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DEVELOPMENT AND ANALYSIS OF A MATHEMATICAL MODEL
FOR THE LIFE CYCLE OF SCHISTOSOMIASIS

A Thesis
Presented For the
Master of Arts
Degree
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Jeffrey Lawrence Pierce

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ABSTRACT

Schistosomiasis is a helminth infection with an intermediate host (snails) and a definitive host (man). This paper presents a mathematical model for the life cycle of schistosomiasis. The continuous model consists of a system of three ordinary differential equations. Existence of limit cycles, stability of equilibrium, and persistence for two cases of the general model are presented. Numerical solutions to these two cases, plus, numerical solutions to a third case, not geometrically solveable, are also presented.

The general system is found to have no limit cycles, or cycle graphs, in the population quadrant. There is a breakpoint and a threshold value for the mean number of worms per human host (for fixed numbers of healthy and infected snails). A globally stable, positive unique equilibrium exists for the healthy and infected snail populations for a constant infectivity rate.

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CHAPTER I

INTRODUCTION

Schistosomiasis is a disease caused by three species of flatworms, also known as blood flukes. Cohen (1976) estimates that one out of every twenty people in the world have some form of schistosomiasis. The disease is concentrated among the poor and underdeveloped countries, who are least financially able to defend themselves against it. Evidence presented by Jordan and Webbe (1969) suggests that only a proportion of those infected by any of the three schistosomes actually die of the disease. There is little doubt, however, that schistosomiasis can cause considerable pathological changes in a large portion of the population.

As Cohen (1976) tells us, no mathematical model for schistosomiasis has been developed that actually represents what is known about the natural history of the disease. There have been several different types of models proposed. Goffman and Warren (1970) apply the Kermack-McKendrick theory to the epidemiology of schistosomiasis. Dietz (1975) gives a stochastic model for the formulation of parasite pairs in the human host. Cohen (1973) presents a dynamic model in which he considers the proportions of the population never infected, currently infected, and previously infected. The model presented in this paper is based on a classical model by MacDonald (1965). Unfortunately, George W. MacDonald died in 1967 before he could fully explore the model he had developed. Ludwig and Haytock (1976) help the mathematician understand MacDonald's model by deriving the mathematical equations for the model.

The following description of the life cycle of schistosomiasis is attributed to Jordan and Webbe (1969). The three species of schistosomes which cause schistosomiasis are Schistosoma mansoni, Schistosoma haematobium, and Schistosoma japonicum. The three species of snails which serve as the intermediate host for the three species of schistosomiasis above, are Biomphalaria glabrata, Bulinus truncatus, and Oncomelania quadrasi, respectively. The sexual stage of a schistosome occurs in man (the definitive host). The asexual stage of a schistosome occurs in the snail (the intermediate host). Eggs produced in the definitive host leave man in the faeces or the urine. Eggs that reach water hatch a free swimming stage called a miracidium. The miracidium can swim for up to twenty-four hours. If the miracidium reaches a snail of the right genotype within this twenty-four hour period, the miracidium will develop through two larval stages, in about four to seven weeks, into thousands of free swimming cercariae. The miracidium is asexual, while the cercariae are sexual. The cercariae can swim for up to forty-eight hours. Each cercaria that penetrates the skin of a human host becomes a wormlike "schistosomule". If the cercaria penetrates the skin of a host in which it can't develop, the cercaria will die and produce a skin irritation on this host. The schistosomule migrates to the lung, producing a cough in the human host. The schistosomule then appears in the liver, where it matures and mates. After mating, the worm pair migrates to the blood vessels in the lining of the small and large intestines. After a period of five to six weeks, eggs begin to appear in the faeces or urine of the human host. The female is estimated to lay from one hundred to three

hundred eggs per day for her lifetime. MacDonald (1965) estimates the mean life of a female worm to be about three years. MacDonald (1965) also considers the worms to be monogamous.

The symptoms of the disease result from infection caused by the eggs that become trapped in the tissue near where they are laid. Other eggs are washed to the spleen and liver where they cause similar types of fibrosis and granuloma.

In this thesis, I develop a general model for the life cycle of schistosomiasis. In the next chapter I give the assumptions and hypotheses on which the model is based. I also develop the general forms of the three nonlinear differential equations which form the model. The first two differential equations attempt to model the growth rates for the healthy and infected snail populations. The third differential equation models the growth rate of the mean number of worms per human host. Once the general model is formulated, Chapter three is devoted to analysis of equilibria and existence of limit cycles. This analysis is applied to two specific cases of the general model. In the first case second degree nonlinearities are incorporated in the density dependence and interaction terms of the equations for the growth rates of the healthy and infected snails. In the second case, I employ second order nonlinearities in the density dependence terms, and use third order nonlinearities in the interaction terms of the growth rate equations of the healthy and infected snails. In Chapter three, the main goal is to investigate the existence and stability of equilibria for the system of differential equations that form the model. In Chapter four, numerical solutions, with sensitivity results, for the

two cases of the general model are presented, and for a third system which I cannot solve geometrically.

CHAPTER II

DEVELOPMENT OF THE GENERAL MODEL FOR THE LIFE
CYCLE OF SCHISTOSOMIASIS

MacDonald (1965) proposed improved control measures for schistosomiasis, and argued for the need for a mathematical model of human schistosomiasis. Ludwig and Haytock (1976) expounded on MacDonald's writings, and supplied the mathematical details for MacDonald's work. The results obtained by Ludwig and Haytock (1976) will be given later.

The quantities of interest that are incorporated as state variables in the model are the number of healthy snails, the number of infected snails, and the mean number of worms per human host. Let H denote the number of healthy snails, I denote the number of infected snails, and m denote the mean number of worms per human host.

We first consider the growth rate of the number of healthy snails. The healthy snail population is assumed to have an intrinsic growth rate a_0 . We also assume that a snail may leave the healthy snail population by becoming infected. The healthy snail population is also assumed to be subject to density dependence and interspecific interaction, both to varying degrees of nonlinearity. Under the above assumptions, H will satisfy the following equation:

$$(2.1) \quad \frac{dH}{dt} = a_0 H - c(m)H - a_1 H^\ell - a_2 I^d H^n,$$

where $c(m)$ is the infectivity rate, ℓ , d , and n are positive real numbers. The form of $c(m)$ will be developed later.

Next, the growth rate of the number of infected snails is considered. The only positive contribution to the infected snail population is from the number of healthy snails that become infected. The population of infected snails is assumed to be subject to density dependence and interspecific interaction, both to varying degrees of nonlinearity. I also assume the infected snails have a large death rate. This hypothesis is supported by experiments conducted by Pan (1965). Under the above assumptions, I will satisfy the following equation:

$$(2.2) \quad \frac{dI}{dt} = c(m)H - \delta I - b_1 I^u - b_2 I^v H^w ,$$

where δ is the death rate mentioned above, u , v , and w are positive integers, and b_1 and b_2 are nonnegative real numbers, both not zero at the same time.

The final consideration is the rate of change of the mean number of worms per human host, m . The worms are assumed to have some positive death rate, and the only positive contribution to the growth rate of the worms is from the cercariae that make it to the human host. Since cercariae can only originate from infected snails, this positive contribution is assumed to come from the fraction of snails that are infected. Under these assumptions, m will satisfy the following equation:

$$(2.3) \quad \frac{dm}{dt} = -c_0 m + c_1 I / (I + H) .$$

Here, c_0 is the death rate mentioned above, and c_1 is a factor which takes into account the number of cercariae produced per infected snail that reach a human host.

The form of $c(m)$ used by Ludwig and Haytock (1976) is given below, where it is assumed that $c(m)$ is proportional to the mean number of paired worms, $P(m)$. Assumed that the number of male and female parasites in the human host are random variables, each with a Poisson distribution. Under the above assumptions, the form of $P(m)$, as given by Ludwig and Haytock (1976), is

$$P(m) = m(1 - e^{-(I_0(m) + I_1(m))}) ,$$

where

$$I_0(m) = \sum_{q=0}^{\infty} \frac{1}{(q!)^2} \left(\frac{m}{2}\right)^{2q} ,$$

and

$$I_1(m) = \sum_{q=0}^{\infty} \frac{1}{q!(q+1)!} \left(\frac{m}{2}\right)^{2q+1} .$$

This derivation is given in detail by Ludwig and Haytock (1976). The general model is the system of nonlinear ordinary differential equations (2.1), (2.2), and (2.3).

At this point it is convenient to summarize the work of Ludwig and Haytock (1976). They use two equations, the first one being

$$(2.4) \quad \frac{dI}{dt} = -\delta I + c(m) I/S ,$$

where I denotes the number of infected snails, and S the total number of snails. δ and $c(m)$ are the same as discussed previously. The second equation they use is

$$(2.5) \quad \frac{dm}{dt} = -rm + A I/S ,$$

where m is the mean number of worms per human host, r is the death rate, and A is a factor which considers the number of cercariae produced per infected snail that make it to a human host. Ludwig and Haytock (1976) do not consider the dynamics of the healthy snail population. They let $c(m)$ be a constant for purposes of equilibrium analysis, and find that (2.4) has a unique, positive, and globally stable equilibrium I_* , where $I_* = \frac{c(m)}{c(m)+\delta} S$. By substituting for $I/S \approx I_*/S$ (near equilibrium), they get $\frac{dm}{dt} = -rm + \frac{ABP(m)}{BP(m)+\delta}$, where B is some factor independent of m . This last equation is found to have three equilibrium solutions, $m \equiv 0$, $m \equiv m_b$ and $m \equiv m_*$. m_b is called the breakpoint, and m_* the threshold. If $m(t)$ is any solution with $m(t) < m_b$, $m(t) \rightarrow 0$ as $t \rightarrow \infty$. If $m(t)$ is any solution with $m(t) > m_b$, $m(t) \rightarrow m_*$ as $t \rightarrow \infty$. The results obtained in this paper are similar to these results obtained by Ludwig and Haytock (1976). There are some differences, however. Note that the infected snail population of Ludwig and Haytock (1976) always has a unique positive equilibrium. This is not the case with the model of this paper, as will be seen in the next chapter.

The form given for $c(m)$ by Ludwig and Haytock (1976) in this chapter is the form used by MacDonald (1965). For the numerical solutions presented in Chapter four, I do not use this form. I consider the cases where $c(m)$ is a constant, a linear function of m , and a quadratic function of m .

CHAPTER III

EXISTENCE OF LIMIT CYCLES, PERSISTENCE, STABILITY
AND UNIQUENESS OF EQUILIBRIA

Recall that the system of differential equations that compose the model is

$$(3.1) \quad \frac{dH}{dt} = a_0 H - c(m)H - a_1 H^2 - a_2 I^d H^n ,$$

$$(3.2) \quad \frac{dI}{dt} = c(m)H - \delta I - b_1 I^u - b_2 I^v H^w ,$$

and

$$(3.3) \quad \frac{dm}{dt} = -c_0 m + c_1 I/(I+H) .$$

This differs from Ludwig and Haytock (1976) in that there is an equation for the growth rate of the healthy snails, and in the equation for the growth rate of the infected snails, density dependence and interspecific interaction has been added.

Persistence for the healthy and infected snail populations is the property that

$$\limsup_{t \rightarrow \infty} H(t) > 0 ,$$

and

$$\limsup_{t \rightarrow \infty} I(t) > 0 ,$$

where $H(t)$ and $I(t)$ are solutions to (3.1) and (3.2). For the next theorem, the assumption is made that the mean number of worms in the human host, m , is a constant, so that $c(m)$ is also a constant.

Theorem 3.1. The HI-system formed by (3.1) and (3.2) cannot persist if $a_0 \leq c(m)$, for $c(m)$ a constant.

Proof: Note that for $c(m)$ a constant, the intrinsic growth rate of H is given as $a_0 - c(m)$. Recall that a_0 , a_1 , and a_2 are positive real numbers. Let $H(0) > 0$ and $I(0) > 0$. Since the right hand sides of (3.1) and (3.2) are continuously differentiable, $H(t) > 0$ and $I(t) > 0$ for all time t . Since $a_1 > 0$, and $a_2 > 0$,

$$-a_1 H^\ell - a_2 I^d H^n < 0 .$$

Also, since $a_0 \leq c(m)$,

$$\frac{dH}{dt} = (a_0 - c(m))H - a_1 H^\ell - a_2 I^d H^n < 0$$

for all time $t > 0$, hence $\lim_{t \rightarrow \infty} H(t)$ exists. Suppose $H(t)$ approaches some positive number; $\lim_{t \rightarrow \infty} H(t) = h > 0$. This implies that $\frac{dH}{dt}$ approaches $(a_0 - c(m))h - a_1 h^\ell - a_2 I^d h^n < 0$, which is a contradiction, since $\frac{dH}{dt}$ must approach zero if $H(t)$ approaches h .

Therefore

$$\lim_{t \rightarrow \infty} H(t) = 0 .$$

A similar argument works for $I(t)$. Suppose $I(t)$ approaches some positive number; $\lim_{t \rightarrow \infty} I(t) = i > 0$. Now $\frac{dI}{dt} = c(m)H - \delta I - b_1 I^u - b_2 I^v H^w < 0$ for all time $t > t_*$ for some t_* , since $H(t) \rightarrow 0$ as $t \rightarrow \infty$. So, $\frac{dI}{dt}$ approaches $-\delta i - b_1 i^u < 0$. This is a contradiction, since $\frac{dI}{dt}$ must approach zero if $I(t)$ approaches i . Therefore,

$$\lim_{t \rightarrow \infty} I(t) = 0 .$$

This implies that neither H nor I can persist. This completes the proof.

The previous theorem yields the following necessary condition for persistence of H and I :

$$a_0 > c(m) , \text{ for } c(m) \text{ constant.}$$

The next consideration is the existence of limit cycles for the HI-system formed by (3.1) and (3.2) for the case where $c(m)$ is a constant. The two following theorems are used to show that there are no limit cycles.

Theorem 3.2. Coleman (1976) (Dulac's Theorem). If a continuous function $B(X, Y)$ exists so that

$\frac{\partial(BF)}{\partial X} + \frac{\partial(BG)}{\partial Y} \neq 0$, then the sytem $\frac{dX}{dt} = F(X, Y)$,
and $\frac{dY}{dt} = G(X, Y)$ has no limit cycle.

Theorem 3.3. The HI-system formed by equation (3.1) and (3.2) has no limit cycle (for $c(m)$ a constant).

Proof: Let $B(H, I) = 1/H$,

$$F(H, I) = a_0 H - c(m)H - a_1 H^\ell - a_2 I^d H^n ,$$

and

$$G(H, I) = c(m)I - \delta I - b_1 H^u - b_2 I^v H^w .$$

Now,

$$B(H, I)F(H, I) = a_0 - c(m) - a_1 H^{\ell-1} - a_2 I^d H^{n-1} ,$$

and

$$B(H, I)G(H, I) = c(m) - \delta I/H - b_1 I^u/H - b_2 I^v H^{w-1} .$$

So that

$$\begin{aligned} \frac{\partial(BF)}{\partial H} + \frac{\partial(BG)}{\partial I} &= -(\ell - 1)a_1 H^{\ell-2} - a_2(n - 1)I^d H^{n-2} \\ &\quad - \delta/H - b_1 u I^{u-1}/H - b_2 v I^{v-1} H^{w-1} < 0 \end{aligned}$$

for all $H > 0$, and $I > 0$, since ℓ and n are positive real numbers, and a_1 , a_2 , δ , b_1 , and b_2 are positive real numbers. Thus, by Theorem 3.2, the HI-system formed by (3.1) and (3.2) has no limit cycle. This concludes the proof.

Now, consider the case of the general model formed by (3.4)-(3.6).

$$(3.4) \quad \frac{dH}{dt} = a_0 H - c(m)H - a_1 H^2 - a_2 IH,$$

$$(3.5) \quad \frac{dI}{dt} = c(m)H - \delta I - b_1 I^2 - b_2 IH,$$

and

$$(3.6) \quad \frac{dm}{dt} = -c_0 m + c_1 I/(I+H).$$

Let us first examine the flow of solutions along the H and I -isoclines to see that there is a unique, positive, and not unstable equilibrium. To get the H -isocline, let $\frac{dH}{dt} = 0$. (3.4) implies that

$$H = 0 \quad \text{or} \quad I = -a_1/a_2 H + \frac{a_0 - c(m)}{a_2}.$$

Let $F_1(H) = -a_1/a_2 H + (a_0 - c(m))/a_2$. $F_1(H)$ is a linear equation in H with slope $-a_1/a_2$ and I -intercept $(a_0 - c(m))/a_2$, and H -intercept $(a_0 - c(m))/a_1$. To get the I -isocline, let $\frac{dI}{dt} = 0$. (3.5) implies that

$$b_1 I^2 + (b_2 H + \delta)I - c(m)H = 0.$$

This is a quadratic equation in I for fixed H . If $H = 0$, then $I = 0$, and $I = -\delta/b_1$ are the I -intercepts of the I -isocline. The graph of the H -isocline, and the I -isocline is given by figure 3.1, along with the flow of solutions along the isoclines in the population quadrant.

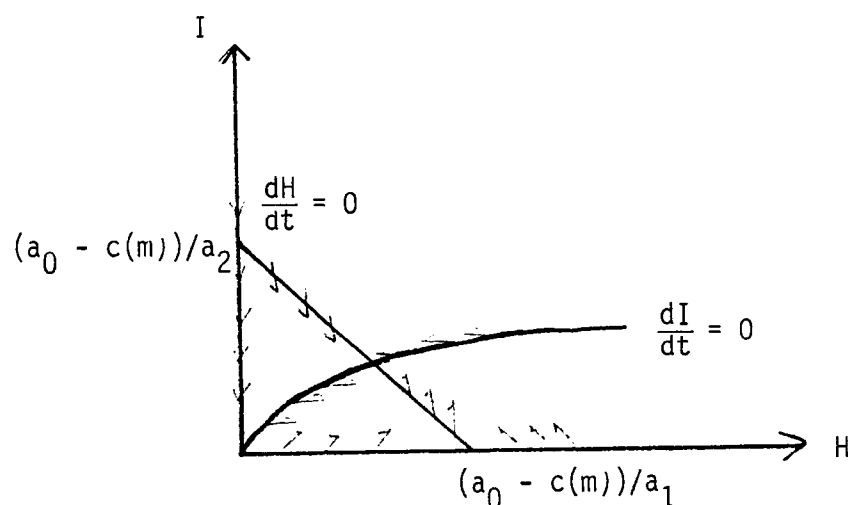


Figure 3.1. Flow of solutions of (3.4) and (3.5) along the isoclines in the population quadrant.

The positive equilibrium shown in Figure 3.1 is unique. To see this, consider the H and I -isoclines. The H -isocline is a straight line with negative slope. The I -isocline is a parabola, which opens to the right, and whose vertex is to the left of the vertical axis. The only possible way to have two positive equilibria is for the H -isocline to intersect the I -isocline in two places in the quadrant $H > 0$ and $I > 0$. This cannot happen, since the I -intercepts of the I -isocline are not both positive. Therefore the positive equilibrium is unique. Theorem 3.3 tells us that there are no limit cycles. Since there are no attractors on the positive I -axis there can be no cycle graphs. So, from observing Figure (3.1), and noting that there are no limit cycles or cycle graphs, the equilibrium must be globally stable.

The next consideration is the m equation:

$$\frac{dm}{dt} = -c_0 m + c_1 I / (I+H) .$$

Using (3.5) gives

$$I / (I+H) = c(m) / (c(m) + \delta + b_1 I + b_2 H) .$$

At equilibrium $I = I_*$ and $H = H_*$, so

$$c(m) / (c(m) + \delta + b_1 I_* + b_2 H_*) = c(m) / (c(m) + q) ,$$

where $q = \delta + b_1 I_* + b_2 H_*$.

Also at equilibrium $\frac{dm}{dt} = 0$, which yields

$$c(m) = g c_0 m / (-c_0 m + c_1) .$$

Recalling that $c(m)$ can be written as $BP(m)$, and letting $\alpha(m) = P(m)/m$ gives

$$B\alpha(m) = g c_0 / (-c_0 m + c_1) ,$$

which gives

$$(3.7) \quad \alpha(m) = q c_0 / B(-c_0 m + c_1) .$$

The m equilibria are fixed points of (3.9). The graphs of $y = \alpha(m)$, provided by Ludwig and Haytock (1976) and of $y = q c_0 / B(-c_0 m + c_1)$ are given by Figure 3.2.

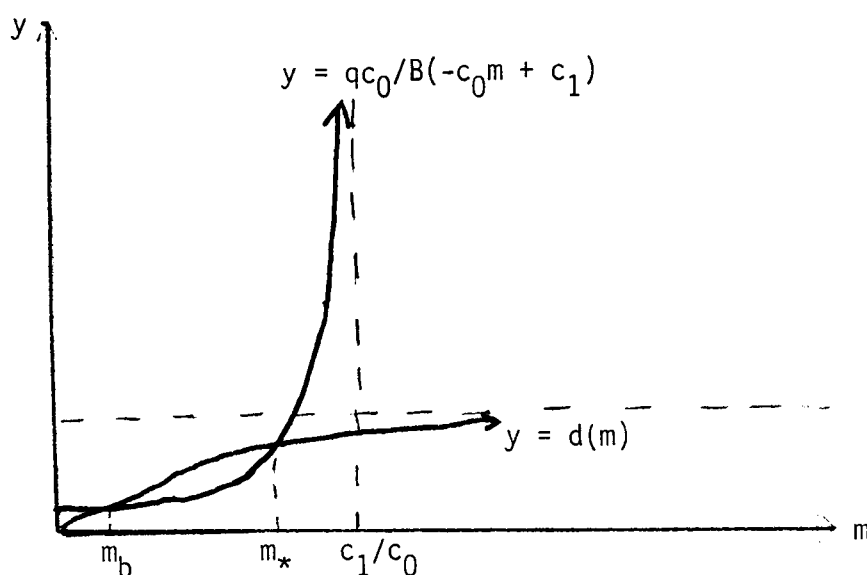


Figure 3.2. Equilibria of 3.6, with stability.

As seen in Figure 3.2, there are two equilibria, m_* , called the "threshold", and m_b , called the breakpoint". Stability of m_b and m_* can be seen by looking at the sign of dm/dt . Note, the equilibrium analysis for the m -equation is for nonconstant $c(m)$. In the case where $c(m)$ is a constant, and m is a positive constant, there is a unique positive equilibrium for the system formed by (3.4)-(3.6). In the case where $c(m)$ is nonconstant, there can be three equilibria; (H_*, I_*, m_b) , (H_*, I_*, m_*) , and $(H_*, I_*, 0)$. These results are similar to those of Ludwig and Haytock (1976) in that there are three equilibria for the m -equation. However, Ludwig and Haytock (1976) do not consider the dynamics for H and I along with those of m . Notice that an increase in m_b would be desirable, since $m \rightarrow 0$ if $m(t) < m_b$. By looking at equilibrium components, MacDonald (1965) found that the only chance to accomplish this in a human population is through a combined program of increased sanitation, reduced exposure to contaminated water, or the destruction of the snail population.

Let us now consider another case of the general model:

$$(3.7) \quad \frac{dH}{dt} = a_0H - c(m)H - a_1H^2 - a_2IH^2,$$

$$(3.8) \quad \frac{dI}{dt} = c(m)H - \delta I - b_2IH^2,$$

and

$$(3.9) \quad \frac{dm}{dt} = -c_0m + c_1I/(I+H).$$

Here, another degree of nonlinearity has been added to the interaction terms in the H and I equations. Also, since the infected snail population is usually smaller than the healthy snail population, thus less subject to density dependence, the density dependence term has been dropped from the I equation.

Let us examine the H and I -isoclines for a fixed value of m to help determine the existence and stability of a positive equilibrium for the HI-system formed by (3.7) and (3.8). To get the H -isocline, let the right hand side of (3.7) be zero. This yields

$$(3.10) \quad H = \frac{a_0 - c(m)}{a_1 + a_2 I} .$$

Recall that $a_0 > c(m)$, so that $H > 0$. To describe the isocline note that (3.10) has the properties that as I approaches $-a_1/a_2$, H approaches infinity, and as I approaches infinity, H approaches zero. The H -isocline with $a_0 > c(m)$ is one branch of a hyperbola. The H -intercept is $(a_0 - c(m))/a_1$. To get the I -isocline, let $\frac{dI}{dt}$ in (3.8) be zero. This yields

$$I = c(m)H/(\delta + b_2 H^2) .$$

When $H = 0$, $I = 0$. As H goes to infinity, I goes to zero. Also I reaches a maximum value at $H = (\delta/b_2)^{1/2}$. Figure 3.3 gives the graph of the H and I isoclines, along with the flow of solutions along the isoclines. Note the possibility for multiple equilibria exists. However, by applying Descartes rule of signs it can

be shown that the equilibrium is unique if $b_2 a_0 - b_2 c(m) - a_2 c(m) < 0$. Recall that the I-isocline was given by

$$I = c(m)H / (\delta + b_2 H^2) .$$

Substituting this into the equation $\frac{dH}{dt} = 0$ gives $a_0 H - c(m)H - a_1 H^2 - \frac{c(m)H}{(\delta + b_2 H^2)} H^2 = 0$. Multiplying both sides by $\delta + b_2 H^2$, and noting that both sides are divisible by H , gives

$$\begin{aligned} & -a_1 b_2 H^3 + (a_0 b_2 - c(m)b_2 - a_2 c(m))H^2 - a_1 \delta H \\ & + (a_0 \delta - c(m)\delta) = 0 . \end{aligned}$$

If $a_0 b_2 - c(m)b_2 - a_2 c(m) < 0$, Descartes rule of signs implies that there is only one real root, therefore, the equilibrium illustrated by Figure 3.3 is unique.

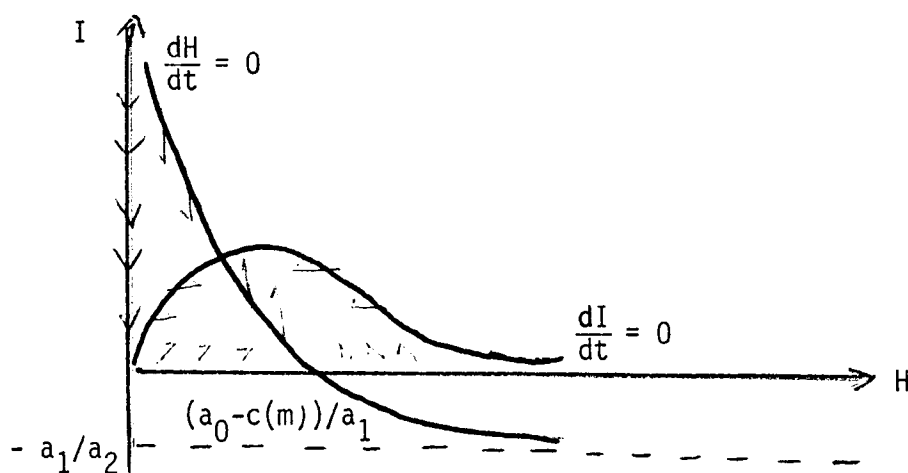


Figure 3.3. Flow of solutions of (3.7) and (3.8) along the H and I -isoclines.

Now, Theorem (3.3) tells us that there are no limit cycles. Absence of an attractor on the positive I-axis does not allow a cycle graph. From these facts, and from observing Figure 3.3 it is evident that the positive unique equilibrium is globally stable (for a fixed m).

Now, consider the m equation:

$$\frac{dm}{dt} = -c_0 m + c_1 I/(I+H) .$$

(3.8) gives

$$I/(I+H) = c(m)/(c(m) + \delta + b_2 H^2) .$$

At equilibrium, $H = H_*$ and $I = I_*$, so

$$I_*/(I_* + H_*) = c(m)/(c(m) + \delta + b_2 H_*^2) .$$

Let

$$p = \delta + b_2 H_*^2 .$$

$\frac{dm}{dt} = 0$ implies that

$$-c_0 m + c_1 c(m)/(c(m) + p) = 0 ,$$

which gives

$$\dot{c}(m) = pc(m)/(-c_0m + c_1) .$$

This is almost identical to the results obtained for the first case. The only difference is that instead of $c(m) = q c_0m/(-c_0m + c_1)$, there is

$$c(m) = p c_0m/(-c_0m + c_1) .$$

As before, let $\alpha(m) = P(m)/m$, which gives

$$(3.11) \quad \alpha(m) = c_0 p/B(-c_0m + c_1) .$$

The m -equilibria are fixed points of (3.11). The graphs of the left and right hand sides of (3.11), as functions of m , are given by Figure 3.4, along with stability of the m equilibria.

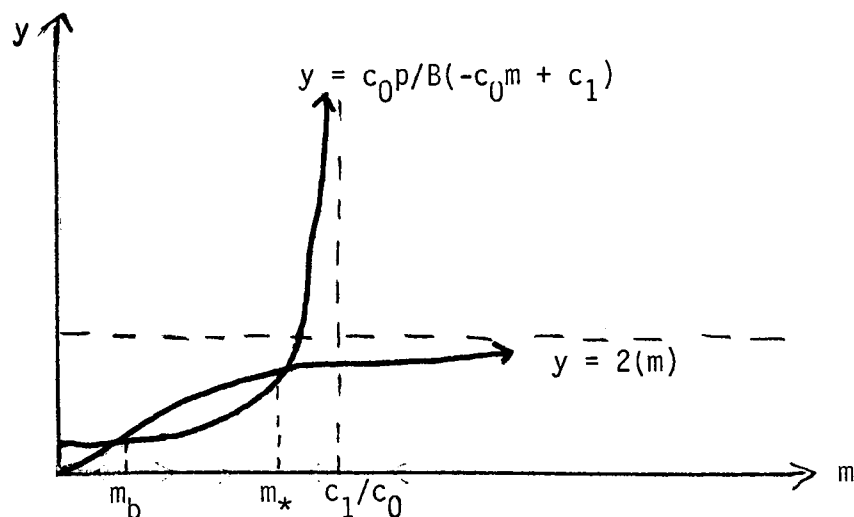


Figure 3.4. The m equilibria of (3.9) with stability indicated.

Once again, for a fixed m , there is a positive unique and stable equilibrium for the system formed by (3.7)-(3.9). For nonconstant $c(m)$, there are three equilibria for the system formed by (3.7)-(3.9); $(H_*, I_*, 0)$, (H_*, I_*, m_b) , and (H_*, I_*, m_*) . If $m(0) > m_b$, the equilibrium reached is (H_*, I_*, m_*) . If $m(0) < m_b$, the equilibrium reached is $(H_*, I_*, 0)$. The results are similar to those of Ludwig and Haytock (1976), in that there are three equilibria for the m equation. However, Ludwig and Haytock (1976) do not consider the dynamics of H , I , and m as a system. In the next chapter numerical solutions to the H and I equations of the two cases just discussed (for a fixed m) are presented, along with some sensitivity results. Also a case that the author cannot solve geometrically is solved numerically.

CHAPTER IV

NUMERICAL SOLUTIONS WITH SENSITIVITY STUDIES

In this chapter, numerical solutions to the HI-systems discussed in the latter part of Chapter three are presented. Consider the equations below:

$$(4.1) \quad \frac{dH}{dt} = a_0 H - c(m)H - a_1 H^2 - a_2 IH ,$$

$$(4.2) \quad \frac{dI}{dt} = c(m)I - \delta I - b_1 I^2 - b_2 IH ,$$

$$(4.3) \quad \frac{dm}{dt} = -c_0 m + c_1 I/(I+H) ,$$

$$(4.4) \quad \frac{dH}{dt} = a_0 H - c(m)H - a_1 H^2 - a_2 IH^2 ,$$

$$(4.5) \quad \frac{dI}{dt} = c(m)H - \delta I - b_2 IH^2 , \text{ and } \cdot$$

Equations (4.1) and (4.2) will be referred to as HI-system (I) , and equations (4.4) and (4.5) as HI-system (II). Note that in the case of a fixed value of m , $c(m)$ is a constant, and (4.1), (4.2), (4.4), and (4.5) are independent of m . Numerical solutions are obtained for the three dimensional systems formed by (4.1)-(4.3), and (4.4), (4.5), and (4.3) in the case where $c(m)$ is a linear function of m , and where $c(m)$ is a quadratic function of m . Although a three dimensional system is solved in the case of a nonconstant $c(m)$, the graph of the HI-phase plane is presented.

the graph of the HI-phase plane is presented.

The numerical method used is the Adams Predictor-Corrector method, also called DGEAR, using functional iteration. This does not require the user to supply a subroutine that calculates the Jacobian at each iteration. The Adams Predictor-Corrector method can be used with the Jacobian calculated internally.

The first consideration is the HI-system (I) with constant, linear, and quadratic infectivity rates. The initial values are $H = 50$, $I = 25$, and $m = 5$. Experiments by Pan (1965) suggest that the death rate of the infected snails should be chosen relatively large (e.g. larger than .4). The interaction and density dependence coefficients will be chosen small (e.g. less than .1) since that contribution to the growth rate is usually small. The intrinsic growth rate of the healthy snails, the infectivity rate, $c(m)$, the death rate of the worms in the human host, c_0 , and the proportion of cercariae that survive to reach a human host, c_1 will be chosen in the mid-range, since I am aware of no biological data that has been gathered to estimate these coefficients.

Numerical solutions to HI-system (I) are presented in Figures 4.1 -4.8. For Figures 4.1 - 4.8 the following set of parameter values will be used, unless indicated otherwise; $c(m) = .4$, $a_0 = .5$, $\delta = .51$, $a_1 = a_2 = b_1 = b_2 = .01$; $c_0 = .05$, and $c_1 = .5$. H_* and I_* will denote the H and I equilibrium values, respectively. The initial values used for all numerical work in this chapter are $H(0) = 50$, $I(0) = 25$, and $m(0) = 5$.

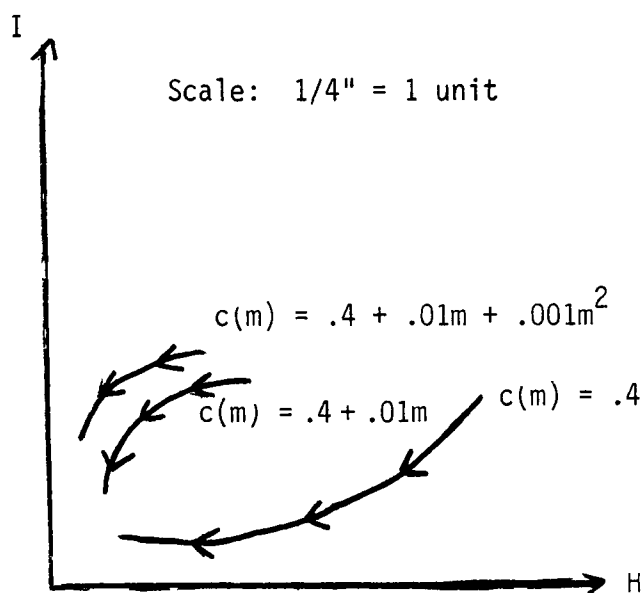


Figure 4.1. Numerical solutions to HI-system (I) with $H_* = 2.103$ and $I_* = 1.579$ when $c(m) = .4$, $H_* = 1.95$ and $I_* = 3.1$ when $c(m) = .4 + .01m$, and $H_* = 1.55$ and $I_* = 4.728$ when $c(m) = .4 + .01m + .001m^2$.

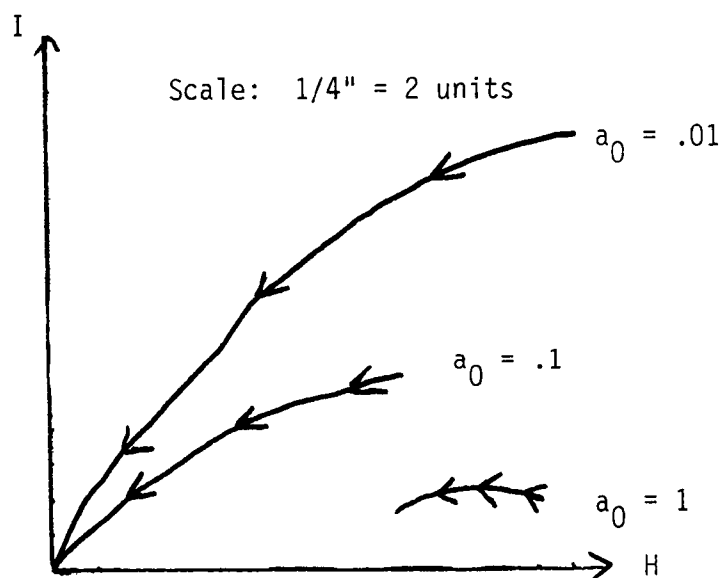


Figure 4.2. Numerical solutions to HI-system (I) with $H_* = 23.481$ and $I_* = 1.555$ when $a_0 = 1$, and extinction when $a_0 = .01$ or $a_0 = .1$.

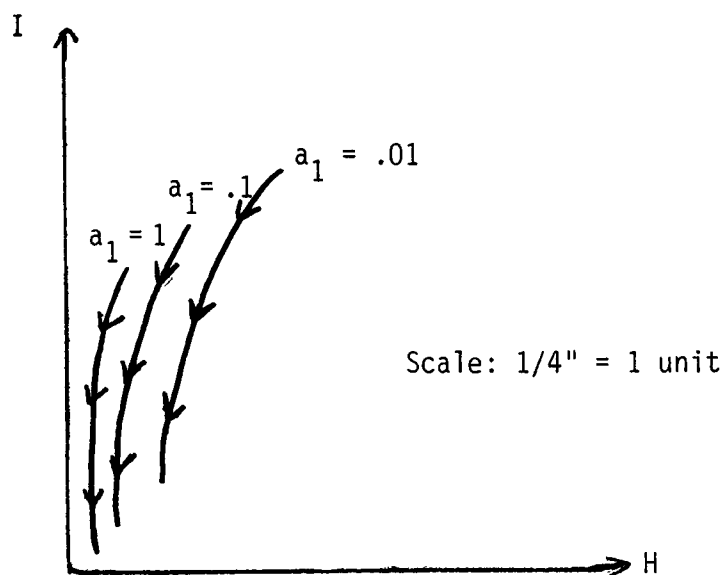


Figure 4.3. Numerical solutions to HI-system (I) with $H_* = 2.103$ and $I_* = 1.579$ when $a_1 = .01$, $H_* = .933$ and $I_* = .710$ when $a_1 = .1$, and $H_* = .099$ and $I_* = .078$ when $a_1 = 1$.

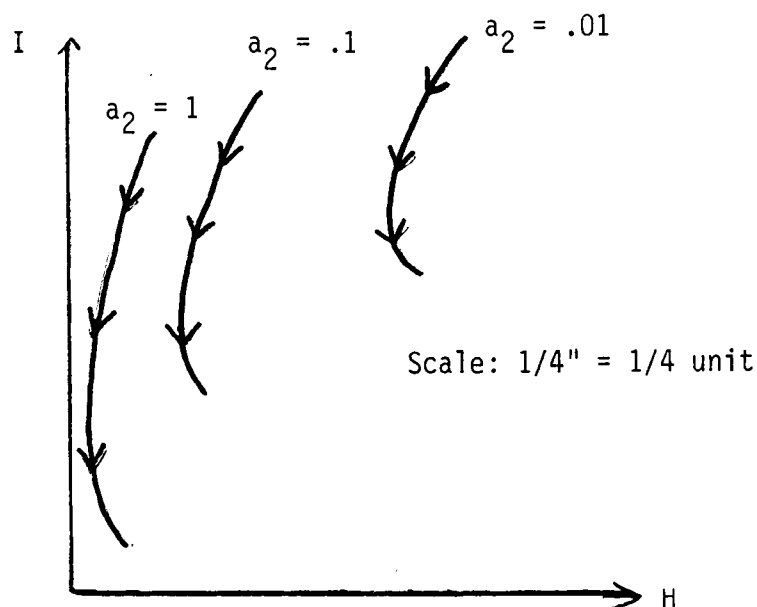


Figure 4.4. Numerical solutions to HI-system (I) with $H_* = 2.103$ and $I_* = 1.579$ when $a_2 = .01$, $H_* = 1.086$ and $I_* = .820$ when $a_2 = .1$, and $H_* = .352$ and $I_* = 2.74$ when $a_2 = 1$.

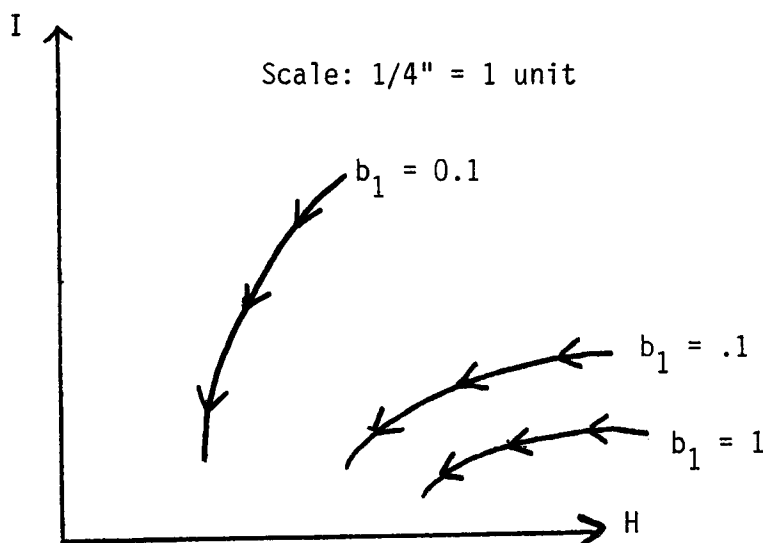


Figure 4.5. Numerical solutions to HI-system (I) with $H_* = 2.103$ and $I_* = 1.579$ when $b_1 = .01$, $H_* = 3.612$ and $I_* = 1.768$ when $b_1 = .1$, and $H_* = 4.836$ and $I_* = 1.067$ when $b_1 = 1$.

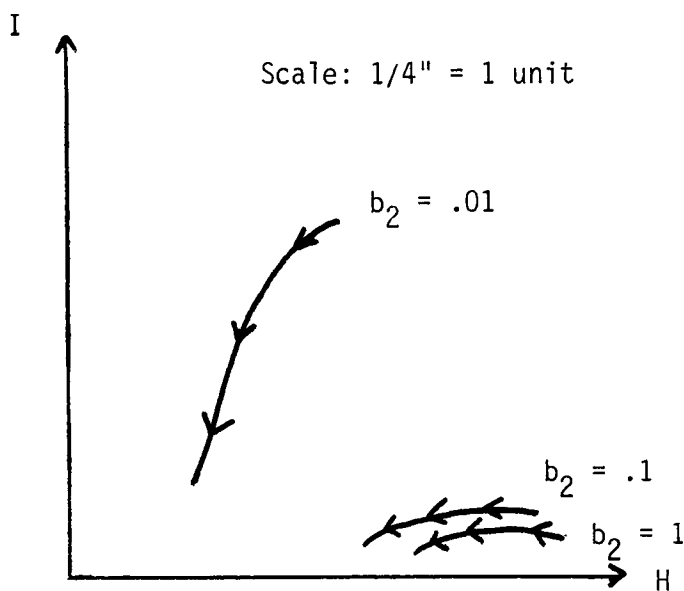


Figure 4.6. Numerical solutions to HI-system (I) with $H_* = 2.103$ and $I_* = 1.579$ when $b_2 = .01$, $H_* = 6.442$ and $I_* = .552$ when $b_2 = .1$, and $H_* = 9.602$ and $I_* = .041$ when $b_2 = 1$.

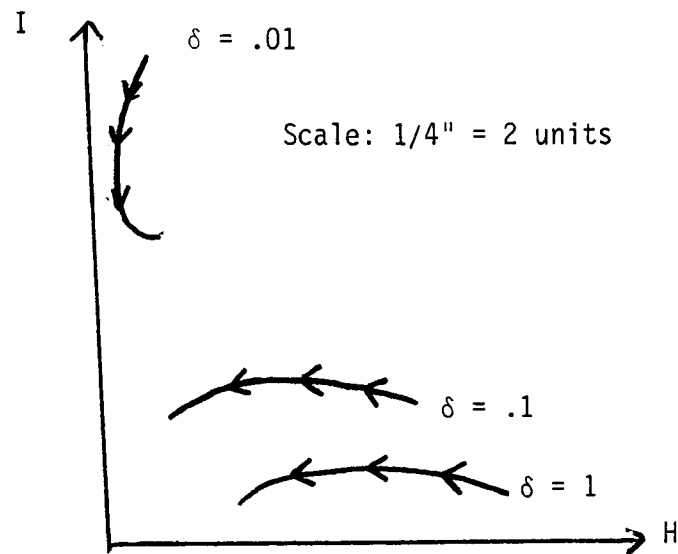


Figure 4.7. Numerical solutions to HI-system (I) with $H_* = .596$ and $I_* = 9.404$ when $\delta = .01$, $H_* = 1.902$ and $I_* = 4.256$ when $\delta = .1$, and $H_* = 4.162$ and $I_* = 1.402$ when $\delta = 1$.

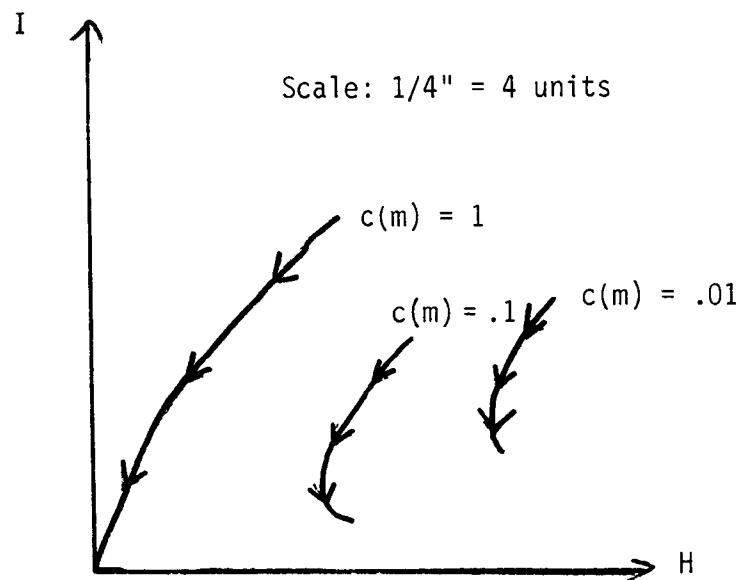


Figure 4.8. Numerical solutions to HI-system (I) with $H_* = 48.512$ and $I_* = .487$ when $c(m) = .01$, $H_* = 30.522$ and $I_* = .61$ when $c(m) = .1$, and extinction when $c(m) = 1$.

Numerical solutions to HI-system (II) are given by Figures 4.9-4.15. For Figures 4.9-4.15 the following set of parameter values is used, unless indicated otherwise: $c(m) = .4$, $a_0 = .5$, $\delta = .51$, $a_1 = a_2 = b_2 = .01$, $b_1 = 0$, $c_0 = .5$, and $c_1 = .5$. H_* and I_* are the H and I equilibrium values, respectively.

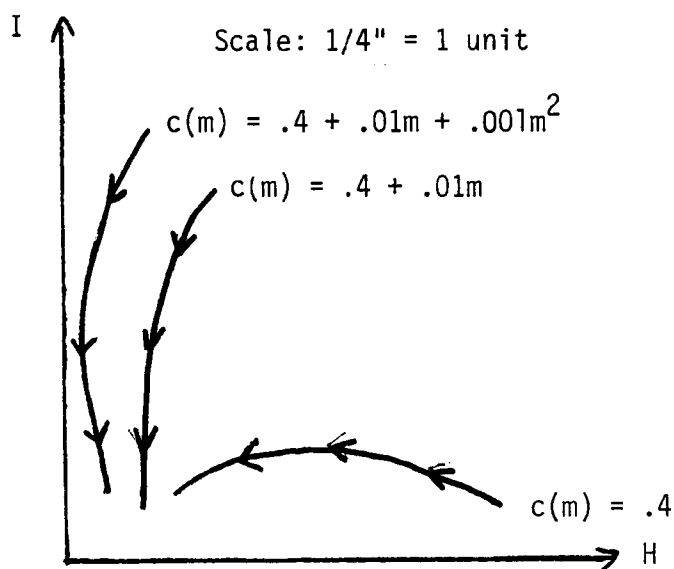


Figure 4.9. Numerical solutions to HI-system (II) with $H_* = 3.224$ and $I_* = 2.1$ when $c(m) = .4$, $H_* = 2.191$ and $I_* = 2.181$ when $c(m) = .4 + .01m$, and $H_* = 1.552$ and $I_* = 2.932$ when $c(m) = .4 + .01m + .001m^2$.

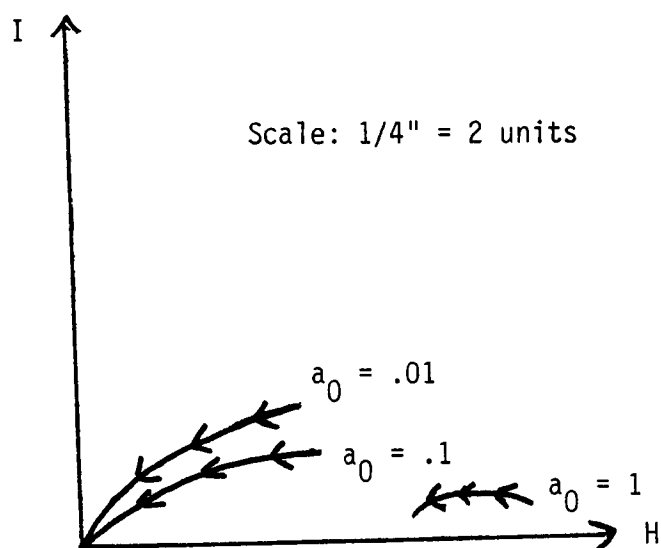


Figure 4.10. Numerical solutions to HI-system (II) with $H_* = 23.406$ and $I_* = 1.563$ when $a_0 = 1$, and extinction when $a_0 = .01$ or $a_0 = 1$.

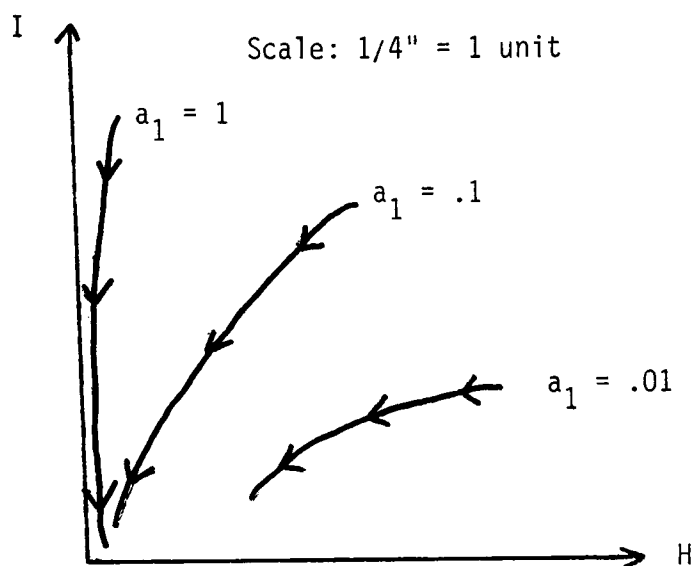


Figure 4.11. Numerical solutions to HI-system (II) with $H_* = 3.224$ and $I_* = 2.191$ when $a_1 = .01$, $H_* = .934$ and $I_* = .720$ when $a_1 = .1$, and $H_* = .1$ and $I_* = .078$ when $a_1 = 1$.

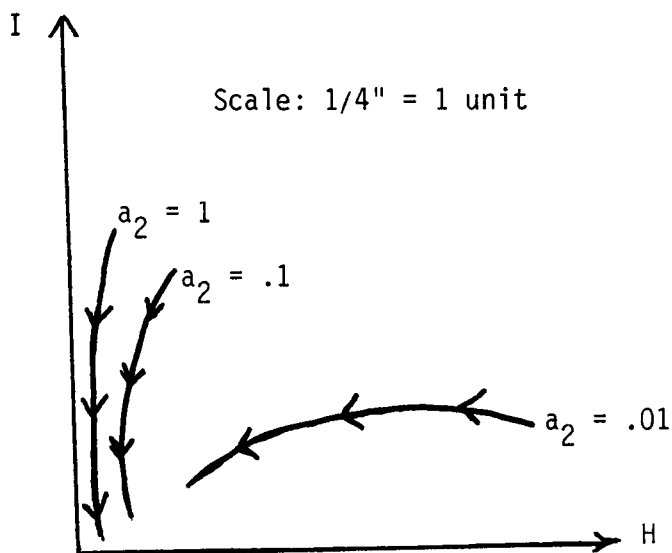


Figure 4.12. Numerical solutions to HI-system (II) with H_* 3.224 and $I_* = 2.191$ when $a_2 = .01$, $H_* = 1.07$ and $I_* = .827$ when $a_2 = .1$, and $H_* = .351$ and $I_* = .274$ when $a_2 = 1$.

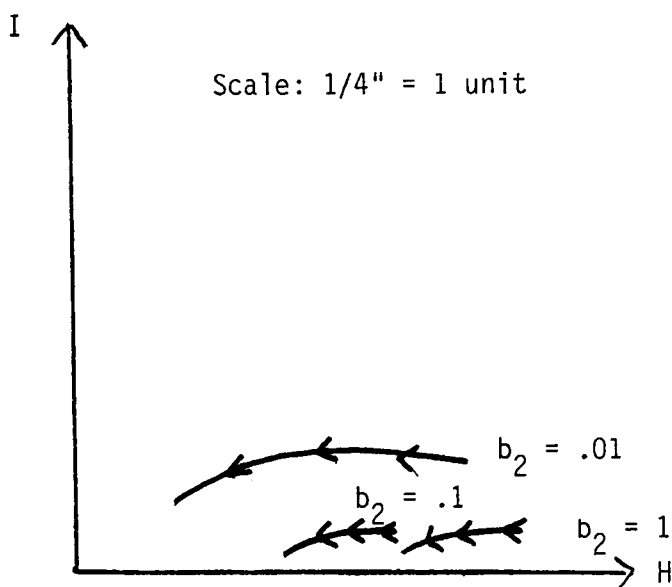


Figure 4.13. Numerical solutions to HI - system (II) with $H_* = 3.224$ and $I_* = 2.191$ when $b_2 = .01$, $H_* = 6.438$ and $I_* = .553$ when $b_2 = .1$, and $H_* = 9.602$ and $I_* = .041$ when $b_2 = 1$.

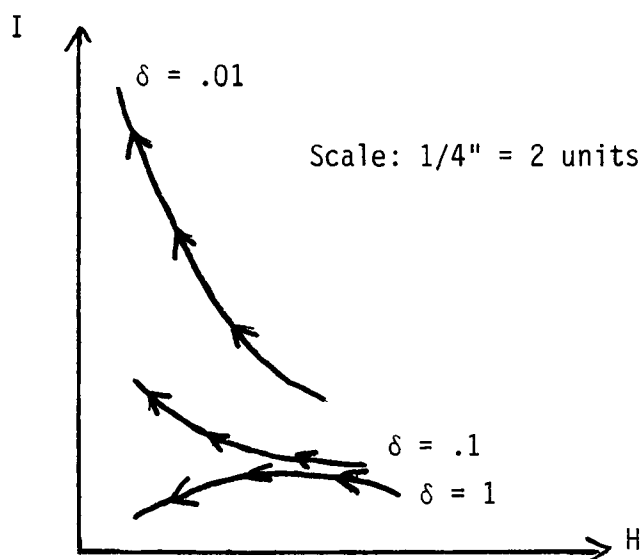


Figure 4.14. Numerical solutions to HI-system (II) with $H_* = .555$ and $I_* = 16.987$ when $\delta = .01$, $H_* = 1.627$ and $I_* = 5.146$ when $\delta = .1$, and $H_* = 4.142$ and $I_* = 1.414$ when $\delta = 1$.

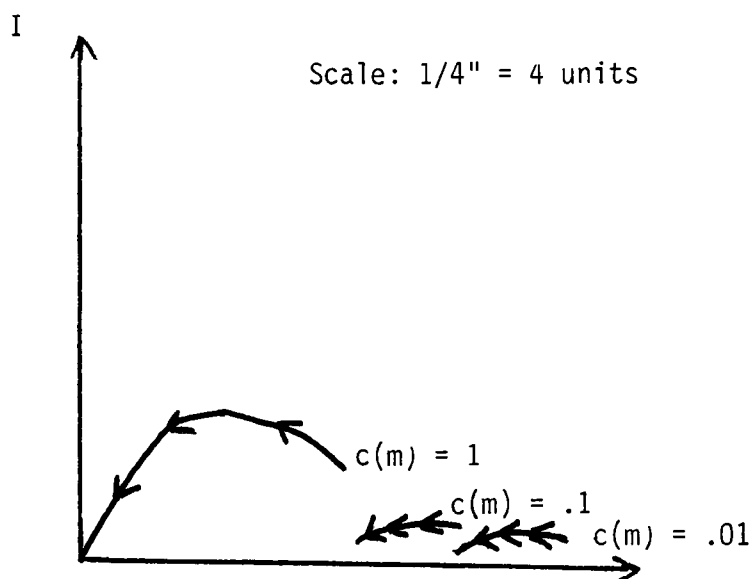


Figure 4.15. Numerical solutions to HI-system (II) with $H_* = 48.021$ and $I_* = .023$ when $c(m) = .01$, $H_* = 30.51$ and $I_* = .3$ when $c(m) = .1$, and extinction when $c(m) = 1$.

A few points can be made using the previous numerical results. If the density dependence or interaction coefficient in the H equation gets large (near one), the equilibrium values for H and I get small (less than one). If the density dependence or interaction coefficient in the I equation gets large (near one), the equilibrium value for H increases, while the equilibrium value for I decreases. If the death rate of the infected snails gets small, the H equilibrium value decreases, while the I equilibrium value decreases. Also, if the intrinsic growth rate of the healthy snails gets small (less than the infectivity rate) or the infectivity rate gets large (greater than the intrinsic growth rate of the healthy snails) the system will go to extinction, as expected. For HI-system (I), note from Figure 3.1, the y -intercept of $y = qc_0/(B(-c_0m + c_1))$ is c_0q/c_1B , where

$$q = \delta + b_1I_* + b_2H_*, \text{ and } H_* \text{ and } I_*$$

are the H and I equilibrium values, respectively. Notice that if either I_* or H_* increase, the y intercept c_0q/c_1B increases, causing the two equilibria for the m -equation to move closer; m_* , the breakpoint, is increased, and m_b , the threshold, is decreased.

For HI-system (II), note from Figure (3.5), the y -intercept of $y = pc_0/(B(-c_0m + c_1))$ is pc_0/Bc_1 , where $p = \delta + b_2H_*^2$. So, if H_* increases, the y -intercept increases, forcing m_b , the breakpoint, to increase, and m_* , the threshold, to decrease. Note that I_* has no effect on the m equilibria in this case.

The last part of this chapter is devoted to numerical solutions to a case of the general model for which equilibria for the HI-system cannot be easily found geometrically. Consider the following set of equations,

$$(4.7) \quad \frac{dH}{dt} = a_0 H - c(m)H - a_1 H^3 - a_2 I^2 H^2 ,$$

$$(4.8) \quad \frac{dI}{dt} = c(m)H - \delta I - b_1 I^2 - b_2 I^3 H^2 ,$$

and

$$(4.9) \quad \frac{dm}{dt} = -c_0 m + c_1 I/(I+H) .$$

Equations (4.7) and (4.8) will be referred to as HI-system (III). A relatively large death rate, δ , will be used, as suggested by the experiments of Pan (1965). Small density dependence and interaction coefficients are chosen, since it is assumed that these effects are relatively small. Mid-range values will be used for the intrinsic growth rate of the healthy snails, and for the constant infectivity rate.

Numerical solutions to HI-system (III) are presented in Figures 4.16-4.23. For Figures 4.16-4.23 the following set of parameters will be used, unless indicated otherwise; $a_0 = .5$, $c(m) = .4$, $\delta = .51$, $a_1 = a_2 = b_1 = b_2 = .01$, $c_0 = .3$, and $c_1 = .4$. Again, H_* and I_* will denote the H and I equilibrium values, respectively.

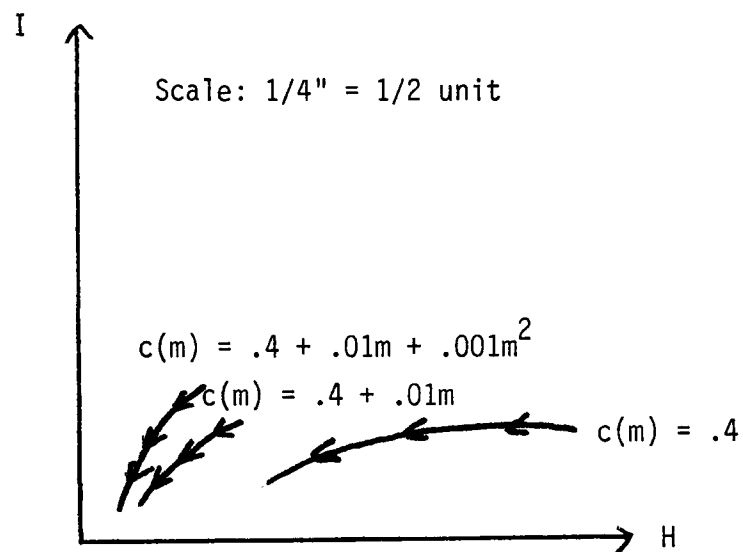


Figure 4.16. Numerical solutions to HI-system (III) with $H_* = 2.238$ and $I_* = 1.492$ when $c(m) = .4$, $H_* = 1.379$ and $I_* = 1.039$ when $c(m) = .4 + .01m$, and $H_* = 1.378$ and $I_* = 1.040$ when $c(m) = .4 + .01m + .001m^2$.

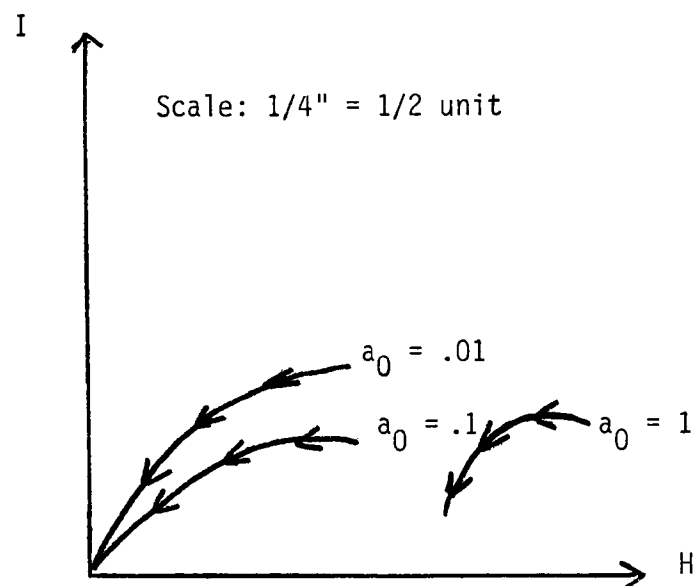


Figure 4.17. Numerical solutions to HI-system (III) with $H_* = 6.079$ and $I_* = 1.946$ when $a_0 = 1$, and extinction when $a_0 = .01$ or $a_0 = .1$.

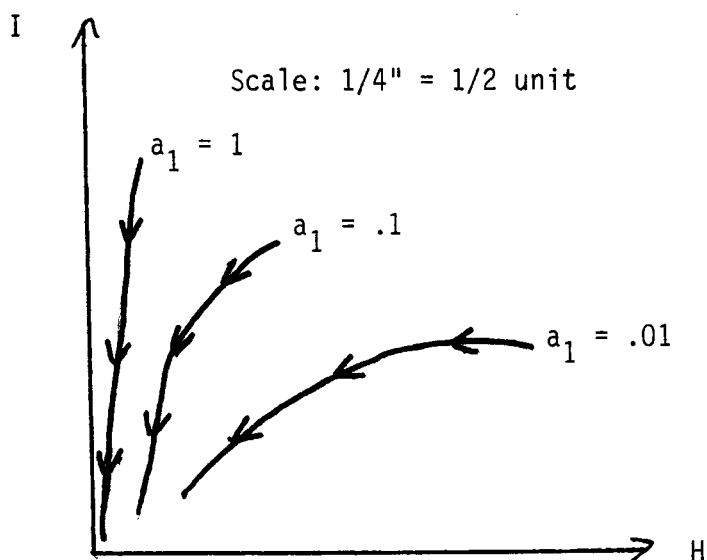


Figure 4.18. Numerical solutions to HI-system (III) with $H_* = 2.238$ and $I_* = 1.492$ when $a_1 = .01$, $H_* = .972$ and $I_* = .246$ when $a_1 = .1$, and $H_* = .315$ and $I_* = .246$ when $a_1 = 1$.

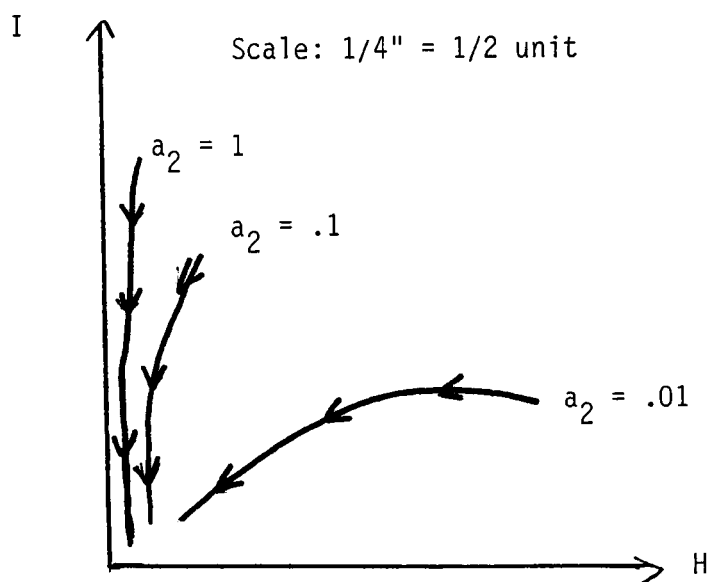


Figure 4.19. Numerical solutions to HI-system (III) with $H_* = 2.238$ and $I_* = 1.492$ when $a_2 = .01$, $H_* = 1.150$ and $I_* = .868$ when $a_2 = .1$, and $H_* = .544$ and $I_* = .422$ when $a_2 = 1$.

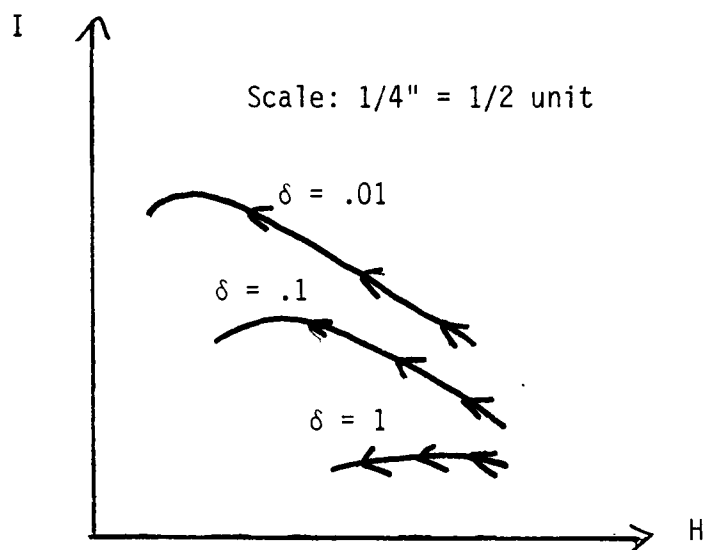


Figure 4.20. Numerical solutions to HI-system (III) with $H_* = .692$ and $I_* = 3.904$ when $\delta = .01$, $H_* = 1.132$ and $I_* = 2.702$ when $\delta = .1$, and $H_* = 2.702$ and $I_* = .998$ when $\delta = 1$.

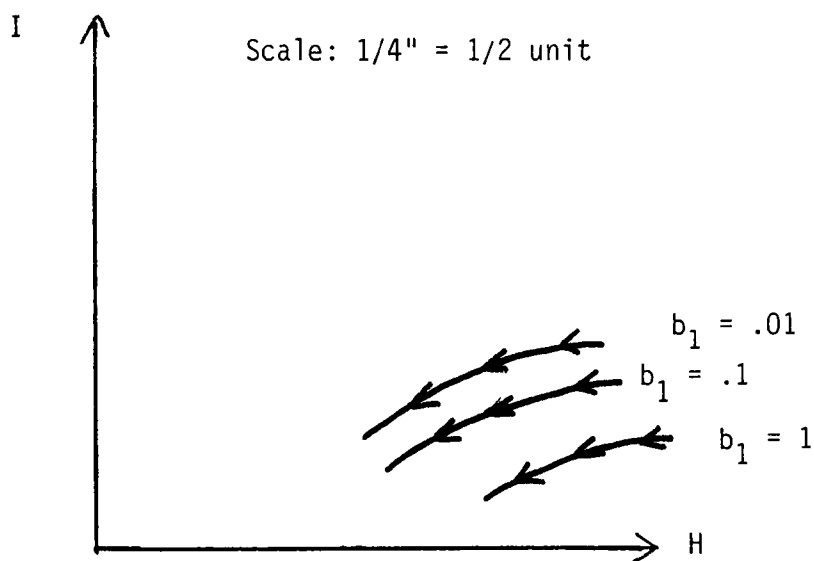


Figure 4.21. Numerical solutions to HI-system (III) with $H_* = 2.238$ and $I_* = 1.492$ when $b_1 = .01$, $H_* = 2.397$ and $I_* = 1.332$ when $b_1 = .1$, and $H_* = 2.846$ and $I_* = .817$ when $b_1 = 1$.

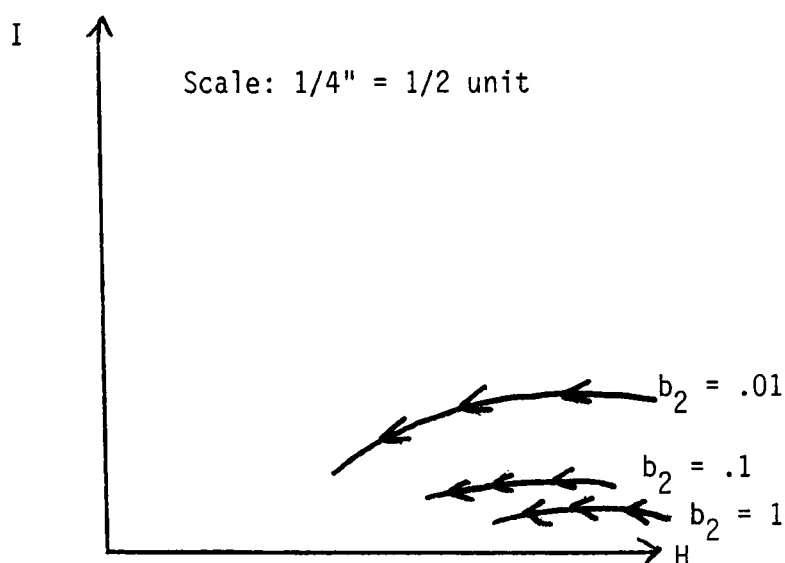


Figure 4.22. Numerical solutions to HI-system (III) with $H_* = 2.238$ and $I_* = 1.492$ when $b_2 = .01$, $H_* = 2.775$ and $I_* = .909$ when $b_2 = .1$, and $H_* = 3.107^2$ and $I_* = .333$ when $b_2 = 1$.

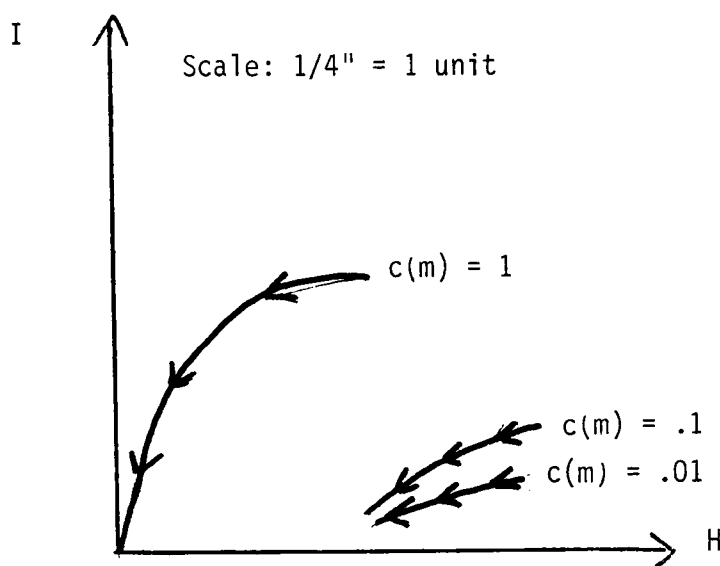


Figure 4.23. Numerical solutions to HI-system (III) with $H_* = 6.992$ and $I_* = .122$ when $c(m) = .01$, $H_* = 6.042$ and $I_* = .759$ when $c(m) = .1$, and extinction when $c(m) = 1$.

The numerical behavior of solutions to HI-system (III) differ very little from solutions to HI-systems (I) and (II). As the density dependence or interaction coefficient in the H equation gets large (near one), the H and I equilibrium values decrease. When the density dependence or interaction coefficient in the I equation gets large (near one), the I equilibrium value decreases, and the H equilibrium value increases. If the death rate of the infected snails, δ , gets large (near one) the I equilibrium value increases. Also, if a_0 gets small (near zero and less than $c(m)$) or $c(m)$ gets large (near one and greater than a_0), the system goes to extinction.

CHAPTER V

SUMMARY

In this paper a necessary condition for persistence of the general HI-system (for a constant infectivity rate) was presented along with a theorem which guarantees no limit cycles existence for this HI-system. Two cases of the general model were considered. In each case, uniqueness and stability of a positive equilibrium were established. There were three equilibrium solutions to the m equation in each case. So, there were three equilibria for the three dimensional systems in the case of a nonconstant infectivity rate. In this respect, the results are similar to those of Ludwig and Haytock (1976), Since they also discovered three equilibrium solutions for m . However, they did not consider the dynamics of H , I , and m as a system.

In the case of second degree nonlinearities in the density dependence and interaction terms in (3.1) and (3.2), increases in the equilibrium values, H_* or I_* , will cause an increase in the breakpoint, m_b . H_* is increased when b_1 (see Figure 4.5) and/or b_2 (see Figure 4.6), in (3.2) are large (near one) or δ (see Figure 4.7) in (3.2) is large (near one). I_* is increased when $c(m)$ is near a_0 , but less than a_0 . I_* is also increased if $c(m)$ is less than a_0 , and δ (see Figure 4.7), in (3.2) is small (near zero).

In the case of second degree nonlinearity in the density dependence term of (3.1), and third degree nonlinearities in the interaction terms in both (3.1) and (3.2), an increase in the equilibrium value H_* will cause an increase in m_b , G_* is increased when a_0 is

larger (near one), $c(m)$ (see Figure 4.15) is smaller (near zero), and/or when b_2 or δ (see Figure 4.6 and 4.7) of (3.2) is large (near one).

In any case, if the value of the breakpoint, m_b , is to be lowered there must be some type of forced density dependence and/or interaction in both the healthy and infected snail populations. This might be accomplished by destroying part of the snail habitat, forcing the snails to live in a more restricted environment. Also, by destroying the snails, the life cycle of schistosomiasis can be interrupted.

Chemical treatment of the water, which destroys the cercariae without harming the other species which might be using the same water would facilitate a significant break in the life cycle of schistosomiasis.

I have no knowledge of any vaccine that is available for schistosomiasis, although the drug praziquantel is available (as a safe antihelminthic agent for schistosomiasis) according to Anderson and May (1982). The results obtained in this paper do not differ enough for the results discussed by Ludwig and Haytock (1976) in their discussion of MacDonald's (1965) paper on helminth infections to offer any new approaches in the control of schistosomiasis.

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VITA

Jeffrey Lawrence Pierce was born in Elizabethton, Tennessee on March 14, 1961. He graduated from Elizabethton Comprehensive High School in 1979. In May, 1983, he received a Bachelor of Arts degree in Mathematics from Maryville College in Maryville, Tennessee.

In September, 1983, he accepted a teaching assistantship at the University of Tennessee, Knoxville and began study towards a Master of Arts degree. He received this degree with a major in Mathematics. He has accepted a teaching position at Louisburg College, Louisburg, North Carolina. He is married to the former Katherine Sperry of Knoxville.