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**THE POPULATION DYNAMICS OF
BOVINE TUBERCULOSIS
IN POSSUMS**

A thesis presented in partial fulfilment of
the requirements for the degree of

Master of Science

in Mathematics at

Massey University

Maree Sleeman
1991

ABSTRACT

With the recent outcry concerning the spread of Bovine Tuberculosis throughout the New Zealand Possum population, there is an increasing need to study some of the diverse modelling approaches to this problem. This thesis centres on modelling the epidemics of this disease using two and three-dimensional dynamical systems, which describe the change in the possum population and change in the number of individuals that are diseased.

Introductory material is covered in Chapter One, which reports on the first, through to some of the most recent research completed in the area of disease epidemics. A review of the previous model of possum tuberculosis is also introduced.

Chapter Two looks at the effects on the dynamics of the model of changing the recovery curve parameter, which measures the degree of recovery of possums following a control operation. Detailed steady-state analysis is carried out on the system and local stability determined.

In Chapter Three, a three-dimensional model is investigated that allows for a latent period following infection of disease. Instead of a possum being able to spread the disease immediately after becoming infected itself, there is a latent time until the disease becomes contagious. An in-depth description is given as to how this model originates, then steady-state analysis is explored, and finally local stability of the steady-states is examined.

Restricting the contact rate of an individual possum with the rest of the population is the model studied in Chapter Four. Rather than a possum being able to come in contact with the whole population in a set time, as was the situation in the previous models, the number of contacts is fixed at some realistic value for the given time period. Steady-state analysis is carried out for this new model, along with the local stability analysis.

Chapter Five looks at the various models and how they relate to the model in Chapter Two, as this model is the base for the subsequent ones. Computer generated plots are examined in order to display the numerical differences between the models. A brief comparison is given between these and some other models in the literature, and concludes by discussing some of the advantages and disadvantages of the various models.

Finally, Chapter Six discusses the need for implementing spatially distributed models in the future, to allow for patchiness within the population.

ACKNOWLEDGEMENTS

I wish to express my sincere appreciation to my supervisor, Dr Michael Carter for his continual advice and encouragement throughout the course of this thesis.

Thanks also to Professor Graeme Wake for his helpful suggestions and enthusiasm while I was completing this research.

I would also like to thank Dr Nigel Barlow for providing the base for this research and for his helpful advice and suggestions.

My sincere thanks to Michael Charleston for the valuable time he spent proof reading my thesis, and to Robert Crawford for the endless assistance he gave me with the computational side of my work.

A special thank you to Veronique Rochecouste whose friendship, support and encouragement was greatly appreciated during the rough times, and throughout the completion of this thesis.

Finally, my heartfelt thanks to Aaron Mills, without whose love, support and patience, this work would not have got around to completion.

Thank you all.

DEDICATION

I would like to dedicate this thesis to Mum and Dad for all their advice, encouragement and support they have given me over the years. Words cannot adequately express my gratitude, but thank you. I love you both.

CONTENTS

1 INTRODUCTION	
1.1 The Possum Problem and Current Research in Epidemics	1
1.2 Review of a Previous Model Studied on Tb in Possums	4
2 MODEL 2: Decreasing the Recovery Curve Parameter θ to 1	
2.1 Introduction	6
2.2 Boundedness of Solutions	6
2.3 Solutions at Equilibrium	8
2.4 Existence of Non-Zero Equilibria	9
2.5 Bifurcations of Equilibria	11
2.6 Tracking the Non-Zero Equilibria	16
2.7 Stability of the Non-Zero Equilibria	22
2.8 Summary	27
3 MODEL 3: Introduction of a Latent Period following Infection	
3.1 Introduction	28
3.2 Formulating the Three Equation Model	28
3.3 Boundedness of Solutions	30
3.4 Solutions at Equilibrium	31
3.5 Existence of Non-Zero Equilibria	33
3.6 Bifurcations of Equilibria	38
3.7 Tracking the Non-Zero Equilibria	40
3.8 Stability of the Non-Zero Equilibria	44
3.9 Summary	49
4 MODEL 4: Restriction on the Contact Rate Per Individual	
4.1 Introduction	50
4.2 Boundedness of Solutions	51
4.3 Solutions at Equilibrium	51
4.4 Existence of a Non-Zero Equilibrium	52
4.5 Bifurcations of Equilibria	53
4.6 Tracking the Non-Zero Equilibrium	60
4.7 Stability of the Non-Zero Equilibrium	62
4.8 Summary	66

CONTENTS

5	DISCUSSION	67
6	FURTHER RESEARCH	73
7	APPENDIX	74
8	LIST OF REFERENCES	87

§1 Introduction

1.1 The Possum Problem and Current Research in Epidemics

The population dynamics of possums in New Zealand has been of interest because of the destruction of local flora caused by high densities of this introduced marsupial. However, serious attempts to study and to control the possum population were not initiated until the possums were implicated in the late 1960s and early 1970s as a reservoir for tuberculosis (Tb), *Mycobacterium bovis*, and as a source of infection of dairy cattle. During the 1970s, possum surveys found tuberculous possums on or near properties with persistent cattle Tb problems and large-scale possum control operations using poison were initiated. The subsequent decline in cattle tuberculosis in the areas that were treated gave further confirmation to their implication as a primary source of this infection. A detailed description of this background material can be found in the 1986 issue of *Surveillance* [9] which is devoted to this problem.

The high number of possums in the country and their broad distribution make a general population control strategy economically impractical and possibly infeasible without unacceptable side effects. Consequently, a detailed quantitative assessment of the population dynamics of possums and of cost effective control strategies has become desirable. A model of this type has been proposed by Dr Nigel Barlow from the Ministry of Agriculture and Fisheries, who also performed several computer simulations based on this model which are being currently used as a basis for control strategies.

In this thesis we shall derive and study a number of models based around Dr Barlow's for the population and disease dynamics of possums, incorporating such things as vertical transmission, density-dependent mortality, a latency period following infection and a restriction on the contact rate per individual. All this, in an attempt to produce a model that is the most biologically realistic to the dynamics of tuberculosis in possums from which appropriate control strategies can possibly be implemented.

Some of the earliest classical work on the theory of epidemics was due to Kermack and McKendrick (1927, cited in [6]), who addressed the problem of outbreaks of disease within a population. One such model, although crude, compared rather well with data for death by plague in Bombay during an epidemic in 1906.

The interaction between epidemiology and population dynamics has been studied by Anderson and May [2] who considered models for both microparasites and macroparasites. They investigated how threshold phenomena for the persistence of epidemics were modified

when the population size was variable. They further discussed how a population could be regulated by an infective disease, and also compared theoretical predictions with some data.

Anderson *et al* [1] discuss a similar model for the spread of fox rabies in Europe, assuming a logistic growth of foxes in the absence of disease. They found that the fox population would either settle to a disease-free equilibrium density or that rabies would settle to a regulated state, (below that of the disease-free equilibrium level), which would either be a stable constant value or stable cycle; the cyclic solutions tending to arise when the carrying capacity of the habitat was relatively large and when there was a latent period of the proper length. They concluded that the model predicted patterns of population behaviour in striking agreement with observed epidemiological trends.

In further research completed by Anderson and May [3], they looked at several different models which described the population dynamics of any microparasitic infection that was directly transmitted among invertebrate hosts, and explored the circumstances under which the parasitic infection would regulate the host populations for the various models. This regulated state was either a stable constant value or a stable cyclic oscillation; the latter case occurring when highly pathogenic microparasites produced large numbers of relatively long-lived infective stages with relatively low intrinsic growth rates.

Badger tuberculosis was the next piece of research discussed in depth by Anderson and Trewthella [4]. They reviewed the various processes which influenced badger abundance and presented available data. Using this information, they formulated simple models for the dynamics of badger populations in the absence of disease and decided that non-linear functions were required so that density-dependent constraints began to operate as the density of badgers approached the carrying capacity of the habitat. Local stability analysis revealed either a non-oscillatory return to equilibrium, damped oscillation or instability depending on threshold values.

Next they examined the information on the epidemiology of Tb and presented data relevant to the dynamics of disease transmission, then constructed simple models of disease spread and examined the factors determining infection prevalence. From the analysis, the models suggested the interaction between badger and disease was stable and that oscillatory fluctuations would rapidly damp to a steady state. The models also suggested that the disease acted to depress significantly badger density below disease-free levels. The level of disease prevalence predicted from the models broadly matched those observed in the field.

Finally, they concluded that the persistence of bovine Tb in badger populations was enhanced by the probable involvement of pseudo-vertical transmission and the presence of carriers; both factors acting to suppress the critical density of susceptible animals necessary for the maintenance of the infection within the host population.

More from a mathematical approach to the problem of epidemics within a population was a paper studied by Pugliese [11], in which he used a two equation system to depict the change in a total population and change in the number of diseased subjects within that

population. (As Pugliese's work is very similar to the models we investigate in the subsequent analysis, a little more depth will be added in reviewing his papers.)

A generalised mortality function was implemented along with a non-specific function to describe the contact rate between diseased and non-diseased individuals. Infected individuals were expected to reproduce at a lesser rate than those of non-infected, while a specified proportion of the offspring of infecteds were born diseased. Thus, the possibility of vertical transmission was considered in the model.

The results showed that above a certain threshold, the population would tend to either a diseased steady-state (which was proved to be globally stable) or a steady-state in which there existed infected individuals but no susceptible individuals. Below this threshold, the population tended to a disease-free equilibrium. No limit cycles were found, so all trajectories would converge to an equilibrium. The final piece of analysis involved a small extension to the model to allow for a vaccinated class of individuals, for which similar equilibria and stability results were obtain as above, except that the stability of the endemic (or diseased) equilibrium was only proved locally.

Lastly was a further paper studied by Pugliese [10] in which he introduced a latent period, i.e. the diseased individuals from [11] were divided into exposed individuals (infected but not contagious) and infectious individuals (contagious), giving a three equation dynamical system.

Again he utilised a generalised function to describe the population mortality and a general function for the contact rate. Exposed and infective individuals reproduced at differing rates, with two specific cases being examined. Firstly, the fertility of exposed individuals was at the same rate as that of susceptibles with infectives reproducing at some lesser rate and secondly, neither exposed nor infective individuals contributed to the reproductive effort of the population. For this study, it was assumed that all newborns were susceptibles, eliminating vertical transmission. This was done since the exclusion of vertical transmission did not change the results in [11] but made the mathematics easier.

The results showed that when the fertility of exposed individuals was equal to that of susceptible individuals, the model appeared to be respondent to the biology and gave rise to a picture similar to that of most epidemic models with the possibility of oscillations. Namely, there was a clear threshold below which there was a global convergence to a disease-free equilibrium, and above to a diseased equilibrium.

When the fertility of exposed and infective individuals was zero, the threshold phenomenon was much weaker. Below this threshold the disease-free equilibrium was stable; above, it was unstable and there existed a diseased equilibrium. However, this diseased equilibrium was not necessarily unique and it could exist below the threshold. Multiple equilibria would not arise if mortality and contact rate were linear with population size but could arise if one of these was relaxed. The diseased equilibrium only existed in an

intermediate range of values and was always unstable. From almost all initial values, there was a convergence either to the disease-free equilibrium or to a zero population.

1.2 Review of a Previous Model Studied on Tb in Possums

This now brings us up to the research which I completed in 1989, [13], where I used a two-equation system to model the spread of bovine tuberculosis in possums. I shall introduce the equations now so that the reader can familiarise themselves with the basic model and how it was derived.

From [13], we have:

$$\frac{dH}{dt} = H(a-b-sH^\theta) - \alpha D \quad (\text{A})$$

$$\frac{dD}{dt} = \beta D(H-D) - D(\alpha + b + sH^\theta) + \frac{aD}{2} \quad (\text{B})$$

where $\theta=3$.

The first equation states that the total population of possums (H) increases at a per capita rate equal to the birth rate minus the death rate in the absence of disease, where $b+sH^\theta$ is the combined density-dependent and independent per capita mortality rate. In the presence of disease, there is an additional loss of αD possums each year, where D is the population of diseased possums; α being the age-independent death rate due to disease.

The second equation describes the change in the number of diseased individuals which increases in proportion to the number of contacts between the susceptibles and diseased, with each diseased animal infecting a proportion β of the susceptibles each year. An additional $\frac{aD}{2}$ become diseased each year by pseudo-vertical transmission i.e. transmission of disease from parent to offspring. Death of diseased animals occurs at a rate $\alpha + b + sH^\theta$, α being the excess over the usual natural mortality rate due to the presence of disease.

In all four equilibria were found for this system of equations, with the most trivial being a zero equilibrium which was always unstable. Further analysis showed a Disease-free equilibrium whose stability depended on parameter values and an Endemic equilibrium (i.e. an equilibrium with non-zero disease and population numbers), whose value *and* stability was determined by parameter values. The remaining equilibrium corresponded to negative population size, so because of the irrelevance of such a solution in the study no further analysis was carried out on this solution.

The most significant finding from the analysis was that at a particular parameter threshold, the Endemic equilibrium entered the feasible region by bifurcating with the Disease-free equilibrium. (The feasible region is the region in phase-space for which population and disease numbers are positive and the number of diseased individuals is at most equal to the total population size). At this bifurcation threshold there was an *exchange of stability* between the two equilibria. Below this threshold, the Endemic equilibrium was outside the feasible region and unstable with the Disease-free equilibrium stable, while above this threshold the Endemic equilibrium was inside the feasible region and stable with the Disease-free equilibrium unstable. This can be represented by the following bifurcation diagram:

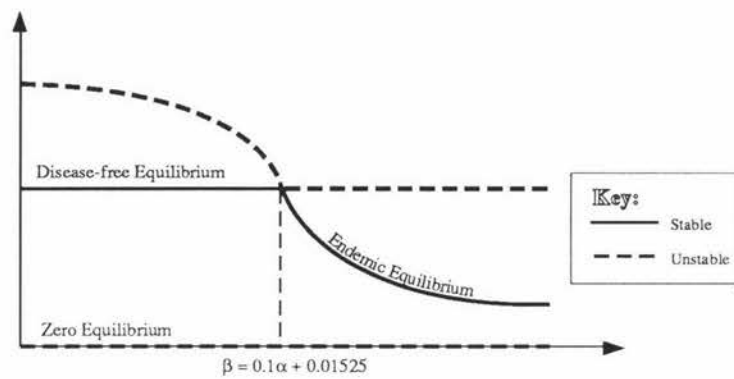


Figure 1.1

Figure 1.2 (taken from [13]) depicts the graph of the equations (A) and (B) at equilibrium ($\frac{dH}{dt} = \frac{dD}{dt} = 0$), with the positive intersection point of (A) and (B) representing the Endemic equilibrium. As parameters vary, this intersection point varies and thus represents the path or *track* of the Endemic equilibrium.

The final piece of analysis showed that solutions to the system remained bounded once they entered the feasible region.

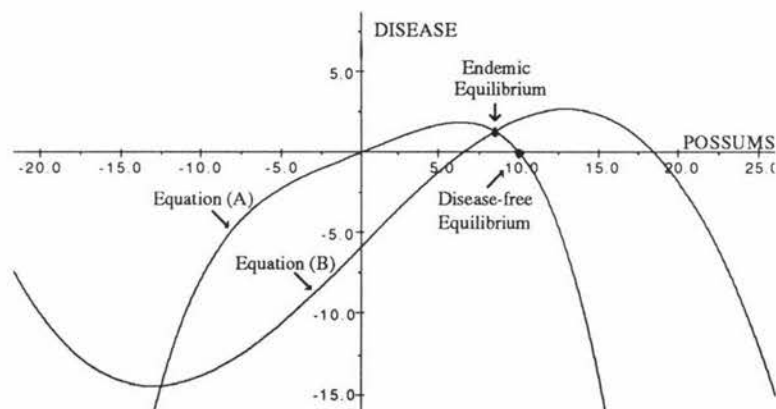


Figure 1.2

§2 Model 2: Decreasing the Growth Curve Parameter θ to 1

2.1 Introduction

In the previous model [13] we had $\theta = 3$ as this supposedly gave the best fit to a recovery curve for relative possum densities following control (also see [7]), implying that our density-dependent mortality function $b+sH^\theta$ was a cubic in H . However, as proposed by Dr Barlow, $\theta=1$ can also adequately describe the growth recovery curve. By setting θ to 1 our mortality function would become linear and analysis of the model would be made a great deal easier. The question to then ask would be "does this have a significant change on the dynamics of the system?". To answer this we proceed with the following analysis.

If we set $\theta=1$ in equations (A) and (B) in [13], then our system, $\frac{dr}{dt}$, becomes:

$$\frac{dH}{dt} = H(a-b-sH) - \alpha D \quad (\text{A}')$$

$$\frac{dD}{dt} = \beta D(H-D) - D(\alpha+b+sH) + \frac{aD}{2} \quad (\text{B}')$$

with all parameters as in [13] (see Appendix) with the exception that the density-dependent constraint

$$s = \frac{a-b}{K^\theta} = \frac{a-b}{K}.$$

2.2 Boundedness of Solutions

We begin the analysis by checking that the solutions remain in the feasible region once they enter it as was the case for the previous model.

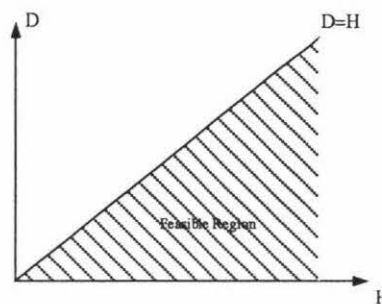


Figure 2.1

If the angle between the inward unit normal to a feasible region boundary and the system trajectory is less than 90° , then obviously no trajectory can leave the feasible region along that boundary. If this is the case for all boundaries, then the feasible region will be invariant.

We will have such an angle if $\frac{dr}{dt} \cdot \underline{n} > 0$ for all boundaries. Firstly, consider the boundary $D = H$. The inward unit normal vector to this boundary is $\underline{n} = (1, -1)$, so that

$$\frac{dr}{dt} \cdot \underline{n} = H(a-b-sH) - \alpha D - \beta D(H-D) + D(\alpha + b + sH) - \frac{aD}{2}$$

and we have $D = H$, so

$$\begin{aligned} \frac{dr}{dt} \cdot \underline{n} &= H(a-b-sH) + H(b+sH) - \frac{aH}{2} \\ &= aH - \frac{aH}{2} = \frac{aH}{2} > 0. \end{aligned}$$

Next, take the boundary $D = 0$. The inward unit normal vector is then $\underline{n} = (0, 1)$. Thus:

$$\frac{dr}{dt} \cdot \underline{n} = 0.$$

This simply means that the trajectories travel along the boundary $D = 0$. That is, perpendicular to the inward normal. Thus the trajectories do not leave at this feasible region boundary.

Finally, consider any trajectory that might lie on the intersection of the two boundaries. Since we have just shown that any trajectory on or within the boundaries $D = 0$ and $H = D$ remains inside the feasible region, the only possible way a trajectory could leave the region at this intersection would be if there were a discontinuity in $\frac{dr}{dt}$ at the intersection. However, the right-hand sides of equations (A') and (B') are both polynomials and are therefore continuous for all H and D . This enables us to conclude that

Theorem 2.2.1: *Any solution starting on or within the boundaries of the feasible region will remain there as $t \rightarrow \infty$. Also, any solution that enters the feasible region at any time will remain in that region as $t \rightarrow \infty$.*

2.3 Solutions at Equilibrium

At equilibrium $\frac{dH}{dt} = \frac{dD}{dt} = 0$. So from (A'), we get

$$D = \frac{H(a-b-sH)}{\alpha} \quad (1)$$

and from (B')

$$D \left[\beta(H-D) - D(\alpha+b+sH) + \frac{a}{2} \right] = 0$$

$$\Rightarrow D = 0 \quad \text{or} \quad \beta(H-D) - (\alpha+b+sH) + \frac{a}{2} = 0.$$

If $D = 0$, then from (1)

$$\begin{aligned} H(a-b-sH) &= 0 \\ \Rightarrow H &= 0 \quad \text{or} \quad H = \left(\frac{a-b}{s} \right). \end{aligned}$$

Thus, we have a *no possum-no disease* equilibrium $H_z = (0,0)$ and a *disease-free* equilibrium at $H_d = \left(\frac{a-b}{s}, 0 \right) = (H^*, 0)$.

The Jacobian matrix at H_z is

$$J = \begin{bmatrix} a-b & -\alpha \\ 0 & \frac{a}{2} - b - \alpha \end{bmatrix}$$

whose eigenvalues are $\lambda_1 = a-b$ and $\lambda_2 = \frac{a}{2} - b - \alpha$. Since $a > b$, $\lambda_1 > 0$, and we can state the following

Theorem 2.3.1: *The no possum-no disease equilibrium, H_z , is always UNSTABLE.*

The Jacobian matrix at H_d is given by

$$J = \begin{bmatrix} b-a & -\alpha \\ 0 & \beta H^* - \alpha - \frac{a}{2} \end{bmatrix}$$

whose eigenvalues are $\lambda_1 = b-a$ and $\lambda_2 = \beta H^* - \alpha - \frac{a}{2}$. Since $a > b$, $\lambda_1 < 0$. For $\lambda_2 < 0$, we require that

$$\beta H^* - \alpha - \frac{a}{2} < 0$$

$$\Rightarrow \beta < \frac{1}{H^*} \left(\alpha + \frac{a}{2} \right).$$

If we let $\beta_t = \left(\frac{s}{a-b} \right) \left(\alpha + \frac{a}{2} \right)$, then we can state the following:

Theorem 2.3.2: *If $\beta < \beta_t$, the disease-free equilibrium H_d is ASYMPTOTICALLY STABLE. If $\beta > \beta_t$, then H_d is UNSTABLE.*

2.4 Existence of Non-Zero Equilibria

If $D \neq 0$ then

$$\beta(H-D) - (\alpha+b+sH) + \frac{a}{2} = 0. \quad (2)$$

Substituting expression (1) for D , we find

$$\beta \left(H - \frac{H(a-b-sH)}{\alpha} \right) - (\alpha+b+sH) + \frac{a}{2} = 0$$

$$\Rightarrow \beta s H^2 + H(\beta(\alpha-a+b) - \alpha s) + \alpha \left(\frac{a}{2} - \alpha - b \right) = 0. \quad (3)$$

This has solutions when

$$H = \frac{-(\beta(\alpha+b-a) - \alpha s) \pm \sqrt{(\beta(\alpha+b-a) - \alpha s)^2 - 4\alpha\beta s \left(\frac{a}{2} - \alpha - b \right)}}{2s\beta}$$

$$\Rightarrow H = \frac{\alpha s - \beta(\alpha+b-a)}{2s\beta} \pm \frac{\sqrt{\beta^2(\alpha+b-a)^2 - 2\alpha\beta s(\alpha+b-a) + \alpha^2 s^2 - 4\alpha\beta s \left(\frac{a}{2} - \alpha - b \right)}}{2s\beta}$$

$$\Rightarrow H = \frac{\alpha s - \beta(\alpha+b-a)}{2s\beta} \pm \frac{\sqrt{\beta^2(\alpha+b-a)^2 + \alpha^2 s^2 + 2\alpha\beta s(\alpha+b)}}{2s\beta}. \quad (4)$$

Notice that the solutions for H are real since the parameter values are all positive.

$$\text{Let } H = A \pm B \text{ where } A = \frac{\alpha s - \beta(\alpha+b-a)}{2s\beta} \text{ and}$$

$$B = \frac{\sqrt{(\beta(\alpha+b-a) - \alpha s)^2 - 4\alpha\beta s(\frac{a}{2} - \alpha - b)}}{2s\beta}.$$

We need to determine what the signs of the roots are for particular parameter values.

1. If $\alpha \leq \frac{a}{2} - b$ then $A > 0$, $B > 0$ and $|A| \geq |B|$ by inspection.
2. If $\frac{a}{2} - b < \alpha \leq a - b$ then $A > 0$, $B > 0$ and $|A| < |B|$, again by inspection.
3. If $\alpha > a - b$ then either:
 - a. If $\alpha s \geq \beta(\alpha+b-a)$ then $A \geq 0$, $B > 0$ and $|A| < |B|$,
 - or b. If $\alpha s < \beta(\alpha+b-a)$ then $A < 0$, $B > 0$ and $|A| < |B|$.

In case 1, we will find (4) has either two positive solutions, or one positive and one zero solution. For case 2, (4) will have one positive and one negative solution and finally in case 3, a. and b. both lead to (4) having one positive and one negative solution. Thus, we can summarise:

Theorem 2.4.1: *Given that $D \neq 0$, if $\alpha > \frac{a}{2} - b$ then there exists one positive non-zero solution to (4) and one negative solution. If $\alpha < \frac{a}{2} - b$ then there exist two positive non-zero solutions to (4), and finally if $\alpha = \frac{a}{2} - b$ then there is one positive and one zero solution to (4).*

We need to clearly label these two equilibria so that no confusion arises in the subsequent analysis as to which equilibrium we are dealing with. Let us label the equilibrium that has the larger value of H the *Endemic equilibrium*, H_e while the other equilibrium which has the smaller H value be labelled the *Wandering equilibrium*, H_w .

2.5 Bifurcations of Equilibria

A bifurcation point can be described as an intersection point of two solution branches. The necessary condition for a real bifurcation is:

$$H(a-b-sH)-\alpha D = \beta D(H-D)-D(\alpha+b+sH)+\frac{aD}{2} = \det(\text{Jacobian}) = 0.$$

Let us check to see if we have bifurcations in this new system. The Jacobian matrix is given by

$$J = \begin{bmatrix} a-b-2sH & -\alpha \\ \beta D-sD & \beta H-2\beta D-\alpha-b-sH+\frac{a}{2} \end{bmatrix}.$$

Now substituting (2) into this, we find that $\det(\text{Jacobian}) = 0$ becomes

$$\det \begin{bmatrix} a-b-2sH & -\alpha \\ \beta D-sD & -\beta D \end{bmatrix} = 0,$$

giving us

$$-\beta D(a-b-2sH) + \alpha(\beta D-sD) = 0 \quad (5)$$

$$\Rightarrow D(\alpha(\beta-s) - \beta(a-b-2sH)) = 0$$

$$\Rightarrow D = 0 \text{ or } \alpha(\beta-s) - \beta(a-b-2sH) = 0$$

$$\Rightarrow D = 0 \text{ or } H = \frac{\alpha s - \beta(a-b-2sH)}{2s\beta}.$$

Firstly, if $D = 0$, then from (1) we find that real bifurcations occur when

$$H = 0 \text{ and } H = \left(\frac{a-b}{s} \right).$$

In the previous work, we found that there was a bifurcation of the Disease-free Equilibrium with the Endemic Equilibrium at a critical parameter value. Do we have the same phenomenon here? The critical parameter condition from the previous model would correspond in this model to

$$\beta_t = \left(\frac{a-b}{s}\right)\left(\alpha + \frac{a}{2}\right). \quad (6)$$

The expression for our Endemic Equilibrium is given by

$$H = \frac{\alpha s - \beta(\alpha+b-a)}{2s\beta} + \frac{\sqrt{(\beta(\alpha+b-a)-\alpha s)^2 - 4\alpha\beta s\left(\frac{a}{2} - \alpha - b\right)}}{2s\beta}.$$

So at β_t , we find after expanding and simplifying that this becomes

$$H = \frac{1}{2s\beta_t} \left(\frac{-s\alpha(\beta_t+2\alpha)}{2(a-b)} + \frac{as}{2} + \frac{3s\alpha}{2} + \sqrt{\left(\frac{s(a(a-b)+a\alpha+2\alpha^2)}{2(a-b)}\right)^2} \right)$$

Since $a > b$, we have $\frac{s(a(a-b)+a\alpha+2\alpha^2)}{2(a-b)} > 0$. Thus

$$H = \frac{1}{2s\beta_t} \left(\frac{-s\alpha(\beta_t+2\alpha)}{2(a-b)} + \frac{as}{2} + \frac{3s\alpha}{2} + \left(\frac{s(a(a-b)+a\alpha+2\alpha^2)}{2(a-b)}\right) \right)$$

Simplifying again, this gives

$$\begin{aligned} H &= \frac{1}{2s\beta_t} (s(a+2\alpha)) \\ &= \frac{1}{2s\left(\frac{s}{a-b}\right)\left(\alpha + \frac{a}{2}\right)} (s(a+2\alpha)) \\ &= \left(\frac{a-b}{s}\right). \end{aligned}$$

Hence:

Theorem 2.5.1: *As β passes through the critical value of β_t , the Endemic equilibrium bifurcates with the Disease-free equilibrium.*

Secondly, the bifurcation at $H = 0$ would be expected to be the Wandering equilibrium bifurcating with the Zero equilibrium as H_w passes through the origin at a critical α value. To verify this, we look at the expression which determines our Wandering equilibrium:

$$H = \frac{\alpha s - \beta(\alpha+b-a)}{2s\beta} - \frac{\sqrt{\beta^2(\alpha+b-a)^2 - 2\alpha\beta s(\alpha+b-a) + \alpha^2 s^2 - 4\alpha\beta s(\frac{a}{2} - \alpha - b)}}{2s\beta}.$$

So at $\alpha_t = \frac{a}{2} - b$, this becomes

$$H = \frac{1}{2s\beta} \left(\left(\frac{a}{2} - b \right) s + \beta \left(\frac{a}{2} \right) - \sqrt{\left(\beta \left(\frac{a}{2} \right) + s \left(\frac{a}{2} - b \right) \right)^2} \right)$$

$$\Rightarrow H = \frac{1}{2s\beta} \left(\left(\frac{a}{2} - b \right) s + \beta \left(\frac{a}{2} \right) - \beta \left(\frac{a}{2} \right) - s \left(\frac{a}{2} - b \right) \right)$$

$$\therefore H = 0.$$

Thus:

Theorem 2.5.2: As α passes through the critical value of α_t the Wandering equilibrium bifurcates with the Zero equilibrium.

If $D \neq 0$ in (5) then we have

$$H = \frac{\alpha s - \beta(\alpha+b-a)}{2s\beta}.$$

Now from (4), this would mean that

$$\beta^2 (\alpha+b-a)^2 + 2\alpha\beta s(\alpha+b) + \alpha^2 s^2 = 0. \quad (7)$$

If we solve this for β , we obtain

$$\beta = \frac{-2\alpha s(\alpha+b) \pm \sqrt{(2\alpha s)^2 (\alpha+b)^2 - 4(\alpha+b-a)^2 (\alpha^2 s^2)}}{2(\alpha+b-a)^2} \quad (8)$$

$$\Rightarrow \beta = \frac{-2\alpha s(\alpha+b) \pm 2\alpha s \sqrt{2a(\alpha+b-\frac{a}{2})}}{2(\alpha+b-a)^2}.$$

Let $\beta = \frac{1}{2(\alpha+b-a)^2} (A \pm 2\alpha s \sqrt{B})$, where $A = -2\alpha s(\alpha+b)$ and $B = 2a(\alpha+b-\frac{a}{2})$. If $\alpha < \frac{a}{2} - b$, then $B < 0$ and so our β solution will be complex. If $\alpha > \frac{a}{2} - b$, then we note that $A < 0$, $B > 0$ and from (8), $|A| > |B|$. This will result in two negative β solutions. In either

case, the values of β which satisfy (7) are not within our parameter space. Thus, we can rule out the possibility of a bifurcation in our system at $H = \frac{\alpha s - \beta(\alpha - a + b)}{2s\beta}$.

The necessary condition for a complex or Hopf bifurcation (if any exist) is

$$H(a-b-sH) - \alpha D = \beta D(H-D) - D(\alpha + b + sH) + \frac{aD}{2} = \text{Tr (Jacobian)} = 0,$$

where $\text{Tr (Jacobian)} = 0$

$$\Rightarrow \text{Tr} \begin{bmatrix} a-b-2sH & -\alpha \\ \beta D - sD & -\beta D \end{bmatrix} = 0$$

$$\Rightarrow a-b-2sH - \beta D = 0$$

$$\Rightarrow D = \frac{a-b-2sH}{\beta}.$$

If we substitute this into equation (2), we obtain the following expression for H:

$$\beta \left(H - \frac{a-b-2sH}{\beta} \right) - (\alpha + b + sH) + \frac{a}{2} = 0$$

$$\Rightarrow H = \frac{\alpha + \frac{a}{2}}{\beta + s}. \quad (9)$$

Substituting H back into (2), we get

$$D = \frac{(a-b)\beta - s(b+2\alpha)}{\beta(\beta+s)}. \quad (10)$$

Now, if we substitute (9) and (10) into equation (1), the other equation which determines the non-zero solutions, we obtain a condition on parameters for a complex bifurcation to exist.

From (1), we find

$$\frac{(a-b)\beta - s(b+2\alpha)}{\beta(\beta+s)} = \left(\frac{\alpha+\frac{a}{2}}{\beta+s}\right) \left(a-b-s\left(\frac{\alpha+\frac{a}{2}}{\beta+s}\right)\right) \frac{1}{\alpha}.$$

Rearranging and simplifying, we obtain an expression for β :

$$\frac{a}{2}(b-a)\beta^2 - \frac{s}{4}(a^2 - 2a(b+2\alpha) + 4\alpha(b+\alpha))\beta - \alpha s^2(b+2\alpha) = 0 \quad (11)$$

If we solve this for β , we get

$$\beta = \frac{-s}{4a(a-b)} \left(a^2 - 2ab - 2a\alpha + 4\alpha b + 4\alpha^2 \pm (a+2\alpha)\sqrt{a^2 - 4ab - 12a\alpha + 4(b+\alpha)^2} \right)$$

For our complex bifurcation to exist, we require that at least one of these solutions for β is real and positive. If we assume the solutions to (11) are real, then this implies

$$a^2 - 4ab - 12a\alpha + 4(b+\alpha)^2 \geq 0. \quad (12)$$

Now we will show that when (11) has real solutions they are both negative. For this to happen, we require

$$\begin{aligned} a^2 - 2ab - 2a\alpha + 4\alpha b + 4\alpha^2 &> (a+2\alpha)\sqrt{a^2 - 4ab - 12a\alpha + 4(b+\alpha)^2} \\ \Rightarrow (a^2 - 2ab - 2a\alpha + 4\alpha b + 4\alpha^2)^2 &> (a+2\alpha)^2 (a^2 - 4ab - 12a\alpha + 4b^2 + 8b\alpha + 4\alpha^2). \end{aligned}$$

Expanding this and simplifying, we find

$$4a(a^2 + 6ab - 8b^2 + 13a\alpha - 12b\alpha + 4\alpha^2) > 0.$$

Now we know from (12) that

$$\begin{aligned} 4\alpha^2 &\geq -a^2 + 4ab + 12a\alpha - 4b^2 - 8b\alpha \\ \Rightarrow 4a(a^2 + 6ab - 8b^2 + 13a\alpha - 12b\alpha + 4\alpha^2) &\geq 10ab - 12b^2 + 25a\alpha - 20b\alpha \\ &= 2b(5a - 6b) + 5\alpha(5a - 4b) > 0. \end{aligned}$$

Thus we can conclude that

$$a^2 - 2ab - 2a\alpha + 4\alpha b + 4\alpha^2 > (a+2\alpha)\sqrt{a^2 - 4ab - 12a\alpha + 4(b+\alpha)^2}.$$

This tells us that when (11) has real solutions they are indeed negative. Because we assumed $\beta \geq 0$ for this model, this allows us to draw the following conclusion:

Theorem 2.5.3: *There are no complex bifurcations in this model for the parameter ranges specified.*

2.6 Tracking the Non-Zero Equilibria

Now, we investigate the Wandering equilibrium's position relative to the feasible region when $\alpha < \frac{a}{2} - b$, i.e., H_w positive.

Consider the equations (1) and (2) which govern the non-zero solutions:

From (1)
$$D = \frac{H(a-b-sH)}{\alpha}$$

and from (2):
$$D = H \left(\frac{\beta-s}{\beta} \right) + \frac{\frac{a}{2}-b-\alpha}{\beta} \tag{2'}$$

Now consider the graph of (1) in Figure (2.2). $D=0$ in (1) when $H=0$ and $H=\left(\frac{a-b}{s}\right)$, while D has its maximum at $D_{\max} = \left(\frac{a-b}{s}\right)\left(\frac{a-b}{2}\right)\frac{1}{\alpha}$ where $H_{\max} = \left(\frac{a-b}{2s}\right)$. Since $\alpha < \frac{a}{2} - b < \frac{a-b}{2}$, D_{\max} must be larger H_{\max} , telling us that the maximum of (1) is outside the feasible region:

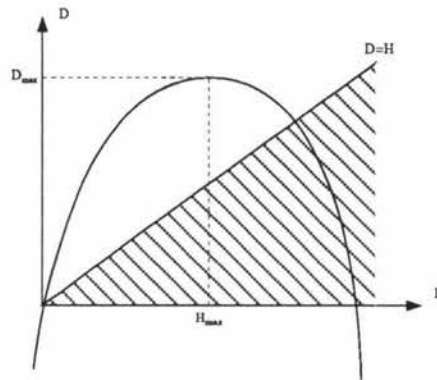


Figure 2.2

Next, let us determine where (1) and (2') intersect the feasible region boundary $H=D$.

(1) $\Rightarrow H = D$ when

$$H = \frac{H(a-b-sH)}{\alpha}$$

$$\Rightarrow H = \frac{a-b-\alpha}{s} \quad \text{and therefore } D = \frac{a-b-\alpha}{s},$$

and (2') $\Rightarrow H = D$ when

$$H = H\left(\frac{\beta-s}{\beta}\right) + \frac{\frac{a}{2}-b-\alpha}{\beta}$$

$$H = \frac{\frac{a}{2}-b-\alpha}{s} \quad \text{and therefore } D = \frac{\frac{a}{2}-b-\alpha}{s}.$$

Because $\frac{a-b-\alpha}{s} > \frac{\frac{a}{2}-b-\alpha}{s}$, the point of intersection of (1) with $H=D$ must be greater than that of (2'). This important point is needed when considering the possible alternative graphs of (2'). Also note that since $\alpha < \frac{a}{2}-b$, the intercept of (2') is positive, and lastly the slope of (2') is at most unity.

If $\beta > s$, then the slope of (2') will be positive, giving us the following:

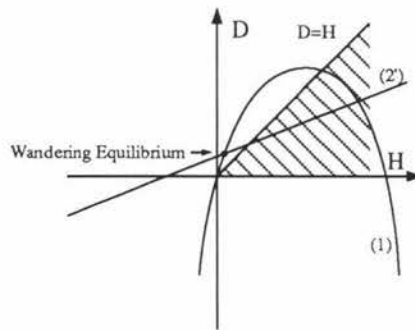


Figure 2.3

This is the only possible situation which satisfies all the above requirements for $\beta > s$. Thus our Wandering equilibrium is outside the feasible region.

If $\beta = s$, then the slope of (2') will be zero, producing the following:

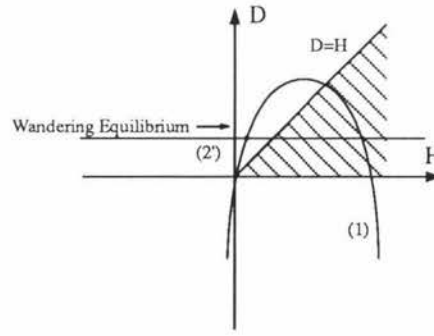


Figure 2.4

Wherever (2') falls, the Wandering equilibrium will be outside the feasible region.

Finally, if $\beta < s$ then the slope of (2') will be negative, giving us either of the following:

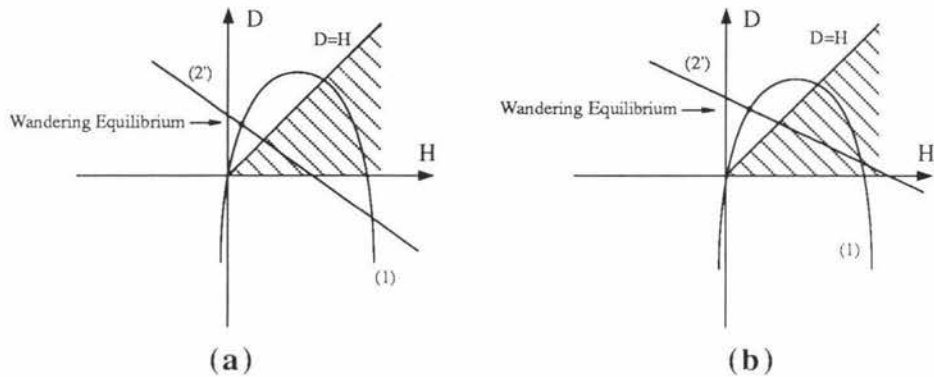


Figure 2.5

Again, in either event, the Wandering equilibrium is outside the feasible region. Thus

Theorem 2.6.1: *When the Wandering equilibrium is positive, i.e., $\alpha < \frac{a}{2} - b$, it will always be outside the feasible region.*

We now investigate the Endemic equilibrium's position relative to the feasible region when β varies about β_t . Again, we make use of equation (1) and (2'), whose intersection governs the non-zero solutions.

If β is slightly perturbed so that $\beta < \beta_t$, then at $H = \left(\frac{a-b}{s}\right)$, (2') becomes

$$D = H \left(\frac{\beta-s}{\beta} \right) + \frac{\frac{a}{2}-b-\alpha}{\beta} < \left(\frac{a-b}{s} \right) \left(1 - \frac{s}{\left(\frac{s}{a-b} \right) \left(\alpha + \frac{a}{2} \right)} \right) + \left(\frac{\frac{a}{2}-b-\alpha}{\frac{s}{a-b} \left(\alpha + \frac{a}{2} \right)} \right) = 0$$

$$\therefore D < 0.$$

In this instance, the intersection point corresponding to the Endemic equilibrium will have a value of D that is negative and a value of H that is greater than $\left(\frac{a-b}{s}\right)$ when $\beta < \beta_t$. Thus when $\beta < \beta_t$, the Endemic equilibrium is outside the feasible region. See below:

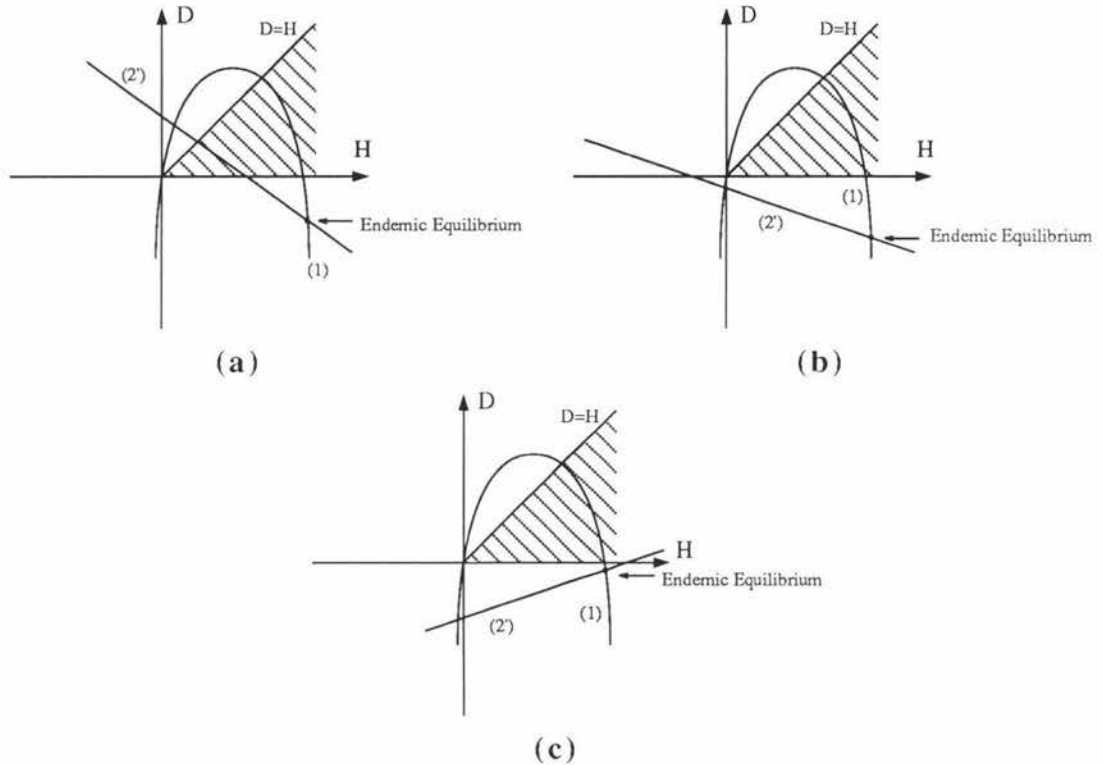


Figure 2.6

Similarly, if β is slightly perturbed the other way so that $\beta > \beta_t$, then at $H = \left(\frac{a-b}{s}\right)$, we find (2') becomes

$$D = H\left(\frac{\beta-s}{\beta}\right) + \frac{\frac{a}{2}-b-\alpha}{\beta} > 0$$

$$\therefore D > 0.$$

This tells us that the intersection point of (1) and (2') which corresponds to the Endemic equilibrium will have a value of D that is positive and because of the shape of (1), it will have a value of H that is less than $\left(\frac{a-b}{s}\right)$ when $\beta > \beta_t$. See below:

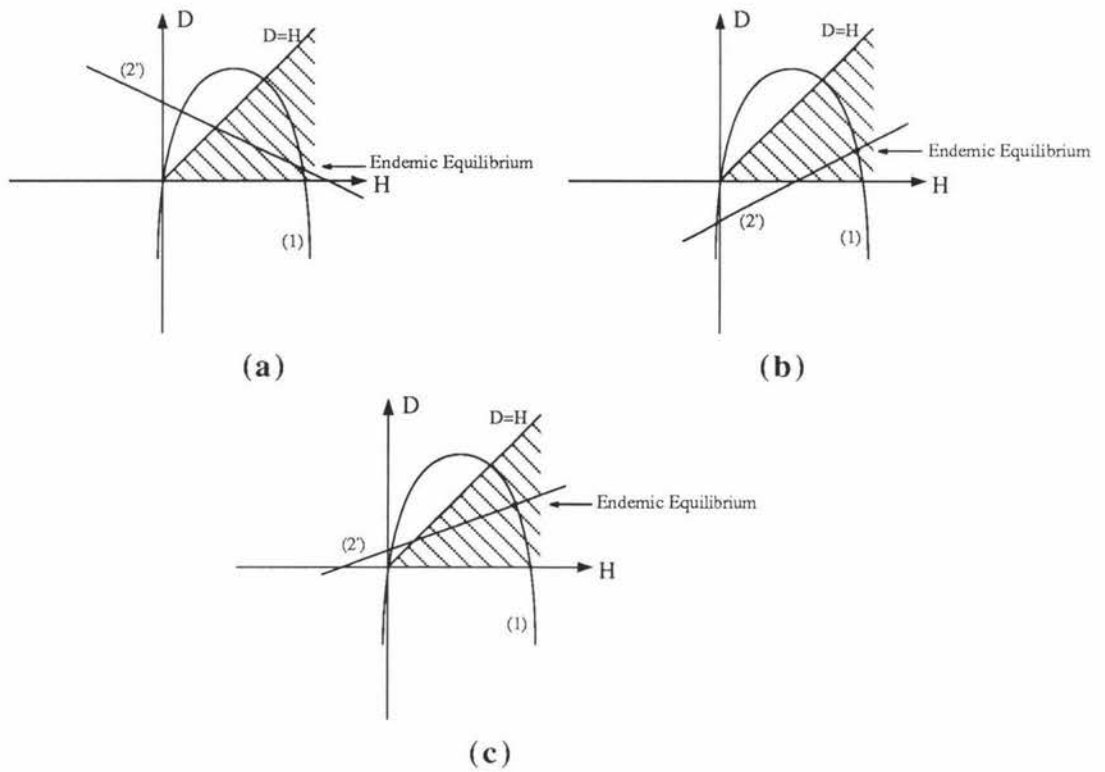


Figure 2.7

When $D > 0$, does the Endemic equilibrium remain inside the feasible region as β varies further? To answer this, we use the same approach as for the Wandering equilibrium, the only difference being that we have an extra condition on (2') which is that $\beta > \beta_t$.

Let us consider the three alternatives: $\beta_t < s$, $\beta_t = s$ and $\beta_t > s$. In the first case, from (6), we get

$$\frac{\alpha + \frac{a}{2}}{a-b} < 1$$

$$\Rightarrow \frac{a}{2} - b - \alpha > 0.$$

This tells us that the intercept of (2') is positive and that the slope is negative (because $\beta_t < s$). From the working in Theorem 2.6.1, if $\alpha < \frac{a-b}{2}$, the *maximum* (or turning point) of (1) will be above the line $H=D$. In this case we have $\alpha < \frac{a}{2} - b < \frac{a-b}{2}$ so that the maximum *is* above the feasible region. Thus we can sketch the following picture, which describes the situation when $\beta_t < s$:

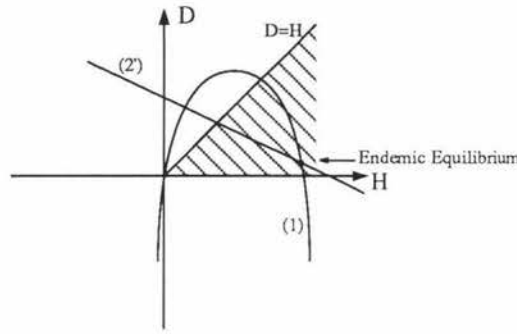


Figure 2.8

Thus the Endemic equilibrium remains inside the feasible region when $\beta_t < s$.

In the second instance when $\beta_t = s$, from (6) we find

$$\frac{a}{2} - b - \alpha = 0.$$

This gives an intercept and slope of zero for (2'). Again, because $\alpha < \frac{a-b}{2}$, the maximum of (2') will be above the feasible region. This is just the following:

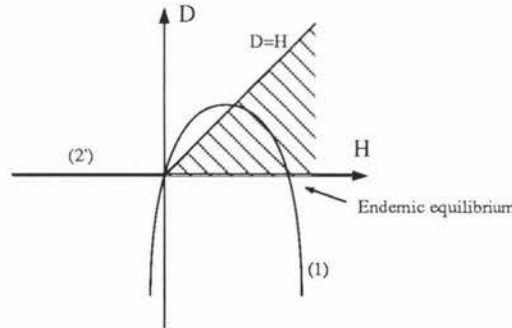


Figure 2.9

As this is still part of the feasible region, we can say that when $\beta_t = s$, the intersection point of (1) and (2') corresponding to the Endemic equilibrium is within the feasible region.

Now in the final instance when $\beta_t > s$, again from (6) we get

$$\frac{a}{2} - b - \alpha < 0.$$

This tells us that the intercept of (2') is negative and the slope is positive but at most unity. As to where the maximum of (2') will lie, we have two possibilities: If $\frac{a}{2} - b < \alpha < \frac{a-b}{2}$, then the maximum is above the feasible region, and if $\alpha \geq \frac{a-b}{2}$ the maximum will be either be on or below the line $H=D$. This results in either of the following situations:

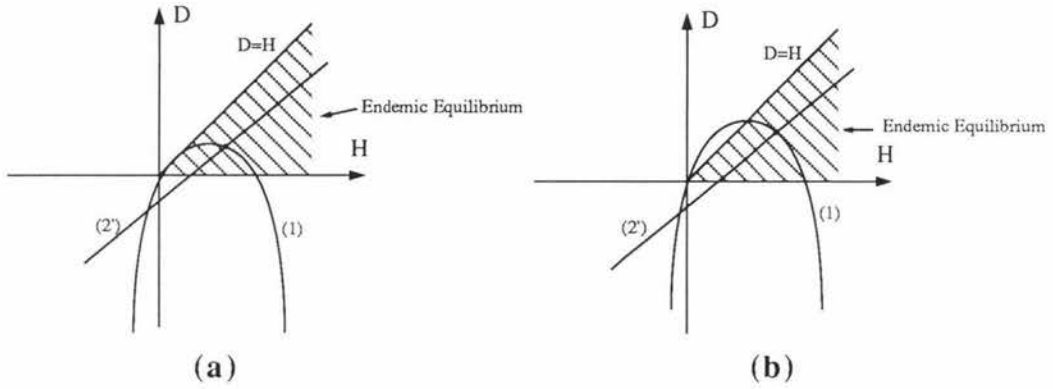


Figure 2.10

In each case, the intersection of (1) with (2') corresponding to the Endemic equilibrium will be within the feasible region. To summarise:

Theorem 2.6.2: When $\beta < \beta_t$, the Endemic equilibrium has $D < 0$, $H > \left(\frac{a-b}{s}\right)$. When $\beta > \beta_t$, the Endemic equilibrium has $D > 0$, $H < \left(\frac{a-b}{s}\right)$ and remains inside the feasible region.

2.7 Stability of the Non-Zero Solutions

The Jacobian matrix for this system is given by

$$J = \begin{bmatrix} a-b-2sH & -\alpha \\ \beta D-sD & \beta H-2\beta D-\alpha-b-sH+\frac{a}{2} \end{bmatrix}.$$

From (1), we can say that

$$a-b-2sH = \frac{\alpha D}{H} - sH,$$

and from (2), we find

$$\beta H = \beta D + \alpha + b + sH + \frac{a}{2}.$$

This gives us the following Jacobian matrix:

$$J = \begin{bmatrix} \frac{\alpha D}{H} & -\alpha \\ \beta D - sD & -\beta D \end{bmatrix}$$

which has the characteristic equation

$$\lambda^2 - \lambda \left(\frac{\alpha D}{H} - sH - \beta D \right) - \beta D \left(\frac{\alpha D}{H} - sH \right) + \alpha D(\beta - s) = 0. \quad (13)$$

Let us investigate the stability of the Endemic Equilibrium at the bifurcation $H = \left(\frac{a-b}{s} \right)$, $D = 0$. If we substitute these values of H and D into (13), we get

$$\begin{aligned} \lambda^2 - \lambda \left(s \left(\frac{a-b}{s} \right) \right) &= 0 \\ \Rightarrow \lambda(\lambda - (b-a)) &= 0. \end{aligned}$$

This gives eigenvalues $\lambda_1 = 0$ and $\lambda_2 = b-a$. Since $a > b$, $\lambda_2 < 0$. However, because there exists a zero eigenvalue, the Principle of Linearised Stability (see Theorem 1.1.2 in [12]) fails to draw a conclusion. Thus, we need to find out what happens to these eigenvalues when the Endemic equilibrium is slightly perturbed from $H = \left(\frac{a-b}{s} \right)$, $D = 0$.

Consider the graph of the function $\lambda^2 - \lambda(b-a)$ whose zeros are the eigenvalues at this equilibrium.

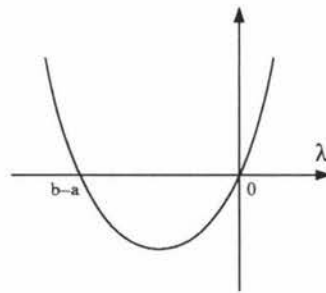


Figure 2.11

At an equilibrium close to $H = \left(\frac{a-b}{s} \right)$, $D = 0$, the eigenvalues will be the zeros of a function which is obtained from this by a slight perturbation. Any such slight perturbation of this function will cause the Endemic equilibrium to become stable or unstable depending entirely on which way the zero eigenvalue perturbs.

If we investigate where (13) intersects the vertical axis after the Endemic equilibrium has been slightly perturbed from $H = \left(\frac{a-b}{s}\right)$, $D = 0$, then this will indicate whether the zero eigenvalue has become positive or negative.

From (13), the vertical axis intercept term is given by:

$$\begin{aligned} & -\beta D \left(\frac{\alpha D}{H} - sH \right) + \alpha(\beta D - sD) \\ & = \frac{-\alpha\beta D^2}{H} + s\beta DH + \alpha\beta D - \alpha sD \end{aligned} \quad (14)$$

We are interested in the sign of (14) when $H \approx \left(\frac{a-b}{s}\right)$, $D \approx 0$ and $\beta \approx \beta_t$. The first term in expression (14) can be neglected as it will be a second order small quantity. So we find (14) becomes

$$\begin{aligned} & s\beta DH + \alpha\beta D - \alpha sD \\ & = D (s\beta H + \alpha\beta - \alpha s) \\ & = D \left(s \left(\frac{s}{a-b} \right) \left(\alpha + \frac{a}{2} \right) + \alpha \left(\frac{s}{a-b} \right) \left(\alpha + \frac{a}{2} \right) - \alpha s \right) \\ & = D \left(s\alpha + \frac{sa}{2} + \alpha \left(\frac{s}{a-b} \right) \left(\alpha + \frac{a}{2} \right) - \alpha s \right) \\ & = D \left(\frac{sa}{2} + \alpha\beta_T \right). \end{aligned}$$

Since $\frac{sa}{2} + \alpha\beta_t > 0$ we can say that if $D < 0$, (14) < 0 and alternatively if $D > 0$, (14) > 0 .

This gives us the following:

If $D < 0$, the vertical axis intercept of (13) will also be negative and the formerly zero eigenvalue will become positive. Thus the Endemic equilibrium will be unstable:

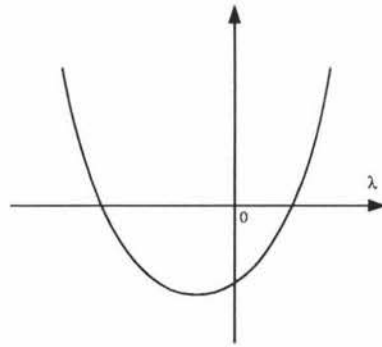


Figure 2.12

If $D > 0$ then the vertical axis intercept of (13) will be positive and so the formerly zero eigenvalue will become negative and hence the Endemic equilibrium will be stable:

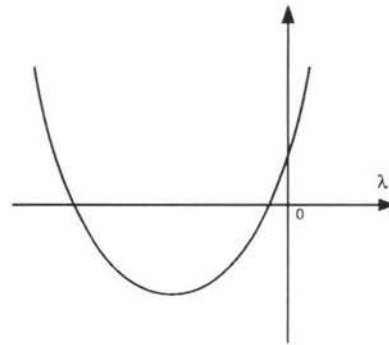


Figure 2.13

We conclude:

Theorem 2.7.1: *A change of stability occurs when the Endemic equilibrium bifurcates with the Disease-free equilibrium. Namely, if $D < 0$ the Endemic equilibrium becomes UNSTABLE and if $D > 0$, the Endemic equilibrium becomes STABLE.*

Now we consider the stability of the Wandering equilibrium. Consider again the Jacobian matrix for the system:

$$J = \begin{bmatrix} a-b-2sH & -\alpha \\ \beta D-sD & \beta H-2\beta D-\alpha-b-sH+\frac{a}{2} \end{bmatrix}.$$

We know from Theorem 2.6.1 that at α_t , the Wandering equilibrium has a solution of $H = D = 0$. So our Jacobian becomes

$$J = \begin{bmatrix} a-b & -\alpha_t \\ 0 & -\alpha_t-b+\frac{a}{2} \end{bmatrix}$$

which has eigenvalues:

$$\lambda_1 = a-b \quad \text{and} \quad \lambda_2 = -\alpha_t - b + \frac{a}{2}$$

However, $\alpha_t = \frac{a}{2} - b$ so that $\lambda_2 = 0$. Now consider the graph of the function $\lambda(\lambda - a + b)$ whose zeros are the eigenvalues at H_w :

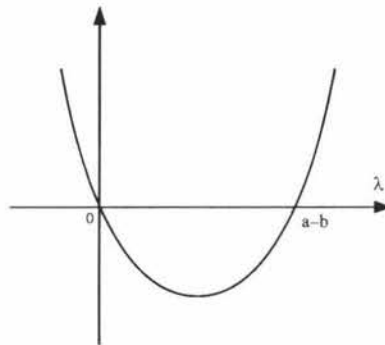


Figure 2.14

At a slight perturbation from α_t , $H \approx 0$, $D \approx 0$ and λ_2 will become either positive or negative depending on which way α is perturbed from α_t . However, because $\lambda_1 = a-b > 0$ there will still be a positive eigenvalue and so at an equilibrium close to α_t , we will have instability. We conclude:

Theorem 2.7.2: *At an equilibrium close to the origin, i.e., $\alpha \approx \alpha_t$, the Wandering equilibrium remains UNSTABLE.*

The only way an equilibrium can lose its stability (or instability) is by bifurcating with another equilibrium. Now because we have ruled out the possibility of any further bifurcations (other than the two specified), this implies that there will be no further stability changes of the non-zero solutions when parameters are taken beyond the critical bifurcation values. In the case of the Wandering Equilibrium, when α moves further away from α_t , it will remain unstable. Similarly for the Endemic Equilibrium, when β is varied beyond β_t , there will be no further change of stability after that at β_t .

2.8 Summary

The results obtained for this model are the standard results for most epidemic models: there exists a threshold below which the disease goes into extinction and above which there exists one stable endemic equilibrium.

Adding some depth to this, our analysis found that there is a bifurcation between the Endemic and the Disease-free equilibria at a particular parameter threshold. Below this threshold, the Endemic equilibrium is outside the biologically feasible region and unstable with the Disease-free equilibrium stable, while above this threshold the Endemic equilibrium is within the feasible region and stable with the Disease-free equilibrium unstable. One could describe this situation as a *swapping of stability* between the two equilibria at the bifurcation threshold. Any solution that enters the feasible region is bounded there as time increases.

Another bifurcation was discovered, between a Zero equilibrium and a Wandering equilibrium at a different parameter threshold than the one above. Both equilibria remained unstable and the Wandering equilibrium remained outside the feasible region irrespective of parameter values. This bifurcation existed in the previous model I examined [13] but was not recognised because the non-zero solutions had to be found numerically (due to the higher degree of the equations). The critical parameter condition for the Wandering equilibrium to bifurcate with the Zero equilibrium was not within the parameter range of the computed solutions, so it *appeared* that nothing of interest happened to the Wandering equilibrium. However, computer solutions now confirm that such a bifurcation occurs in the previous model at that threshold value.

No periodic (or Hopf) bifurcations were found in this model, so that all trajectories converged to some equilibrium.

§3 Model 3: Introduction of a Latent Period following Infection

3.1 Introduction

In the previous section, individuals with tuberculosis were just classified as diseased. However, tuberculosis can be separated into two major stages. First, the animal becomes infected, which means that it has acquired the disease but it is not contagious and secondly the disease becomes more pronounced and the animal becomes infectious, which implies contagious. The reason for an extension of this type is to make the model appear slightly more realistic. Unfortunately, in the field it is very difficult to distinguish infected possums from infectious ones so that such parameters like latent period for the disease to become infectious are very hard to establish. Thus, while introducing the two stages of infection may increase the realism of the model, it also introduces (more) problems of unknown parameter values.

Anyway, we will investigate this model and see if it displays the same or similar characteristics as the two equation model. If it does, this means we need not bother with this separation of diseased individuals and the extra work which it requires to get an overview of the situation.

A similar analysis format will be used as in section 2.

3.2 Formulating the Three Equation Model

As with the two equation model, the total population of possums (H) is divided into susceptibles (S) and diseased. However, for this study we introduce a latent period following infection. Thus, diseased individuals are classified into two types: Infected (M), i.e. diseased but not contagious and infectious (Y), diseased and contagious.

The possibility of pseudo-vertical transmission of disease is allowed for, as was the case for the previous model, where $\left(1 - \frac{a}{2}\right)$ represents the proportion of newborns of infectious individuals that are susceptible and $\frac{a}{2}$ is the proportion that is born infected.

It is assumed that the disease is not so debilitating that all individuals do not contribute equally to the reproductive effort of the population.

Non-disease related mortality is given by the standard density-dependent function $b+sH$ with infectious individuals suffering an additional mortality α . Thus, the life expectancy of a diseased possum is $\frac{1}{\alpha+b}$. The number of new infectives increases by the number of contacts

between infectious and susceptible animals, each infectious one infecting a proportion β of the susceptibles each year. Possums are assumed to pass from the latent or infected class to the infectious state at a per capita rate v , such that the average incubation period is $\frac{1}{v}$.

These assumptions are depicted schematically by the following:

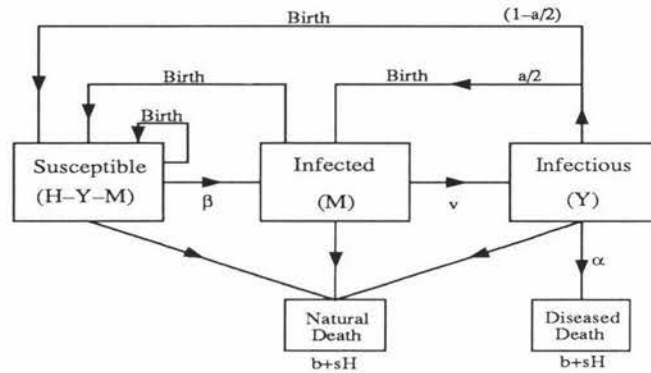


Figure 3.1

These biological assumptions lead us to the following set of first order differential equations for the dynamics of possum populations infected with bovine tuberculosis:

$$\frac{dS}{dt} = aH - \frac{a}{2}Y - \beta SY - S(b+sH) \quad (1a)$$

$$\frac{dM}{dt} = \beta YS - M(v+b+sH) + \frac{a}{2}Y \quad (1b)$$

$$\frac{dY}{dt} = vM - Y(\alpha+b+sH) \quad (1c)$$

where $H=S+Y+M$.

Adding the three equations in (1), we obtain

$$\frac{dH}{dt} = H(a-b-sH) - \alpha Y. \quad (2)$$

We could use, instead of system (1), a system obtained by using (2) and any two equations of system (1) remembering the identity $H=S+Y+M$. We will use equation (2) along with (1b) and (1c) in future analysis and call this system $\frac{dc}{dt}$.

3.3 Boundedness of Solutions

First, let us define the feasible region for this present model. Using the variables H , M and Y , this is the region in 3-space for which H , M and Y are positive and $H \geq M+Y$, or in other words, it is the biologically feasible region such that population and disease numbers must be positive and total disease must be at most equal to the population size. This is represented by the following:

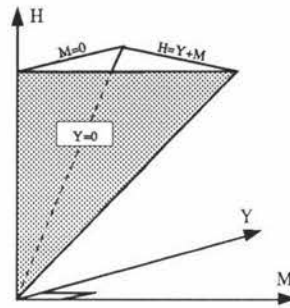


Figure 3.2

It would be convenient if solutions which enter the feasible region or are within previously, remain there as time increases, as was the case for the previous models.

The feasible region will be invariant if

$$\frac{dc}{dt} \cdot \mathbf{n} \text{ (inward normal vector to boundary)} > 0 \text{ for all boundaries.}$$

We start by investigating the surface $Y=0$. The unit normal to this plane, pointing into the feasible region is $(0,0,1)$. Thus

$$\frac{dc}{dt} \cdot \mathbf{n} = vM > 0 \text{ since } v, M > 0.$$

Next, consider the surface $M=0$. The unit normal is then $(0,1,0)$. Thus

$$\frac{dc}{dt} \cdot \mathbf{n} = \beta Y(H-Y) + \frac{a}{2}Y > 0 \text{ since } H > Y \text{ and } a, \beta, Y \text{ and } H > 0.$$

Thirdly, consider the surface $H=Y+M$. The unit normal is $(1,-1,-1)$. Thus

$$\frac{dc}{dt} \cdot \mathbf{n} = \frac{dH}{dt} - \frac{dM}{dt} - \frac{dY}{dt}$$

$$\begin{aligned}
&= H(a-b-sH)-\alpha Y-\beta Y(H-Y-M)+M(v+b+sH)-\frac{a}{2}Y-vM+Y(\alpha+b+sH) \\
&= H(a-b-sH)-\beta Y(H-Y-M)+M(b+sH)-\frac{a}{2}Y+Y(b+sH).
\end{aligned}$$

Now, we know that $H=Y+M$, so this gives

$$\frac{dc}{dt} \cdot \underline{n} = aH - \frac{a}{2}Y = a\left(H - \frac{Y}{2}\right) > 0 \text{ as } H > Y \text{ and } a, H \text{ and } Y \text{ are all } > 0.$$

Finally, let us consider any trajectory that might happen to lie on the intersection of two boundaries. Since we have just shown that any trajectory on or within the three boundaries $H=M+Y$, $Y=0$, $M=0$ remains inside the feasible region, then the only reason that a trajectory could leave this region at the intersection of two boundaries is if $\frac{dc}{dt}$ were discontinuous at this point of intersection. However, since the components of $\frac{dc}{dt}$ are all polynomials, this tells us that they are continuous for all H , M and Y . Hence:

Theorem 3.3.1: *Any solution starting on or within the boundaries of the feasible region will remain there as $t \rightarrow \infty$. Also, any solution that enters the feasible region at any time, will remain there as $t \rightarrow \infty$.*

3.4 Solutions at Equilibrium

Again, using the variables H , M and Y , at equilibrium we know $\frac{dH}{dt} = \frac{dM}{dt} = \frac{dY}{dt} = 0$. So from (2) we get

$$Y = \frac{H(a-b-sH)}{\alpha}. \quad (3)$$

From (1c), we obtain:

$$M = \frac{Y(\alpha+b+sH)}{v} = \frac{H(a-b-sH)(\alpha+b+sH)}{\alpha v}, \quad (4)$$

so that (1b) gives us

$$\beta Y(H-Y-M) - \frac{Y(\alpha+b+sH)(v+b+sH)}{v} + \frac{aY}{2} = 0$$

$$\therefore Y \left(\beta(H-Y-M) - \frac{(\alpha+b+sH)(v+b+sH)}{v} + \frac{a}{2} \right) = 0 \quad (5)$$

$$\Rightarrow Y = 0 \text{ or } \beta(H-Y-M) - \frac{(\alpha+b+sH)(v+b+sH)}{v} + \frac{a}{2} = 0.$$

If $Y=0$, then from (3)

$$H(a-b-sH) = 0$$

$$\Rightarrow H = 0 \text{ or } H = \left(\frac{a-b}{s} \right),$$

and from (4), if $Y=0$ then $M=0$.

Thus, we have a *Zero* equilibrium $H_z=(0,0,0)$ and a *Disease-free* equilibrium at $H_d = \left(\frac{a-b}{s}, 0, 0 \right) = (H^*, 0, 0)$.

The Jacobian matrix at H_z is

$$J = \begin{bmatrix} a-b & 0 & -\alpha \\ 0 & -v-b & \frac{a}{2} \\ 0 & v & -\alpha-b \end{bmatrix}$$

whose eigenvalues are $\lambda_1=a-b$ and the eigenvalues of

$$A = \begin{bmatrix} -v-b & \frac{a}{2} \\ v & -\alpha-b \end{bmatrix}.$$

Since $a>b$, $\lambda_1>0$, giving us the following:

Theorem 3.4.1: *The Zero equilibrium H_z is always UNSTABLE.*

The Jacobian matrix at H_d is given by

$$J = \begin{bmatrix} b-a & 0 & -\alpha \\ 0 & -v-a & \beta H^* + \frac{a}{2} \\ 0 & v & -\alpha-a \end{bmatrix}$$

whose eigenvalues are $\lambda_1=b-a$ and the eigenvalues of

$$B = \begin{bmatrix} -(v+a) & \beta H^* + \frac{a}{2} \\ v & -(\alpha+a) \end{bmatrix}.$$

We can see that $\text{Tr } B < 0$ and

$$\det B = (v+a)(\alpha+a) - v\beta H^* - \frac{av}{2}.$$

For this equilibrium to be stable, we require $\text{Tr } B < 0$ and $\det B > 0$. Thus

$$(v+a)(\alpha+a) - v\beta H^* - \frac{av}{2} > 0 \text{ i.e. } \beta < \frac{1}{H^*} \left(\frac{(v+a)(\alpha+a) - \frac{av}{2}}{v} \right).$$

If we let $\beta_c = \left(\frac{a-b}{s} \right) \left(\frac{(v+a)(\alpha+a) - \frac{av}{2}}{v} \right)$, then we can state the following

Theorem 3.4.2: *If $\beta < \beta_c$, then the Disease-free equilibrium H_d is ASYMPTOTICALLY STABLE. If $\beta > \beta_c$, then H_d is UNSTABLE.*

3.5 Existence of Non-Zero Equilibria

If $Y \neq 0$ in (5), then

$$\beta(H-Y-M) - \frac{(\alpha+b+sH)(v+b+sH)}{v} + \frac{a}{2} = 0. \quad (5')$$

Substituting (3) and (4) into this, we find

$$\beta \left(H - \frac{H(a-b-sH)}{\alpha} - \frac{H(\alpha+b+sH)(a-b-sH)}{v\alpha} \right) = \frac{(\alpha+b+sH)(v+b+sH) - \frac{av}{2}}{v}.$$

Expanding out and simplifying, we obtain

$$\beta H = \frac{\alpha \left(s^2 H^2 + sH(\alpha + 2b + v) + (\alpha + b)(v + b) - \frac{av}{2} \right)}{(s^2 H^2 + sH(v + \alpha + 2b - a) + (b - a)(\alpha + b + v) + \alpha v)} = W(H). \quad (6)$$

Let $W(H) = \frac{F(H)}{G(H)}$, where $F(H) = \alpha \left(s^2 H^2 + sH(\alpha + 2b + v) + (\alpha + b)(v + b) - \frac{av}{2} \right)$ and $G(H) = s^2 H^2 + sH(v + \alpha + 2b - a) + (b - a)(\alpha + b + v) + \alpha v$. The easiest way to determine the non-zero solutions is to attempt to graph $W(H)$ against H and find out where this function intersects the function βH . Let us first see if we can say anything about the slope of $W(H)$.

$$W(H) = \frac{\alpha \left(s^2 H^2 + sH(\alpha + 2b + v) + (\alpha + b)(v + b) - \frac{av}{2} \right)}{\left(s^2 H^2 + sH(v + \alpha + 2b - a) + (b - a)(\alpha + b + v) + \alpha v \right)} = \frac{F(H)}{G(H)}$$

$$\begin{aligned} \text{So that } W'(H) &= \frac{1}{G(H)^2} \left(\alpha \left[s^2 H^2 + sH(v + \alpha + 2b - a) + \alpha v - (a - b)(v + b + \alpha) \right] \left[2s^2 H + s(v + \alpha + 2b) \right] \right. \\ &\quad \left. - \alpha \left[s^2 H^2 + sH(v + \alpha + 2b) + (v + b)(\alpha + b) - \frac{av}{2} \right] \left[2s^2 H + s(v + \alpha + 2b - a) \right] \right) \\ &= \frac{\alpha}{G(H)^2} \left[2s^2 H^4 + s^3 H^2(v + \alpha + 2b) + 2s^3 H^2(v + \alpha + 2b - a) + s^2 H(v + \alpha + 2b - a)(v + \alpha + 2b) \right. \\ &\quad \left. + 2s^2 H(\alpha v - (a - b)(v + \alpha + b)) + s(\alpha v - (a - b)(v + \alpha + 2b))(v + \alpha + 2b) \right] \\ &\quad - \frac{\alpha}{G(H)^2} \left[2s^4 H^3 + s^3 H^2(v + \alpha + 2b - a) + 2s^3 H^2(v + \alpha + 2b) + s^2 H(v + \alpha + 2b)(v + \alpha + 2b - a) \right. \\ &\quad \left. + 2s^2 H^2 \left((v + b)(\alpha + b) - \frac{av}{2} \right) + s \left((v + b)(\alpha + b) - \frac{av}{2} \right) (v + \alpha + 2b - a) \right]. \end{aligned}$$

After a great deal of expanding and simplifying, we obtain

$$W'(H) = \frac{-\alpha \alpha s}{G(H)^2} \left(s^2 H + sH(v + 2b + 2\alpha) + b(v + \alpha + b) + \frac{v}{2}(v + \alpha + a) + \alpha^2 \right).$$

Given that all parameters are positive, we can say that for $H > 0$, $W'(H) < 0$.

The next thing to note is that we will have a horizontal asymptote occurring at $W(H) = \alpha$. Vertical asymptotes are given by the solutions of $G(H) = 0$, i.e.,

$$G(H) = s^2 H^2 + sH(v + \alpha + 2b - a) + (b - a)(\alpha + b + v) = 0.$$

Solving for H , we get

$$H = \frac{1}{2s^2} \left(-s(v+\alpha+2b-a) \pm \sqrt{s^2(v+\alpha+2b-a)^2 - 4s^2((b-a)(\alpha+b+v)+\alpha v)} \right).$$

Simplifying, gives

$$H = \frac{1}{2s} \left(-(v+\alpha+2b-a) \pm \sqrt{(v-\alpha)^2 + a(a+2v+2\alpha)} \right).$$

If we let $H = \frac{1}{2s} (A \pm B)$ where $A = -(v+\alpha+2b-a)$ and $B = \sqrt{(v-\alpha)^2 + a(a+2v+2\alpha)}$ then because of the parameter ranges, $A < 0$ and $B > 0$. However, we are unable to say anything about $|A|$ compared to $|B|$, so we consider both cases again. First, if $|A| > |B|$ then $G(H)=0$ will have two negative solutions. On the other hand, if $|A| < |B|$, $G(H)=0$ will have one positive and one negative solution.

Now let us look at where $W(H)=0$

$$F(H) = \alpha \left(s^2 H^2 + sH(\alpha+2b+v) + (\alpha+b)(v+b) - \frac{av}{2} \right) = 0.$$

Solving this for H, we find

$$\begin{aligned} H &= \frac{1}{2s^2} \left(-s(\alpha+2b+v) \pm \sqrt{s^2(v+\alpha+2b)^2 - 4s^2 \left((v+b)(\alpha+b) - \frac{av}{2} \right)} \right) \\ &= \frac{1}{2s} \left(-(\alpha+2b+v) \pm \sqrt{(v+\alpha+2b)^2 - 4(v+b)(\alpha+b) + 2av} \right). \end{aligned}$$

Simplifying, we get

$$H = \frac{1}{2s} \left(-(\alpha+2b+v) \pm \sqrt{(v-\alpha)^2 + 2av} \right).$$

Let $H = \frac{\alpha}{2s} (C \pm D)$ where $C = -(\alpha+2b+v)$ and $D = \sqrt{(v-\alpha)^2 + 2av}$. We notice straight away that $C < 0$ and $D > 0$. We are unable, again, to say anything about $|C|$ compared to $|D|$. So we will consider both cases. If $|C| > |D|$ then $F(H)=0$ has two negative solutions. If $|C| < |D|$, $F(H)=0$ will have one positive and one negative solution.

The possible solutions and asymptote combinations we can have for $W(H)$ are:

Case 1: $|A| > |B|$ and $|C| > |D|$

Case 2: $|A| < |B|$ and $|C| > |D|$

Case 3: $|A| > |B|$ and $|C| < |D|$

Case 4: $|A| < |B|$ and $|C| < |D|$

In Case 3, we have one positive and one negative solution to $F(H)=0$ and two negative vertical asymptotes, looking something like the following:

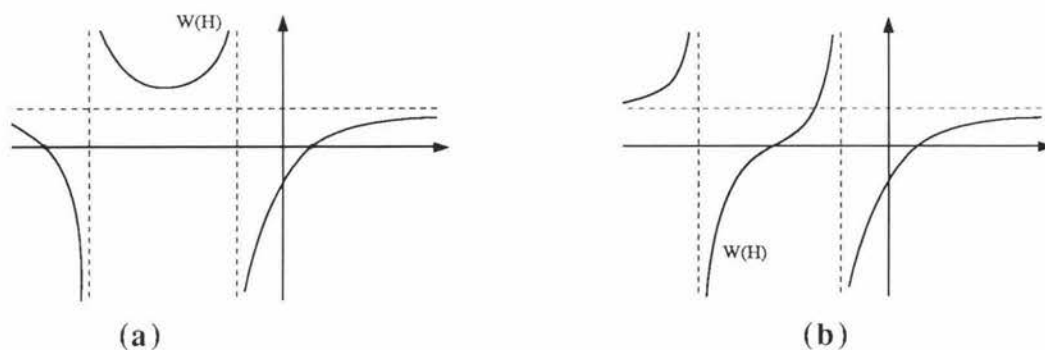


Figure 3.3

However, because we have found that the slope of $W(H)$ is decreasing for $H > 0$ this case has to be ruled out. Similarly we may rule out other instances where the slope of $W(H)$ is increasing.

If the solutions were in Case 1, we find that we have two negative solutions to $F(H)=0$ and two negative asymptotes, so that there would be one positive and two negative intersections occurring between $W(H)$ and βH :

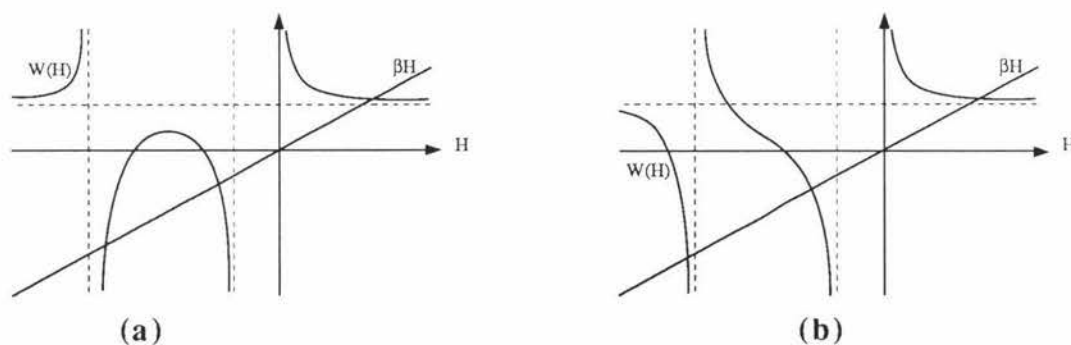


Figure 3.4

Case 2 would produce two negative solutions to $F(H)=0$ with one positive and one negative asymptote, giving one positive and two negative intersections between $W(H)$ and βH :

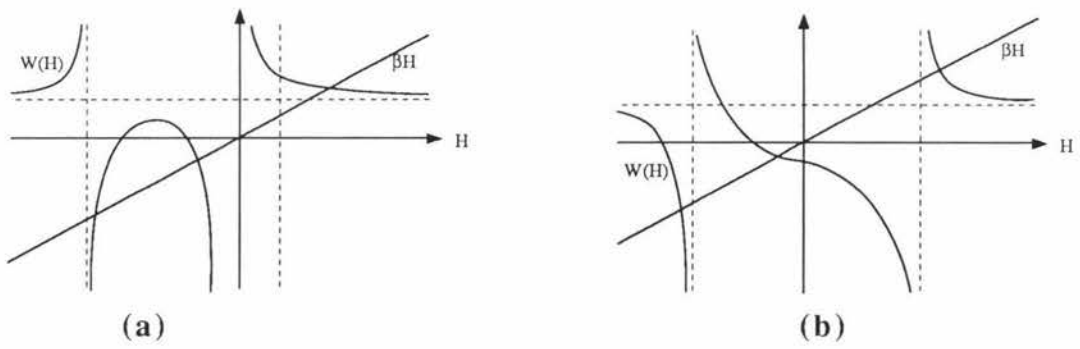


Figure 3.5

Finally, for Case 4, we would have one positive and one negative solution to $F(H)=0$ and one positive and one negative asymptote, producing two positive and one negative intersection between $W(H)$ and βH :

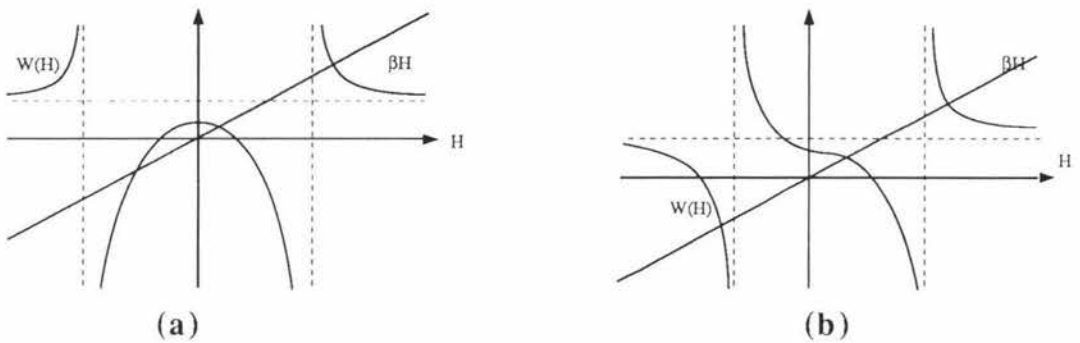


Figure 3.6

To find out what parameter conditions give rise to this particular scenario, we look at the solutions of $F(H)=0$. These are given by

$$\frac{1}{2s} \left(-(v+\alpha+2b) \pm \sqrt{(v+\alpha+2b)^2 - 4 \left((v+b)(\alpha+b) - \frac{av}{2} \right)} \right).$$

Now to produce two positive and one negative intersection between $W(H)$ and βH , we require $F(H)=0$ to have one negative and one positive solution. This means that

$$|-(v+\alpha+2b)| < \left| \sqrt{(v+\alpha+2b)^2 - 4 \left((v+b)(\alpha+b) - \frac{av}{2} \right)} \right|.$$

Expanding out the radical expression, we get

$$(v+\alpha+2b)^2 - 4(v+b)(\alpha+b) + 2av = (v+\alpha+2b)^2 - 4b\alpha - 4b^2 + 2v(a-2b-2\alpha).$$

So for this radical expression to be the larger, we need

$$-4b\alpha - 4b^2 + 2v(a - 2b - 2\alpha) > 0$$

$$\text{i.e. } \alpha < \frac{v(a-2b)-2b^2}{2(v+b)} = \alpha_c.$$

This enables us to summarise

Theorem 3.5.1: *If $\alpha > \alpha_c$, then there exist two negative and one positive non-zero solutions to (6). If $\alpha < \alpha_c$, then there exist two positive and one negative non-zero solution to (6). By inspection, if $\alpha = \alpha_c$, then there exists one positive and one negative non-zero solution and one zero solution to (6).*

Again at this stage we will clearly label the three equilibria. Let us call the equilibrium which has the largest H value, the Endemic equilibrium, similarly to the previous model. Label the equilibrium with the smallest H value, which is in fact always negative and was non-existent in the previous model, the Negative equilibrium, and finally let the equilibrium that has an H value between that of the Endemic and the Negative equilibrium be labelled the Wandering equilibrium, as we did in the previous model.

3.6 Bifurcations of Equilibria

In the previous model, we found that there were two real bifurcations: one between the Zero and the Wandering equilibria at a critical α value and the other, the Disease-free equilibrium, bifurcating with the Endemic equilibrium at a critical β value. In the latter case, the critical β condition was related to the stability of the Disease-free equilibrium. Let us see if we get the same phenomenon occurring with this three-dimensional model.

The condition for the Disease-free equilibrium to be stable is that

$$\beta < \left(\frac{s}{a-b}\right) \left(\frac{(v+a)(\alpha+a) - \frac{av}{2}}{v}\right) = \beta_c.$$

Thus, we expect a bifurcation at β_c between the Disease-free equilibrium and the Endemic equilibrium. Now rearranging (6) to a polynomial expression for H, we find that the Endemic equilibrium can be represented as one of the solutions of the following equation:

$$s^2\beta H^3 + (\beta s(v+\alpha+2b-a) - \alpha s^2)H^2 + \left((v\alpha + (b-a)(v+\alpha+b))\beta - \alpha s(\alpha+2b+v) \right)H + \frac{av\alpha}{2} - \alpha(v+b)(\alpha+b) = 0. \quad (7)$$

If this bifurcation takes place, then at β_c we should find that $H = \left(\frac{a-b}{s}\right)$ is one of the solutions of (7). Substituting $H = \left(\frac{a-b}{s}\right)$ and β_c into (7), we get

$$\begin{aligned} & s^2 \left(\frac{s}{a-b}\right) \left(\frac{a-b}{s}\right)^3 \left(\frac{(v+a)(\alpha+a) - \frac{av}{2}}{v}\right) \\ & + \left[\left(\frac{s}{a-b}\right) \left(\frac{a-b}{s}\right)^2 (v+\alpha+2b-a) \left(\frac{(v+a)(\alpha+a) - \frac{av}{2}}{v}\right) - \alpha \left(\frac{a-b}{s}\right)^2 s^2 \right] \\ & + \left(\frac{a-b}{s}\right) \left(\frac{s}{a-b}\right) (v\alpha + (b-a)(v+\alpha+b)) \left(\frac{(v+a)(\alpha+a) - \frac{av}{2}}{v}\right) \\ & - \alpha s \left(\frac{a-b}{s}\right) (\alpha+2b+v) + \frac{av\alpha}{2} - \alpha(v+b)(\alpha+b). \end{aligned}$$

After expanding and simplifying, we obtain

$$\begin{aligned} & \frac{(a-b)^2}{v} (v\alpha + \frac{av}{2} + a\alpha + a^2) + \frac{(a-b)}{v} (v+\alpha+2b-a) (v\alpha + \frac{av}{2} + a\alpha + a^2) \\ & + \frac{1}{v} (v\alpha + (b-a)(v+\alpha+b)) \left(v\alpha + \frac{av}{2} + a\alpha + a^2 \right) - \alpha(\alpha+2b+v)(a-b) \\ & + \frac{av\alpha}{2} - \alpha(v+b)(\alpha+b) \\ & = 0. \end{aligned}$$

Therefore, $H = \left(\frac{a-b}{s}\right)$ is a solution of (7) when $\beta = \beta_c$. We conclude

Theorem 3.6.1: As β passes through the critical value of β_c , the Endemic equilibrium bifurcates with the Disease-free equilibrium.

Now we look at the bifurcation between the Zero and the Wandering equilibria. This took place in the previous model when α passed through the critical value α_c , making the Wandering equilibrium positive.

That critical condition for this model is

$$\alpha < \frac{v(a-2b)-2b^2}{2(v+b)} = \alpha_c.$$

If we are to have a bifurcation at α_c between the Zero and the Wandering equilibria, we need $H = 0$ to be a solution of (7) at α_c . If this is so, then from (7)

$$\frac{av\alpha}{2} - \alpha(v+b)(\alpha+b) = 0$$

$$\Rightarrow \frac{av}{2} - (v+b)(\alpha+b) = 0,$$

so that

$$\begin{aligned} & \frac{av}{2} - (v+b) \left(\frac{v(a-2b)-2b^2}{2(v+b)} + b \right) \\ &= \frac{av}{2} - \frac{1}{2(v+b)} (v(a-2b)-2b^2+2b(v+b)) \\ &= 0. \end{aligned}$$

Therefore $H=0$ is a solution of (7) when $\alpha = \alpha_c$. Thus

Theorem 3.6.2: *As α passes through the critical value of α_c , the Wandering equilibrium bifurcates with the Zero equilibrium.*

3.7 Tracking the Non-Zero Equilibria

Now we look at the positions of the Wandering and the Endemic equilibria in relation to the feasible region for varying parameters.

Substituting for M from (4) into (5'), we can obtain an expression for Y in terms of H , namely

$$Y = \frac{-s^2H^2 - H(s(\alpha+v+2b)-v\beta) - (\alpha+b)(v+b) + \frac{av}{2}}{\beta(\alpha+v+b+sH)}, \quad (8)$$

and from (3), we have

$$Y = \frac{H(a-b-sH)}{\alpha}.$$

The intersections of these two curves represent our non-zero equilibria.

We first investigate the Wandering equilibrium's position relative to the feasible region when α varies about α_c . Consider the graph of (3) and (8). (8) is difficult to sketch as it contains many varying parameters. However, we can see that it has a negative vertical asymptote and an asymptote with negative slope (found by standard methods). Also, from Theorem 3.6.2 we know that at α_c (8) must intersect (3) at the origin. Thus, we have something like the following

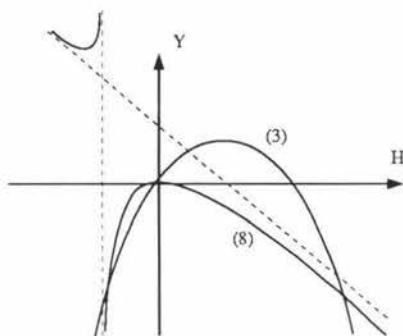


Figure 3.7

If α is slightly perturbed so that $\alpha > \alpha_c$ ($-\alpha < -\alpha_c$), then at $H=0$, we find (8) becomes

$$\begin{aligned} Y &= \frac{-s^2H^2 - H(s(\alpha+v+2b)-v\beta) - (\alpha+b)(v+b) + \frac{av}{2}}{\beta(\alpha+v+b+sH)} < \frac{-\alpha_c(v+b)-b(v+b) + \frac{av}{2}}{\beta(\alpha_c+v+b)} \\ &= \frac{-(v(a-2b)-2b^2)}{2(v+b)} (v+b) - b(v+b) + \frac{av}{2} \\ &= \frac{-av}{2} + \frac{av}{2} \\ &= 0 \end{aligned}$$

$$\therefore Y < 0.$$

This tells us that the intersection point of (3) and (8) which corresponds to the Wandering equilibrium will have a value of Y that is negative and because of the shape of (3), it will have a value of H that is also negative. Substituting Y and H into (4), (the equation for M), we find that M can be either positive or negative depending on the sign of $\alpha+b+sH$. However, in either situation the Wandering equilibrium is outside the feasible region when $\alpha > \alpha_c$.

Alternatively, if $\alpha < \alpha_c$ ($-\alpha > -\alpha_c$), then (8) gives $Y > 0$. In this instance, the intersection point corresponding to the Wandering equilibrium will have a value of Y that is positive and a value of H that is also positive, from Figure (3.7). Using (4) we find that the corresponding M value will be positive as well.

The question remaining now is "does the Wandering equilibrium enter the feasible region at any stage?". Consider Figure 3.6 (a) or (b). Let \hat{H} be the intersection point between $W(H)$ and βH that represents the Wandering equilibrium. In either of these instances we have a solution of $F(H) = 0$ for some $H > \hat{H}$. Now $F'(H) = \alpha(2s^2H + s(\alpha+2b+v)) > 0$ for positive H , so obviously at \hat{H} , $F(H) < 0$. See below:

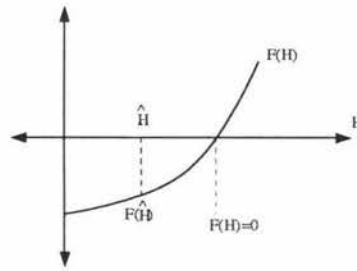


Figure 3.8

We know that $W(H)$ is positive at \hat{H} so $G(H) < 0$. At equilibrium we have (5')

$$\beta(H-Y-M) - \frac{(\alpha+b+sH)(v+b+sH)}{v} + \frac{a}{2} = 0.$$

Substituting (3) and (4) into this and rearranging, we obtain

$$\frac{\beta H}{\alpha v} (s^2 H^2 + sH(v+2b+\alpha-a) + (b-a)(\alpha+b+v) + \alpha v) = \frac{(\alpha+b+sH)(v+b+sH) - \frac{av}{2}}{v}$$

$$\Rightarrow \frac{\beta H}{\alpha v} G(H) = \frac{(\alpha+b+sH)(v+b+sH) - \frac{av}{2}}{v},$$

$$\text{where } G(H) = s^2 H^2 + sH(v+2b+\alpha-a) + (b-a)(\alpha+b+v) + \alpha v.$$

$$\text{But } \frac{(\alpha+b+sH)(v+b+sH) - \frac{av}{2}}{v} = \beta(H-Y-M), \text{ so}$$

$$\frac{\beta H}{\alpha v} G(H) = \beta(H-Y-M)$$

$$\therefore Y + M = \frac{H}{\alpha v} (\alpha v - G(H)) = H \left(1 - \frac{G(H)}{\alpha v} \right) \quad (9)$$

Now if $G(H) < 0$ at \hat{H} , then from (9) $\hat{Y} + \hat{M} > \hat{H}$. We conclude:

Theorem 3.7.1: When $\alpha < \alpha_c$ the Wandering equilibrium is outside the feasible region.

Now to investigate the Endemic equilibrium's position relative to the feasible region when β varies about β_c . Consider again the graph of (3) and (8), but at $\beta = \beta_c$ this time. From Theorem 3.6.1, we have that (8) will intersect (3) at $H = \left(\frac{a-b}{s} \right)$, $Y = 0$. Giving us the following situation:

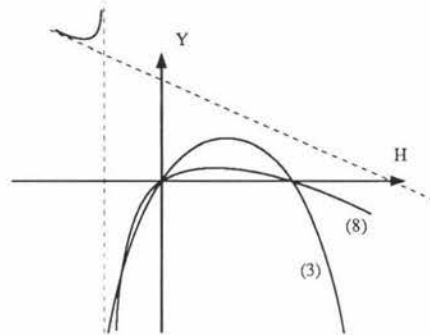


Figure 3.9

Now if β is slightly perturbed such that $\beta < \beta_c$, then at $H = \left(\frac{a-b}{s} \right)$, we find (8) becomes

$$Y = \frac{-s^2 H^2 - H(s(\alpha+v+2b) - v\beta) - (\alpha+b)(v+b) + \frac{av}{2}}{\beta(\alpha+v+b+sH)} < 0$$

This shows us that the intersection point of (3) and (8) which represents the Endemic equilibrium will have a Y value that is negative and because of the shape of (3) in Figure (3.9), it will have a value of H that is greater than $\left(\frac{a-b}{s} \right)$. From (4), M will take on a negative value also. Thus, the Endemic equilibrium is outside the feasible region when $\beta < \beta_c$.

Similarly, if β is perturbed so that $\beta > \beta_c$, then at $H = \left(\frac{a-b}{s}\right)$, (8) gives $Y > 0$. What this tells us is that the intersection point of (3) and (8) corresponding to the Endemic equilibrium will have a value of Y that is positive and, again because of the shape of (3), it will have a H value that is less than $\left(\frac{a-b}{s}\right)$. From (4), we see that M will be positive also. From here we would like to know if the Endemic equilibrium is within the feasible region and if so, whether it stays there as β varies beyond β_c .

Let \bar{H} be the intersection point that corresponds to the Endemic equilibrium. In any instance (from Figures 3.3-3.6) we have a solution to $F(H) = 0$ for some $H < \bar{H}$. As $F'(H) > 0$ for positive H , obviously $F(\bar{H}) > 0$.

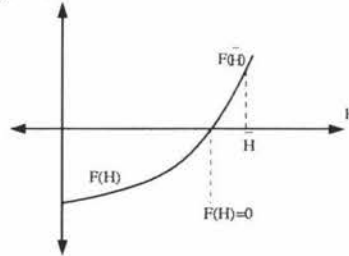


Figure 3.10

Since $F(\bar{H}) > 0$ and $W(\bar{H}) > 0$, then $G(\bar{H}) > 0$. From (9), we again have

$$Y + M = H \left(1 - \frac{G(H)}{\alpha v} \right),$$

so if $G(\bar{H}) > 0$, then $\bar{Y} + \bar{M} < \bar{H}$. Hence

Theorem 3.7.2: *When $\beta < \beta_c$ the Endemic equilibrium is outside the feasible region. When $\beta > \beta_c$ the equilibrium is within the feasible region.*

3.8 Stability of the Non-Zero Equilibria

The Jacobian for the system is given by

$$J = \begin{bmatrix} a-b-2sH & 0 & -\alpha \\ \beta Y - sM & -\beta Y - v - b - sH & \beta H - 2\beta Y - \beta M + \frac{a}{2} \\ -sY & v & -\alpha - b - sH \end{bmatrix}$$

the characteristic equation is

$$\begin{aligned}
& -\lambda^3 + \lambda^2(a-b-2sH-\beta Y-v-b-sH-\alpha-b-sH) - \lambda((a-b-2sH)(-\beta Y-v-b-sH-\alpha-b-sH) \\
& + (\beta Y+v+b+sH)-v(\beta H-2\beta Y-\beta M+\frac{a}{2})-\alpha s Y) \\
& + (a-b-2sH)\left((\beta Y+v+b+sH)(\alpha+b+sH)-v(\beta H-2\beta Y-\beta M+\frac{a}{2})\right) \\
& -\alpha v(\beta Y-sM)+\alpha s Y(\beta Y+v+b+sH) = 0. \tag{10}
\end{aligned}$$

We know from (5') that the equation for the non-zero equilibria is represented by

$$\beta H = \frac{(\alpha+b+sH)(v+b+sH)}{v} - \frac{a}{2} + \beta Y + \beta M.$$

Thus, we can simplify expression (10):

$$\begin{aligned}
& -\lambda^3 + \lambda^2(a-3b-4sH-v-\alpha-\beta Y) - \lambda((a-b-2sH)(-\beta Y-v-\alpha-2b-2sH) + \beta Y(v+\alpha+b+sH) - \alpha s Y) \\
& + \beta Y(a-b-2sH)(v+\alpha+b+sH) - \alpha v(\beta Y-sM) + \alpha s Y(\beta Y+v+b+sH) = 0. \tag{10'}
\end{aligned}$$

From (1c), we know $M = \frac{Y(\alpha+b+sH)}{v}$, so (10') now becomes

$$\begin{aligned}
& -\lambda^3 + \lambda^2(a-3b-4sH-v-\alpha-\beta Y) - \lambda((a-b-2sH)(-\beta Y-v-\alpha-2b-2sH) + \beta Y(v+\alpha+b+sH) - \alpha s Y) \\
& + \beta Y(a-b-2sH)(v+\alpha+b+sH) - \alpha s \beta Y + \alpha s(\alpha+b+sH) + \alpha s Y(\beta Y+v+b+sH) = 0. \tag{11}
\end{aligned}$$

Let us determine the stability of the Endemic equilibrium at the bifurcation $H = \left(\frac{a-b}{s}\right)$,

$M=Y=0$. We see that (10) then becomes

$$-\lambda^3 + \lambda^2(a-3b-4(a-b)-v-\alpha) - \lambda(a-b-2(a-b))(-v-\alpha-2b-2(a-b)) + (a-b-2(a-b)) = 0$$

$$\Leftrightarrow -\lambda(\lambda^2 - \lambda(b-3a-v-\alpha) + (a-b)(v+\alpha+2a)) = 0$$

$$\Leftrightarrow \lambda = 0 \text{ or } \lambda = \frac{b-3a-v-\alpha}{2} \pm \frac{\sqrt{(b-3a-v-\alpha)^2 - 4(a-b)(v+\alpha+2a)}}{2}$$

$$\Leftrightarrow \lambda_1 = 0, \lambda_2 = b-a \text{ and } \lambda_3 = -2a-v-\alpha.$$

Obviously, λ_2 and $\lambda_3 < 0$. However because $\lambda_1 = 0$, the Principal of Linearised Stability fails and we are unable to draw a conclusion. We need to find out what happens to these eigenvalues when the equilibrium is slightly removed from the bifurcation point.

Consider the following graph of the function

$$F(\lambda) = -\lambda^3 + \lambda^2(b - 3a - v - \alpha) - \lambda(a - b)(v + \alpha + 2a)$$

whose zeros are the eigenvalues at this equilibrium value:

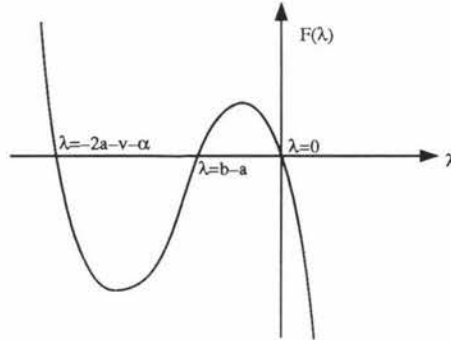


Figure 3.11

At an equilibrium close to $H = \left(\frac{a-b}{s}\right)$, $M=Y=0$, the eigenvalues will be the zeros of a function which is obtained from this by a small perturbation. Any such slight perturbation of this function will cause the equilibrium to become stable or unstable depending on which way the zero eigenvalue moves.

If we look at where the function cuts the $F(\lambda)$ axis, then (this will enable us to say that) if the $F(\lambda)$ axis intercept is positive then the formerly zero eigenvalue will become positive and so, the equilibrium will be unstable. Similarly, if the $F(\lambda)$ axis intercept is negative, then the formerly zero eigenvalue will become negative making the equilibrium stable.

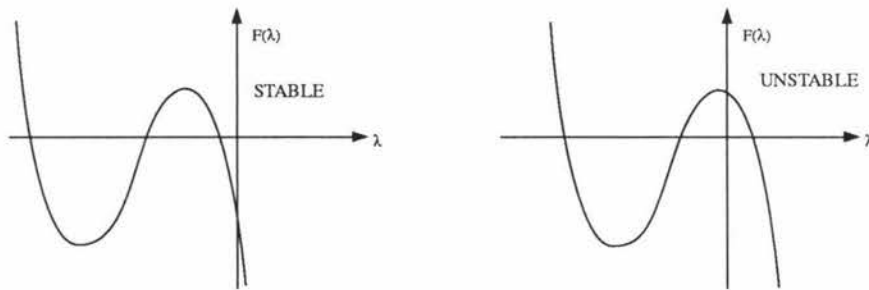


Figure 3.12

From (11), the term which corresponds to the $F(\lambda)$ intercept is

$$\beta Y(a - b - 2sH)(\alpha + v + b + sH) - \alpha v \beta Y + \alpha s Y(\alpha + b + sH) + \alpha s Y(v + b + sH) + \alpha s \beta Y^2 \tag{12}$$

If we substitute for $a - b - 2sH$ using (3), we get

$$\left(\frac{\alpha\beta Y^2}{H} - \beta s Y H\right)(\alpha + v + b + sH) - \alpha v \beta Y + \alpha s Y(\alpha + b + sH) + \alpha s Y(v + b + sH) + \alpha s \beta Y^2. \quad (12')$$

Since $Y \approx 0$, $\frac{\alpha\beta Y^2}{H}$ and $\alpha s \beta Y^2$ will be second order small quantities and can be neglected. So (11') becomes

$$Y(-s\beta H(\alpha + v + b + sH) - v\alpha\beta + \alpha s(\alpha + b + sH) + \alpha s(v + b + sH)). \quad (13)$$

Let us investigate the sign of $-s\beta H(\alpha + v + b + sH) - v\alpha\beta + \alpha s(\alpha + b + sH) + \alpha s(v + b + sH)$ at $H \approx \left(\frac{a-b}{s}\right)$ $\beta \approx \beta_c$. (13) then becomes

$$-s\left(\frac{(v+a)(\alpha+a) - \frac{av}{2}}{v}\right)(\alpha + v + a) - \alpha\left(\frac{s}{a-b}\right)\left(\frac{(v+a)(\alpha+a) - \frac{av}{2}}{v}\right) + \alpha s(\alpha + 2a + v).$$

Expanding out and rearranging, we get

$$\frac{-s(2a^4 + a^3(3v + 4\alpha - 2b) + a^2(v^2 + 3\alpha v + 2\alpha^2 - b(3v + 4\alpha)) + a(v\alpha(v + 2\alpha) - b(v^2 + \alpha v + 2\alpha^2)) + 2v^2\alpha^2)}{2v(a-b)}.$$

Factorising gives

$$\frac{-s(a(a-b)(2a^2 + 4a\alpha + v^2 + 2\alpha^2) + 3a^3v(1-b) + va\alpha(3a-b) + a\alpha v^2 + 2av\alpha^2 + 2v^2\alpha^2)}{2v(a-b)}$$

$$= \tau \text{ (say).}$$

Since $a > b$ and $1-b > 0$, $\tau < 0$ for all a, b, v and $\alpha > 0$.

If $Y < 0$, the vertical axis intercept of (13) will be positive and the formerly zero eigenvalue will become positive. Thus, the Endemic equilibrium will be unstable. If $Y > 0$, then the vertical axis intercept of (13) will be negative and the formerly zero eigenvalue will become negative. Thus, the Endemic equilibrium will be stable, enabling us to conclude

Theorem 3.7.1: *A change of stability occurs when the Endemic equilibrium bifurcates with the Disease-free equilibrium. Namely, if $Y < 0$ the Endemic equilibrium is UNSTABLE, and if $Y > 0$, the Endemic equilibrium is STABLE.*

Now let us determine the stability of the Wandering equilibrium at the bifurcation $H=M=Y=0$. The Jacobian matrix will therefore be

$$J = \begin{bmatrix} a-b & 0 & -\alpha \\ 0 & -v-b & \frac{a}{2} \\ 0 & v & -\alpha-b \end{bmatrix},$$

giving a characteristic polynomial

$$(a-b-\lambda)(\lambda^2+\lambda(v+2b+\alpha_c)+(v+b)(\alpha_c+b)-\frac{av}{2}) = 0 \quad (14)$$

$$\Rightarrow (a-b-\lambda)\left(\frac{-v-2b-\alpha_c \pm \sqrt{(v-\alpha_c)^2+2av}}{2}\right) = 0,$$

which has solutions $\lambda_1, \lambda_2, \lambda_3$ where

$$\lambda_1 = a-b, \quad \lambda_2 = \frac{-v-2b-\alpha_c + \sqrt{(v-\alpha_c)^2+2av}}{2}$$

and
$$\lambda_3 = \frac{-v-2b-\alpha_c - \sqrt{(v-\alpha_c)^2+2av}}{2}.$$

Note that $\lambda_1 > 0$ and $\lambda_3 < 0$. Now $\alpha_c = \frac{v(a-2b)-2b^2}{2(v+b)}$, so that λ_2 becomes

$$\frac{1}{2} \left(\frac{2(v+b)(-v-2b)-(v(a-2b)-2b^2)}{2(v+b)} + \sqrt{\left(\frac{2v(v+b)-(v(a-2b)-2b^2)}{2(v+b)} \right)^2 + 2av} \right).$$

After simplifying

$$\lambda_2 = \frac{1}{2} \left(\frac{-2(v+b)^2-av}{2(v+b)} + \sqrt{\left(\frac{2(v+b)^2-av}{2(v+b)} \right)^2} \right)$$

$$\therefore \lambda_2 = 0.$$

Now consider the graph of (14) whose zeros are the eigenvalues at H_w :

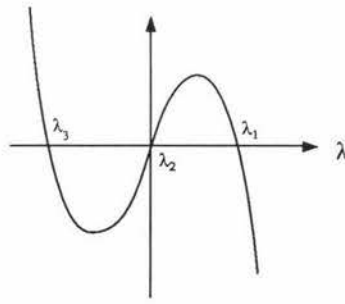


Figure 3.13

At a slight perturbation from α_c , $H \approx 0$, $Y \approx 0$ and $M \approx 0$ and λ_3 will become either positive or negative depending on which way α is perturbed from α_c . However, because $\lambda_1 = a - b > 0$, there will still be a positive eigenvalue and so at an equilibrium close to α_c the Principal of Linearised Stability concludes that we will have instability. Hence

Theorem 3.7.2: *At an equilibrium close to the origin ($\alpha \approx \alpha_c$), the Wandering equilibrium remains UNSTABLE.*

3.8 Summary

A very similar picture emerged from the analysis of this 3-dimensional system to the previous model. There was a threshold above which there existed a stable endemic steady state and below which the disease became extinct. Again, this threshold was a bifurcation threshold between the Disease-free and the Endemic equilibria. Above it, the Endemic equilibrium remained within the feasible region and was stable with the Disease-free equilibrium unstable, while below the threshold the Endemic equilibrium was outside the feasible region and unstable with the Disease-free equilibrium stable.

Similarly, there was a bifurcation between the Wandering and the Zero equilibria, at a different parameter threshold than the one above. Both equilibria remained unstable and the Wandering equilibrium never entered the feasible region.

Another equilibrium existed but corresponded to negative disease and population numbers, so because of the biological irrelevance of such an equilibrium, no further analysis was carried out.

Hopf bifurcations were not checked in this model as the algebra involved in this process was too complicated.

Introduction of a latency period had the overall effect that when decreased, it reduced the total density of possums, increased the prevalence of infection and increased the amplitude of the oscillations to equilibrium. Similarly, when the latency period was increased there was an increase in density of possums, a decrease in the prevalence and the oscillations to equilibrium were damped.

§4 Model 4: Restriction on the Contact Rate per Individual

4.1 Introduction

In the previous 2D model, the term which represented the increase in diseased individuals from diseased animals interacting with the rest of the population can be given by

$$\beta DH \left(\frac{H-D}{H} \right),$$

where β is the transmission coefficient, DH is the number of diseased animals interacting with the whole population and $\left(\frac{H-D}{H} \right)$ is the proportion of the population that become infected. If, instead of the diseased animals interacting with the whole population each diseased animal is restricted to associate with a fixed number of possums, then we could view the model as slightly more realistic for the simple reason that a particular possum can only interact with a certain number of other possums in a given time. What this would mean in mathematical terms, is that our contact term would become

$$k D \left(\frac{H-D}{H} \right)$$

where k incorporates the previous β (transmission coefficient) and also includes an interaction coefficient. This would result in the following system, $\frac{d\mathbf{u}}{dt}$:

$$\frac{dH}{dt} = H(a-b-sH) - \alpha D \quad (\mathbf{A}'')$$

$$\frac{dD}{dt} = \frac{kD(H-D)}{H} - D(\alpha+b+sH) + \frac{aD}{2} \quad (\mathbf{B}'')$$

Before we begin, we make the restriction that $H \neq 0$ to avoid any problems with (B''). Since very small H , (total population size), is not really important in this study, this seems acceptable. Let us investigate this particular restriction on contact rate to see if it has a major affect on the structure of the model.

4.2 Boundedness of Solutions

Again we begin by checking that solution to this system remain bounded once they enter the feasible region. If $\frac{d\mathbf{u}}{dt} \cdot \underline{\mathbf{n}} > 0$ on all feasible region boundaries, then the feasible region will be invariant.

Consider first the boundary $D = H$. The inward normal vector is $\underline{\mathbf{n}} = (1, -1)$, so that:

$$\frac{d\mathbf{u}}{dt} \cdot \underline{\mathbf{n}} = H(a-b-sH) - \alpha D - \frac{kD}{H} (H-D) + D(\alpha+b+sH) - \frac{aD}{2}$$

where $D = H$. This then becomes

$$\frac{d\mathbf{u}}{dt} \cdot \underline{\mathbf{n}} = \frac{aH}{2} > 0$$

Next, take the boundary $D = 0$. The inward normal vector is then $\underline{\mathbf{n}} = (0, 1)$. Thus

$$\frac{d\mathbf{u}}{dt} \cdot \underline{\mathbf{n}} = 0.$$

Again, this means that the trajectories travel along the boundary $D = 0$, and never leave the feasible region.

The only other way a system trajectory could leave the feasible region is at the intersection of the two boundaries. This only occurs at the origin, the point which we know causes difficulties. So if we disregard this point, which is what we will be doing throughout the rest of the analysis, then everywhere else the feasible region will be invariant.

4.3 Solutions at Equilibrium

Equilibria occur when $\frac{dH}{dt} = \frac{dD}{dt} = 0$. From (A''), we get:

$$D = \frac{H(a-b-sH)}{\alpha} \tag{1}$$

and from (B''):

$$D \left[\frac{k(H-D)}{H} - (\alpha+b+sH) + \frac{a}{2} \right] = 0 \tag{2}$$

$$\Rightarrow D = 0 \text{ or } \frac{k(H-D)}{H} - (\alpha+b+sH) + \frac{a}{2} = 0$$

If $D = 0$, then from (1)

$$H(a-b-sH) = 0$$

$$\Rightarrow H = 0 \text{ or } H = \left(\frac{a-b}{s}\right)$$

Since $H \neq 0$, we can only have an equilibrium at $H = \left(\frac{a-b}{s}\right)$ when $D = 0$. This represents a Disease-free equilibrium, $H_d = \left(\left(\frac{a-b}{s}\right), 0\right) = (H^*, 0)$.

The Jacobian matrix at H_d is

$$J = \begin{bmatrix} b-a & -\alpha \\ 0 & k-\alpha-\frac{a}{2} \end{bmatrix},$$

whose eigenvalues are $\lambda_1 = b-a < 0$ and $\lambda_2 = k-\alpha-\frac{a}{2}$. For H_d to be stable, we require that:

$$\lambda_2 = k-\alpha-\frac{a}{2} < 0$$

$$\Rightarrow k < \alpha + \frac{a}{2} = k_c$$

Thus, we can state the following:

Theorem 4.3.1: *If $k < k_c$, the Disease-free equilibrium H_d is STABLE. If $k > k_c$, then H_d is UNSTABLE.*

4.4 Existence of a Non-Zero Equilibrium

If $D \neq 0$ in (2), then:

$$\frac{k(H-D)}{H} - (\alpha+b+sH) + \frac{a}{2} = 0 \quad (3)$$

Substituting (1) for D, we obtain

$$\frac{k}{H} \left[H - \frac{H(a-b-sH)}{\alpha} \right] - (\alpha+b+sH) + \frac{a}{2} = 0.$$

Simplifying, we get

$$H = \frac{(k-\alpha)(\alpha+b) - a(k - \frac{\alpha}{2})}{(\alpha-k)s}. \quad (4)$$

Solving (3) for D gives

$$D = \frac{H(k + \frac{a}{2} - \alpha - b - sH)}{k}, \quad (5)$$

and substituting (4) into (5), we end up with the following expression for D:

$$D = \left[\frac{(k-\alpha)(\alpha+b) - a(k - \frac{\alpha}{2})}{(\alpha-k)s} \right] \left[\frac{\frac{a}{2} + \alpha - k}{\alpha - k} \right]. \quad (6)$$

Summarising

Theorem 4.4.1: *There exists one non-zero equilibrium which we will call the Endemic equilibrium, whose solution is given by (4) and (6).*

4.5 Bifurcations of Equilibria

The necessary condition for a real bifurcation is

$$H(a-b-sH) - \alpha D = \frac{kD(H-D)}{H} - D(\alpha+b+sH) + \frac{aD}{2} = \det(\text{Jacobian}) = 0$$

The Jacobian matrix for this system is given by

$$J = \begin{bmatrix} a-b-2sH & -\alpha \\ k\frac{D^2}{H^2} - sD & k - \frac{2kD}{H} - \alpha - b - sH + \frac{a}{2} \end{bmatrix}.$$

Substituting (3) into this, we find

$$J = \begin{bmatrix} a-b-2sH & -\alpha \\ k\frac{D^2}{H^2} - sD & -\frac{kD}{H} \end{bmatrix}, \quad (7)$$

so that $\det(\text{Jacobian})=0$ becomes

$$\begin{aligned} & -\frac{kD}{H} [a-b-2sH] + \alpha \left[k\frac{D^2}{H^2} - sD \right] = 0 \\ \Rightarrow & D \left[-\frac{k}{H}(a-b-2sH) + \alpha \left(k\frac{D}{H^2} - s \right) \right] = 0 \\ \Rightarrow & D = 0 \quad \text{or} \quad -\frac{k}{H}(a-b-2sH) + \alpha \left(k\frac{D}{H^2} - s \right) = 0. \end{aligned}$$

If $D = 0$, then from (1), $H = \frac{a-b}{s}$. We therefore have a bifurcation occurring at the Disease-free equilibrium. If we make the assumption that it is the Endemic equilibrium H_e that bifurcates with the Disease-free equilibrium as was the case in previous models, then this would mean that $H = \frac{a-b}{s}$, $D = 0$ must be a solution to

$$\frac{k(H-D)}{H} - \alpha - b - sH + \frac{a}{2} = 0,$$

which enables us to obtain a parameter threshold for this bifurcation to occur, namely

$$\begin{aligned} & k - \alpha - b - (a-b) + \frac{a}{2} = 0 \\ \Rightarrow & k = \alpha + \frac{a}{2} = k_c. \end{aligned}$$

Hence

Theorem 4.5.1: *As k passes through the critical value of k_c , the Endemic equilibrium bifurcates with the Disease-free equilibrium.*

If $D \neq 0$, then

$$-\frac{k}{H} (a-b-2sH) + \alpha \left(\frac{\alpha D}{H^2} - s \right) = 0.$$

From (1), we have $a-b-2sH = \frac{\alpha D}{H} - sH$, giving us:

$$-\frac{k}{H} \left(\frac{\alpha D}{H} - sH \right) + \frac{\alpha k D}{H^2} - \alpha s = 0$$

$$\therefore ks - \alpha s = 0$$

$$\Rightarrow s(k-\alpha) = 0.$$

Since $s \neq 0$, $\alpha = k$. However, as this does not satisfy equation (4) this tells us that there are no further real bifurcations in the system.

There are three necessary conditions that need to be satisfied in order for there to be a complex or Hopf bifurcation. Suppose the eigenvalues of the Jacobian matrix are given by:

$$\lambda = a(k) \pm b(k) i,$$

i.e.,

$$\lambda = \frac{a-b-2sH - \frac{kD}{H} \pm \sqrt{\left(a-b-2sH - \frac{kD}{H}\right)^2 - 4\left(\alpha \left(\frac{kD^2}{H^2} - sD\right) - \frac{kD}{H} (a-b-2sH)\right)}}{2}$$

As in Chapter 2, the first requirement for a complex bifurcation is that $a(k) = 0$ (i.e. $\text{tr}(\text{Jac}) = 0$). If we treat k as our bifurcation parameter, then at $k = k^*$, $a(k^*) = 0$.

From (7), $\text{tr}(\text{Jac}) = 0$

$$\Rightarrow a-b-2sH - \frac{kD}{H} = 0$$

$$\Rightarrow k = \frac{H(a-b-2sH)}{D}.$$

Substituting (4) and (5) into this, we find

$$k = \frac{a}{2} + \alpha - sH = k^* \quad \text{or} \quad H = \frac{\frac{a}{2} + \alpha - k}{s}.$$

Now for H to actually obtain this value

$$\frac{\frac{a}{2} + \alpha - k}{s} = \frac{(k - \alpha)(\alpha + b) - a(k - \frac{\alpha}{2})}{(\alpha - k)s}.$$

Rearranging for k , we get

$$k^2 + k(\frac{a}{2} - b - 3\alpha) + \alpha(2\alpha + b) = 0.$$

If we solve this for our bifurcation parameter, we find

$$k = \frac{3\alpha + b - \frac{a}{2}}{2} \pm \frac{1}{4} \sqrt{a^2 - 4a(b + 3\alpha) + 4b^2 + 8b\alpha + 4\alpha^2} = k_1^*, k_2^*.$$

Because all parameters in this model are positive, we must ensure that these solutions for k are real and positive. Notice that the radical term is a quadratic in α , so for this expression to be positive, $\alpha < \frac{3a}{2} - b - \sqrt{2a(a-b)}$ or $\alpha > \frac{3a}{2} - b + \sqrt{2a(a-b)}$. In the first instance when $\alpha < \frac{3a}{2} - b - \sqrt{2a(a-b)}$, we have:

$$\begin{aligned} \frac{3\alpha + b - \frac{a}{2}}{2} &< \frac{3\left(\frac{3a}{2} - b - \sqrt{2a(a-b)}\right) + b - \frac{a}{2}}{2} \\ &= 4a - 3b - 3\sqrt{2a(a-b)}. \end{aligned}$$

For the specified a and b , this expression is negative, so

$$\frac{3\alpha + b - \frac{a}{2}}{2} < 0.$$

Thus, the first part of our k solution is negative. To determine the magnitude of $\frac{3\alpha + b - \frac{a}{2}}{2}$ in relation to the radical term, we can rewrite the above solutions for k as

$$k = \frac{-\left(\frac{a}{2} - b - 3\alpha\right)}{2} \pm \frac{1}{4} \sqrt{\left(\frac{a}{2} - b - 3\alpha\right)^2 - 4\alpha(2\alpha + b)}.$$

By inspection, we can see that the first expression will dominate the radical expression, so our two solutions for k , k_1^* and k_2^* , will be negative and so $\alpha < \frac{3a}{2} - b - \sqrt{2a(a-b)}$ will not represent a valid complex bifurcation.

If, on the other hand, $\alpha > \frac{3a}{2} - b + \sqrt{2a(a-b)}$, then

$$\frac{3\alpha + b - \frac{a}{2}}{2} > \frac{3\left(\frac{3a}{2} - b + \sqrt{2a(a-b)}\right) + b - \frac{a}{2}}{2}$$

$$= 4a - 2b + 3\sqrt{2a(a-b)} > 0$$

$$\therefore \frac{3\alpha + b - \frac{a}{2}}{2} > 0.$$

We know that the k solutions are dominated by this term, so our solutions for k will be positive for $\alpha > \frac{3a}{2} - b + \sqrt{2a(a-b)}$. This in turn implies that H can have a value of $\frac{\frac{a}{2} + \alpha - k}{s}$ under these parameter conditions.

Can we say anything about the sign of H and D when $\alpha > \frac{3a}{2} - b + \sqrt{2a(a-b)}$ and $k = k_1^*$ or $k = k_2^*$? If we substitute k_1^* and k_2^* into $H = \frac{\frac{a}{2} + \alpha - k}{s}$, we find that

$$H = \frac{\frac{a}{2} + \alpha - k}{s} = \frac{\frac{a}{2} + \alpha - \left(\frac{3\alpha + b - \frac{a}{2}}{2} \pm \frac{1}{4}\sqrt{(a-2b)^2 - 4\alpha(3a-2b-\alpha)}\right)}{s}$$

$$\therefore H = \frac{1}{4s} \left(3a - 2\alpha - 2b \pm \sqrt{(a-2b)^2 - 4\alpha(3a-2b-\alpha)}\right).$$

If $\alpha > \frac{3a}{2} - b + \sqrt{2a(a-b)}$, then the first part of this expression becomes

$$3a - 2b - 2\alpha < 3a - 2b - 2\left(\frac{3a}{2} - b + \sqrt{2a(a-b)}\right)$$

$$= -2\sqrt{2a(a-b)} < 0$$

$$\therefore 3a - 2b - 2\alpha < 0$$

To determine the magnitude of $3a-2b-2\alpha$ in relation to the radical expression, we see that:

$$(3a-2\alpha-2b)^2 = 9a^2+4\alpha^2+4b^2-12a\alpha-12ab+8\alpha b,$$

so that the radical term can be given by

$$(a-2b)^2-4\alpha(3a-2b-\alpha) = (3a-2\alpha-2b)^2 + 8a(b-a)$$

Since $b-a < 0$,

$$|\sqrt{(a-2b)^2-4\alpha(3a-2b-\alpha)}| < |3a-2\alpha-2b|.$$

Hence, the two solution we obtain for H are negative when $\alpha > \frac{3a}{2} - b + \sqrt{2a(a-b)}$ and $k=k_1^*$ or $k=k_2^*$.

Now we know that D is given by (6), namely:

$$D = H \left(\frac{\frac{a}{2} + \alpha - k}{\alpha - k} \right)$$

If we already know that $H < 0$, then we have to determine the sign of $\left(\frac{\frac{a}{2} + \alpha - k}{\alpha - k} \right)$. At

$$k = \frac{3\alpha + b - \frac{a}{2}}{2} \pm \frac{1}{4} \sqrt{(a-2b)^2 - 4\alpha(3a-2b-\alpha)}.$$

$$\frac{\frac{a}{2} + \alpha - k}{\alpha - k} = \frac{3a-2b-2\alpha \pm \sqrt{(a-2b)^2 - 4\alpha(3a-2b-\alpha)}}{a-2b-2\alpha \pm \sqrt{(a-2b)^2 - 4\alpha(3a-2b-\alpha)}} \quad (8)$$

From the working just done, we can say that the numerator expression is negative. As for the denominator, if $\alpha > \frac{3a}{2} - b + \sqrt{2a(a-b)}$, then the first part becomes

$$a-2b-2\alpha < a-2b-2\left(\frac{3a}{2} - b + \sqrt{2a(a-b)}\right)$$

$$= -2a-2\sqrt{2a(a-b)} < 0$$

$$\therefore a-2b-2\alpha < 0.$$

Now to check the magnitude of $a-2b-2\alpha$ in relation to the radical expression, we see that the term under the radical can be represented by

$$(a-2b)^2-4\alpha(3a-2b-\alpha) = (a-2b-2\alpha)^2 + 8a(b-\alpha).$$

Again, for $\alpha > \frac{3a}{2} - b + \sqrt{2a(a-b)}$, this becomes

$$= (a-2b-2\alpha)^2 + 8a\left(2b - \frac{3a}{2} - \sqrt{2a(a-b)}\right).$$

For the specified a and b , $2b - \frac{3a}{2} - \sqrt{2a(a-b)} < 0$

$$\Rightarrow |(a-2b-2\alpha)| > |\sqrt{(a-2b)^2-4\alpha(3a-2b-\alpha)}|$$

Hence, our denominator and numerator are negative in (8). Thus for $\alpha > \frac{3a}{2} - b + \sqrt{2a(a-b)}$, and $k=k_1^*$ or $k=k_2^*$, we have H and D negative. At this stage we could stop because any chance of a Hopf bifurcation occurs outside the biologically feasible region. However, we continue because the next requirement for such a bifurcation fails.

The next condition for the Hopf bifurcation is that $b(k) < 0$, at k^* .

$$\Rightarrow \frac{4k^*D}{H}(a-b-2sH) - 4\alpha\left(\frac{k^*D^2}{H^2} - sD\right) < 0$$

$$\Rightarrow 4D\left(\frac{k^*}{H}(a-b-2sH) - \alpha\left(\frac{k^*D}{H^2} - s\right)\right) < 0$$

$$\Rightarrow D > 0 \text{ and } \frac{k^*}{H}(a-b-2sH) - \alpha\left(\frac{k^*D}{H^2} - s\right) < 0$$

$$\text{or } D < 0 \text{ and } \frac{k^*}{H}(a-b-2sH) - \alpha\left(\frac{k^*D}{H^2} - s\right) > 0.$$

In the first case, we have $D > 0$ which contradicts the working above that says $D < 0$. In the second instance, $D < 0$ and

$$\frac{k^*}{H}(a-b-2sH) - \alpha\left(\frac{k^*D}{H^2} - s\right) > 0.$$

From (1), we know that $a-b-2sH = \frac{\alpha D}{H} - sH$, so that

$$\begin{aligned} & \frac{k^*}{H} \left(\frac{\alpha D}{H} - sH \right) - \alpha \left(\frac{k^* D}{H} - s \right) > 0 \\ \Rightarrow & -k^* s + \alpha s > 0 \\ \Rightarrow & s(\alpha - k^*) > 0. \end{aligned}$$

Since $s > 0$, $\alpha > k^*$. Now $k^* = \frac{a}{2} + \alpha - sH$, so

$$\begin{aligned} & \alpha > \frac{a}{2} + \alpha - sH \\ \Rightarrow & H > \frac{a}{2s}. \end{aligned}$$

Again, we have a contradiction as $\frac{a}{2s}$ is positive. Thus, our second necessary condition for a complex bifurcation fails, enabling us to conclude that there is no Hopf bifurcation in the system, for the specified parameter values.

4.6 Tracking the Non-Zero Equilibria

Now, we investigate the Endemic equilibrium's position relative to the feasible region about the bifurcation value k_c . Consider equations (1) and (5) whose non-zero intersection determines the Endemic solution. From Theorem 4.5.1, we know that the Endemic equilibrium bifurcates with the Disease-free equilibrium when $k = k_c$. So what happens to the Endemic equilibrium as k varies about k_c ?

If k is slightly perturbed so that $k < k_c$, then at $H = \frac{a-b}{s}$, we find (5) becomes:

$$\begin{aligned} D &= \frac{H(k + \frac{a}{2} - \alpha - b - sH)}{k} < \left(\frac{a-b}{s} \right) \left(\frac{k_c - \alpha - \frac{a}{2}}{k_c} \right) \\ &= 0 \end{aligned}$$

$$\therefore D < 0$$

This tells us that the intersection point of (1) and (5) corresponding to the Endemic equilibrium will have a value of D that is negative and because of the shape of (1), it will have a value of H that is greater than $\frac{a-b}{s}$:

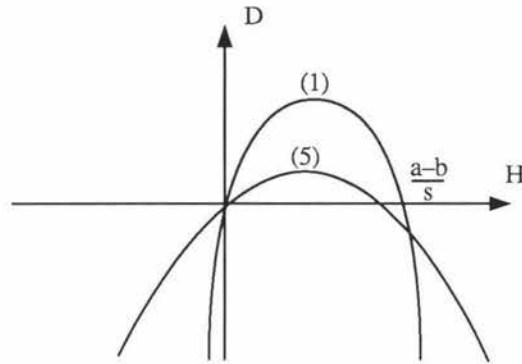


Figure 4.1

Similarly, if k is perturbed the other way so that $k > k_c$, then at $H = \frac{a-b}{s}$, (5) becomes

$$D = \frac{H(k + \frac{a}{2} - \alpha - b - sH)}{k} > \left(\frac{a-b}{s}\right) \left(\frac{k_c - \alpha - \frac{a}{2}}{k_c}\right)$$

$$= 0$$

$$\therefore D > 0$$

In this instance, the intersection point of (1) and (5) corresponding to the Endemic equilibrium will have a value of D that is positive and a value of H that is less than $\frac{a-b}{s}$.

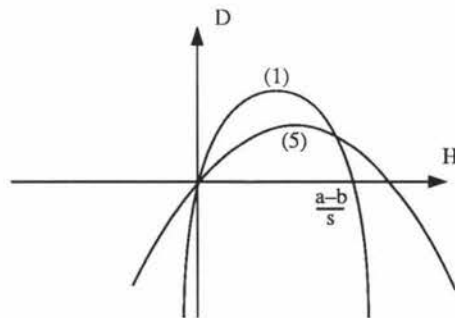


Figure 4.2

Concluding

Theorem 4.6.1: If $k < k_c$, then the Endemic equilibrium is outside the feasible region, with a D value that is negative and an H value that is greater than $\left(\frac{a-b}{s}\right)$. If $k > k_c$, then the

Endemic equilibrium enters the feasible region with a corresponding value of D that is positive and an H value that is less than $\left(\frac{a-b}{s}\right)$.

Now if $D > 0$, does the Endemic equilibrium remain inside the feasible region, i.e., $H > D$? (4) and (6) give us the exact position of the Endemic equilibrium, namely

$$H = \frac{(k-\alpha)(\alpha+b)-a(k-\frac{\alpha}{2})}{(\alpha-k)s}$$

$$D = \left[\frac{(k-\alpha)(\alpha+b)-a(k-\frac{\alpha}{2})}{(\alpha-k)s} \right] \left[\frac{\frac{a}{2}+\alpha-k}{\alpha-k} \right] = H \left[\frac{\frac{a}{2}+\alpha-k}{\alpha-k} \right].$$

What we obviously need to establish, is the magnitude of $\frac{\frac{a}{2}+\alpha-k}{\alpha-k}$. First, we know that for $D > 0$, $k > \alpha + \frac{a}{2}$, (Theorem 4.5.1). Now

$$\frac{\frac{a}{2}+\alpha-k}{\alpha-k} = \frac{\frac{a}{2}}{\alpha-k} + 1.$$

Because $k > \alpha + \frac{a}{2}$, $\alpha-k < 0$. Thus $\frac{\frac{a}{2}}{\alpha-k} < 0$, implying that the magnitude of $\frac{\frac{a}{2}+\alpha-k}{\alpha-k}$ is less than unity. Hence, we conclude

Theorem 4.6.2: *When $D > 0$, the Endemic equilibrium is inside the feasible region.*

4.7 Stability of the Non-Zero Equilibrium

Consider again the Jacobian for the system given by (7):

$$J = \begin{bmatrix} a-b-2sH & -\alpha \\ k\frac{D^2}{H^2}-sD & -\frac{kD}{H} \end{bmatrix},$$

which gives the following characteristic equation

$$\lambda^2 - \lambda \left(a - b - 2sH - \frac{kD}{H} \right) - \frac{kD}{H} (a - b - 2sH) + \alpha \left(\frac{kD^2}{H^2} - sD \right) = 0. \quad (8)$$

Let us investigate the stability of the Endemic equilibrium at the bifurcation $H = \left(\frac{a-b}{s} \right)$, $D = 0$.

If we substitute these values of H and D into (8), we get

$$\lambda^2 - \lambda \left(a - b - 2s \left(\frac{a-b}{s} \right) \right) = 0$$

$$\Rightarrow \lambda^2 - \lambda(b-a) = 0$$

$$\Rightarrow \lambda_1 = 0 \text{ and } \lambda_2 = b-a.$$

Since $a > b$, $\lambda_2 < 0$. However, $\lambda_1 = 0$, for which the Principle of Linearised Stability fails to draw a conclusion about the stability of this equilibrium. This means that higher order terms are making a contribution towards the stability, so we need to find out what happens to these eigenvalues when the equilibrium is slightly perturbed from $H = \left(\frac{a-b}{s} \right)$, $D = 0$.

Consider the graph of the function $\lambda^2 - \lambda(b-a)$ whose zeros are the eigenvalues at this equilibrium.

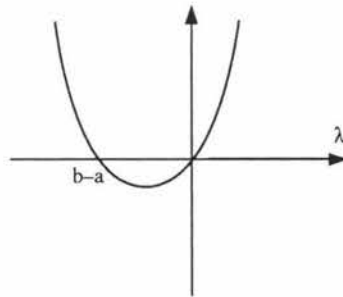


Figure 4.3

At an equilibrium close to $H = \left(\frac{a-b}{s} \right)$, $D = 0$, the eigenvalues will be the zeros of a function which is obtained from this by a slight perturbation. Any such slight perturbation of this function will cause the Endemic equilibrium to become stable or unstable depending entirely on which way the zero eigenvalue perturbs.

If we investigate where (8) intersects the vertical axis after the Endemic equilibrium has been slightly perturbed from the bifurcation point, then this will indicate whether the zero eigenvalue has become positive or negative.

From (8), the vertical axis term is given by

$$\frac{kD^2}{H^2} (a-b-2sH) + \left(\frac{kD^2}{H^2} - sD \right) \quad (9)$$

Since $D \approx 0$, $\frac{kD^2}{H^2} \approx 0$. So we end up with

$$\begin{aligned} & -\frac{kD}{H}(a-b-2sH) + \alpha(-sD) \\ = & D \left(-\frac{k}{H}(a-b-2sH) - \alpha s \right) \end{aligned}$$

Now at $H \approx \left(\frac{a-b}{s} \right)$, this becomes

$$\begin{aligned} & D \left(-\frac{ks}{a-b}(b-a) - \alpha s \right) \\ = & sD(k - \alpha). \end{aligned}$$

At $k \approx k_c$, we finally get

$$sD \left(\frac{a}{2} + \alpha - \alpha \right) = \frac{as}{2} D.$$

Since $\frac{as}{2} > 0$ we can say that if $D < 0$, (9) < 0 and alternatively if $D > 0$, (9) > 0 . This gives us the following:

If $D < 0$, the vertical axis intercept of (8) will also be negative and the formerly zero eigenvalue will become positive. Thus the Endemic equilibrium will be unstable.

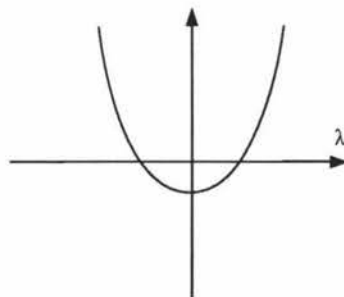


Figure 4.4

If $D > 0$ ($k > k_c$), then the vertical axis intercept of (8) will be positive and so the formerly zero eigenvalue will become negative and hence the Endemic equilibrium will be stable.

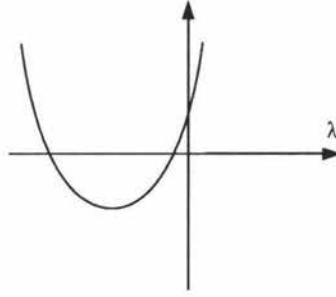


Figure 4.5

Thus, we summarise:

Theorem 4.7.1: *A change of stability occurs when the Endemic equilibrium bifurcates with the Disease-free equilibrium. Namely, if $D < 0$ the Endemic equilibrium becomes UNSTABLE and if $D > 0$, the Endemic equilibrium becomes STABLE.*

When $D > 0$ and the Endemic equilibrium is stable, do we have asymptotic stability (real eigenvalues) or spiralling stability (complex eigenvalues)? To determine this we need to look at the sign of the discriminant of the Jacobian matrix, which is given by

$$\text{dis} = \left(a - b - 2sH - \frac{kD}{H} \right)^2 - 4\alpha \left(\frac{kD^2}{H^2} - sD \right) + \frac{4kD}{H} (a - b - 2sH)$$

Substituting our Endemic solution into this ((4) and (5)), we find:

$$\begin{aligned} \text{dis} &= 4\alpha^2 (a^2 - 2a(b+k) + (b+k)^2) - 4k\alpha (a - (b+k))(3a - 2(b+k)) + k^2(3a - 2(b+k)) \\ &= \left[2\alpha(a - (b+k)) - k(3a - 2(b+k)) \right]^2 > 0 \end{aligned}$$

Hence, the eigenvalues for the Endemic solution are real.

Theorem 4.7.2: *When $D > 0$, the Endemic equilibrium is ASYMPTOTICALLY STABLE.*

4.8 Summary

The overall picture emanating from this model is again very similar to the results obtained in chapters 2 and 3. There was a bifurcation threshold below which the Endemic equilibrium was outside the feasible region and unstable with the Disease-free equilibrium stable and above which the Endemic equilibrium was within the feasible region and *asymptotically* stable throughout that entire region, with the Disease-free equilibrium unstable. Once again, any solution that entered the feasible region was bounded there as time increased.

A slight problem arose with the Endemic solution when the mortality rate due to disease (α) approached the same value as the contact term (k); the Endemic solution became infinite. However, this occurred below the bifurcation threshold so that the Endemic equilibrium was outside the biologically feasible region anyway.

Hopf bifurcations were checked and after lengthy analysis it was established that such bifurcations could not occur for the specified parameter values.

§5 Discussion

Before we start, so as no confusion arises when discussing the difference between models, let us reiterate them:

Model 1: Two dimensional model with $\theta=3$. (Previous work [3]).

Model 2: Two dimensional model with $\theta=1$. (Chapter 2).

Model 3: Three dimensional model with $\theta=1$. (Chapter 3).

Model 4: Two dimensional model with fixed contact rate. (Chapter 4).

As this research used Model 2 as the base we will compare Models 1, 3 and 4 to this base model, in order to determine whether changes to Model 2 are advantageous or not in terms of overall possum dynamics. In discussing the differences between the models we will firstly look at the difference in dynamics and then use computer generated plots to investigate the numerical differences between the models.

We begin this discussion by looking at Model 1 ($\theta=3$) in relation to Model 2 ($\theta=1$), the difference being that the growth curve parameter θ has been reduced from 3 in Model 1 to 1 in Model 2. This had no dramatic change on the dynamics from Model 1 to Model 2. Both had a Zero equilibrium that bifurcated with a Wandering equilibrium at a particular parameter threshold. This threshold condition was the same for both models except for the value of θ . The Zero and Wandering equilibria were always unstable in both models, and the Wandering equilibrium always remained outside the feasible region. Both models had a Disease-free equilibrium that bifurcated with an Endemic equilibrium at another parameter threshold, which was exactly the same for both models. Above this parameter threshold both models had the Endemic equilibrium stable inside the biologically feasible region with the Disease-free equilibrium unstable, while below this threshold the Endemic equilibrium was outside the feasible region and unstable with the Disease-free equilibrium stable.

There was a numerical difference in the non-zero solutions (Wandering and Endemic equilibria) between the two models for the reason that one of the two equations whose intersection determined the non-zero solutions was not the same in each model. In Model 1 this equation was a cubic while in Model 2 it was a linear function. Contour plots showing the varying Endemic solution for the specified parameter ranges are depicted in Plot 1 and Plot 2 which correspond to Model 1 and Model 2 respectively. For $\alpha > 0.6$ the two models have almost identical levels of possum density (H), while for $\alpha < 0.6$ Model 1 has greater density than Model 2. For $\beta < 0.2$ both models are sensitive to $\alpha > 0.2$, i.e., small changes in α result in large changes in the level of possum density. For $\alpha < 0.25$ both models are insensitive to $\beta > 0.2$, i.e., large changes in β , when $\beta > 0.2$, result in little or no change in possum density.

In terms of prevalence of infection ($\frac{D}{H}$), Plots 7 and 8, Model 1 has higher overall prevalence than Model 2.

Thus, the overall effect of reducing θ to 1 has been to lower the density of possums in the Endemic state, as well as lowering the prevalence of infection. There was no significant change in the structure of the equilibria, only in the actual non-zero values. However, the analysis of Model 2 was made easier by the reduction in the order of the equations.

Now we look at the differences between Model 2 and Model 3 (latent period following infection, $\frac{1}{v}$). Although one model was represented by a system of two equations and the other by three, the overall dynamics of the two were still the same. Both models had a Wandering equilibrium that bifurcated with a Zero equilibrium at a particular parameter threshold. This threshold condition was a little different between the models as Model 3 allowed for a latent period. However, we now show that as the latent period becomes minute ($\frac{1}{v} \rightarrow 0$), the bifurcation threshold for Model 3 is the same as that for Model 2.

From Chapter 3, the bifurcation threshold of Model 3 is given by

$$\alpha_c = \frac{v(a-2b)-2b^2}{2(v+b)},$$

So that as $\frac{1}{v} \rightarrow 0$, ($v \rightarrow \infty$), we find

$$\begin{aligned} \lim_{v \rightarrow \infty} \alpha_c &= \lim_{v \rightarrow \infty} \left(\frac{a-2b-\frac{2b^2}{v}}{\frac{2(v+b)}{v}} \right) \\ &= \frac{a-2b}{2} = \frac{a}{2} - b = \alpha_t \text{ (from Model 2).} \end{aligned}$$

As $\frac{1}{v} \rightarrow 0$, the bifurcation between the Zero and the Wandering equilibria in Model 3 occurs at the same parameter threshold as that for Model 2.

These two equilibria remained unstable in both models with the Wandering equilibrium staying outside the feasible region in both instances.

Both models had a Disease-free equilibrium and an Endemic equilibrium that bifurcated at another parameter threshold. Again, this threshold condition was different between the models, but again we show that as the latent period approaches zero, the two conditions become the same. From Chapter 3, the bifurcation threshold is given by

$$\beta_c = \left(\frac{s}{a-b} \right) \left(\frac{(v+a)(\alpha+a) - \frac{av}{2}}{v} \right)$$

So that as $\frac{1}{v} \rightarrow 0$, ($v \rightarrow \infty$), we find

$$\begin{aligned} \lim_{v \rightarrow \infty} \beta_c &= \left(\frac{s}{a-b} \right) \lim_{v \rightarrow \infty} \left(\frac{v(\alpha+a) + a(\alpha+a) - \frac{av}{2}}{v} \right) \\ &= \left(\frac{s}{a-b} \right) \left(\alpha + a - \frac{a}{2} \right) = \left(\frac{s}{a-b} \right) \left(\alpha + \frac{a}{2} \right) = \beta_t \text{ (from Model 2).} \end{aligned}$$

So as $\frac{1}{v} \rightarrow 0$, the bifurcation between the Disease-free and the Endemic equilibria in Model 3 occurs at the same parameter threshold as for Model 2.

Above this threshold, both models had the Endemic equilibrium inside the feasible region and stable with the Disease-free equilibrium unstable, while below this threshold both models had the Endemic equilibrium outside the feasible region and unstable with the Disease-free equilibrium stable.

Numerically there was a difference in the non-zero equilibria, again brought about by the fact that one of the two equations governing the non-zero equilibria was different between models. (The non-zero equilibria for Model 3 could also be represented by two equations, (3) and (8)). Closer inspection now reveals that as the latent period becomes minute, the equation in Model 3 approaches the corresponding equation in Model 2.

From Chapter 2, this equation is represented by (2'):

$$D = H \left(\frac{\beta-s}{\beta} \right) + \frac{\frac{a}{2} - b - \alpha}{\beta},$$

but from Chapter 3, it is represented by (8):

$$Y = \frac{-s^2 H^2 - H (s(\alpha+v+2b) - v\beta) - (\alpha+b)(v+b) + \frac{av}{2}}{\beta(\alpha+v+b+sH)}.$$

Now as the latent period becomes minute ($\frac{1}{v} \rightarrow 0$ or $v \rightarrow \infty$), the number of individuals in the latent stage will also become minute and in fact Y will represent all the diseased individuals, i.e., $Y \equiv D$. This means that (8) becomes

$$\lim_{v \rightarrow \infty} Y = \lim_{v \rightarrow \infty} \left(\frac{\frac{-s^2H^2 - vH(s-\beta) - sH(\alpha+2b) - v(\alpha+b) - b(\alpha+b) + \frac{av}{2}}{v}}{\frac{v\beta + \beta(\alpha+b+sH)}{v}} \right)$$

$$= \frac{-H(s-\beta) - (\alpha+b) + \frac{a}{2}}{\beta} = H \left(\frac{\beta-s}{\beta} \right) + \frac{\frac{a}{2} - b - \alpha}{\beta} = (2') \text{ from Model 2.}$$

This means that when the latent period following infection approaches zero, the Wandering and Endemic equilibria from Model 3 are exactly the same as those from Model 2.

This is verified by comparing Plot 2 with Plots 3, 4 and 5. In Plot 3 when the latent period ($\frac{1}{v}$) is relatively large, there is higher possum density than in Model 2. As ($\frac{1}{v}$) decreases (Plots 4 and 5) the density of possums approaches that of Model 2. (Compare Plot 2 with Plot 5). Prevalence of infection has similar behaviour. When ($\frac{1}{v}$) is relatively large, prevalence is lower than in Model 2, (Plot 8 V Plot 9). When the latent period decreases (Plot 10 and 11) the prevalence of infection approaches that of Model 2. (Compare Plot 8 with Plot 11).

Thus, the overall effect of extending Model 2 to allow for a latent period following infection has been that when there was a latent period of a set length, there was an increase in the density of possums, a decrease in the prevalence of infection, and oscillations to equilibrium were damped compared to Model 2. When the latent period was zero, Model 3 exactly mimicked Model 2.

Finally, we compare Model 2 with Model 4 (fixed contact rate). Although the characteristics were similar, there were distinct differences between the models. No Wandering equilibrium existed in Model 4 as it did in Model 2. However both models had an Endemic equilibrium which bifurcated with a Disease-free equilibrium at particular parameter threshold. The threshold condition for Model 4 differed from that of Model 2 by a factor of $\left(\frac{a-b}{s}\right)$. Again, above the threshold, both models had the Endemic equilibrium stable inside the feasible region with the Disease-free equilibrium unstable, while below the threshold the Endemic equilibrium was outside the feasible region and unstable with the Disease-free equilibrium stable. When the Endemic equilibrium in Model 4 was stable the approach to the equilibrium was asymptotic, whereas in Model 2 the approach could be either asymptotic or spiralling towards equilibrium, depending on parameter values.

There were noticeable numerical differences between these two models, again because one of the two equations whose intersection determined the non-zero solutions was not the same for both models. In Model 2 this equation was a linear function while in Model 4 it was a quadratic expression.

These differences are easy to discern by comparing Plot 2 with Plot 6, which have quite distinct differences in the level of possum density. In Plot 6, for $\alpha > 0.5$, the model is extremely sensitive to high k (remembering that k represents an interaction coefficient as well as incorporating the transmission coefficient β), i.e., small changes in k result in large changes in the density of possums.

With respect to prevalence of infection, (Plots 8 and 12), there are again very clear differences between Model 2 and Model 4.

In terms of correlation between the models presented here and other research, all our models exhibit the standard results for most epidemic models: there exists a threshold below which disease goes into extinction and above which there exists an endemic equilibrium which is stable.

Similar models to these have been studied by Pugliese, [10] and [11]. Because Pugliese uses a generalised function to describe the mortality and a generalised function for the contact rate [11], Pugliese's models encompasses Model 1, 2 and 4, (as the differences between our models was in the mortality and contact rates). So it is not surprising then that the results obtained from Models 1, 2 and 4 are just specific cases of the results obtained from [11]. In [10] Pugliese introduced a latency period following infection (as we did in Model 3), and again used generalised function to describe the mortality and contact rates. Model 3 was just a particular case of [10], so again it is no surprise that our results paralleled those of Pugliese.

Finally, we briefly discuss the advantages and disadvantages of the various models examined in this thesis, including Model 1 from [13]. Model 1 with $\theta=3$ gave the best fit to a recovery curve for relative possum densities following control, which in turn implies that Models 2, 3 and 4 are not as biologically realistic with $\theta=1$. The only real disadvantage with $\theta=3$ was in the analysis of the model, as the degree of the equations was higher. Model 2 on the other hand was easier to analyse because $\theta=1$ enabled us to find the non-zero equilibria analytically rather than numerically. Model 3 introduced a latent period following infection which made this model more realistic but also introduced more problems of unknown parameter values, e.g., length of latent period. Another difficulty with this was that in the field it is very hard to distinguish infected individuals from infectious ones, so estimations would not be very precise. On the mathematical side Model 3 displayed exactly the same characteristics as Model 2 when the latent period was small, so there was no real advantage in including a latent period. Lastly, Model 4 was certainly the easiest to analyse as there was only one non-zero equilibrium which was represented by a simple analytic expression. Having a fixed contact rate made this model more realistic for the reason that an individual possum could only have contact with a fixed number of possums in a set time. The only problems that occurred with this model was that there were difficulties with the Zero equilibrium (origin) as this did not satisfy one of the differential equations. However, as this equilibrium was not important (zero possums and disease) it was just ignored. The other problem arose with the non-zero equilibrium. Given a particular parameter combination, this equilibrium became

infinite. However, this occurred outside the biologically feasible region so again this problem was ignored.

§6 A NEED FOR FURTHER RESEARCH

The primary objective of this thesis was to investigate various time-dependent dynamical systems which modelled the spread of bovine tuberculosis in possums, assuming a uniform spread of the population. However, emphasis now needs to be placed on the spatial spread of the Tb infection caused by migration of the possums in light of the fact that the density of the disease varies considerably. This is a very important aspect of the possum problem because of the observed patchiness of regions of high infection and because population control programmes are directed only to areas of high infection rate in which the infection can be reintroduced via migration.

Although we considered vertical transmission in this thesis from females passing the disease to their offspring, there are other unusual and interesting aspects associated with the Tb infection in possums. The spatial spread of the disease is enhanced by the tendency of juvenile possums to migrate over large distances. Thus age-structure occurs both due to vertical transmission and due to this tendency of the young to migrate. Finally, there is another coupling of space with disease transmission which occurs due to the inclination of individual possums to use more than one den site within their home territory. This is a more restricted spatial effect than the one due to migration.

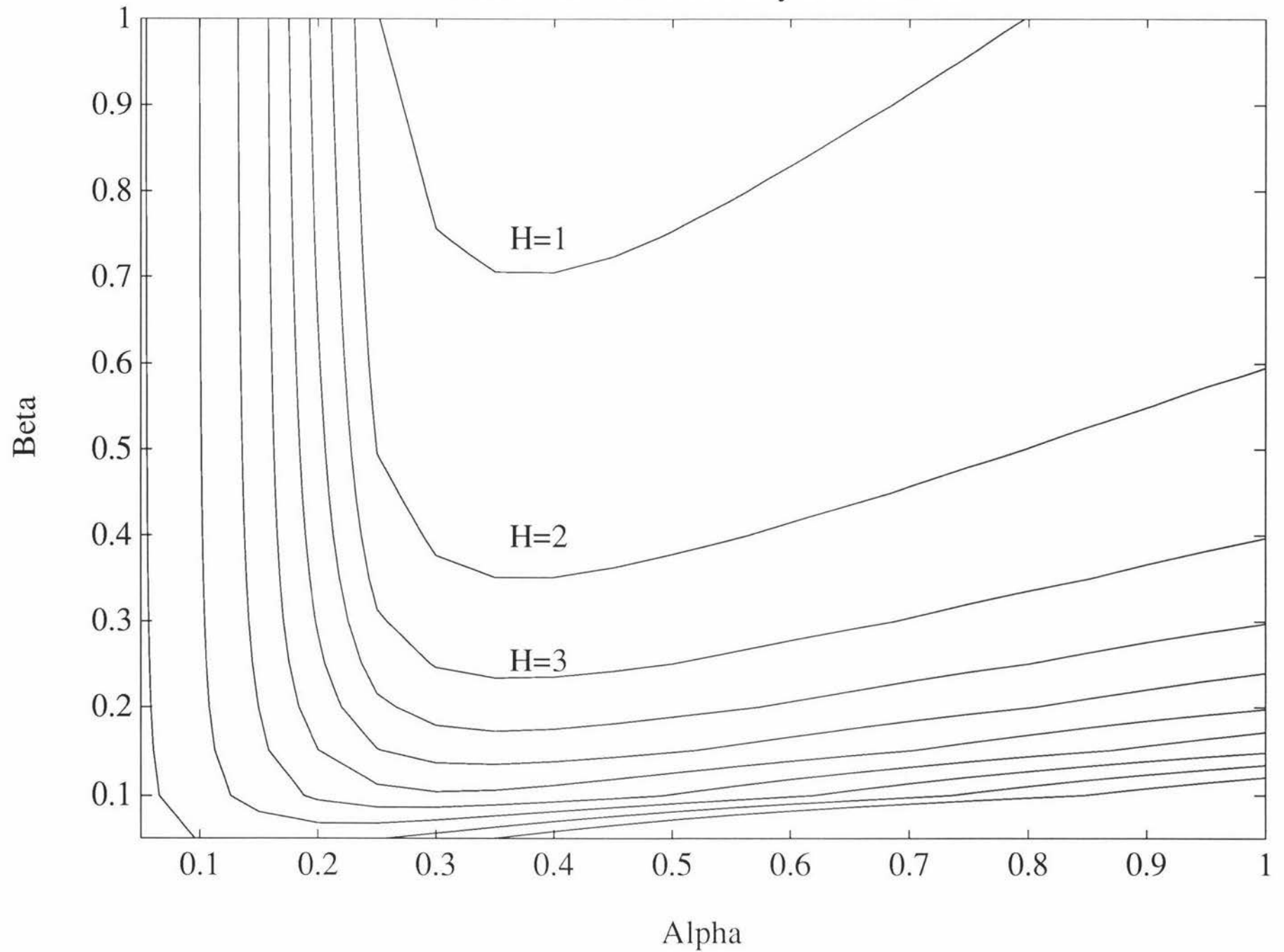
Thus, the importance of analytical modelling as well as simulation needs to be stressed. Particular mention needs to be made of the large number of parameters involved, which precludes comprehensive simulation. Also the effect of neglecting dispersion will need to be investigated. The analytical investigation is crucial for establishing thresholds at which the model will exhibit gross parametric sensitivity. This is especially true for the incorporation of age structure where the equations will be hyperbolic (in the age variables) as well as being parabolic (in the spatial variables). This comprehensive type of model has not been investigated anywhere in the literature.

APPENDIX

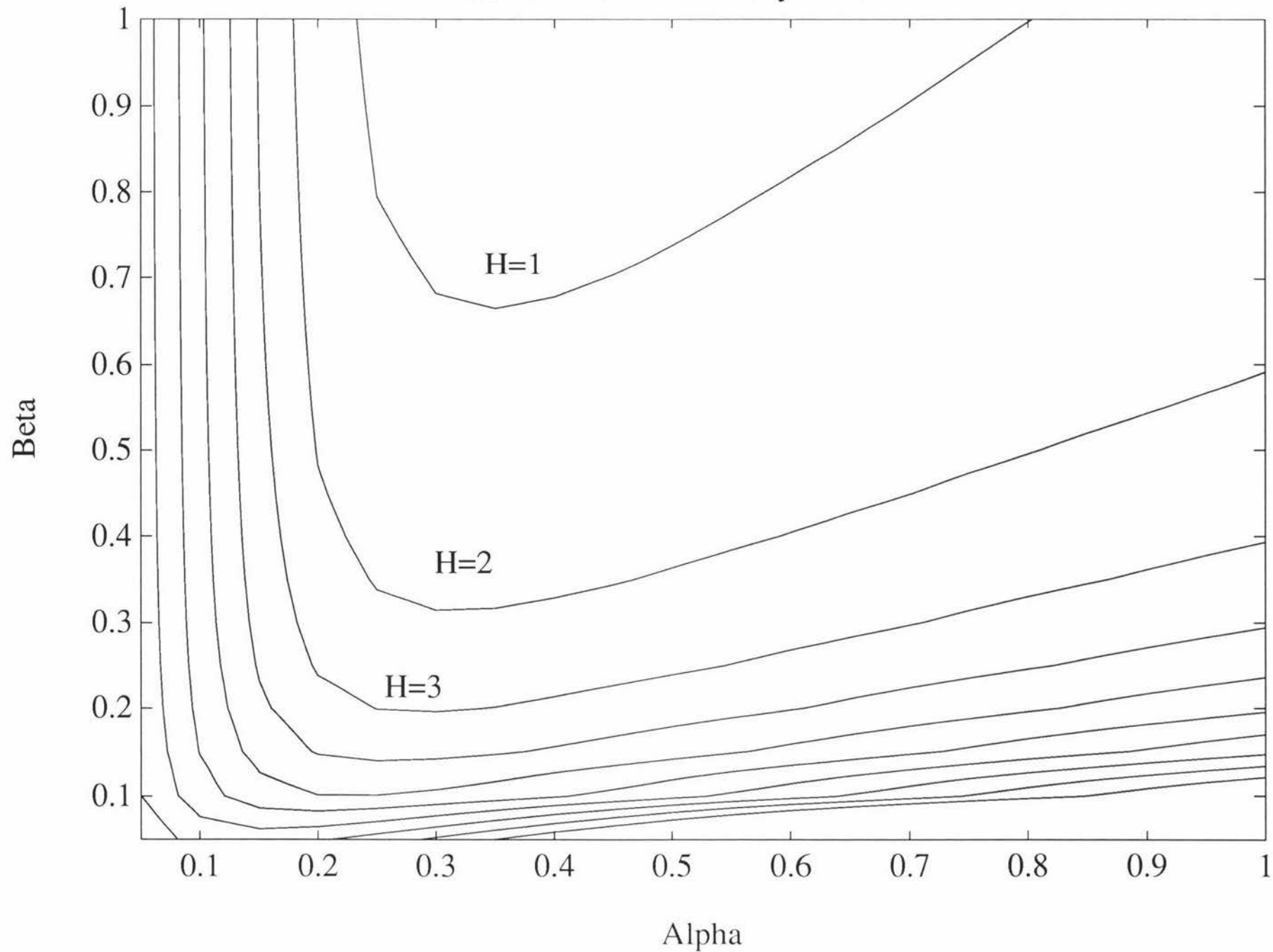
PARAMETERS AND INITIAL VALUES

<u>Symbol</u>	<u>Parameter</u>	<u>Value</u>
a	Exponential birth rate	0.305 yr ⁻¹ .
b	Exponential death rate	0.105 yr ⁻¹ .
k	Interaction and transmission coefficient	0 < k < 1 (yr ⁻¹ ha).
K	Host equilibrium density in the absence of disease	10 ha ⁻¹ .
s	Density-dependent coefficient, ($\frac{a-b}{K^\theta}$)	0.0002 yr ⁻¹ ha.
v	$\frac{1}{\text{latent period}}$	v ≥ 0 (t ⁻¹)
θ	Population growth curve shape parameter	3 or 1.
α	Additional age independent mortality rate due to disease	0 < α < 1 (yr ⁻¹).
β	Transmission coefficient	0 < β < 1 (yr ⁻¹ ha).

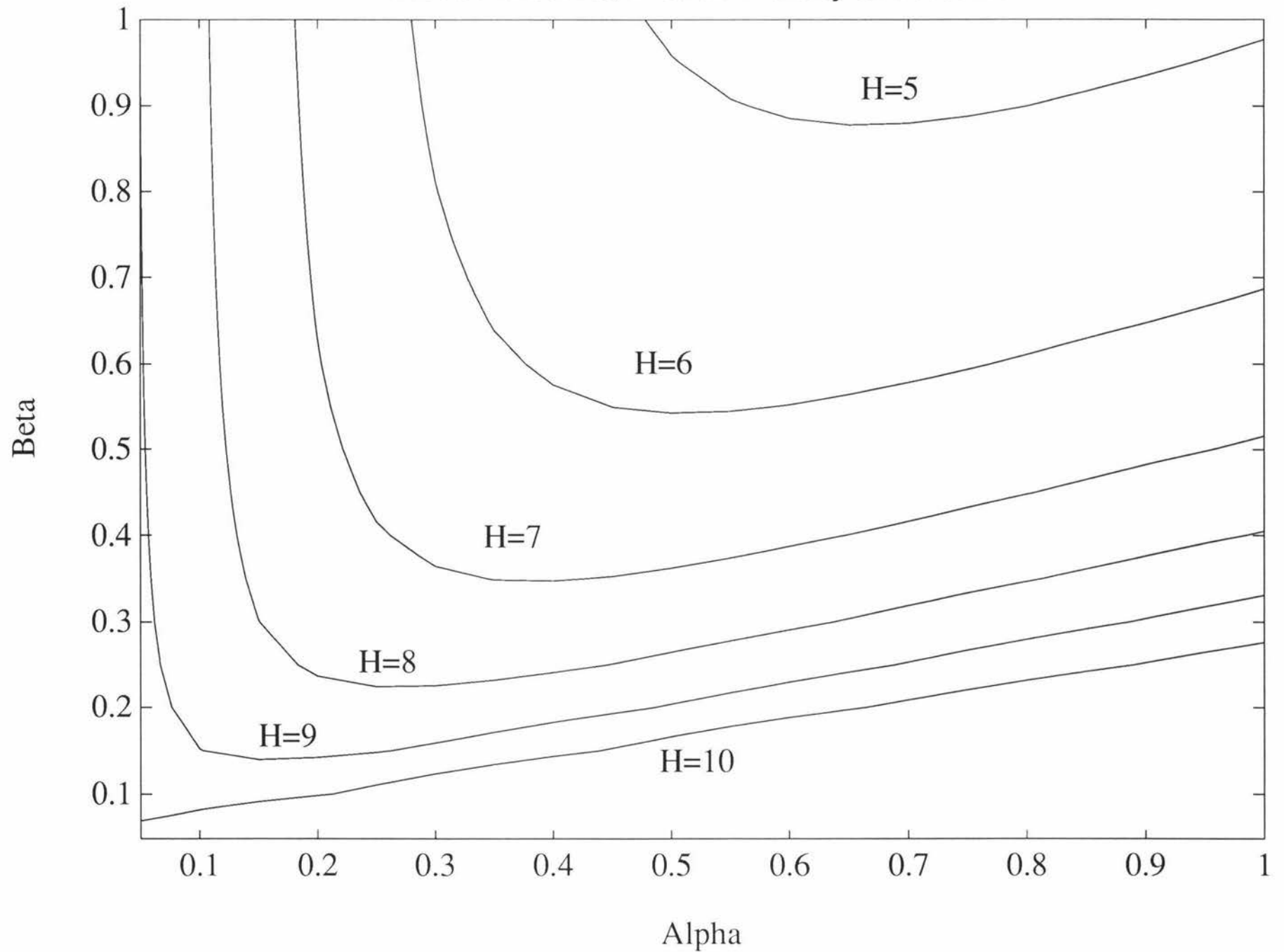
Plot 1: Model 1: Density of Possums



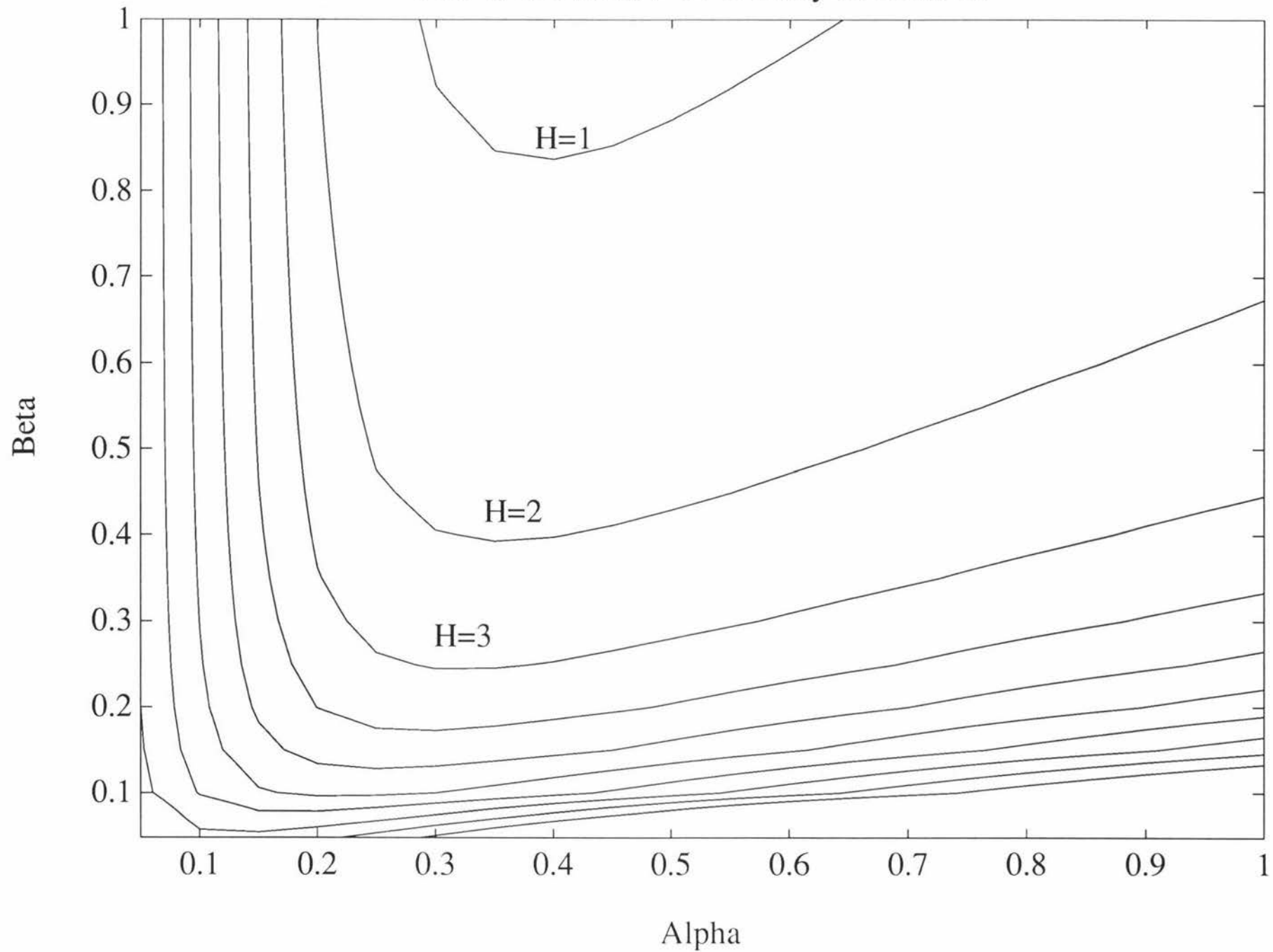
Plot 2: Model 2: Density of Possums



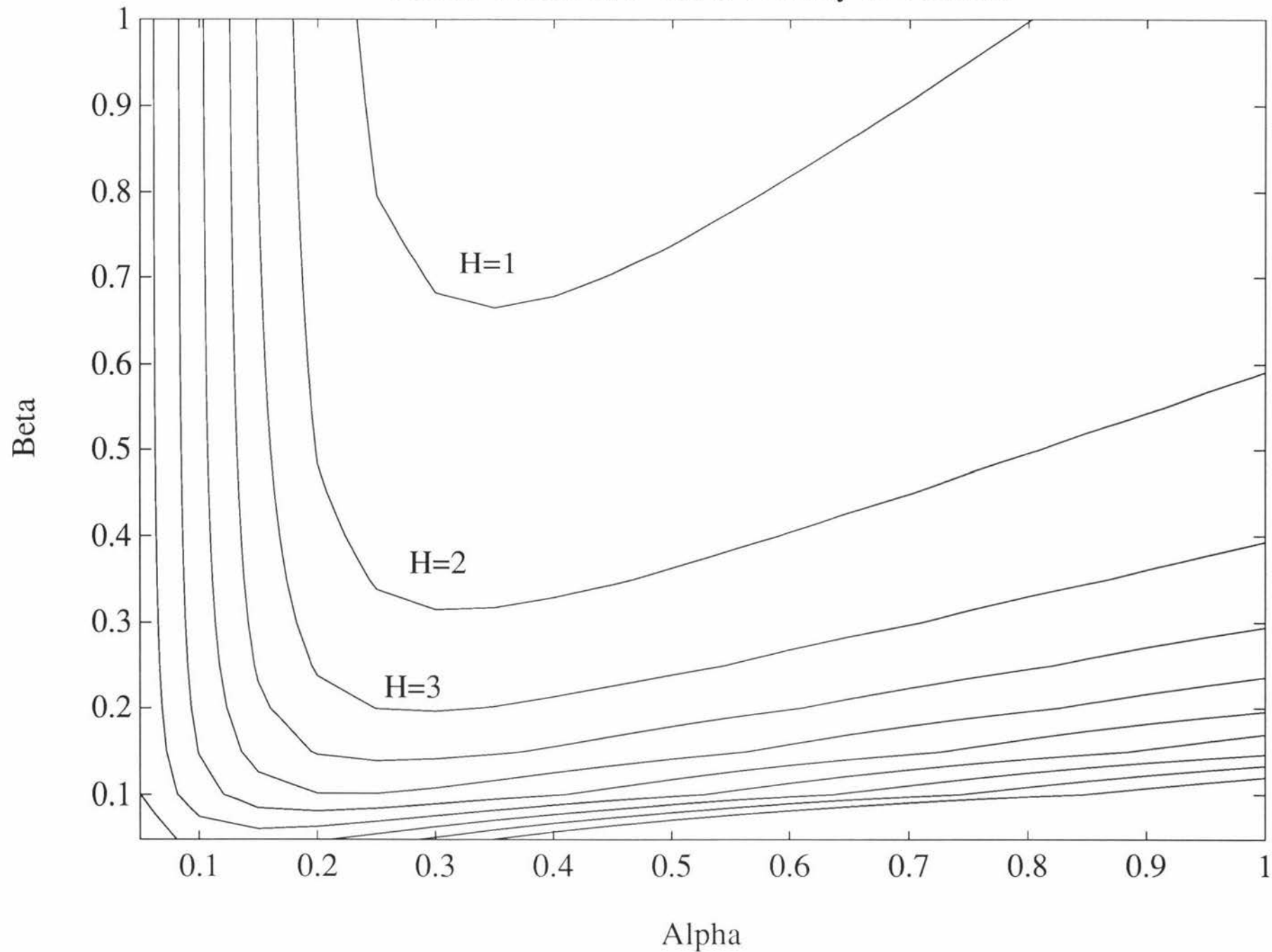
Plot 3: Model 3, $\nu=0.25$: Density of Possums



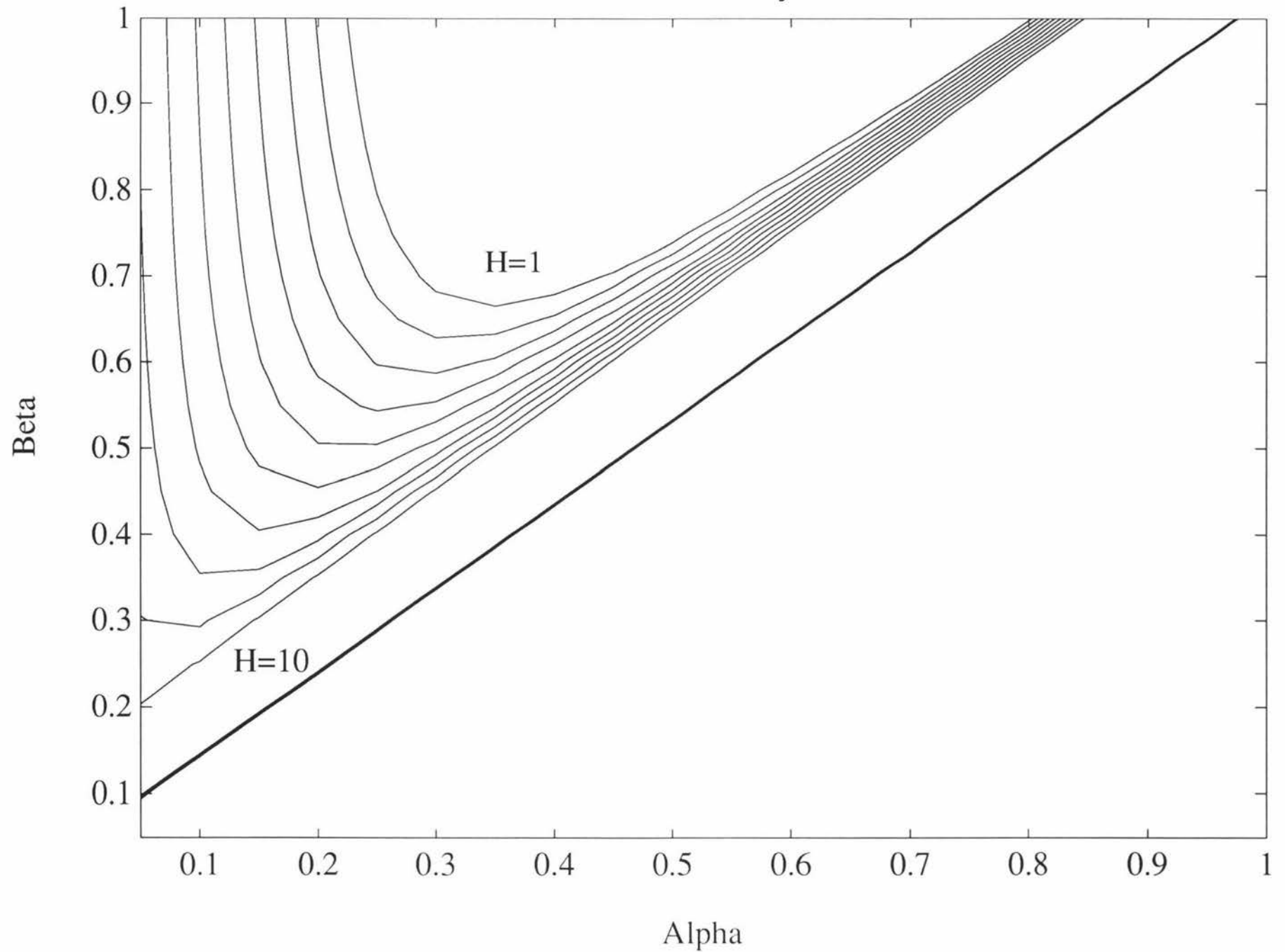
Plot 4: Model 3, $v=3$: Density of Possums



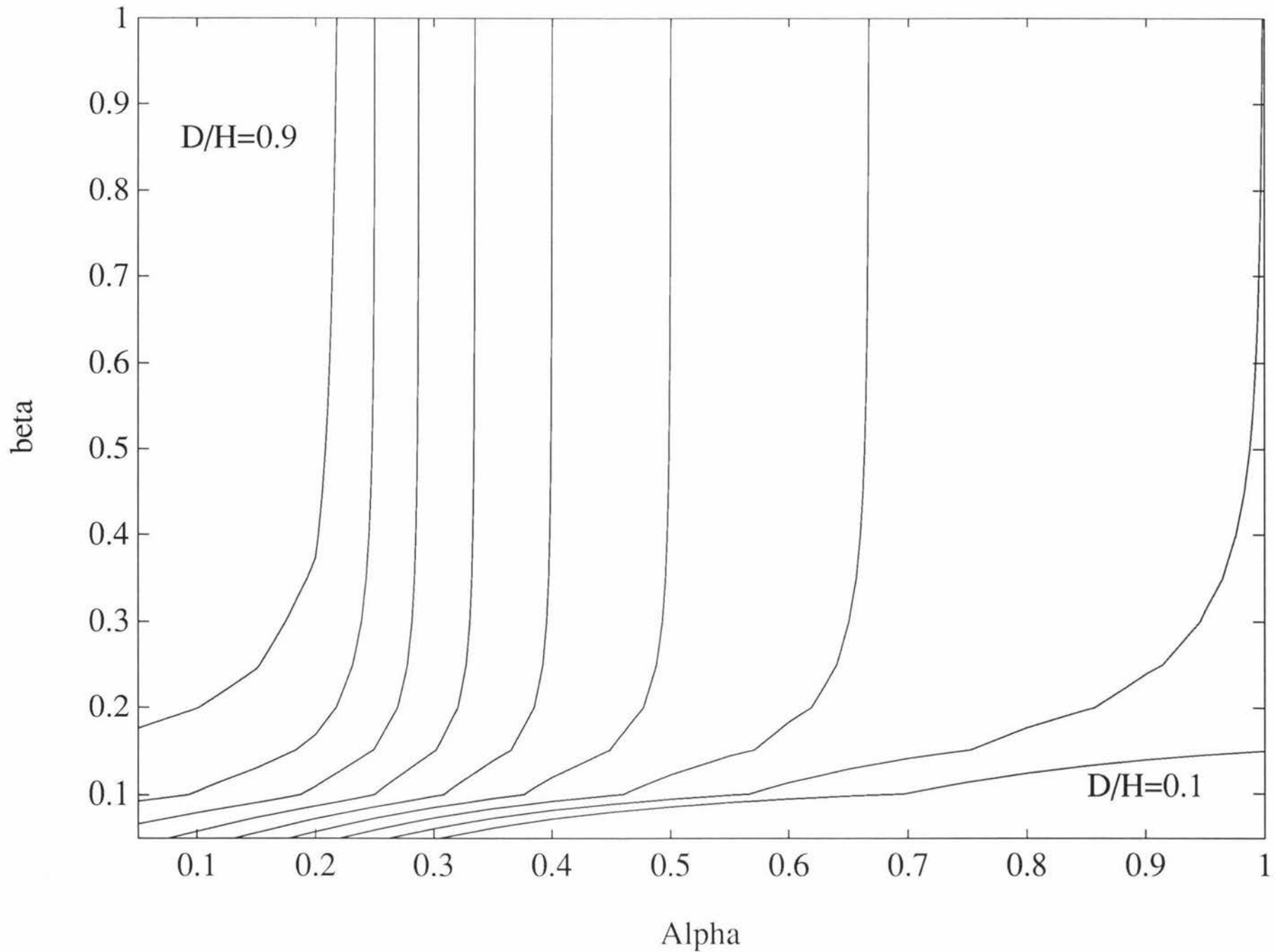
Plot 5: Model 3, $v=1000$: Density of Possums



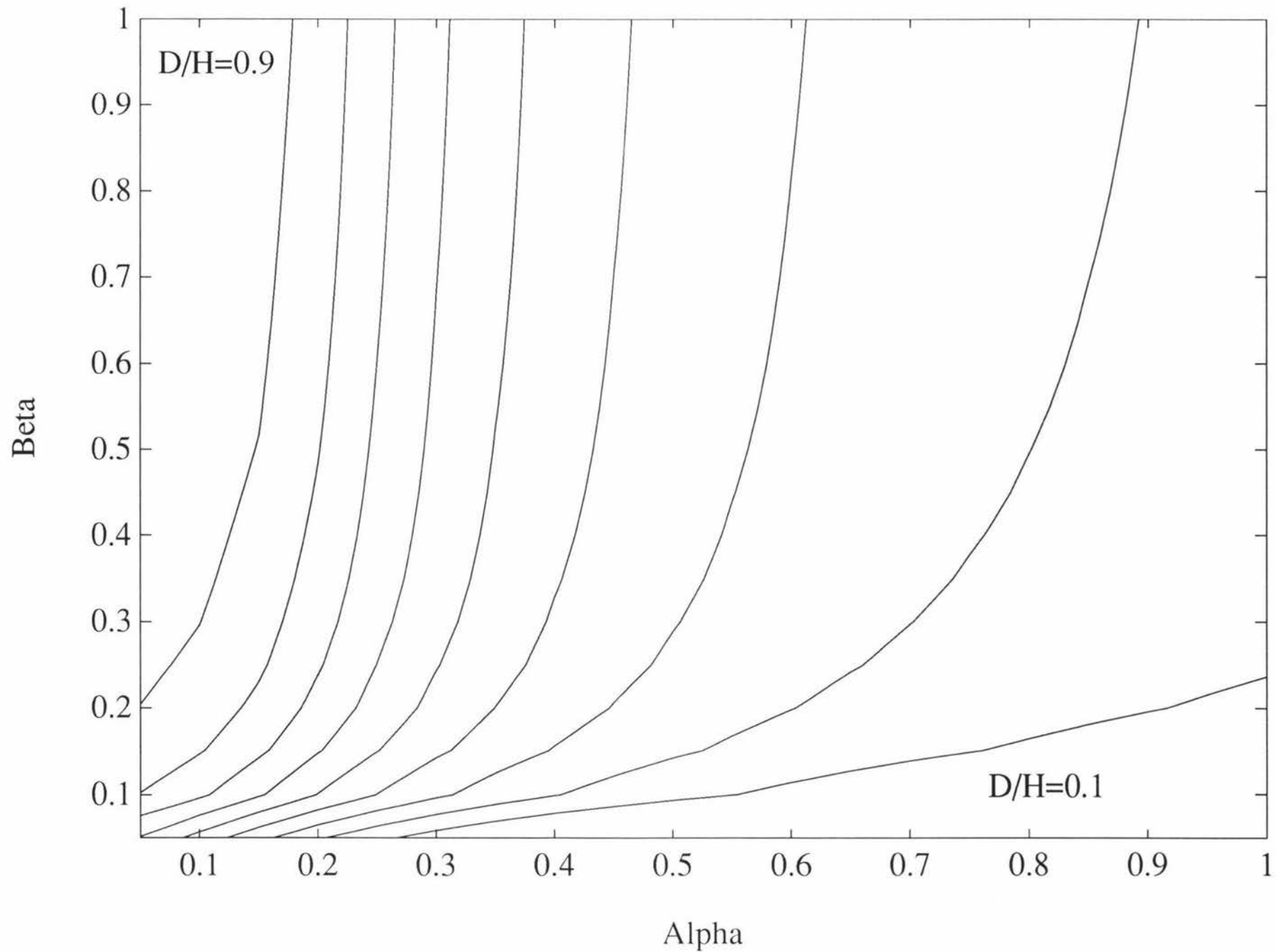
Plot 6: Model 4: Density of Possums



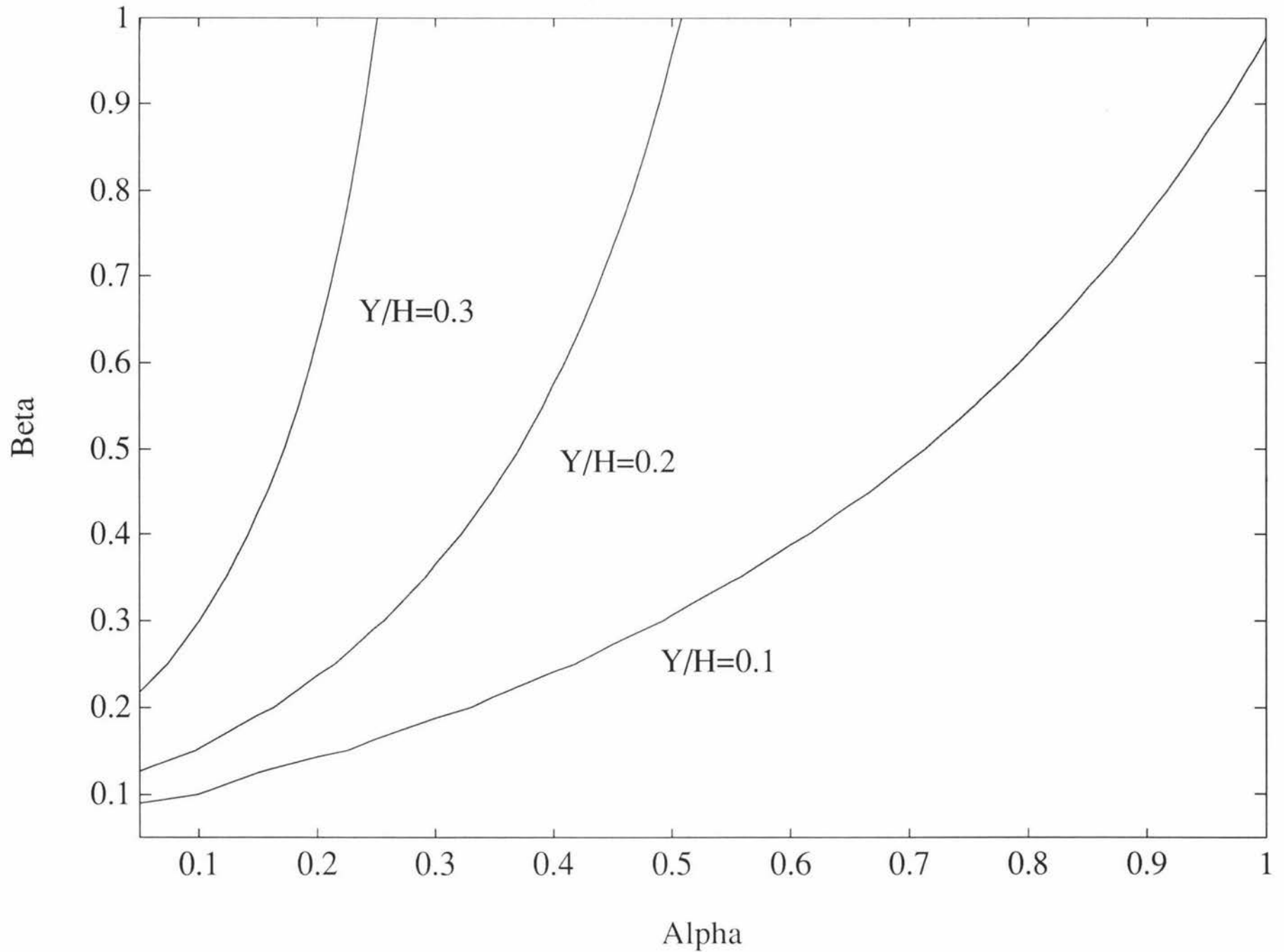
Plot 7: Model 1: Prevalence of Infection



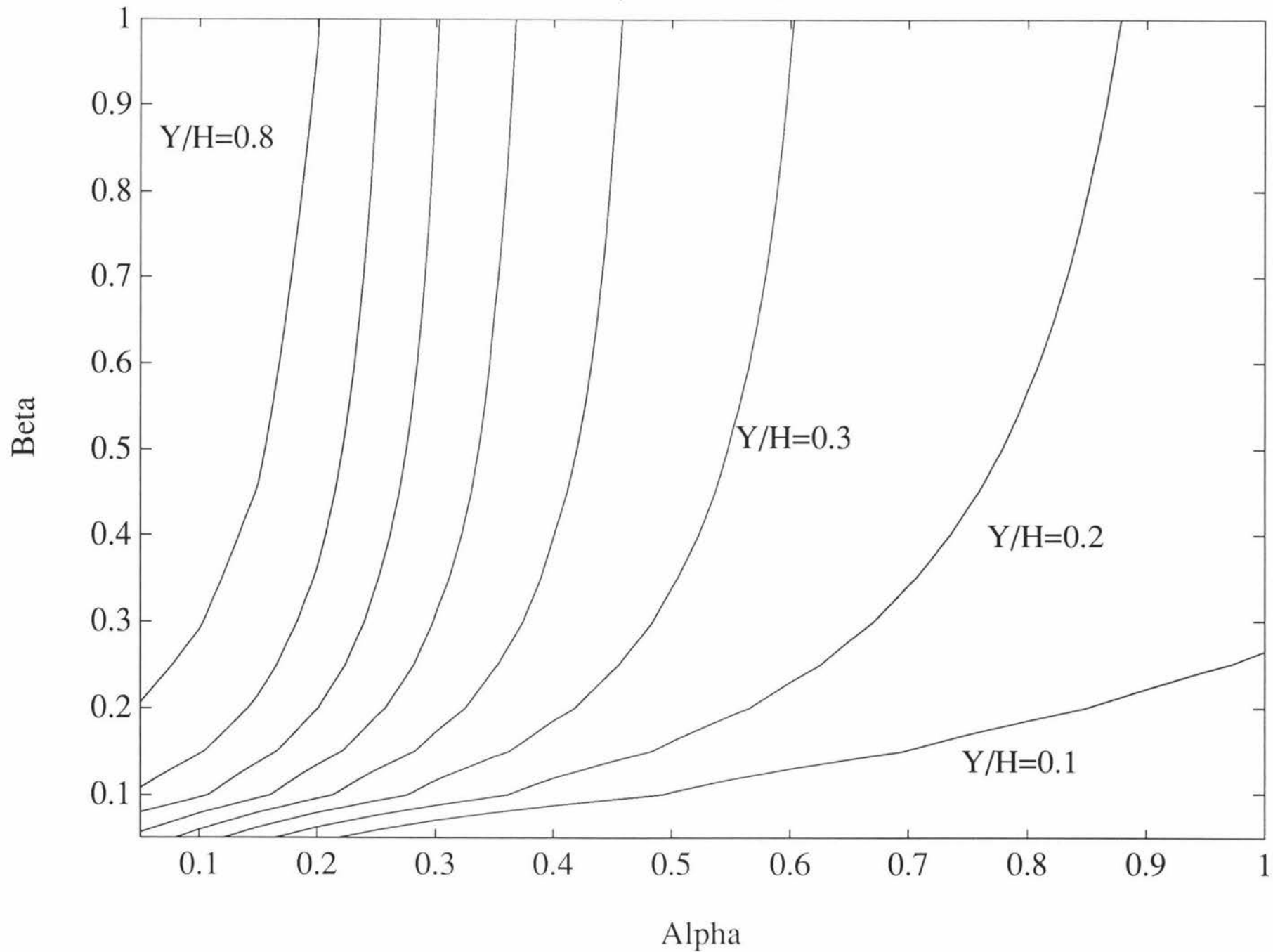
Plot 8: Model 2: Prevalence of Infection



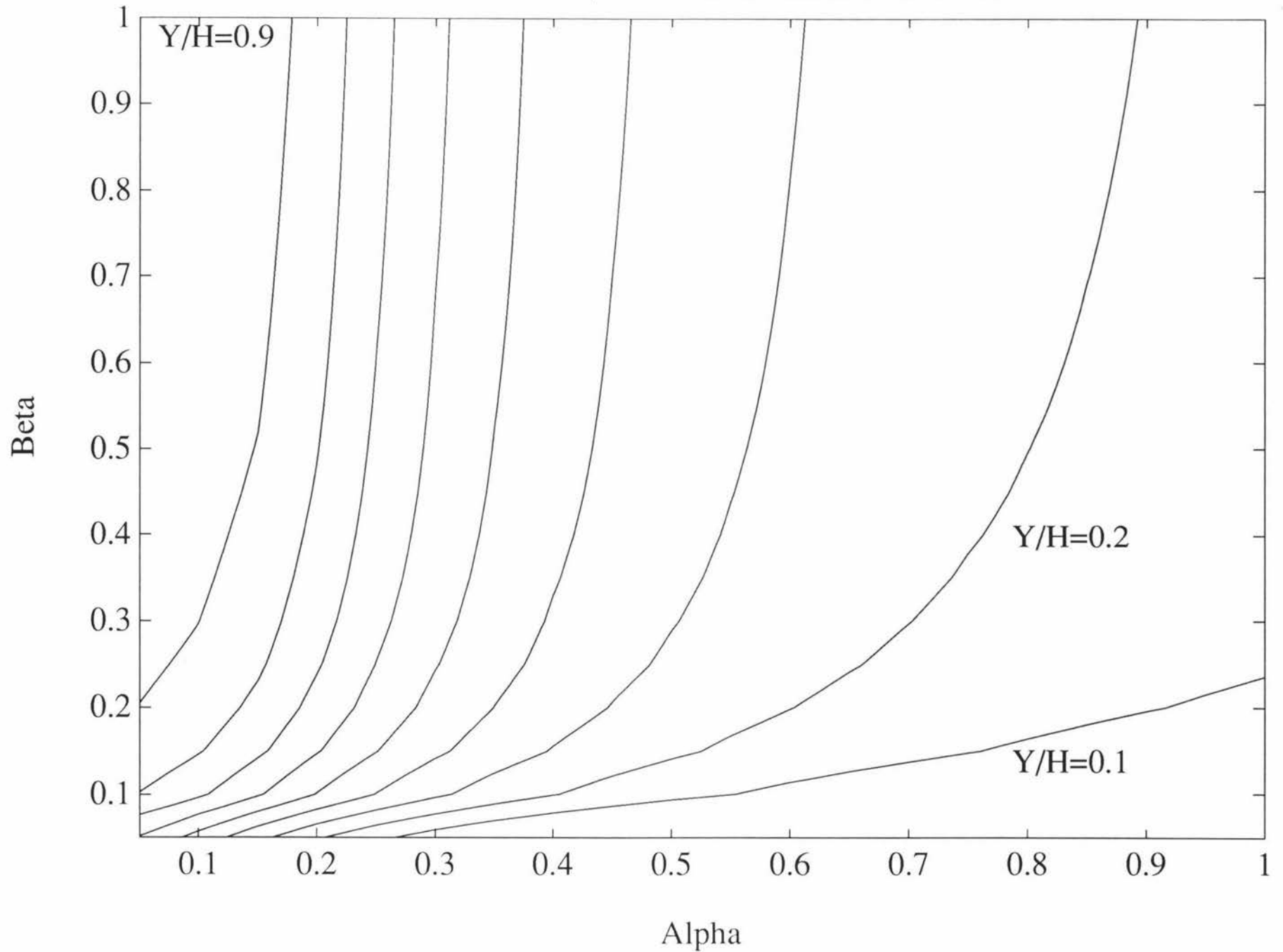
Plot 9: Model 3, $\nu=0.25$: Prevalence of Infection



Plot 10: Model 3, $\nu=3$: Prevalence of Infection



Plot 11: Model 3, $v=1000$: Prevalence of Infection



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