expressions for
the equilibrium values of the state variables.

\[ S^*_S = \frac{\mu + d}{\beta} (1 - e^{-\mu R_0}), \]

\[ S^*_A = \frac{\mu + d}{\beta} (e^{-\mu R_0}), \]

\[ I^*_S = \frac{R_0 \mu^2 (\mu + d)(R_0 - 1)}{\beta (\mu (R_0 - 1) - d)} \left( \frac{1 - e^{-(\mu + d)r}}{\mu + d} - \frac{1 - e^{-\mu R_0}}{\mu R_0} \right), \] \hspace{1cm} (6.18)

\[ I^*_A = \frac{R_0 \mu^2 (\mu + d)(R_0 - 1)}{\beta (\mu (R_0 - 1) - d)} \left( \frac{e^{-(\mu + d)r}}{\mu + d} - \frac{e^{-\mu R_0}}{\mu R_0} \right). \]

We note that \( I^*_A \) is positive for, if \( \mu (R_0 - 1) - d > 0 \), then

\[ \frac{e^{-(\mu + d)r}}{\mu + d} > \frac{e^{-\mu R_0}}{\mu R_0}, \]

while if \( \mu (R_0 - 1) - d < 0 \), the direction of the inequality is reversed.

Mean age when first infected

The average age at infection, \( \bar{a} \) is given by

\[ \bar{a} = \frac{\int_0^\infty a \lambda(a) s(a) da}{\int_0^\infty \lambda(a) s(a) da}, \]

so that at equilibrium we have

\[ \bar{a} = \frac{\int_0^\infty a \lambda(a) (\mu + d) e^{-\mu R_0} da}{\int_0^\infty (\mu + d) e^{-\mu R_0} da}. \]

Hence we have \( \bar{a} = \frac{1}{\mu R_0} \), or alternatively, if the mean life expectancy is \( \bar{w} \) then \( R_0 = \bar{w}/\bar{a} \). This, we note en passant, is a straightforward way to obtain an estimate of \( R_0 \) in the field and justifies our using \( R_0 \) in the explicit expressions for \( s^*(a) \) and \( i^*(a) \).

6.5.2 Transforming system (6.14) into a set of delay differential equations

With the same assumptions as we made in the previous section, with \( \beta, \mu \) and \( d \) independent of age and \( \gamma = 0 \), we now transform system (6.14) from p.d.e.s to delay differential equations. For the susceptible class we have

\[ \frac{\partial s}{\partial a} + \frac{\partial s}{\partial t} = -(\beta I(t) + \mu) s(a, t), \] \hspace{1cm} (6.19)

where

\[ I(t) = \int_0^\infty i(a, t) da = I_A(t) + I_J(t). \]
If we integrate equation (6.19) with respect to $a$ from $\tau$ to $\infty$ we obtain
\[
\frac{dS_A}{dt} = s(\tau, t) - s(\infty, t) - \int_{\tau}^{\infty} (\beta I(t) + \mu)s(a, t)\, da.
\]
For obvious reasons $s(\infty, t) = 0$.

We can find an expression for $s(\tau, t)$, the number of susceptible juveniles reaching maturity, as follows. Define
\[
s_\xi(a) = s(a, \xi + a),
\]
then, for $t > a$,
\[
\frac{ds_\xi}{da} = \left[ \frac{\partial s}{\partial a} + \frac{\partial s}{\partial t} \right] = -(\beta I(a + \xi) + \mu)s(a, a + \xi).
\]
Thus we have
\[
\frac{ds_\xi}{da} = -(\beta I(a + \xi) + \mu)s_\xi,
\]
which we can integrate to obtain
\[
s_\xi(a) = s_\xi(0)e^{-\int_0^a (\beta I(\theta + \xi) + \mu)\, d\theta}.
\] (6.20)
Here $s_\xi(0) = s(0, \xi) = B(N_A(\xi))$.

If on the other hand $a > t$, we define
\[
s_\eta(a) = s(t + \eta, t),
\]
then
\[
\frac{ds_\eta}{dt} = \left[ \frac{\partial s}{\partial a} + \frac{\partial s}{\partial t} \right]_{a=t+\eta} = -(\beta I(t) + \mu)s(t + \eta, t),
\]
which we can integrate to obtain
\[
s_\eta(a) = s_\eta(0)e^{-\int_0^a (\beta I(\theta) + \mu)\, d\theta},
\] (6.21)
with $s_\eta(0) = s_0(a - t)$.

We have $t > \tau$ so we now substitute $a = \tau$ and $\xi = t - \tau$ in (6.20) and we have
\[
s(\tau, t) = B(N_A(t - \tau))e^{-\mu(\tau)}e^{-\int_0^\tau (\beta I(t) + \mu)\, d\theta}.
\] (6.22)
We can interpret the biological significance of equation (6.22) as showing that the rate of maturation of juveniles is equal to the birth rate at time $t - \tau$, multiplied by the probability that those born are still alive at maturity $\tau$ later and multiplied by the probability that they are still uninfected by the time that they reach maturity.

Thus the delay differential equations for $S$ are
\[
\frac{dS_A}{dt} = B(N_A(t - \tau))e^{-\int_0^{t-\tau} (\beta I(\theta + t - \tau) + \mu)\, d\theta} - B(I(t))S_A(t) - \mu S_A(t)
\]
\[
\frac{dS_I}{dt} = B(N_A(t)) - B(N_A(t - \tau))e^{-\int_0^{t-\tau} (\beta I(\theta + t - \tau) + \mu)\, d\theta} - B(I(t))S_I(t) - \mu S_I(t).
\] (6.23)
We can now derive delay differential equations for \( I \) from the second equation of system (6.14), once more with \( \beta, \mu \) and \( d \) independent of age and \( \gamma = 0 \)
\[
\frac{\partial i}{\partial a} + \frac{\partial i}{\partial t} = \beta I(t)s(a, t) - (\mu + d)i(a, t).
\] (6.24)

Integrating equation (6.24) with respect to \( a \) from \( \tau \) to \( \infty \) we obtain, with \( i(\infty, t) = 0 \),
\[
\frac{dI_A}{dt} = i(\tau, t) + \int_\tau^\infty (\beta I(t)s(a, t) - (\mu + d)i(a, t)) \, da.
\]

We solve equation (6.24) for \( t \in [0, \tau] \) by the method of characteristics to find \( i(\tau, t) \), the rate of maturation of infected juveniles. We find that
\[
i(\tau, t) = \int_0^\tau \beta s(\xi, t - \tau + \xi)I(t - \tau + \xi)e^{-(\mu + d)(\tau - \xi)} \, d\xi.
\] (6.25)

The right hand side of equation (6.25) expresses the rate of maturation of infective juveniles as the integral from \( 0 \) to \( \tau \) of the density of susceptible juveniles becoming infected at age \( \xi \), multiplied by the force of infection at the time they are infected and multiplied by the probability that they remain alive from age \( \xi \) until maturity.

The differential equations for \( I \) are therefore
\[
\frac{dI_A}{dt} = \int_0^\tau \beta s(\xi, t - \tau + \xi)I(t - \tau + \xi)e^{-(\mu + d)(\tau - \xi)} \, d\xi
\]
\[
+ \beta S_A(t)I(t) - (\mu + d)I_A(t)
\]
\[
+ \int_0^\tau \beta s(\xi, t - \tau + \xi)I(t - \tau + \xi)e^{-(\mu + d)(\tau - \xi)} \, d\xi
\]
\[
- (\mu + d)I_J(t).
\] (6.26)

We can thus restate the age structured SIS model as equations (6.23) and (6.26) together with the initial conditions
\[
S_A(0) = S_A(0) > 0, \quad S_J(0) = S_J(0) > 0, \quad I_A(0) = I_A(0) > 0, \quad I_J(0) = 0,
\]
\[
S_A(\theta) > 0, S_J(\theta) > 0, I_A(\theta) > 0, I_J(\theta) > 0 \quad \text{for} \quad \theta \in [-\tau, 0].
\]

We consider that \( I_A^0 \) represents the addition of a single infective individual to a population consisting entirely of susceptibles.
6.5.3 Analysing the SI model as a system of delay differential equations

Collecting the results of the previous sections, the age-structured SI model with constant $\mu, \beta, d$ can thus be written as follows

\[
\frac{dS_A}{dt} = B(N_A(t - \tau)) e^{-\int_0^\tau (\beta I(\theta + t - \tau) + \mu) d\theta} - \beta I(t)S_A(t) - \mu S_A(t),
\]

\[
\frac{dS_J}{dt} = B(N_A(t)) - B(N_A(t - \tau)) e^{-\int_0^\tau (\mu + \beta I(\theta + t - \tau)) d\theta} - \beta I(t)S_J(t) - \mu S_J(t),
\]

\[
\frac{dI_A}{dt} = \int_0^\tau \beta s(\xi, t - \tau + \xi) I(t - \tau + \xi) e^{-(\mu + d)(\tau - \xi)} d\xi + \beta S_A(t) I(t) - (\mu + d) I_A(t),
\]

\[
\frac{dI_J}{dt} = \beta S_J(t) I(t) - \int_0^\tau \beta s(\xi, t - \tau + \xi) I(t - \tau + \xi) e^{-(\mu + d)(\tau - \xi)} d\xi - (\mu + d) I_J(t),
\]

with the following definitions and conditions

\[
S_A(0) = S^0_A > 0, \quad S_J(0) = S^0_J > 0, \quad I_A(0) = I^0_A > 0, \quad I_J(0) = 0,
\]

\[
S_A(\theta) > 0, S_J(\theta) > 0, I_A(\theta) > 0, I_J(\theta) > 0 \quad \text{for} \quad \theta \in [-\tau, 0],
\]

\[
S(t) = S_A(t) + S_J(t), \quad I(t) = I_A(t) + I_J(t),
\]

\[
s(a, t) = B(N_A(t - a)) e^{-\int_0^{t-a} \beta I(\theta) d\theta} - \int_{t-a}^t \beta I(\theta) d\theta,
\]

\[
n_A = S_A + I_A.
\]

6.5.4 Positivity of the state variables in system (6.27)

Lemma 6.5.1 All the state variables remain non-negative for all $t > 0$.

We have already proved that $S(t)$ and $I(t)$ are positive in Section 6.5. We now need to prove the positivity and boundedness of the adult and juvenile susceptible and infective classes.

We have already shown that

\[
s(a, t) = B(N_A(t - a)) e^{-\int_0^{t-a} \beta I(\theta) d\theta} - \int_{t-a}^t \beta I(\theta) d\theta,
\]

\[
i(a, t) = \int_0^a \beta s(\xi, t - a + \xi) I(t - a + \xi) e^{-(\mu + d)(a - \theta)} d\xi,
\]

for $t > a$, where $a$ is a variable of integration such that $a \in [0, \tau]$. Thus (6.27) is valid for $t > \tau$ and we can use the expressions in (6.28) to restate the first
of the equations of system (6.27) in the form
\[
\frac{dS_A}{dt} = B(S_A(t - \tau) + I_A(t - \tau))
\]
\[
e^{-\int_0^\tau (\beta I_A(\theta + t - \tau) + I_J(\theta + t - \tau)) + \mu)d\theta} - \beta I(t)S_A(t) - \mu S_A(t).
\]

We can now apply Theorem 5.2.1 on p 81 of [49] to (6.29). On the right hand side we put \( S_A(t) = 0 \) and we see immediately that all of the remaining terms are non-negative when all of the other state variables (including those with delays) are non-negative. Then we can conclude that \( S_A(t) \geq 0 \) for all \( t > 0 \).

We can similarly use expressions in (6.28) to restate the third of the equations of system (6.27) in the form
\[
\frac{dI_A}{dt} = \int_0^\tau \beta B(S_A(t - \tau) + I_A(t - \tau)) e^{-\mu t} - \int_{t-\tau}^{t-\tau+\xi} \beta I(\theta)d\theta
\]
\[
(I_A(t - \tau + \xi) + I_J(t - \tau + \xi))e^{-(\mu + \delta)(\tau - \xi)}d\xi
\]
\[+\beta S_A(t)(I_A(t) + I_J(t)) - (\mu + \delta)I_A(t).
\]

If we set \( I_A(t) = 0 \) on the right hand side of (6.30) we see immediately that all of the remaining terms are non-negative when all of the other state variables, including those with delays, are non-negative. Then we can conclude that \( I_A(t) \geq 0 \) for all \( t > 0 \).

We can use the expressions in (6.28) to express \( S_J(t) \) and \( I_J(t) \) as follows:
\[
S_J(t) = \int_0^\tau B(S_A(t - a) + I_A(t - a)) e^{-\mu a} - \int_{t-a}^{t^-a+\xi} \beta I(\theta)d\theta
\]
\[a
\]
\[e^{-\int_{t-a}^{t-a+\xi} \beta I(\theta)d\theta} I(t - a + \xi) e^{-(\mu + \delta)(a - \xi)}d\xi da.
\]

The right hand sides of (6.31) are the integrals of exponentials and of terms we have either defined or shown to be positive. Hence \( S_J(t) \geq 0 \) and \( I_J(t) \geq 0 \). Thus we can conclude that, for \( t > \tau \), all the state variables are positive.

For \( t \leq \tau \) we must use the following expression for \( s(a, t) \) obtained from (6.21):
\[
s(a, t) = s_0(a - t)e^{-\int_0^t (\beta I(\theta) + \mu)d\theta},
\]
where the initial age density \( s_0(a) \geq 0 \) by assumption. Repeating the previous argument with this expression for \( s(a, t) \) allows us to conclude that
$S_A(t), S_J(t), I_A(t), I_J(t)$ are all non-negative for $t < \tau$. This completes the proof of Lemma 6.5.1.

6.5.5 Boundedness

Lemma 6.5.2 All the state variables are bounded from above.

In Section 6.5 we showed that $S(t)$ is bounded from above. Since $S(t) = S_A(t) + S_J(t)$ and $S_A(t)$ and $S_J(t)$ are positive, it follows that $S_A(t)$ and $S_J(t)$ are bounded from above. We can establish what these bounds are.

From the properties of $B$ we have that $\sup_{N_0 > 0} B(N_A) = B < \infty$, thus, from the first equation of system (6.27) we deduce that

\[
\frac{dS_A}{dt} \leq \bar{B} - \int_0^\tau (\mu + \beta I(\theta + t - \tau)) d\theta - \beta I(t)S_A(t) - \mu S_A(t).
\]

Since $S_A(t), I(t) \geq 0$

\[
\frac{dS_A}{dt} \leq \bar{B} - \int_0^\tau (\beta I(\theta + t - \tau) + \mu) d\theta - \mu S_A(t) \leq \bar{B} e^{-\mu \tau} - \mu S_A(t)
\]

and thus

\[
S_A(t) \leq \frac{1}{\mu} (\bar{B} e^{-\mu \tau} - Ce^{-\mu t}),
\]

where $C$ is a constant, therefore

\[
\limsup_{t \to \infty} S_A(t) \leq \frac{1}{\mu} \bar{B} e^{-\mu \tau}.
\]

Self-evidently, there will be fewer susceptibles in the presence of infection than in its absence. Thus, if we assume that there is no infective class then we must have

\[
\frac{dS(t)}{dt} = B(N_A(t)) - \mu S(t) \leq \bar{B} - \mu S(t),
\]

so that

\[
S(t) \leq \frac{1}{\mu} (\bar{B} - Ke^{-\mu t}) \quad \text{where } K \text{ is a constant},
\]

therefore

\[
\limsup_{t \to \infty} S(t) \leq \frac{1}{\mu} \bar{B}.
\]

Finally, from equation (6.31), with $I = 0$ we have the inequality

\[
S_J(t) \leq \int_0^\tau \bar{B} e^{-\int_{t-a}^{t} \mu d\eta} da = \frac{\bar{B}}{\mu} (1 - e^{-\mu \tau}).
\]

In Section 6.5 we showed that $I(t)$ is bounded from above. Since $I(t) = I_A(t) + I_J(t)$ and $I_A(t)$ and $I_J(t)$ are positive, it follows that $I_A(t)$ and $I_J(t)$ are bounded from above.
We now establish a bound for \( I_J(t) \). Let \( \limsup_{t \to \infty} I(t) = \bar{I} \). Then we can write, from (6.31)

\[
\limsup_{t \to \infty} I_J(t) \leq \int_0^\infty \int_0^a \beta \bar{B} I e^{-\mu a} e^{-(\mu + d)(e^{-\xi} - 1)} d\xi da.
\]

Integrating, we obtain

\[
\limsup_{t \to \infty} I_J(t) \leq \frac{\beta \bar{B} \bar{I} \left( d(1 - e^{-\mu a}) + e^{-\mu a}(e^{-d} - 1) \right)}{\mu d(\mu + d)}.
\]

We see, by differentiating the right hand side of the above inequality and by using numerical simulation on a wide range of parameters where necessary, that this bound for \( \limsup_{t \to \infty} I_J(t) \) is increasing in \( \tau \), the age at maturity, as would be expected, but decreasing in \( \mu \), the natural death rate and in \( d \), the death rate from disease, for which a biological explanation is not evident.

We are, however, not able to find a more useful estimate of \( \bar{I} \) than \( \frac{\bar{B}}{\mu} \). This completes the proof of Lemma 6.5.2. \( \Box \)

6.5.6 Global stability of the infection free equilibrium

Lemma 6.5.3 If \( \frac{\beta \bar{B}}{\mu} < \mu + d \) then the IFE of (6.27) is globally stable.

Adding the last two equations in system (6.27) gives

\[
\frac{dI}{dt} = \beta S(t) I(t) - (\mu + d)I(t). \tag{6.32}
\]

Now, we have shown that \( \limsup_{t \to \infty} S(t) \leq \frac{1}{\mu} \bar{B} \), thus for any \( \epsilon > 0 \) there is a \( T_\epsilon > 0 \) such that \( S(t) \leq \frac{\bar{B}}{\mu} + \epsilon \) for \( t > T_\epsilon \). Consequently, for \( t > T_\epsilon \),

\[
\frac{dI}{dt} \leq \beta \left( \frac{\bar{B}}{\mu} + \epsilon \right) I(t) - (\mu + d)I(t).
\]

\[
I(t) \leq I(0)e^{\left( \frac{\beta \bar{B}}{\mu} + \epsilon \right)(\mu + d)t}.
\]

If \( \frac{\beta \bar{B}}{\mu} < \mu + d \), then, by continuity we must be able to choose a value of \( \epsilon \) sufficiently small and a suitable \( T_\epsilon \) such that

\[
\beta \left( \frac{\bar{B}}{\mu} + \epsilon \right) < \mu + d
\]

and hence

\[
\limsup_{t \to \infty} I(t) \leq 0.
\]

Since \( I(t) \geq 0 \) we must have \( \lim_{t \to \infty} I(t) = 0 \).
We defined $R_0 = \frac{\beta B(N_A^*)}{\mu(\mu + d)}$ and by definition, $B(N_A^*) \leq B$. Hence if $\beta B \leq \mu(\mu + d)$ then $R_0 \leq 1$.

However, the converse is not the case and we have not yet established that the infection free equilibrium is globally stable if $R_0 < 1$.

Another approach to computing the equilibrium quantities

At equilibrium we can write system (6.27) in the following form, where the starred quantities represent equilibrium values of the state variables,

\[ B(N_A^*) e^{-(\beta(I_A^* + I_J^*) + \mu)t} - \beta S_A^*(I_A^* + I_J^*) - \mu S_A^* = 0, \]
\[ B(N_A^*)(1 - e^{-(\beta(I_A^* + I_J^*) + \mu)t}) - \beta S_J^*(I_A^* + I_J^*) - \mu S_J^* = 0, \]
\[ \int_0^t \beta s^*(\xi)(I_A^* + I_J^*) e^{-(\mu + d)(t - \xi)} d\xi + \beta S_A^*(I_A^* + I_J^*) - (\mu + d)I_A^* = 0, \]
\[ \beta S_J^*(I_A^* + I_J^*) - \int_0^t \beta s^*(\xi)(I_A^* + I_J^*) e^{-(\mu + d)(t - \xi)} d\xi - (\mu + d)I_J^* = 0. \]

We can solve this set of simultaneous equations by making the substitution $\lambda = \beta(I_A^* + I_J^*)$, using the previously derived expression for $s^*(t) = B(N_A^*) e^{-(\lambda^* + \mu)t}$ and finally substituting $\lambda^* = \mu(R_0 - 1)$, to obtain the identical expressions for the equilibrium populations as in equation (6.18).

6.5.7 Applying the renewal equation method to system (6.14)

If we let $\gamma(a) = 0$ for simplicity and solve system (6.14) by the method of characteristics we obtain

\[ s(a, t) = \begin{cases} B(t - a) e^{-\int_0^t (\lambda(a, t - a + \alpha) + \mu(a)) d\alpha} & : t > a \\ s_0(a - t) e^{-\int_{a-t}^0 (\lambda(a, t - a + \alpha) + \mu(a)) d\alpha} & : t < a \end{cases}, \]

\[ \int_0^a (\lambda(\theta, t - a + \theta) B(t - a) e^{-\int_0^\theta (\lambda(a, t - a + \alpha) + \mu(a)) d\alpha}) d\theta : t > a \]

\[ \int_{a-t}^a (\lambda(\theta, t - a + \theta) s_0(a - t) e^{-\int_{a-t}^\theta (\lambda(a, t - a + \alpha) + \mu(a)) d\alpha}) d\theta + s_0(a - t) e^{-\int_{a-t}^0 (\mu(a) + d(a)) d\theta} \]

\[ : t < a. \]

We define the birth function $B(.)$ in a different manner from before, namely

\[ B(t) = \int_0^\infty (b_0(a)s(a, t) + b_1(a)i(a, t)) da, \]

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where $b_s$ and $b_i$ are age dependant birth rates for the susceptible and infected classes respectively. If we suppose that $t$ is large enough that we can ignore the case that $t < a$ then we have

$$B(t) = \int_0^\infty b_s(a) B(t-a) e^{-\int_0^a (\lambda(a,t-a+a)+\mu(a))da} da$$

$$+ \int_0^\infty b_i(a) \int_0^a \left( \lambda(\theta, t-a+\theta) B(t-a) e^{-\int_0^a (\lambda(a,t-a+a)+\mu(a))da} - e^{-\int_0^a (\mu(a)+d(a))da} \right) d\theta da$$

if $B(t) = ce^{\psi t}$ then we obtain the characteristic equation

$$\int_0^\infty b_s(a) e^{-\psi a} e^{-\int_0^a (\lambda(a,t-a+a)+\mu(a))da} da +$$

$$\int_0^\infty b_i(a) \int_0^a \left( \lambda(\theta, t-a+\theta) e^{-\psi a} e^{-\int_0^a (\lambda(a,t-a+a)+\mu(a))da} - e^{-\int_0^a (\mu(a)+d(a))da} \right) d\theta da = 1.$$
so that we have

\[
\lambda X + X' = -B^*e^{-\int_0^a \beta(a,b)Y(b)db} - \mu(a)X(a) + \gamma(a)Y(a),
\]

\[
\lambda Y + Y' = B^*e^{-\int_0^a \beta(a,b)Y(b)db} - (\mu(a) + d(a) + \gamma(a))Y(a).
\]

In order to make any progress we now assume that all the parameters are constant. Then the integral term in the two equations above becomes \(\int_0^a Y(b)db\). This we take to be \(y_0\), the number of infectives introduced to the equilibrium system.

Thus we now have the o.d.e. system

\[
\begin{align*}
\lambda X + X' &= -\beta y_0 B^* e^{-\mu a} - \mu X + \gamma Y \\
\lambda Y + Y' &= \beta y_0 B^* e^{-\mu a} - (\mu + d + \gamma)Y.
\end{align*}
\] (6.33)

The o.d.e. for \(Y\) is decoupled from that for \(X\) and we solve it to give

\[
Y(a) = \frac{\beta B^* y_0 e^{-\mu a}}{\lambda + d + \gamma} \left(1 - e^{-\lambda + d + \gamma a}\right) + Y(0) e^{-(\lambda + d + \gamma)a},
\]

while the solution for \(X\) is

\[
X(a) = e^{-\mu a} \left( -\frac{\beta y_0 B^*}{\lambda} (1 - e^{-\lambda a}) + \frac{\gamma \beta y_0 B^*}{\lambda + d + \gamma} \left(1 - e^{-\lambda a}\right) - \frac{1}{\gamma + d} \left(e^{-\lambda a} - e^{-(\lambda + d + \gamma)a}\right) \right).
\]

We can also linearise the model without age structure, system (6.12) around the IFE, \((\bar{B}_\mu,0)\), with \(\bar{N}_A(t) = N_A(t) - N_A^*, \bar{S}(t) = S(t) - \bar{S}_\mu\) and \(\bar{I}(t) = I(t)\) to give us

\[
\frac{d\bar{S}}{dt} = B'(N^*_A)\bar{N}_A(t) - \frac{\beta B^* 1}{\mu} \bar{S} + \gamma \bar{I}
\]

\[
\frac{d\bar{I}}{dt} = \frac{\beta B^* 1}{\mu} - (\mu + d + \gamma)\bar{I}.
\]

Solving these equations for \(\bar{I}(t)\) we obtain

\[
\bar{I}(t) = \bar{I}(0) e^{(\frac{\beta B^* 1}{\mu} - (\mu + d + \gamma)t)}.
\]

We have thus found a value for \(\lambda\) in equation (6.33). Recalling the definition of \(R_0\) from (6.13) we can put

\[
\bar{I}(t) = \bar{I}(0) e^{(\mu + d + \gamma)(R_0 - 1)t}.
\]

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and can therefore express the density function of infected animals close to the IFE as follows

\[ i(a, t) = \left( \frac{\mu y_0(a) R_0 e^{-\mu a}}{R_0 - \frac{\mu}{\mu + d + \gamma}} \right) \left( 1 - e^{-(\mu + d + \gamma) R_0} \right) e^{(\mu + d + \gamma)(R_0 - 1)t}. \]

### 6.5.8 The full SIS model

If we now amend the model represented by system (6.14) to take account of recovery of infectives, so that \( \gamma \neq 0 \), we have the following equations;

\[
\frac{\partial s(a, t)}{\partial a} + \frac{\partial s(a, t)}{\partial t} = -\lambda(a, t)s(a, t) - \mu(a)s(a, t) + \gamma(a)i(a, t),
\]

\[
\frac{\partial i(a, t)}{\partial a} + \frac{\partial i(a, t)}{\partial t} = \lambda(a, t)s(a, t) - (\mu(a) + d(a))i(a, t) - \gamma(a)i(a, t),
\]

where all the parameters and variables have the same meanings as in equation (6.14) and where the initial and boundary conditions are

\[
s(0, t) = B(N_A(t)), \quad i(0, t) = 0, \quad s(a, 0) = s_0(a) > 0, \quad i(a, 0) = i_0(a) > 0
\]

and \( \lambda \), the force of infection is given by

\[
\lambda(a, t) = \int_0^\infty \beta(a, \alpha) i(a, \alpha) d\alpha.
\]

At an equilibrium in time, if \( \lambda, \beta, \mu, d \) and \( \gamma \) are constant we have

\[
\frac{ds}{da} = -s + \gamma i,
\]

\[
\frac{di}{da} = \lambda s - (\mu + d + \gamma)i.
\]

Solving these two simultaneous o.d.e.s we have the following expressions for \( s(a) \) and \( i(a) \)

\[
s(a) = \frac{\theta}{\lambda} e^{-\psi a} \left( (\mu + \gamma + d - \psi) \sinh \phi a + \phi \cosh \phi a \right),
\]

\[
i(a) = \theta e^{-\psi a} \sinh \phi a,
\]

where

\[
\theta = \frac{\lambda B(N_A)}{\phi}, \quad \psi = \frac{2\mu + \lambda + \gamma + d}{2},
\]

\[
\phi = \frac{1}{2} \sqrt{(\lambda + 2\mu + \gamma + d)^2 - 4(\mu(\mu + \gamma + d) + \lambda(\mu + d))},
\]

and

\[
\lambda = \frac{\mu(\mu + \gamma + d)(R_0 - 1)}{\mu + d}, \quad R_0 = \frac{\beta B(N_A)}{\mu(\mu + d + \gamma)}.\]
We can compute values for $S_j^*$, $S_A^*$, $I_j^*$ and $I_A^*$ by straightforwardly integrating these expressions for $s(a)$ and $i(a)$ between the appropriate limits, but the results are algebraically unwieldy.

6.6 An age-structured SEI model

In much the same way as for the SI model we can define an age structured SEI model, with $\sigma(a)$ the per capita rate of passing from the latent ($\epsilon$) to the infectious class and with all the other parameters and variables having the same meanings as for the SI model, as follows:

\[
\begin{align*}
\frac{\partial s}{\partial a} + \frac{\partial s}{\partial t} &= -(\lambda(a, t) + \mu(a)) s(a, t), \\
\frac{\partial e}{\partial a} + \frac{\partial e}{\partial t} &= \lambda(a, t)s(a, t) - (\mu(a) + \sigma(a))e(a, t), \\
\frac{\partial i}{\partial a} + \frac{\partial i}{\partial t} &= \sigma(a)e(a, t) - (\mu(a) + d(a))i(a, t), \\
s(0, t) &= B(N_A(t)), \quad e(0, t) = 0, \quad i(0, t) = 0, \\
s(a, 0) &= s_0(a), \quad e(a, 0) = 0, \quad i(a, 0) = i_0(a) > 0,
\end{align*}
\]

(6.34)

\[
\lambda(a, t) = \int_0^\infty \beta(a, \alpha)i(\alpha, t)d\alpha.
\]

6.6.1 Equilibrium age distribution

In the same manner and with the same notation as for the SI model, if we consider the parameters $\mu, \beta, \sigma$ and $d$ to be constant and $t$ large enough that we may consider that the system has reached equilibrium, we can solve equation (6.34) to obtain the following implicit equations for the age density of the state variables for the endemic equilibrium, assuming that the basic reproductive ratio for the system is greater than unity.

\[
s(a) = B(N_A^*)e^{-(\lambda^*+\mu)a},
\]

\[
\epsilon(a) = \frac{\lambda^*B(N_A^*)}{\lambda^* - \sigma} \left( e^{-(\mu+\sigma)a} - e^{-(\mu+\lambda^*)a} \right),
\]

(6.35)

\[
i(a) = \frac{\sigma\lambda^*B(N_A^*)}{\lambda^* - \sigma} \left( \frac{e^{-(\lambda^*+\mu)a} - e^{-(\mu+d)a}}{\lambda^* - d} - \frac{e^{-(\sigma+\mu)a} - e^{-(\mu+d)a}}{\sigma - d} \right).
\]

Once more $N_A^*$ is the adult population at equilibrium and $\lambda^*$, the equilibrium force of infection, is given by $\lambda^* = \beta I^*$.

Computing $I^*$ by integrating the last equation of (6.35) and substituting $\lambda^* = \beta I^*$ we have

\[
I^* = \frac{B(N_A^*)\sigma\beta - \mu(\mu + \sigma)(\mu + d)}{\beta(\mu + \sigma)(\mu + d)},
\]

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so that the condition for $I^* > 0$ is

$$R_0 := \frac{B(N_A^*)\beta}{\mu(\mu + \sigma)(\mu + d)} > 1.$$ 

Moreover, we immediately have $\lambda^* = \mu(R_0 - 1)$, so that we have the following explicit expressions for the age distributions at equilibrium

$$s(a) = \frac{\mu(\mu + \sigma)(\mu + d)}{\beta \sigma} R_0 e^{-\mu R_0 a},$$

$$\epsilon(a) = \frac{\mu^2 R_0 (R_0 - 1)(\mu + \sigma)(\mu + d)}{\beta \sigma(\mu(R_0 - 1) - \sigma)} \left( e^{-(\mu+\sigma)a} - e^{-\mu R_0 a} \right),$$

$$i(a) = \frac{\mu^2 R_0 (R_0 - 1)(\mu + \sigma)(\mu + d)}{\beta(\mu(R_0 - 1) - \sigma)} \times \left( \frac{e^{-\mu R_0 a} - e^{-(\mu+d)a}}{\mu(R_0 - 1) - d} - \frac{e^{-(\mu+\sigma)a} - e^{-(\mu+d)a}}{\mu(R_0 - 1) - d} \right).$$

Integrating each of the equations in system (6.36) with respect to $a$ from 0 to $\infty$ we obtain the expressions for the equilibrium populations of each of the three disease classes analogous to those already derived in Chapter 4, namely

$$S^* = \frac{(\mu + d)(\mu + \sigma)}{\beta \sigma}, \quad E^* = \frac{\mu(R_0 - 1)(\mu + d)}{\sigma \beta}, \quad I^* = \frac{\mu(R_0 - 1)}{\beta}.$$ 

We can obtain values for the equilibrium population of the six classes by integrating equation (6.36) between appropriate limits as follows

$$S_j^* = \frac{(\mu + d)(\mu + \sigma)}{\beta \sigma} (1 - e^{-\mu R_0 \tau}),$$

$$S_A^* = \frac{(\mu + d)(\mu + \sigma)}{\beta \sigma} (e^{\mu R_0 \tau}),$$

$$E_j^* = \frac{\mu^2 R_0 (R_0 - 1)(\mu + \sigma)(\mu + d)}{\beta \sigma(\mu(R_0 - 1) - \sigma)} \left( \frac{1 - e^{(\mu+\sigma)\tau}}{\mu + \sigma} - \frac{1 - e^{-\mu R_0 \tau}}{\mu R_0} \right),$$

$$E_A^* = \frac{\mu^2 R_0 (R_0 - 1)(\mu + \sigma)(\mu + d)}{\beta \sigma(\mu(R_0 - 1) - \sigma)} \left( \frac{e^{-\mu R_0 \tau}}{\mu + \sigma} - \frac{e^{-\mu R_0 \tau}}{\mu R_0} \right),$$

$$I_j^* = \frac{\mu^2 R_0 (R_0 - 1)(\mu + \sigma)(\mu + d)}{\beta(\mu(R_0 - 1) - \sigma)(\mu(R_0 - 1) - d)} \left( 1 - e^{-\mu R_0 \tau} \right) \left( \frac{1 - e^{-\mu R_0 \tau}}{\mu R_0(\mu(R_0 - 1) - d)} \right) - \frac{1 - e^{-(\sigma+\mu)\tau}}{(\sigma - d)(\sigma + \mu)} \left( \frac{1 - e^{-(\mu+d)\tau}(\mu(R_0 - 1) - \sigma)}{(\mu(R_0 - 1) - d)(\sigma - d)(\mu + d)} \right),$$

$$I_A^* = \frac{\mu^2 R_0 (R_0 - 1)(\mu + \sigma)(\mu + d)}{\beta(\mu(R_0 - 1) - \sigma)(\mu(R_0 - 1) - d)} \left( \frac{e^{-\mu R_0 \tau}}{\mu R_0(\mu(R_0 - 1) - d)} \right) - \frac{e^{-(\sigma+\mu)\tau}}{(\sigma - d)(\sigma + \mu)} \left( \frac{e^{-(\mu+d)\tau}(\mu(R_0 - 1) - \sigma)}{(\mu(R_0 - 1) - d)(\sigma - d)(\mu + d)} \right).$$

(6.37)
Reducing to a system of delay differential equations

In order to obtain a closed set of delay differential equations and for use in analysing the linearisation around the infection-free equilibrium, \( i(a, t) \) we need to obtain expressions for \( s(a, t), \epsilon(a, t) \). We solve system (6.34) using the method of characteristics and consider \( t \) sufficiently large that we can take \( t > a \). The solution is as follows;

\[
s(a, t) = B(N_a(t - a))e^{-\mu a}e^{-\int_{t-a}^{t} \beta I(\theta) d\theta}.
\]

The age density of susceptibles is the product of \( B(N_a(t - a)) \), the number of animals born at time \( t - a \), \( e^{-\mu a} \), the probability that they have survived to age \( a \) and \( e^{-\int_{a}^{\infty} \beta I(\theta) d\theta} \), the probability that they remain uninfected to age \( a \).

\[
\epsilon(a, t) = \int_{0}^{a} \beta s(\xi, t - a + \xi)I(t - a + \xi)e^{-(\mu + \sigma)(a - \xi)}d\xi.
\]

The age density of latents is the product of the density of susceptibles born at time \( t - a \) and infected at age \( \xi \in (0, a) \), multiplied by \( e^{-\mu(\sigma)a} \), the probability that they survive from age \( \xi \) to age \( a \) and have not yet become infectious, integrated over all possible ages of infection from birth to age \( a \). If we substitute for \( s(\xi, t - a + \xi) \) we obtain

\[
\epsilon(a, t) = \int_{0}^{a} \beta B(N_a(t - a))I(t - a + \xi)e^{-(\mu + \sigma)(a - \xi)}d\xi.
\]

Finally, solving system (6.34) for \( i(a, t) \);

\[
i(a, t) = \sigma \int_{0}^{a} \epsilon(\xi, t - a + \xi)e^{-(\mu + \phi)(a - \xi)}d\xi.
\]

The age density of the infectious class is the product of the density of latents born at time \( t - a \) and, passing into the infectious class at age \( \xi \in (0, a) \) and then surviving until age \( a \), integrated over all possible ages of infection from birth to age \( a \). If we substitute for \( \epsilon(\xi, t - a + \xi) \) we obtain

\[
i(a, t) = \sigma \int_{0}^{a} \int_{0}^{\xi} \beta B(N_a(t - a))I(t - \phi)e^{-(\mu + \phi)(\xi - \phi)}e^{-(\mu + \sigma)(\xi - \phi)}d\phi d\xi.
\]

By the same process that we used for the SI model, with the age of reproductive maturity \( \tau \), we can now reduce the p.d.e.s of system (6.34) to the following set
of delay differential equations:

\[
\begin{align*}
\frac{dS_A}{dt} &= B(N_A(t - \tau)) e^{-\int_0^\tau \beta I(\xi + t - \tau) d\xi} e^{-\mu t} - \beta I(t) S_A(t) - \mu S_A(t), \\
\frac{dS_I}{dt} &= B(N_A(t)) - B(N_A(t - \tau)) e^{-\int_0^\tau \beta I(\xi + t - \tau) d\xi} e^{-\mu t} - \beta I(t) S_I(t) - \mu S_I(t), \\
\frac{dE_A}{dt} &= \int_0^\tau \beta s(\xi, \xi + t - \tau) I(\xi + t - \tau) e^{-(\mu + \sigma) (\tau - \xi)} d\xi + \beta I(t) S_A(t) - (\mu + \sigma) E_A(t), \\
\frac{dE_I}{dt} &= \beta S_I(t) I(t) - \int_0^\tau \beta s(\xi, \xi + t - \tau) I(\xi + t - \tau) e^{-(\mu + \sigma) (\tau - \xi)} d\xi - (\mu + \sigma) E_I(t), \\
\frac{dI_A}{dt} &= \sigma \int_0^\tau e(\xi, \xi + t - \tau) e^{-(\mu + \sigma) (\tau - \xi)} d\xi + \sigma E_A(t) - (\mu + d) I_A(t), \\
\frac{dI_I}{dt} &= \sigma E_I(t) - \sigma \int_0^\tau e(\xi, \xi + t - \tau) e^{-(\mu + \sigma) (\tau - \xi)} d\xi - (\mu + d) I_I(t),
\end{align*}
\]

with initial conditions

\[
S_A(0) = S_A^0, \quad S_I(0) = S_I^0, \quad E_A(0) = 0, \quad E_I(0) = 0, \quad I_A(0) > 0, \quad I_I(0) = 0,
\]

\[
S_A(\theta) > 0, \quad S_I(\theta) > 0, \quad E_A(\theta) > 0, \quad E_I(\theta) > 0, \quad I_A(\theta) > 0, \quad I_I(\theta) > 0,
\]

for \( \theta \in [-\tau, 0] \).

The expressions for \( s(\xi, \xi + t - \tau) \) and \( e(\xi, \xi + t - \tau) \) are those we derived at the start of this section. If we consider an equilibrium in time, set the right hand sides of (6.38) equal to zero and solve for the equilibrium values of the state variables we recover the expressions in equation (6.37).

We linearise system (6.38) around the infection-free equilibrium, defining

\[
X_A(t) = S_A(t) - S_A^*, \quad X_I(t) = S_I(t) - S_I^*, \\
Y_A(t) = E_A(t), \quad Y_I(t) = E_I(t), \\
Z_A(t) = I_A(t), \quad Z_I(t) = I_I(t), \quad Z(t) = I(t), \\
\hat{N}_A(t) = N_A(t) - N_A^*,
\]

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and ignoring quadratic and higher order terms as follows;

\[
\frac{dX_A}{dt} = -B(N_A)\left(\int_{t-r}^{t} \beta Z(\xi) d\xi + \hat{N}_A(t-r)B'(N_A')e^{-\mu r} \right)
- \beta Z(t)S_A' - \mu X_A,
\]

\[
\frac{dX_J}{dt} = \hat{N}_A(t)B'(N_A) + \left( B(N_A)\int_{t-r}^{t} \beta Z(\xi) d\xi - \hat{N}_A(t-r)B'(N_A') \right) e^{-\mu r}
- \beta Z(t)S_J' - \mu X_J,
\]

\[
\frac{dY_A}{dt} = \beta \int_0^t B(N_A)e^{-\mu \xi}Z(t-r+\xi)e^{-(\mu+\sigma)(r-\xi)}d\xi
-(\mu + \sigma)Y_A(t) + \beta Z(t)S_A',
\]

\[
\frac{dY_J}{dt} = -\beta \int_0^t B(N_A)e^{-\mu \xi}Z(t-r+\xi)e^{-(\mu+\sigma)(r-\xi)}d\xi
-(\mu + \sigma)Y_J(t) + \beta Z(t)S_J',
\]

\[
\frac{dZ_A}{dt} = \beta \sigma \int_0^t \int_0^t B(N_A)e^{-\mu \xi}Z(t-r+\xi)e^{-(\mu+\sigma)(r-\xi)}d\xi - \sigma Y_A(t) + (\mu + d)Z_A(t),
\]

\[
\frac{dZ_J}{dt} = -\beta \sigma \int_0^t \int_0^t B(N_A)e^{-\mu \xi}Z(t-r+\xi)e^{-(\mu+\sigma)(r-\xi)}d\xi + \sigma Y_J(t) - (\mu + d)Z_J(t).
\]  

We look for solutions to (6.39) of the form

\[
X_A(t) = c_1 e^{\lambda t}, \quad X_J(t) = c_2 e^{\lambda t}, \quad Y_A(t) = c_3 e^{\lambda t},
\]

\[
Y_J(t) = c_4 e^{\lambda t}, \quad Z_A(t) = c_5 e^{\lambda t}, \quad Z_J(t) = c_6 e^{\lambda t}.
\]

From the first two equations of (6.39) we have, with \( B = B(N_A) \) and \( B' = B'(N_A') \) for convenience

\[
\lambda c_1 = \left( B\beta(c_3 + c_6)\left(1 - \frac{e^{-\lambda r}}{\lambda} \right) - B'(c_1 + c_3 + c_5)e^{-\lambda r} \right)e^{-\mu r}
- \beta(c_3 + c_6)S_A' - \mu c_1,
\]

\[
\lambda c_2 = B'(c_1 + c_3 + c_5) + \left( B\beta(c_3 + c_6)\left(1 - \frac{e^{-\lambda r}}{\lambda} \right) - B'(c_1 + c_3 + c_5)e^{-\lambda r} \right)e^{-\mu r}
- \beta(c_3 + c_6)S_J' - \mu c_2.
\]  

(6.40)
In the absence of infection \( c_3, c_4, c_5 \) and \( c_6 = 0 \) and we can therefore write (6.40) as

\[
\begin{pmatrix}
B'e^{-(\lambda+\mu)\tau} - \lambda - \mu & 0 \\
B'(1 - e^{-(\lambda+\mu)\tau}) - \mu - \lambda
\end{pmatrix}
\begin{pmatrix}
c_1 \\
c_2
\end{pmatrix}
= \begin{pmatrix}
0 \\
0
\end{pmatrix}.
\]

For non-trivial solutions we must have

\[(\lambda + \mu)(B'e^{-(\lambda+\mu)\tau} - (\lambda + \mu)) = 0,
\]

with two negative real roots if \( B'e^{-\mu\tau} < \mu \).

**Remark 6.6.1** In a non-age model in the absence of infection we have \( \frac{dS}{dt} = B(S) - \mu S \) leading to a stable equilibrium if \( B' < \mu \).

The remaining equations obtained by substitution of the Ansatz into (6.39) are

\[
\lambda c_3 = \frac{B\beta(c_5 + c_6)e^{-\mu\tau}}{\lambda + \sigma} \left(1 - e^{-(\lambda + \sigma)\tau}\right) - (\mu + \sigma)c_3 + \beta(c_5 + c_6)S_A, \\
\lambda c_4 = -\frac{B\beta(c_5 + c_6)e^{-\mu\tau}}{\lambda + \sigma} \left(1 - e^{-(\lambda + \sigma)\tau}\right) - (\mu + \sigma)c_4 + \beta(c_5 + c_6)S_A, \\
\lambda c_5 = \frac{\beta\sigma Be^{-\mu\tau}}{\lambda + \sigma} \left(\frac{\lambda + \sigma}{(\mu + \sigma)(\lambda + \mu + 2\sigma)}e^{-(\lambda+\mu+2\sigma)\tau} + \frac{1}{\lambda + \mu + 2\sigma}\right)
\left(-\frac{e^{-(\lambda+\sigma)\tau}}{\mu + \sigma}\right) + \sigma c_3 - (\mu + d)c_5, \\
\lambda c_6 = -\frac{\beta\sigma Be^{-\mu\tau}}{\lambda + \sigma} \left(\frac{\lambda + \sigma}{(\mu + \sigma)(\lambda + \mu + 2\sigma)}e^{-(\lambda+\mu+2\sigma)\tau} + \frac{1}{\lambda + \mu + 2\sigma}\right)
\left(-\frac{e^{-(\lambda+\sigma)\tau}}{\mu + \sigma}\right) + \sigma c_4 - (\mu + d)c_6.
\]

The characteristic equation for this set of six equations for the condition that there are non-trivial solutions for \( c_1 \ldots c_6 \) is a transcendental equation (in \( e^{-\lambda\tau} \)) also containing powers of \( \lambda \) up to \( \lambda^{11} \). There is no prospect of any analytical progress.

We can, however, by integrating the expressions we have derived for \( s(a, t), e(a, t) \) and \( i(a, t) \) with respect to \( a \), between appropriate limits, obtain expressions for the total sizes of each of the six state variables as functions of \( t \), in the form of delay integral equations.

We have, changing variables with \( \psi = t - \alpha \) the following expressions for the juvenile state variables (the adult equivalents have same form, except that the first integral has limits from \( -\infty \) to \( t - \tau \) and must be split into two ranges,
\((-\infty, 0]\) and \([0, t-\tau]\).

\[
S_J(t) = \int_{t-\tau}^{t} B(N_A(\psi)) e^{-\mu(t-\psi)} e^{\int_{\psi}^{t} -B(\theta)d\theta} d\psi,
\]

\[
E_J(t) = \int_{t-\tau}^{t} \int_{0}^{t-\psi} \beta B(N_A(\psi)) I(\psi + \xi) e^{-\int_{\psi}^{\psi+\xi} B(\theta)d\theta} e^{-\mu(\xi+\psi) e^{\int_{\psi}^{\psi+\xi} -B(\xi+\psi) d\xi}} d\xi d\psi,
\]

\[
I_J(t) = \int_{t-\tau}^{t} \int_{0}^{t-\psi} \int_{0}^{\xi} \sigma B(N_A(\psi)) I(\psi + \phi)
\]
\[
\quad + e^{-\int_{\psi}^{\psi+\xi} B(\theta)d\theta} e^{-\mu(\xi+\psi) e^{\int_{\psi}^{\psi+\xi} -B(\xi+\psi) d\xi}} d\phi d\xi d\psi.
\]

We can now linearise the expression for \(I_J(t)\) about the IFE with the substitutions in (6.39) and ignoring quadratic and higher order terms we have

\[
Z_J(t) = \int_{t-\tau}^{t} \int_{0}^{t-\psi} \int_{0}^{\xi} \sigma B(N_A^*) Z(\psi + \phi) e^{-\mu(\xi+\psi) e^{\int_{\psi}^{\psi+\xi} -B(\xi+\psi) d\xi}} d\phi d\xi d\psi.
\]

We now consider a solution of the form \(Z_J(t) = a_1 e^{\lambda t},\quad Z_A(t) = a_2 e^{\lambda t}\), substitute into the above equation, evaluate the integrals and simplify, putting \(A = \sigma B(N_A^*)(a_1 + a_2)/a_1\), to obtain the following equation for \(\lambda\)

\[
\frac{A}{(\lambda + \sigma)(\lambda + d)(d - \sigma)} \left( \frac{(d - \sigma)(1 - e^{-\mu t})}{\mu} \right)
\]
\[
- \frac{(\lambda + d)(1 - e^{-(\lambda + \mu + d)t})}{\lambda + \mu + d} + \frac{(\lambda + \sigma)(1 - e^{-(\lambda + \mu + \sigma)t})}{\lambda + \mu + \lambda + d}
\] = 1.

Finally we note that we can collapse the age-structured SO model to a non-age-structured SEI model similar to that we have already studied in Chapter 4, (differing in the use of a general as opposed to a logistic fecundity function) and which we have shown to have a globally stable IFE. Since we have shown that all three state variables in the non-age-structured model are non-negative and can show this to be true for the six state variables of the age-structured model we may conjecture that the age-structured model will also have a globally stable IFE.
Chapter 7

Infection by both air-borne and soil transmission and direct contact

We now consider infection carried through bacteria in the air and through contact with faecal matter in the soil arising from infective animals as well as infection from direct contact with infective animals. The basic model equations and supporting assumptions are those used in system (2.1) (using a constant birth rate $\Lambda$ to allow us to focus on the epidemic dynamics) together with an equation modelling the production of air-borne and faecal bacteria and their exponential decay.

\[
\begin{align*}
\frac{dS_c}{dt} &= \Lambda_c - \mu_c S_c + \gamma_c I_c - \beta_c S_c I_c - \xi_c S_c I_b - \hat{\theta}_c A S_c, \\
\frac{dI_c}{dt} &= \beta_c S_c I_c + \xi_c S_c I_b + \hat{\theta}_c A S_c - \mu_c I_c - \gamma_c I_c, \\
\frac{dS_b}{dt} &= \Lambda_b - \mu_b S_b + \gamma_b I_b - \beta_b S_b I_b - \xi_b S_b I_c - \hat{\theta}_b A S_b, \\
\frac{dI_b}{dt} &= \beta_b S_b I_b + \xi_b S_b I_c + \hat{\theta}_b A S_b - \mu_b I_b - \gamma_b I_b, \\
\frac{dA}{dt} &= \hat{\lambda} I_c + \phi I_b - \mu A,
\end{align*}
\]

\[N = S_c + I_c, \quad N_b = S_b + I_b,\]

\[S_c(0) > 0, \quad I_c(0) \geq 0, \quad S_b(0) > 0, \quad I_b(0) \geq 0, \quad A(0) \geq 0.\]

The susceptible and infective class densities are $S$ and $I$ respectively, $A$ is the density of bacteria, the subscripts $c, b, A$ refer to cattle, badgers and bacteria respectively, $\mu$ is death rate, $\gamma$ recovery rate, $\beta$ intra-species infectivity rate and $\xi$ interspecies infectivity rate. $\hat{\theta}$ is the infectivity rate from the bacteria. $\hat{\lambda}$ is the rate of production of bacteria by infected cattle and $\phi$ is the rate of production of bacteria by infected badgers. We assume that at $t = 0$ an infective individual is introduced into the system.
We note that by solving the fifth equation of (7.1) we obtain, ignoring transients

\[ A(t) \approx \int_0^t e^{-\delta(t-s)} \left( \lambda I_c(s) + \phi I_b(s) \right) ds. \]

This demonstrates that the parameter \( \delta \) has a key role in determining the impact of past levels of infection on the current levels of bacteria in the environment. The smaller \( \delta \) the greater this “memory” property.

With an equivalent scheme to that used in (2.14), we non-dimensionalise the model with following additional components and rescale time by the average length of the infective period in cattle, \( \frac{1}{\mu_c + \gamma_c} \),

\[
\begin{align*}
v &= \frac{S_c}{N_c^*}, & w &= \frac{I_c}{N_c^*}, & x &= \frac{S_b}{N_b^*}, & y &= \frac{I_b}{N_b^*}, & a &= \frac{A}{\mu_c + \gamma_c}, \\
\lambda &= \frac{\hat{\lambda} A_c}{\mu_c}, & \phi &= \frac{\hat{\phi} A_b (\mu_c + \gamma_c)}{\mu_b (\mu_b + \gamma_b)}, & \delta &= \mu A (\mu_c + \gamma_c) \\
\theta_c &= \hat{\theta}_c, & \theta_b &= \frac{\hat{\theta}_b (\mu_c + \gamma_c)}{\mu_b + \gamma_b}.
\end{align*}
\]

Thus \( \lambda \) and \( \phi \) are measures of the quantity of bacteria produced by infective cattle and badgers respectively over the time that they remain infective. \( R_c, R_b, U_c \) and \( U_b \) are the basic reproductive ratios defined in (2.13) for the two species SIS system (2.1)

\[
\begin{align*}
\frac{dv}{dt} &= \alpha_c (1 - v) + w (1 - \alpha_c) - R_c vw - k U_c vy - \theta_c av, \\
\frac{dw}{dt} &= -w + R_c vw + k U_c vy + \theta_c av, \\
\frac{dx}{dt} &= k a_b (1 - x) + k y (1 - \alpha_b) - k R_b xy - U_b wx - k \theta_b ax, \\
\frac{dy}{dt} &= -k y + k R_b xy + U_b wx + k \theta_b ax, \\
\frac{da}{dt} &= \lambda w + k \phi y - \delta a, \\
v + w &= n_c, & x + y &= n_b,
\end{align*}
\]

where \( v(t), w(t) \) are densities of susceptible and infective cattle respectively, \( x(t), y(t) \) are densities of susceptible and infectious badgers and \( a(t) \) density of bacteria. We expect that \( a >> v, w, x, y \) so that \( \lambda, \phi << \delta \) and \( \theta_b, \theta_c << R_b, R_c \), while \( R_b, R_c, U_b, U_c \) and \( v, x, y, z \) are all of the same order of magnitude. We can verify that the positive cone, \( \mathbb{R}^5 \) is invariant for the state variables and that the state variables are bounded from above.

Finally, we will also make use of the reduction in dimension of the system from
five to three by assuming that $t$ is large enough that we have $n_c \approx 1, n_b \approx 1$ and can thus substitute $v \approx 1 - w$ and $x \approx 1 - y$ to give us
\[
\frac{dv}{dt} = -w + R_c w(1 - w) + kU_c y(1 - w) + \theta_c a(1 - w),
\]
\[
\frac{dy}{dt} = -ky + kR_b y(1 - y) + U_b w(1 - y) + k\theta_b a(1 - y), \tag{7.3}
\]
\[
\frac{da}{dt} = \lambda w + k\phi y - \delta a.
\]

7.1 Cattle in the absence of badgers

We first show the essential results for cattle alone, with the following abbreviated model
\[
\frac{dv}{dt} = \alpha_c (1 - v) + w(1 - \alpha_c) - R_c v w - \theta_c a v,
\]
\[
\frac{dw}{dt} = -w + R_c v w + \theta_c a v, \quad \frac{da}{dt} = \lambda w - \delta a, \tag{7.4}
\]
\[
v(0) = v_0 > 0, \quad w(0) = w_0 > 0, \quad a(0) = 0.
\]

Lemma 7.1.1 System (7.4) exhibits a transcritical bifurcation with bifurcation parameter $R_0 = R_c + \frac{\theta_c \lambda}{\delta}$.

As we would anticipate, there are only two equilibria for system (7.4), the infection-free equilibrium, $(1, 0, 0)$ and the endemic equilibrium;
\[
v^* = \frac{\delta}{R_c \delta + \theta_c \lambda}, \quad w^* = \frac{R_c \delta + \theta_c \lambda - \delta}{R_c \delta + \theta_c \lambda}, \quad a^* = \frac{\lambda(R_c \delta + \theta_c \lambda - \delta)}{\delta(R_c \delta + \theta_c \lambda)}.
\]

We find that the basic reproductive ratio for the system, the principal eigenvalue of the next generation matrix, is $R_0$, where
\[
R_0 = \frac{1}{2} \left( R_c + \sqrt{R_c^2 + \frac{4\theta_c \lambda}{\delta}} \right). \tag{7.5}
\]

The criterion for $w^* > 0$ is $R_0 > 1$, while the eigenvalues of the Jacobian of the linearisation of system (7.4) about the IFE are
\[
\psi_1 = -\alpha_c, \quad \psi_2 = \frac{1}{2}(R_c - 1 - \delta) + \frac{1}{2}\sqrt{(R_c - 1 + \delta)^2 + 4\theta_c \lambda},
\]
\[
\psi_3 = \frac{1}{2}(R_c - 1 - \delta) - \frac{1}{2}\sqrt{(R_c - 1 + \delta)^2 + 4\theta_c \lambda}.
\]

$\psi_1, \psi_2, \psi_3 < 0$ if $R_0 < 1$. For $R_0 > 1, \psi_2 > 0$ while the other eigenvalues remain negative. The solution in this case is dominated by terms of the form $e^{\psi_2 t}$ and the trajectory in phase space from the IFE to the endemic equilibrium is represented by the associated eigenvector $\left( \frac{\delta + \psi_2}{\lambda}, \frac{\delta + \psi_2}{\lambda}, 1 \right)$.

Finally the eigenvalues for the linearisation of system (7.4) about the endemic equilibrium are all negative provided that $R_0 > 1$. Thus the IFE of system (7.4) is linearly stable if $R_0 < 1$, while the endemic equilibrium is linearly stable if $R_0 > 1$. This proves the lemma.
7.2 Inter- and intra-species direct infection and transmission by airborne/soil bacteria

Whether we use the five dimensional system (7.2) or the three dimensional system (7.3) we cannot obtain meaningful explicit algebraic expressions for the endemic equilibrium, nor can we find the eigenvalues of the next generation matrix in a tractable form. We can establish that there are only two equilibria, the infection free equilibrium \((1, 0, 1, 0, 0)\) and the endemic equilibrium \((v^*, w^*, x^*, y^*, a^*)\).

**Conjecture 7.2.1** System (7.2) exhibits a transcritical bifurcation with parameter \(R_{\text{all}}\) defined in equation (7.6).

We find the determinant and the trace of the Jacobian, \(J\), of the linearisation of system (7.2) about the infection free equilibrium to be

\[
\det(J) = a_c a_b k^2 \left( k \theta_b (1 - R_c) + \lambda U_c \\
+ (1 - R_b)(\lambda \theta_c - \delta(1 - R_c)) + U_b (\delta U_c + \phi \theta_c) \right)
\]

\[
\text{trace}(J) = -a_c - k \alpha_b - \delta - (1 - R_c) - k(1 - R_b).
\]

The Routh-Hurwitz conditions for this five dimensional system require, inter alia, that \(\det(J) < 0\) and \(\text{trace}(J) < 0\) for the IFE to be linearly stable. We find that \(\det(J) = 0\) for

\[
\delta = \frac{k \lambda U_c \theta_b + \phi \theta_c U_b + \lambda \theta_c (1 - R_b) + k \phi \theta_b (1 - R_c)}{1 - R_c (1 - R_b) (1 - R_{bc})}
\]

and that

\[
\frac{d \det(J)}{d \delta} = -a_b a_c k^2 ((1 - R_c)(1 - R_b) - U_b U_c).
\]

Thus \(\det(J)\) is decreasing in \(\delta\) (provided that \(\max\{R_c, R_b\} < 1\) and \(0 < R_{bc} < 1\), the condition that there is no endemic disease where only direct infection is considered) and thus the criterion for \(\det(J) < 0\) is \(0 < R_{\text{all}} < 1\) where

\[
R_{\text{all}} = \frac{k \lambda U_c \theta_b + \phi \theta_c U_b + \lambda \theta_c (1 - R_b) + k \phi \theta_b (1 - R_c)}{\delta(1 - R_c)(1 - R_b)(1 - R_{bc})}.
\]

(7.6)

Here, \(R_{bc}\) is the basic reproductive ratio of the two animal system with direct transmission only and is defined in equation (2.11) in Chapter 2.

A sufficient but not necessary criterion for the second condition to be met is also that \(\max\{R_c, R_b\} < 1\) and \(0 < R_{bc} < 1\).

The formulation of \(R_{\text{all}}\) in equation (7.6) is rather unsatisfactory, since it is discontinuous at \(R_{bc} = 1\), \(R_b = 1\) and \(R_c = 1\) and \(R_{\text{all}}\) is not increasing in the individual basic reproductive ratios as we should expect. In practice we need to compute the spectral radius of the next generation matrix but are not able to do so analytically.
Nevertheless if we consider \( R_{all} \) we see that increasing \( \delta \) (e.g. by chemically degrading the bacteria) we reduce \( R_{all} \). We can express the equilibrium quantities of the infective classes and bacteria as

\[
w^* = H, \quad y^* = \frac{H (\delta (1 - R_c + R_b H) - \theta_c \lambda (1 - H))}{k (1 - H) (U_c \delta + \theta_c \phi)},
\]

\[
a^* = \frac{H (U_c \lambda (1 - H) + \phi (1 - R_c + R_b H))}{(1 - H) (U_c \delta + \theta_c \phi)}.
\]

Here, \( H \) is the appropriate root of a non-factorisable cubic equation. We find that \( H = 0 \) when \( R_{all} = 1 \).

### 7.3 Simplification of system (7.2)

An obvious approach to the study of system (7.2) is by setting some of the key parameters to zero. Thus, in particular, we make the assumption that only the cattle excrete bacteria in significant quantities (a suggestion which appeared widely in the media in 2006), i.e. \( \phi = 0 \), and examine some of the results.

#### 7.3.1 No cross-infection

In this model we let \( \phi = 0 \), \( U_c = 0 \) and \( U_b = 0 \) in system (7.2), so that the only inter-species transmission is from air-borne or soil bacteria. We consider an entirely susceptible population of badgers in a closed system with both susceptible and infected cattle at \( t = 0 \).

\[
\begin{align*}
\frac{dv}{dt} &= \alpha_c (1 - v) + w (1 - \alpha_c) - R_c vw - \theta_c av, \\
\frac{dw}{dt} &= -w + R_c vw + \theta_c av, \\
\frac{dx}{dt} &= k \alpha_b (1 - x) + k y (1 - \alpha_b) - k R_b xy - k \theta_b ax, \\
\frac{dy}{dt} &= -k y + k R_b xy + k \theta_b ax, \\
\frac{da}{dt} &= \lambda w - \delta a,
\end{align*}
\]

\( v + w = n_c, \quad x + y = n_b. \)

The initial conditions are \( v(0) = v_0 > 0, w(0) > 0, x(0) = x_0 > 0, y(0) = 0 \) and \( a(0) \geq 0 \). We use these initial conditions throughout all of the model systems in Section 7.3.

**Lemma 7.3.1** System (7.7) has three distinct equilibria and shows two transcritical bifurcations. The IFE is stable if \( R_1 < 1 \), where \( R_1 \) is defined in (7.9). A stable IFE exists in cattle and a stable endemic equilibrium exists in badgers if both \( R_b > 1 \) and \( R_c < 1 - \frac{\theta_c \lambda}{\delta} \). A stable endemic equilibrium exists in both species if both \( R_b > 1 \) and \( R_c > 1 - \frac{\theta_c \lambda}{\delta} \).
We prove this lemma in the remainder of this subsection.

**Remark 7.3.2** In the model represented by system (7.7), cattle can in principle cause the infection in badgers, without themselves suffering endemic disease. Badgers cannot influence the level of infection in cattle.

**Infection free equilibrium** \((1,0,1,0,0)\)

The eigenvalues of the Jacobian of the linearisation of system (7.7) around this equilibrium are

\[
\begin{align*}
\mu_1 &= -\alpha_c, \quad \mu_2 = -k\alpha_b, \quad \mu_3 = -k(1 - R_b), \\
\mu_4 &= \frac{1}{2}(R_c - 1 - \delta) + \frac{1}{2}\sqrt{(R_c - 1 - \delta)^2 + 4\theta_c\lambda + 4\delta(R_c - 1)}, \\
\mu_5 &= \frac{1}{2}(R_c - 1 - \delta) - \frac{1}{2}\sqrt{(R_c - 1 - \delta)^2 + 4\theta_c\lambda + 4\delta(R_c - 1)}.
\end{align*}
\]

(7.8)

Thus we conclude that the IFE is locally stable if both

\[
R_b < 1 \quad \text{and} \quad R_c < 1 - \frac{\theta_c\lambda}{\delta}.
\]

The relative orders of magnitude of the parameters ensure that \(\frac{\theta_c\lambda}{\delta} < 1\).

The IFE can become unstable as \(R_b\) increases through 1, while \(R_c\) remains less than \(\frac{\theta_c\lambda}{\delta}\), in which case the system will move to the endemic state in badgers and the IFE in cattle. The eigenvector associated with \(\mu_3\) is \((0,0,-1,1,0)\) a sign pattern we would expect. If, however, \(R_c + \frac{\theta_c\lambda}{\delta} > 1\), while \(R_b < 1\) then the IFE becomes unstable through the change of sign of \(\mu_4\) along the eigenvector \((X_1, X_2, X_3, X_4, X_5)\), where

\[
\begin{align*}
X_1 &= -\frac{(k(R_b - 1) - \mu_4)((1 - \alpha_c - R_c)(\delta + \mu_4) - \theta_c)}{k\theta_b(\alpha_c + \mu_4)}, \\
X_2 &= -\frac{(\delta + \mu_4)(k(R_b - 1) - \mu_4)}{k\theta_b}, \\
X_3 &= \frac{kR_b - k\alpha_b - \mu_4}{k\alpha_b + \mu_4}, \\
X_4 &= 1, \\
X_5 &= -\frac{1}{k\theta_b}(k(R_b - 1) - \mu_4)
\end{align*}
\]

which points to the endemic disease state in both species.

The eigenvalues of the next generation matrix are the set

\[
\left\{ R_b, \frac{R_c}{2} \left( 1 \pm \sqrt{1 + \frac{4\theta_c\lambda}{R_b^2\delta}} \right) \right\}
\]

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and the largest eigenvalue will be the basic reproductive ratio for system (7.7) which we define as $R_1$, where
\[
R_1 = \max \left\{ R_b, \frac{R_c}{2} \left(1 + \sqrt{1 + \frac{4\theta_c\lambda}{R_c^2\delta}}\right)\right\}. \tag{7.9}
\]

Now, $R_1 < 1$ is equivalent to both $R_b < 1$ and $R_c < 1 - \frac{\theta_c\lambda}{\delta}$, since
\[
\frac{R_c}{2} \left(1 + \sqrt{1 + \frac{4\theta_c\lambda}{R_c^2\delta}}\right) = \frac{R_c}{2} + \sqrt{\frac{R_c^2}{4} + \frac{\theta_c\lambda}{\delta}} < 1
\]
\[
\iff \sqrt{\frac{R_c^2}{4} + \frac{\theta_c\lambda}{\delta}} < 1 - \frac{R_c}{2}
\]
\[
\iff \frac{R_c^2}{4} + \frac{\theta_c\lambda}{\delta} < \left(1 - \frac{R_c}{2}\right)^2 \quad \text{(assuming that $R_c < 2$)}
\]
\[
\iff R_c < 1 - \frac{\theta_c\lambda}{\delta}.
\]

The critical value of $R_c$ is thus $1 - \frac{\theta_c\lambda}{\delta}$, reduced by $\frac{\theta_c\lambda}{\delta}$ compared to the value of the reproductive ratio where the only transmission of the disease is through direct infection. $\frac{\theta_c\lambda}{\delta}$ is the product of the quantity of bacteria produced by an individual cow, the susceptibility of cattle to infection from bacteria per unit time and the mean lifetime of the bacteria. The effect of long-lived bacteria is clear.

**Infection free equilibrium in cattle, endemic equilibrium in badgers**

This equilibrium is $\left(1, 0, \frac{1}{R_b}, 1 - \frac{1}{R_b}, 0\right)$. The eigenvalues of the Jacobian of the linearisation, expressed in terms of the eigenvalues for the infection free equilibrium, are
\[
\nu_1 = \mu_1, \quad \nu_2 = \mu_2, \quad \nu_3 = -\mu_3, \quad \nu_4 = \mu_4, \quad \nu_5 = \mu_5,
\]
where $\mu_i, i = 1 \ldots 5$ are defined in (7.8) and thus we conclude that this equilibrium is locally stable if both
\[
R_b > 1 \quad \text{and} \quad R_c < 1 - \frac{\theta_c\lambda}{\delta}.
\]

**Endemic equilibrium in both species**

The equilibrium values of the state variables are
\[
v^* = \frac{\delta}{R_c\delta + \theta_c\lambda}, \quad w^* = \frac{\theta_c\lambda + \delta(R_c - 1)}{R_c\delta + \theta_c\lambda}, \quad a^* = \frac{\lambda(\theta_c\lambda + \delta(R_c - 1))}{\delta(R_c\delta + \theta_c\lambda)},
\]
\[
x^* = H, \quad y^* = \frac{H\lambda\theta_b(\theta_c\lambda + \delta(R_c - 1))}{\delta(R_c\delta + \theta_c\lambda)(1 - HR_b)}.
\]

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where $H$ is a root of the quadratic $f(z) = 0$, where
\[ f(z) = \delta R_b (R_c \delta + \theta_c \lambda) z^2 - \left( R_c (1 + R_b) \delta^2 - \lambda (\theta_b - \theta_c) - \lambda (\theta_c R_c + \theta_b R_b) \delta + \theta_c \theta_b \lambda^2 \right) z + \delta (R_c \delta + \theta_c \lambda). \]

The values for $(v^*, w^*, a^*)$ are of course identical to those for cattle alone, system (7.4). We require $H > 0$; we find that this implies the constraint $R_c \geq 1 - \frac{\theta_c \lambda}{\delta}$.

We find, by numerical simulation that $\mu_i, i = 1 \ldots 5$ are negative for all positive values of $\theta_b$ and $R_b$. Thus a level of stable endemic disease exists in badgers no matter how low the values of the infectivity parameters, provided that neither is zero. While the local stability of this equilibrium is not obvious analytically, we note that the determinant of the Jacobian of the linearisation of system (7.7) about the endemic equilibrium is zero for $R_c = 1 - \frac{\theta_c \lambda}{\delta}$ and $a^* > 0$ for $R_c > 1 - \frac{\theta_c \lambda}{\delta}$.

Conjecture 7.3.3 The endemic equilibrium of system (7.7) is locally stable if
\[ \min \left\{ R_b, \frac{R_c}{2} \left( 1 + \sqrt{1 + \frac{4 \theta_c \lambda}{R_c^2 \delta^2}} \right) \right\} > 1. \]

Remark 7.3.4 If we construct a model where only badgers excrete bacteria and there is no cross-infection then we obtain the same results as above, with the position of badgers and cattle interchanged.

7.3.2 Air-borne/soil transmission the only infection route

The assumption in this case is that there is neither inter- nor intra-species transmission. The model equations are as follows, using the three-dimensional system of equation (7.3) and assuming that $t$ is large enough to allow us to do so,

\[
\begin{align*}
\frac{dw}{dt} &= -w + \theta_c a (1 - w), \\
\frac{dy}{dt} &= -ky + k \theta_b a (1 - y), \\
\frac{da}{dt} &= \lambda w + k \phi y - \delta a.
\end{align*}
\]

Conjecture 7.3.5 System (7.10) has two equilibria - the IFE and the endemic equilibrium. The system has a transcritical bifurcation with $\tilde{R}_0$ as the bifurcation parameter, where $\tilde{R}_0$ is defined in (7.11).

The infection free equilibrium

The determinant of the Jacobian of the linearisation about the infection free equilibrium is $k(\theta_b \phi + \theta_c \lambda) - \delta k$. This is negative when $\tilde{R}_0 < 1$, where
\[ \tilde{R}_0 = \frac{1}{\delta} (k \theta_b \phi + \theta_c \lambda). \]

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Since the trace of this Jacobian is always negative, this is a condition for stability of the IFE and this form of $R_0$ has an evident biological plausibility as the basic reproductive ratio, being the sum of the products of the rate of bacteria excreted by each species, multiplied by the infectivity of that species to bacteria and the mean lifetime of the bacteria.

$R_0 > 1$ also ensures the existence of each of the three components of the endemic equilibrium. Although we cannot prove analytically the sign of the determinant of the linearisation about the endemic equilibrium, for $R_0 = 1$, this determinant is zero.

The spectral radius of the next generation matrix of system (7.10) is $\sqrt{R_0}$, which suggests that the conjecture is true.

7.3.3 Air-borne/soil transmission and intra-species transmission in cattle only

This model describes a situation where there is no direct transmission between badgers nor any inter-species transmission. We use the three-dimensional model from system (7.3), assuming that $t$ is large enough to permit us to do so, with the assumption once again that only cattle excrete bacteria,

$$\frac{dw}{dt} = -w + R_c w (1-w) + \theta_c a (1-w),$$

$$\frac{dy}{dt} = -ky + k\theta_y a (1-y), \quad \frac{da}{dt} = \lambda w - \delta a.$$  \hspace{1cm} (7.12)

System (7.12) has two equilibria, the IFE and the endemic equilibrium.

Proposition 7.3.6 System (7.12) exhibits a transcritical bifurcation with parameter $\frac{R_c \delta}{\delta - \theta_c \lambda}$.

We prove this proposition as follows.

Infection-free equilibrium

The Jacobian of the linearisation around this equilibrium has the following set of eigenvalues

$$\left\{-k, \quad -\frac{1}{2}(1-R_c+\delta) \pm \frac{1}{2}\sqrt{(\delta+R_c-1)^2 + 4\theta_c \lambda}\right\}.$$  \hspace{1cm} (7.12)

The criterion that all of these eigenvalues are negative is $R_c < 1 - \frac{\theta_c \lambda}{\delta}$. The spectral radius of the next generation matrix is $R_4$, where

$$R_4 = \frac{1}{2} \left( R_c + \sqrt{R_c^2 + \frac{4\theta_c \lambda}{\delta}} \right)$$

and $R_4 < 1$ is equivalent to $R_c < 1 - \frac{\theta_c \lambda}{\delta}$.  \hspace{1cm} (7.12)
The endemic equilibrium

This equilibrium is at

\[ w^* = \frac{\theta_c \lambda + \delta (R_c - 1)}{R_c \delta + \theta_c \lambda}, \quad a^* = \frac{\lambda (\theta_c \lambda + \delta (R_c - 1))}{\delta (R_c \delta + \theta_c \lambda)}, \]
\[ y^* = \frac{\lambda \theta_b (\theta_c \lambda + \delta (R_c - 1))}{\lambda \theta_b (R_c \delta + \theta_c \lambda) + \lambda \delta (\theta_c - \theta_b) + \delta^2 R_c}. \]

We cannot prove the linear stability of this equilibrium with the Routh Hurwitz criteria analytically since the algebra is intractable, although numerical simulation suggests that it is. However we have

\[ \det(J) = \frac{k R_c (\delta (1 - R_c) - \theta_c \lambda)}{(R_c \delta + \theta_c \lambda)^2} \]

which is zero for \( R_c = 1 - \frac{\theta_c \lambda}{\delta} \). It is decreasing in \( R_c \) for \( R_c > 0 \) and negative for \( R_c > 1 - \frac{\theta_c \lambda}{\delta} \), which is the condition for the existence of the endemic state.

If \( R_c > 1 - \frac{\theta_c \lambda}{\delta} \), then \( \text{trace}(J) < 0 \), while \( \frac{d}{dR_c} \text{trace}(J) < 0 \) for all \( R_c > 0 \). We can thus conclude that the equilibrium is unstable for \( R_c > 1 - \frac{\theta_c \lambda}{\delta} \). \( \square \)

7.3.4 Air-borne/soil transmission and cross infection of cattle by badgers only

We consider the situation where both species can acquire the infection from bacteria and that in addition badgers can directly infect cattle. We assume that \( t \) is large enough to permit us to use the three dimensional model and we assume once again that only cattle excrete bacteria.

The model equations are

\[ \frac{dw}{dt} = -w + k U_c y (1 - w) + \theta_c a (1 - w), \quad \frac{dy}{dt} = -ky + k \theta_b a (1 - y), \quad \frac{da}{dt} = \lambda w - \delta a. \hspace{1cm} (7.13) \]

System (7.13) has two equilibria, the IFE and the endemic equilibrium.

**Conjecture 7.3.7** System (7.13) has a transcritical bifurcation with bifurcation parameter \( \frac{k \lambda U_c \theta_b}{\delta - \theta_c \lambda} \).

The infection free equilibrium

The characteristic equation of the Jacobian of the linearisation around this equilibrium is:

\[ \mu^3 + (1 + k + \delta) \mu^2 + (k + \delta + k \delta - \theta_c \lambda) \mu + k \delta - \theta_c \lambda k - \lambda k^2 U_c \theta_b = 0. \hspace{1cm} (7.14) \]
We examine the linear stability of the IFE by verifying the conditions under which the Routh-Hurwitz criteria apply to equation (7.14), which we express as \( a_1 \mu^3 + a_1 \mu^2 + \mu + a_3 = 0 \), namely:

\( a_1 > 0 \implies 1 + \delta + k > 0 \) which is always true,

\( a_3 > 0 \implies k \delta - \theta_c \lambda k - \lambda k^2 U_c \theta_b > 0 \) which is true if \( U_c \frac{\delta - \theta_c \lambda}{k \lambda \theta_b} \),

\( a_1 a_2 - a_3 > 0 \implies (1 + \delta) \left( (1 + k)(k + \delta) - \theta_c \lambda \right) + \lambda k^2 U_c \theta_b > 0 \)

which will certainly be true if \( \delta > \theta_c \lambda \), which we take as true from the relative magnitude of the parameters. Thus if \( U_c \frac{\delta - \theta_c \lambda}{k \lambda \theta_b} \) then the IFE is linearly stable.

Computing the spectral radius of the next generation matrix for this model is not straightforward. We are faced with a characteristic polynomial \( g(z) \) for the matrix of

\[
g(z) = z^3 - \lambda \mu z - \frac{\lambda U_c k \theta_b}{\delta} = 0. \quad (7.15)
\]

By Descartes' rule of signs we can see that there will be only one positive real root for equation (7.15). If we differentiate and solve \( g'(z) = 0 \) for extrema, we find the larger extremum at \( z = 2' \) and verify that this is a minimum, since \( g'' \left( \frac{\lambda \mu}{3 \delta} \right) > 0 \). The maximum occurs at negative \( z \). Since we already know that \( \delta >> \theta_c \lambda \) it follows that this minimum occurs at \( z << \frac{1}{3} \), while we need the condition that the spectral radius is greater than or less than one. We thus conclude that the real positive root is the basic reproductive ratio for the system, \( R_5 \).

We can solve (7.15) to give us the following expression for \( R_5 \) (to make this expression useful we will need to approximate it), which does at least allow us to look at the explicit influence of each of the parameters.

\[
R_5 = \psi + \chi,
\]

where

\[
\psi = \left( \frac{\lambda U_c k \theta_b}{2 \delta} + \sqrt{- \left( \frac{\lambda \theta_c}{3 \delta} \right)^3 + \frac{\lambda^2 U_c^2 k^2 \theta_b^2}{4 \delta^2}} \right)^\frac{1}{2},
\]

\[
\chi = \left( \frac{\lambda U_c k \theta_b}{2 \delta} - \sqrt{- \left( \frac{\lambda \theta_c}{3 \delta} \right)^3 + \frac{\lambda^2 U_c^2 k^2 \theta_b^2}{4 \delta^2}} \right)^\frac{1}{2}.
\]

We find that, as we expect, when \( R_5 = 1 \) we have \( U_c = \frac{\delta - \theta_c \lambda}{k \lambda \theta_b} \).
Endemic equilibrium

The endemic equilibrium is at

\[ w^* = \frac{\delta H}{\lambda \theta_b (1 - H)}, \quad y = H, \quad a^* = \frac{H}{\theta_b (1 - H)}, \] (7.16)

where \( H \) is a solution of the quadratic

\[ k U_c \theta_b (\lambda \theta_b + \delta) H^2 + \left( (\theta_b - \theta_c) - \theta_c \theta_b \lambda - k U_c \theta_b (\delta + 2 \lambda \theta_b) \right) H + \theta_b (\theta_c \lambda + k U_c \lambda \theta_b - \delta) = 0. \]

There is no simple form for \( H \), but \( H = 0 \) when \( U_c = \frac{\delta - \theta_c \lambda}{k \lambda \theta_b} \). There is no simple characteristic polynomial for the Jacobian of the linearisation about the endemic equilibrium, but we note that the determinant of the linearisation is zero when \( U_c = \frac{\delta - \theta_c \lambda}{k \lambda \theta_b} \).

7.3.5 Cattle infected from badgers directly, badgers from airborne/soil transmission

In this model the presence of badgers induces an endemic disease equilibrium in cattle. The model equations are

\[
\frac{dw}{dt} = -w + w U_c (1 - w), \quad \frac{dy}{dt} = -k y + k \theta_b a (1 - y), \quad \frac{da}{dt} = \lambda w - \delta a. \tag{7.17}
\]

Conjecture 7.3.8 System (7.17) has two equilibria, the IFE and the endemic equilibrium and shows a transcritical bifurcation with parameter \( \frac{U_c k \lambda \theta_b}{\delta} \).

The infection free equilibrium

The characteristic polynomial of the Jacobian of the linearisation of system (3.89) is

\[ z^3 + (1 + k + \delta) z^2 + (k + \delta + k \delta) z + k \delta - \lambda k^2 U_c \theta_b = 0. \] (7.18)

Applying the Routh Hurwitz criteria to (7.18) in the same manner as in section 7.3.4, we verify that each of the following is true and thus the IFE is stable provided that \( \frac{U_c k \lambda \theta_b}{\delta} < 1 \).

\[ a_1 > 0 \implies 1 + k + \delta > 0, \]

\[ a_3 > 0 \implies k \delta - \lambda k^2 U_c \theta_b > 0 \text{ if } U_c < \frac{\delta}{k \lambda \theta_b}, \]

\[ a_1 a_2 - a_3 > 0 \implies (1 + k + \delta)(k + \delta + k \delta) - k \delta + \lambda k^2 U_c \theta_b > 0. \]

The spectral radius of the next generation matrix is \( R_\delta \), where

\[ R_\delta = \left( \frac{\lambda k U_c \theta_b}{\delta} \right)^{\frac{1}{2}}. \] (7.19)
Endemic equilibrium

The equilibrium is at

\[ w^* = \frac{\lambda U_c k \theta_b - \delta}{\lambda \theta_b (k U_c + 1)}, \quad y^* = \frac{\lambda U_c k \theta_b - \delta}{U_c k (\lambda \theta_b + \delta)}, \quad a^* = \frac{\lambda U_c k \theta_b - \delta}{\delta \theta_b (k U_c + 1)}. \]

The characteristic polynomial is extremely unwieldy. However we find that all the terms in the expressions for the coefficient of the quadratic term are positive and the same is true for all the terms of the expansion of the product of the coefficients of the quadratic term and the linear term minus the constant term. The constant term itself is positive provided that \( U_c > \frac{\delta}{k \lambda \theta_b} \). (We establish this by showing that the constant is zero for \( U_c = \frac{\delta}{k \lambda \theta_b} \) and its derivative with respect to \( U_c \) is \( k^2 \lambda \theta_b > 0 \).)

7.4 Spatially heterogeneous model

The essential idea is that we have an initial state with an infection free equilibrium and diffusion of badgers through an infinite one dimensional domain (with co-ordinate \( \eta \)) with static cattle and bacteria both static (i.e. in the soil) and advecting (e.g through prevailing wind). An infective is then introduced at \( t = 0 \). This gives us the following model, where the diffusion rate of badgers is \( D \), the advection speed of the bacteria is \( \xi \) and all the other parameters and variables are as in (7.1);

\[
\frac{\partial S_c}{\partial t} = \Lambda_c - \mu_c S_c(\eta, t) + \gamma_c I_c(\eta, t) - \beta_c S_c(\eta, t) I_c(\eta, t)
- \xi_c S_c(\eta, t) I_b(\eta, t) - \delta_c A(\eta, t) S_c(\eta, t),
\]

\[
\frac{\partial I_c}{\partial t} = \beta_c S_c(\eta, t) I_c(\eta, t) + \xi_c S_c(\eta, t) I_b(\eta, t) + \delta_c A(\eta, t) S_c(\eta, t)
- (\mu_c + \gamma_c) I_c(\eta, t),
\]

\[
\frac{\partial S_b}{\partial t} = D \frac{\partial^2 S_b}{\partial \eta^2} + \Lambda_b - \mu_b S_b(\eta, t) + \gamma_b I_b(\eta, t) - \beta_b S_b(\eta, t) I_b(\eta, t)
- \xi_b S_b(\eta, t) I_c(\eta, t) - \delta_b A(\eta, t) S_b(\eta, t),
\]

\[
\frac{\partial I_b}{\partial t} = D \frac{\partial^2 I_b}{\partial \eta^2} + \beta_b S_b(\eta, t) I_b(\eta, t) + \xi_b S_b(\eta, t) I_c(\eta, t)
+ \delta_b A(\eta, t) S_b(\eta, t) - (\mu_b + \gamma_b) I_b(\eta, t),
\]

\[
\frac{\partial A}{\partial t} = \lambda I_c(\eta, t) + \phi I_b(\eta, t) + \xi \frac{\partial A}{\partial \eta} - \mu A(\eta, t).
\]

We assume that at the front of a travelling wave there is a constant number of badgers and that the population of cattle is maintained constant. This
allows us to reduce the dimension of the system from five to three. We non-
dimensionalise with the same scheme as in (7.2) and with \( D = \frac{\partial \alpha_0}{\mu_b (\mu_c + \gamma_c)} \), and 
\[
\xi = \frac{\xi}{\mu_c + \gamma_c}.
\]

\[
\frac{\partial w}{\partial t} = -w + R_c w(1 - w) + kU_c y(1 - w) + \theta_c a(1 - w),
\]

\[
\frac{\partial y}{\partial t} = D \frac{\partial^2 y}{\partial \eta^2} - ky + kR_b y(1 - y) + U_b w(1 - y) + k\theta_b a(1 - y),
\]

(7.21)

\[
\frac{\partial a}{\partial t} = \lambda w + k\phi y + \xi \frac{\partial a}{\partial \eta} - \delta a.
\]

Now we transform the p.d.e.s into o.d.e.s with the substitution \( z = \eta + ct \)

\[
\frac{dw}{dz} = -w + R_c w(1 - w) + kU_c y(1 - w) + \theta_c a(1 - w),
\]

\[
\frac{dy}{dz} = D \frac{d^2 y}{dz^2} - ky + kR_b y(1 - y) + U_b w(1 - y) + k\theta_b a(1 - y),
\]

\[
(c - \xi) \frac{da}{dz} = \lambda w + k\phi y - \delta a.
\]

The boundary conditions are \( w(-\infty) = 0, y(-\infty) = 0, a(-\infty) = 0, w(\infty) = w^*, y(\infty) = y^*, a(\infty) = a^* \), where the starred quantities are the endemic equi-
librium. We use these boundary conditions throughout this section.

Removing the second order derivative we have the four equation system;

\[
\frac{dw}{dz} = \frac{1}{c} \left( -w + R_c w(1 - w) + kU_c y(1 - w) + \theta_c a(1 - w) \right),
\]

\[
\frac{dy}{dz} = p, \quad \frac{dp}{dz} = \frac{1}{D} \left( cp + ky - kR_b y(1 - y) - U_b w(1 - y) - k\theta_b a(1 - y) \right),
\]

\[
\frac{da}{dz} = \frac{1}{c - \xi} \left( \lambda w + k\phi y - \delta a \right).
\]

We investigate a number of models, analogous to the static models studied in
the previous section. We are interested in a travelling wave connecting the
infection free equilibrium with the endemic equilibrium.

**Proposition 7.4.1** Travelling wave solutions connecting the IFE and the en-
demic equilibrium are feasible for systems (7.25) and (7.26). Such solutions
are only possible in system (7.22) if \( R_0 \) and \( c \) are sufficiently small and \( R_c, \lambda \)
and \( \theta_c \) are sufficiently large.

We prove this proposition in the remainder of this section.
7.4.1 No cross-infection

We assume that $U_b = 0, U_c = 0$ and $\phi = 0$. The model system, in the form of o.d.e.s, obtained as described in the previous section is thus

$$\frac{dw}{dz} = \frac{1}{c} \left(- w + R_c w (1 - w) + \theta_c a (1 - w)\right),$$

$$\frac{dy}{dz} = p, \quad \frac{dp}{dz} = \frac{1}{D} \left(cp + ky - kR_b y (1 - y) - k\theta_y a (1 - y)\right),$$

$$\frac{da}{dz} = \frac{1}{c - \xi} \left(\lambda w - \delta a\right).$$

(7.22)

We have already shown that there are three equilibria for the spatially homogeneous version of system (7.22).

We assume that $c < \xi$. The necessity for this assumption can be seen by considering the fourth equation in (7.22) with $w = 0$. We thus have

$$\frac{da}{dz} \bigg|_{w=0} = \frac{-\delta a}{c - \xi}, \quad a(z) = a(0)e^{-\frac{\xi}{c-\xi}z},$$

while the biological reality must be that with no production of bacteria, $\lim_{z \to \infty} a(z) = 0$, which requires that $c < \xi$. From a biological perspective, if badgers can only be infected from bacteria, the rate at which they diffuse must be less than the rate of advection of the bacteria else the infected population will go to zero.

The infection free equilibrium

Linearising (7.22) about the IFE, $(0, 0, 0, 0)$, we compute the characteristic equation of the Jacobian to be $f(s) = 0$, where $f(s)$ is given by,

$$f(s) = (Ds^2 - cs + k(R_b - 1))
\left((c^2 - c\xi)s^2 + ((R_c - 1)(\xi - c) + c\delta)s - \lambda \theta_c + \delta(1 - R_c)\right).$$

(7.23)

The evolution of the linearised system from the IFE will be determined by the roots of $f(s) = 0$, which are the eigenvalues, and their associated eigenvectors. For biological reasonableness, since $w, y$ and $a$ are non-negative, we cannot allow an oscillatory solution so these roots must be real. We thus need to find the conditions on $c$ that the discriminant of the two quadratic terms in $f(s)$ are positive.

From the first term in $f(s)$ we have the condition as $|c| \geq |c_1|$ where

$$c_1 = 2\sqrt{Dk(R_b - 1)},$$

provided that $R_b > 1$, the condition for endemic disease in badgers alone. If $R_b < 1$ then the discriminant of the first term is always positive.

If we call the second term in $f(s)$ $h(s)$, recalling that we must have $c < \xi$
and if we assume \( R < 1 - \frac{\delta^2}{\theta} \), then the graph of \( h(s) \) is an inverted parabola, \( h(0) > 0 \) and there is always a positive real root for \( h(s) = 0 \), thus there is no constraint on \( c \) arising from \( h(s) \).

If, on the other hand \( R > 1 - \frac{\delta^2}{\theta} \) then real roots will only exist for \( h(s) = 0 \) provided that \( c > c_2 \) or \( c < c_3 \) where

\[
\begin{align*}
c_2 &= \frac{\xi \left( (R_c - 1)^2 + \delta(R_c - 1) + 2\delta \theta + 2\sqrt{\lambda \theta \delta (R_c - 1)} \right)}{4\lambda \theta_c + (R_c + \delta - 1)^2}, \\
c_3 &= \frac{\xi \left( (R_c - 1)^2 + \delta(R_c - 1) + 2\delta \theta - 2\sqrt{\lambda \theta \delta (R_c - 1)} \right)}{4\lambda \theta_c + (R_c + \delta - 1)^2}.
\end{align*}
\]

Simulation suggests that both \( c_2 \) and \( c_3 \) are positive.

Thus the minimum wavespeed for a plausible travelling wave solution if \( R < 1 \) is \( c_{\text{min}} = c_1 \) provided that \( c_1 > \xi \). If \( R > 1 \) then \( c_{\text{min}} = \max\{c_1, c_2\} \) is a sufficient, but not necessary condition for a plausible travelling wave solution. If \( c_3 > c > c_1 \) a travelling wave solution is also plausible provided once more that \( c > \xi \).

The eigenvalues of the Jacobian are as follows:

\[
\begin{align*}
\nu_1 &= \frac{1}{2D} \left( c + c^2 - 4Dk(R_c - 1) \right), \\
\nu_2 &= \frac{1}{2D} \left( c - c^2 - 4Dk(R_c - 1) \right), \\
\nu_3 &= -\frac{c\delta + (1 - R_c)(\xi - c) + H}{2c(c - \xi)}, \\
\nu_4 &= -\frac{c\delta + (1 - R_c)(\xi - c) - H}{2c(c - \xi)}.
\end{align*}
\]

Here

\[
H := \sqrt{\left( (1 - R_c)(\xi - c) + c\delta \right)^2 - 4c(c - \xi)(\delta(1 - R_c) - \lambda \theta_c)}. \tag{7.24}
\]

Now, \( \text{Re}(\nu_1) > 0 \) and \( \text{Re}(\nu_2) > 0 \) for \( \nu_1, \nu_2 \in \mathbb{C} \), while if \( \nu_1, \nu_2 \in \mathbb{R} \) then \( \nu_1, \nu_2 > 0 \). There are thus always at least two increasing linearised solutions and thus a positive dominant eigenvalue.

For a travelling wave from the IFE to one of the other equilibria to be feasible we require a particular sign pattern for the eigenvector associated with the dominant eigenvalue, which we label \( (e_1, e_2, e_3, e_4)^T \). The four components of the eigenvectors relate to \( w, y, \alpha, \) and \( \delta \) respectively. Necessarily \( w, y, \alpha, \delta \geq 0 \) so \( \frac{dw}{dz}, \frac{dy}{dz}, \frac{d\alpha}{dz}, \frac{d\delta}{dz} \geq 0 \). We thus need all the components of this eigenvector to be non-negative.

The dominant eigenvalue

Since we have defined our moving co-ordinate \( z = x + ct \), with \( c > 0 \), we are describing a wave which moves from right to left as \( z \) increases. The dominant eigenvalue will thus be the smallest positive eigenvalue. Numerical simulation of a wide range of parameter values suggests that, for real values either \( \nu_1 > \nu_3 > \nu_2 > 0 \) or \( \nu_1 > \nu_2 > \nu_3 > 0 \).
The key eigenvector

If \( \nu_2 \) is the dominant eigenvalue, the associated eigenvector is

\[
\begin{pmatrix}
0, 1, \frac{c - \sqrt{c^2 - 4Dk(1 - R_b)}}{2D}, 0
\end{pmatrix}^T
\]

which has sign pattern \((0, +, +, 0)\) which is acceptable for a travelling wave solution. If however the dominant eigenvalue is \( \nu_3 = (e_1, e_2, e_3, e_4)^T \), we have

\[
e_1 = \frac{1}{4\theta_b k \lambda c^3(c - \xi)^2(c(R_c - 1 + \delta) - \xi(R_c - 1) + H)}
\]

\[
(2k(R_b - 1) + 1 - R_c + \delta)c^4 - \left(\xi(4k(R_b - 1) + 2(R_c - 1) + \delta) + H\right)c^3
\]

\[
+ \left((1 + 2k(R_b - 1) - R_c)\xi^2 + \xi H + (D(R_c - 1)^2 + 2\lambda\theta_c + \delta^2)\right)c^2
\]

\[
- \left(2D\xi((R_c - 1)^2 + \lambda\theta_c) + DH(R_c - 1 - \delta)\right)c,
\]

\[
e_2 = 1, \quad e_3 = \nu_3, \quad e_4 = \frac{2c\lambda e_1}{c(R_c - 1 + \delta) - \xi(R_c - 1) + H}.
\]

where \( H \) has been defined in (7.24).

We cannot make any progress analytically to establish the sign pattern of \( e_1 \) and \( e_4 \). Numerical simulation suggests that no combination of reasonable parameters can give either four non-negative components or four non-positive components. The conclusion is that there does not appear to be a suitable eigenvector sign pattern such that a travelling wave is possible if \( \nu_3 \) is the dominant eigenvalue.

Determining the dominant eigenvalue

It is thus a matter of importance to establish the conditions in which \( \nu_2 < \nu_3 \) if we want to understand when we may expect a travelling wave solution. As \( R_b \) increases with constant \( c \), \( \nu_2 \) increases and then becomes complex with real part \( \frac{\nu_2}{2} \), when \( R_b > 1 \) whereas \( \nu_3 \) is independent of \( R_b \). Since we cannot allow a complex eigenvector, \( c_1 \) must increase once \( R_b > 1 \) since \( c_1 = 2\sqrt{Dk(R_b - 1)} \).

There may thus be a value of \( R_b \) above which \( \nu_2 > \nu_3 \) and no travelling wave is possible. Simulation suggests that this is a relatively small number.

Differentiation shows that \( \nu_2 \) is decreasing in \( c \) and simulation shows that \( \nu_2 \) is also decreasing in \( c \), there is a value of \( c \) above which \( \nu_2 > \nu_3 \) and no travelling wave is possible. Simulation also suggests that \( \nu_2 \) is increasing in \( R_c, \lambda \) and \( \theta_c \) and these parameters do not appear in \( \nu_2 \) so as \( R_c, \lambda \) and \( \theta_c \) increase, at some point \( \nu_2 < \nu_3 \) and a travelling wave is feasible. \( \theta_b \) has no effect on the relative size of the eigenvalues.
We cannot explain this result from a biological perspective at this stage.

7.4.2 Air-borne/soil transmission the only infection route

The first order o.d.e. model system, derived in the same manner as in the preceding section is as follows, once more we assume that only cattle excrete bacteria;

\[
\frac{dw}{dz} = \frac{1}{c} (-w + \theta_c a(1-w)),
\]

\[
\frac{dy}{dz} = p, \quad \frac{dp}{dz} = \frac{1}{D} (cp + ky - k\theta_c a(1-y)), \quad (7.25)
\]

\[
\frac{da}{dz} = \frac{1}{c-\xi} (\lambda w - \delta a).
\]

For system (7.25) there are only two equilibria - the IFE and the endemic equilibrium.

The infection free equilibrium

The characteristic polynomial of the Jacobian of system (7.25) linearised about the IFE is \( h(s) = 0 \), where

\[
h(s) = (Ds^2 - cs - k) \left( (c^2 - c\xi)s^2 + (c(\delta + 1) - \xi)s + \delta - \theta_c\lambda \right).
\]

The discriminant of the first term of \( h(s) \) is always positive as is the discriminant of the second term since we have already established that we must have \( c < \xi \) and \( \delta > \theta_c\lambda \). There is thus no constraint in this case on \( c \) for a travelling wave to be plausible.

The eigenvalues of the Jacobian are

\[
\nu_1 = \frac{c + \sqrt{c^2 + 4Dk}}{2D}, \quad \nu_2 = \frac{c - \sqrt{c^2 + 4Dk}}{2D},
\]

\[
\nu_3 = \frac{c(1 + \delta) - \xi - \sqrt{(c(1 + \delta) + \xi)^2 + 4c\theta_c\lambda(c - \xi)}}{2c(c - \xi)},
\]

\[
\nu_4 = \frac{c(1 + \delta) - \xi + \sqrt{(c(1 + \delta) + \xi)^2 + 4c\theta_c\lambda(c - \xi)}}{2c(c - \xi)},
\]

and we have \( \nu_1 > 0, \; \nu_2 < 0, \; \nu_3 > 0 \) and \( \nu_4 < 0 \).

The dominant eigenvalue

Differentiation shows that \( \nu_1 \) is increasing in \( c \) and simulation suggests that \( \nu_3 \) is also increasing in \( c \). \( \nu_3 \) is increasing in \( \lambda \) and \( \theta_c \) so that for larger values of these parameters \( \nu_1 < \nu_3 \).
The key eigenvector

The eigenvector associated with \( v_1 \) is \( (0, 1, \frac{c + \sqrt{c^2 + 4DK}}{2D}, 0) \) so that a travelling wave would be feasible. If \( v_3 \) is the dominant eigenvalue the associated eigenvector is \( (b_1, b_2, b_3, b_4) \) where

\[
b_1 = \frac{\theta c b_4}{1 + v_3}, \quad b_2 = 1, \quad b_3 = v_3, \quad b_4 = \frac{D}{k \theta b} \left( k + \frac{c v_3}{2D} - v_3^2 \right)
\]

Simulation suggests that, save for unrealistic values of \( \theta c \) and \( \lambda \), we have \( b_1 > 0 \) and \( b_4 > 0 \), while \( b_3 > 0 \) provided that \( \theta c \lambda > \delta \), the condition for the existence of the endemic equilibrium.

We thus conclude that a travelling wave solution is feasible for system (7.25).

7.4.3 Air-borne/soil transmission and intra-species transmission in cattle only

The first order o.d.e. model system, derived as in the same way before is as follows:

\[
\begin{align*}
\frac{dw}{dz} &= \frac{1}{c} (-w + R_c w (1 - w) + \theta \epsilon a (1 - w)), \\
\frac{dy}{dz} &= p, \\
\frac{dp}{dz} &= \frac{1}{D} (cp + ky - k \theta \epsilon a (1 - y)), \\
\frac{da}{dz} &= \frac{1}{c - \xi} (\lambda w - \delta a).
\end{align*}
\]

Once more we assume that only cattle excrete bacteria.

The Jacobian of system (7.26) linearised about the IFE has the characteristic equation \( g(s) = 0 \) where

\[
g(s) = (Ds^2 - cs - k) \left( (c^2 - c \xi) s^2 + (c \delta - c + \xi + R_c (c - \xi)) + R_c \delta - \lambda \theta c - \delta \right).
\]

The discriminants of both the first and the second terms in \( g(s) \) are positive and there are thus no conditions on \( c \) for the existence of real eigenvalues.

The eigenvalues of the Jacobian are

\[
\begin{align*}
\mu_1 &= \frac{c + \sqrt{c^2 + 4DK}}{2D}, \\
\mu_2 &= \frac{c - \sqrt{c^2 + 4DK}}{2D}, \\
\mu_3 &= -c \delta - (c - \xi) (1 - R_c) + \sqrt{Q}, \\
\mu_4 &= -c \delta - (c - \xi) (1 - R_c) - \sqrt{Q},
\end{align*}
\]

where we have defined

\[
Q = \left( (c - \xi) (1 - R_c) - \delta c \right)^2 + 4c \theta \epsilon \lambda (c - \xi).
\]

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The dominant eigenvalue

We have $\mu_1 > 0$, $\mu_2 < 0$, $\mu_3 > 0$ (for $\theta_c \lambda > \delta(R_c - 1)$) and $\mu_4 < 0$. The dominant eigenvalue will thus be $\mu_1$ or $\mu_3$. Simulation suggests that $\mu_3$ is increasing in $R_c$, $\theta_c$ and $\lambda$ while $\mu_1$ is independent of these parameters. Hence as $R_c$, $\theta_c$ and $\lambda$ increase there will be a point such that $\mu_3 > \mu_1$. Provided that $R_c > 1$, simulation suggests that $\mu_3$ is decreasing, while $\mu_1$ is increasing in $c$.

The sign pattern of the key eigenvector

The eigenvector associated with $\mu_1$ is

$$
\left(0, 1, \frac{c + \sqrt{c^2 + 4Dk}}{2D}, 0\right)^T,
$$

which has sign pattern $(0, +, +, 0)$ and is thus acceptable for a travelling wave solution originating at the IFE.

The eigenvector associated with $\mu_3$, we designate as $(\alpha_1, \alpha_2, \alpha_3, \alpha_4)$ where

$$
\alpha_1 = \left(\frac{\delta + \Phi(c - \xi)}{k\theta_c \lambda c(c - \xi)}\right) \left(k\lambda c(c - \xi) - D(\theta_c \lambda - \delta(R_c - 1)) + \Phi(c^2(c - \xi) - D\xi(1 - R_c) + Dc(1 + \delta - R_c))\right),
$$

$$
\alpha_2 = 1, \quad \alpha_3 = -\Phi,
$$

$$
\alpha_4 = \frac{1}{k\theta_c \lambda c(c - \xi)} \left(kc(c - \xi) - D(\theta_c \lambda - \delta(R_c - 1)) + \Phi(c^2(c - \xi) - D\xi(1 - R_c) + Dc(1 + \delta - R_c))\right),
$$

where

$$
\Phi = \frac{c\delta - (R_c - 1)(c - \xi) - \sqrt{Z}}{c(c - \xi)},
$$

$$
Z = \sqrt{(\delta(R_c - 1)(c - \xi) - \delta c)^2 + 4\theta_c \lambda (c - \xi)}.
$$

We find that $\alpha_3 < 0$ for $\theta_c \lambda > \delta(R_c - 1)$ thus suggesting that a travelling wave solution is not plausible if $\mu_3 > \mu_1$ and this condition is satisfied.

It is not possible to make any significant progress with the spatially heterogeneous system corresponding to cattle infected from badgers directly, or to badgers infected from from airborne/soil transmission only as the algebra is intractable.
Conclusions

Introduction of infection transmitted by bacteria in addition to that resulting from direct contact with an infective animal results in models that are substantially more complicated to analyse than those in Chapter 2. The models do throw some light on how tuberculosis might be transmitted if the suggestions of the “pro-badger” lobby are correct, i.e. badgers are infected by the bacteria excreted by infective cattle.
Chapter 8

Discussion, conclusions and future work

Spatially homogeneous SIS models

In a two or more species model, where each species can transmit infection directly to other species as well as within its own species we can establish a basic reproductive ratio for the system, $R_0$. This parameter is the principal eigenvalue of the next generation matrix for the total system. However this expression does not have an obvious biological interpretation. The criterion for linear stability of the endemic equilibrium gives a different form of basic reproductive ratio which is more biologically intuitive, but is only meaningful as a bifurcation parameter.

We are able to prove the conditions for global stability of the endemic disease equilibrium in the two species model. Importantly, the presence of mutually infective species leads to an endemic disease equilibrium with a greater density of infective animals and stable at lower infectivity than for any of the species alone. Indeed each species alone may have a basic reproductive ratio less than unity but the multispecies model may possess an endemic disease equilibrium. Where several species interact, it may be the case that even a relatively low density of one of the species is essential for the stability of the endemic equilibrium and removal of that species will eliminate the equilibrium.

We have found that the analysis of even relatively simple systems, such as these spatially homogeneous SIS models, rapidly leads to algebraic intractability, even to the extent of finding explicit expressions for the equilibrium values of state variables or of eigenvalues of linearisations about endemic equilibria. This makes it difficult to prove, analytically, the effect of the variations in individual parameters, or groups of parameters on the behaviour of the overall system.

Further work

We have considered the key disease parameters, infectivity and recovery rates, to be constant and we have assumed that recovered animals acquire no immunity and are reinfected at the same rate for each subsequent infection. We assume that there are no additional deaths from disease. We thus assume that
all animals transmit infection at the same rate, all susceptibles are equally likely to become infected and the progress of the disease is the same in each animal.

- In practice we might expect that infectivity and susceptibility would differ markedly depending on an animal's age, time since infected and previous history of exposure to the disease and that some animals would acquire at least partial immunity (see for example [28]). The parameters might also be functions of environmental variables and thus infectivity and recovery rates may credibly have a pronounced seasonality.

- We have not been able to demonstrate analytically for a two or more species system the relationship between the equilibrium values of the state variables and the eigenvalues of the linearisation about the endemic equilibrium and $R_0$, the principal eigenvalue of the next generation matrix, although numerical simulation supports our conjecture that one exists.

- While theory suggests that it should be the case, we have not demonstrated that, in the three species model, the basic reproductive ratio greater than unity is the condition for the existence and therefore stability of the endemic equilibrium.

While we can study analytically the asymptotic behaviour of these systems, we are unable make much progress in studying their transient behaviour in an analytical way. In practical terms it is of course the transient behaviour which will be observed and which farmers and policymakers need to understand and much needs to be done to focus on this area.

- We have conjectured that the evolution of the system as it moves away from the infection free equilibrium as infectives are introduced will be determined by $R_0$, both in the case of the time that the system takes to get arbitrarily close to the stable equilibrium and the number of animals infected over a given time period, but this has been shown neither analytically nor by numerical simulation.

**Culling strategies**

For both continuous culling SIS and SEIS models, we have shown that it is possible to remove an endemic equilibrium in a single species by culling the whole population, either on a constant yield or a constant rate basis, without the entire population being eradicated, regardless of the particular fecundity function chosen. With a logistic fecundity function fixed yield culling is only successful in this way provided that the disease is not very contagious, but fixed rate culling is always successful. The same result is also found in the badgers/cattle model. The density of the remaining, infection free population is greater than that of the susceptible endemic equilibrium population. A similar conclusion was reached studying impulse culling one species SIS models. This result, removing the disease without exterminating all the badgers, would potentially be of interest to the animal protection lobby were this behaviour in the model to be replicated in the field.
Destabilising an endemic equilibrium in the single animal model by culling all disease classes requires the lowest rate of culling, although the total number of animals culled over time will be least if only infectives are culled. The practical efficacy of the latter strategy must of course depend on an effective and rapid test for bovine TB in badgers. We have shown the importance of controlling immigration if culling is to be successful.

Further work

- A single species impulsive culling model gives comparable results to the continuous case, indeed we show that the continuous case is the limit of the impulsive case as the frequency of culling increases. We conjecture that this would also be true for impulsive culling in the badger/cattle system but have been unable to show this analytically.

- In the culling models studied, we assume that there are no deaths due to disease. Although including deaths due to disease leads rapidly to algebraic complexity, this is an important area for further work if we are to produce a practically useful model.

- In SEIS impulsive culling models with a fixed length latency period $\tau$ we might anticipate that there would be a relationship between the value of $\tau$ and the time interval between culls in determining the optimum culling strategy.

- We have not modelled vaccination strategies, noting the resistance of the farming industry to the practice. It is nonetheless important for policymakers to model the relative cost effectiveness of vaccination and culling strategies.

Models with a latent period

We have shown that our models for a single species both with an exponentially distributed latent period and a fixed latent period are well posed and proved the criteria for the global stability of the IFE in each case. We have considered only the fixed latent period model in the badger/cattle system and proved the criteria for linear stability of the IFE.

Further work

- We have not investigated the exponentially distributed badger/cattle model either with or without culling, nor have we been able to make much analytical progress in studying the endemic equilibrium. Since a latent period is a realistic feature of $m. bovis$, this is work that would be useful to pursue.

Spatially heterogeneous models

We have shown how an SIS model in which infected badgers diffuse into a population of susceptible animals in an infinite domain can give rise to a travelling wave solution connecting the IFE and the endemic disease equilibrium.
and that we can understand the non-linear problem through considering the linearised problem. The speed at which the disease spreads is increasing in the system basic reproductive ratio.

We have also demonstrated the feasibility of travelling wave solutions connecting the IFE and endemic disease equilibrium in the badger/cattle SIS model system (infected badgers diffusing into a population of susceptible cattle and badgers). However the minimum wavespeed calculated does not appear to depend on the disease parameters, which is not biologically reasonable.

SEIS models with diffusion of infected badgers in one and two species models also show travelling wave solutions which feasibly connect the IFE and endemic disease equilibrium. However we have not been able to establish minimum wavespeeds dependant on disease parameters.

In the single species SIS culling models with diffusion we demonstrate travelling wave solutions connecting the IFE and the endemic equilibrium. We can compute minimum wavespeeds which are decreasing functions of the culling rates for both fixed yield and fixed rate culling.

Constraining the reaction diffusion equations for the single species SIS model to a finite interval we can find constraints on the culling parameter such that the infected class is eliminated with a non-spatially homogeneous infection free population remaining.

Further work

- Both the SIS and SEIS two species reaction diffusion models require further analysis to establish biologically meaningful minimum wavespeeds if they are to provide insight into the rate of spread of the disease in the field.

- Our results have been obtained in one dimensional spatial systems. A more realistic model will need to consider two dimensional spatial systems.

- Developing the spatially heterogeneous culling models with diffusion in finite domains with varying boundary conditions and in particular studying the behaviour of the infected class would seem to provide an effective way to simulate the real world situation.

- We did not study patch models - where animals are contained in a series of patches with assumptions about mixing between patches. Given that the badger is a territorial animal and that cattle are normally constrained to a relatively specific location this would appear to be an attractive model to develop.

Age structured models

We derive general age structured SI and SEI p.d.e. models for a single species and, by considering steady state solutions, find age distributions for the equi-
librium values of the state variables as well as the sizes of the related equi-
librium populations of adults and juveniles. By transforming the p.d.e.s into
delay differential equations, we establish the well posedness of the SI model and
show that if the IFE is globally stable then $R_0 < 1$. We cannot establish the
stronger criterion that if the IFE is stable then $R_0 < 1$. We find an expression
for the age distribution of infectives close to the IFE.

It is difficult to make any analytical progress with the SEI delay differential
equation model.

**Further work**

- The primary interest in studying age-structured models is to be able
to model age-related disease parameters which appear biologically more
realistic than constants and to study the effect of culling with age de-
pendence (such that juveniles are culled at a different rate from adults)

**Transmission by bacteria in addition to direct con-
tact**

Models of the cattle/badger system incorporating bacterial transmission in
addition to SIS transmission add considerable algebraic complexity and the
majority of our results are in the form of conjectures rather than analytical
proofs. Presence of bacteria significantly affects the results by comparison
with SIS models with direct transmission only.

**Further work**

- If the possibility of air and soil borne bacterial transmission is proved in
the field, it will be necessary to incorporate bacteria as a state variable
in the models used elsewhere throughout this work in order to obtain
the most relevant results.

- Further analytical investigation is needed to improve the robustness of
our conjectures.
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