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STOCHASTIC MODELING OF PARASITES IN HOST POPULATIONS

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ABSTRACT

The complexity of the host-parasite relationship, and its depression of host populations has been investigated and successfully modeled for large populations using deterministic methods. These models fail to accurately predict interactions within smaller populations, and require a statistical component to reclaim some degree of accuracy. This research employs stochastic differential equations to better forecast changes in small populations.

1. INTRODUCTION

Experimental and observational studies have shown that parasites can reduce host density and even drive host populations to extinction [8]. Existing deterministic models, unfortunately, fail to explain or model this possibility, and some existing stochastic models, which might include this extinction phenomena, are impractical to simulate (see for example [4, 7, 9, 13, 14, 15, 16, 18] and the reference therein).

In the present investigation, an existing stochastic model developed by Allen [1] is examined. Then, an equivalent stochastic model, which is more computationally convenient, is described (see [2]). The two models are computationally tested for comparison.

In an effort to understand parasite induced host extinction, Ebert et. al. [8] developed an SI deterministic epidemiological model and a stochastic version. Their models include host fecundity and density dependent population constraints, as well as infectious rates. Empirical data based on six different parasites are compared for predictions from the deterministic and stochastic models.

A slightly more complex SIR deterministic model was developed by McCallum [17]. This model includes host fecundity and infectious rates, as well as the introduction of a population of recovered and immune individuals. The results are analyzed for catastrophic outcomes and equilibrium states.

Each of these methods are described deterministically and stochastically.

2. TWO INTERACTING POPULATIONS STOCHASTIC MODELS

2.1. An Existing Stochastic Model

The system depicted in Figure 2.1 illustrates a compartmental analysis of the two interacting populations model developed by Allen [1].

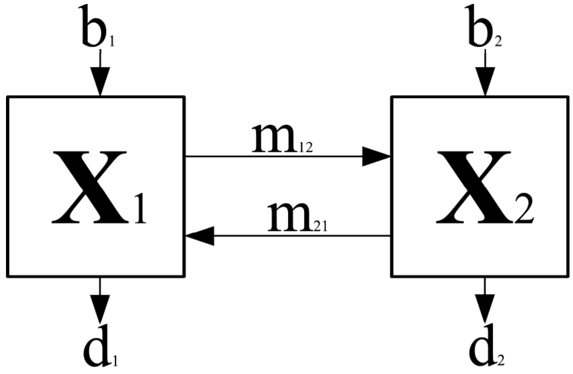

Figure 2.1: *Two Interacting Populations*

This system includes the following vector possibilities as rates of change, with their corresponding probabilities, listed respectively:

$$\begin{array}{ll}
\vec{\eta}_1 = (1,0)^T, & P_1 = b_1 X_1 \Delta t; \\
\vec{\eta}_2 = (-1,0)^T, & P_2 = d_1 X_1 \Delta t; \\
\vec{\eta}_3 = (-1,1)^T, & P_3 = m_{12} X_1 \Delta t; \\
\vec{\eta}_4 = (1,-1)^T, & P_4 = m_{21} X_2 \Delta t; \\
\vec{\eta}_5 = (0,1)^T, & P_5 = b_2 X_2 \Delta t; \\
\vec{\eta}_6 = (0,-1)^T, & P_6 = d_2 X_2 \Delta t; \\
\vec{\eta}_7 = (0,0)^T, & P_7 = 1 - \sum_{i=1}^{6} P_i \\
\sum_{i=1}^{7} P_i = 1 &
\end{array} \tag{2.1}$$

Figure 2.1 includes X_1 and X_2 which are two interacting populations (e.g. Susceptible and Infected), b_i and d_i are the birth and death rates of each population, and m_{ij} are the transfer rates from i to j.These rates of change are each functions which may depend on X_i and t.

Neglecting higher order terms, the mean of this system is [1]:

$$E(\vec{\eta}) = \sum_{i=1}^{7} P_i \vec{\eta}_i = \begin{bmatrix} b_1 X_1 - d_1 X_1 - m_{12} X_1 + m_{21} X_2 \\ b_2 X_2 - d_2 X_2 - m_{21} X_2 + m_{12} X_1 \end{bmatrix} \Delta t = \vec{\mu} dt \tag{2.2}$$

and its covariance matrix is given by [1]:

$$E(\vec{\eta}\,\vec{\eta}^T) = \sum_{i=1}^{7} P_i \vec{\eta}_i \vec{\eta}_i^T = \begin{bmatrix} a & b \\ b & c \end{bmatrix} \Delta t, \tag{2.3}$$

where $a = (b_1 + d_1 + m_{12}) X_1 + m_{21} X_2$, $b = -m_{12} X_1 - m_{21} X_2$ and $c = (b_2 + d_2 + m_{21}) X_2 + m_{12} X_1$.

This covariance matrix has a positive definite square root of the form [1]:

$$B = \frac{1}{\sqrt{r+u+2s+2w}}\begin{bmatrix} r+s+w & -s \\ -s & u+s+w \end{bmatrix}, \tag{2.4}$$

where $r = X_1(b_1+d_1)$, $s = X_1 m_{12} + X_2 m_{21}$, $u = X_2 b_2 + X_2 d_2$ and $w = \sqrt{ru+rs+su}$.

The normal distribution of $\vec{\eta}$ is demonstrated in [1]: $\vec{x}(t+\Delta t) = \vec{x}(t) + \vec{\eta} \;\Leftrightarrow\; \vec{x}(t+\Delta t) = \vec{x}(t) + \vec{\mu}\Delta t + B\sqrt{\Delta t}\vec{\alpha}$, where $\vec{\alpha} = (\alpha_1, \alpha_2)^T$ and $\alpha_i \sim N(0,1)$.

Therefore, as $\Delta t \to 0, \vec{X}(t)$ converges strongly to the solution of the stochastic system:

$$\tfrac{d\vec{X}}{dt} = \vec{\mu} + B\tfrac{d\vec{W}(t)}{dt} \;, \tag{2.5}$$

where $\vec{X} = (X_1(t), X_2(t))^T, \vec{\mu} = \vec{\mu}(t, X_1, X_2), B = B(t, X_1, X_2)$ and $\vec{W}(t)$ is a two dimensional Wiener process.

This model presents an accurate way to examine interactions between two populations, but while this modeling technique continues to hold for greater numbers of distinct populations, the calculation of the covariance matrix B becomes difficult to calculate (see [2] and [3]).

An equivalent method, easier to implement is described in the next subsection.

2.2. An Equivalent Stochastic Model

The method studied in the present investigation has the same vectors and probabilities as (2.1), but one examines each vector change individually, with their probabilities as mean times before occurrence in separate Poisson processes:

$$\begin{cases} \Delta X_1 = r_1 - r_2 - r_3 + r_4 \\ \Delta X_2 = r_3 - r_4 + r_5 - r_6 \end{cases}, \tag{2.6}$$

where

$$\begin{array}{ll} r_1 \sim P(b_1 X_1 \Delta t), & r_4 \sim P(m_{21} X_2 \Delta t), \\ r_2 \sim P(d_1 X_1 \Delta t), & r_5 \sim P(b_2 X_2 \Delta t), \\ r_3 \sim P(m_{12} X_1 \Delta t), & r_6 \sim P(d_2 X_2 \Delta t). \end{array}$$

The Poisson processes are then normalized:

$$\begin{cases} \Delta X_1 = b_1 X_1 \Delta t + \sqrt{b_1 X_1 \Delta t}\Lambda_1 - d_1 X_1 \Delta t - \sqrt{d_1 X_1 \Delta t}\Lambda_2 \\ -m_{12} X_1 \Delta t \qquad - \sqrt{X_1 m_{12} \Delta t}\Lambda_3 + m_{21} X_2 \Delta t + \sqrt{m_{21} X_2 \Delta t}\Lambda_4, \\ \Delta X_2 = m_{12} X_1 \Delta t + \sqrt{m_{12} X_1 \Delta t}\Lambda_3 - m_{21} X_2 \Delta t - \sqrt{m_{21} X_2 \Delta t}\Lambda_4 \\ +b_2 X_2 \Delta t \qquad + \sqrt{b_2 X_2 \Delta t}\Lambda_5 - d_2 X_2 \Delta t - \sqrt{d_2 X_2 \Delta t}\Lambda_6, \end{cases} \tag{2.7}$$

$$\Lambda_i \sim N(0,1), \forall i \in [1, ..., 6]$$

As $\Delta t \to 0$, this system converges to the following Ito stochastic differential equation:

$$\begin{cases} \frac{dX_1}{dt} = X_1(b_1 - d_1 - m_{12}) + X_2 m_{21})dt + \sqrt{b_1 X_1}dW_1(t) \\ \qquad -\sqrt{d_1 X_1}dW_2(t) - \sqrt{m_{12} X_1}dW_3(t) + \sqrt{m_{21} X_2}dW_4(t) \\ \frac{dX_2}{dt} = (m_{12} X_1 + X_2(-m_{21} + b_2 - d_2)dt + \sqrt{m_{12} X_1}dW_3(t) \\ \qquad -\sqrt{m_{21} X_2}dW_4(t) + \sqrt{b_2 X_2}dW_5(t) - \sqrt{d_2 X_2}dW_6(t) \end{cases} \tag{2.8}$$

This system may be rewritten as:

$$\left\{ \tfrac{d\vec{X}}{dt} = \vec{\mu}dt + Gd\vec{W}(t) \right. \;, \tag{2.9}$$

where $\vec{\mu}$ and $\vec{X}$ are the same as in (2.5), $\vec{W}$ is a six dimensional Wiener process, and G is the following matrix:

$$G = \begin{bmatrix} G_1 & -G_2 & -G_3 & G_4 & 0 & 0 \\ 0 & 0 & G_3 & -G_4 & G_5 & -G_6 \end{bmatrix}, \tag{2.10}$$

where $G_1 = \sqrt{b_1 X_1}$, $G_2 = \sqrt{d_1 X_1}$, $G_3 = \sqrt{m_{12} X_1}$,

$G_4 = \sqrt{m_{21} X_2}$, $G_5 = \sqrt{b_2 X_2}$ and $G_6 = -\sqrt{d_2 X_2}$.

The equivalence of these two Stochastic differential equations, proved by Allen et. al. [2], are illustrated in models that follow.

3. A SIMPLE SI MODEL

The following epidemiological model with horizontal transmission was developed in [8]:

$$\begin{cases} \frac{dS}{dt} = b(S + fI)[1 - c(S + I)] - dS - \beta SI \\ \frac{dI}{dt} = -(d + \alpha)I + \beta SI \\ S(0) = S_0 > 0, \\ I(0) = I_0 > 0 \end{cases} \tag{3.1}$$

An extrapolation of a similar compartmental model as in the general form produces Figure 3.2.

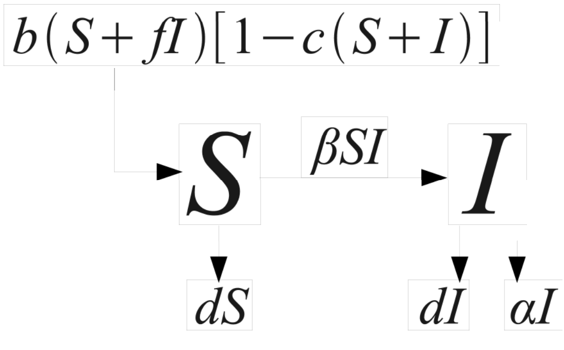

Figure 3.2: *SI Model*

This system includes $S(t)$, $I(t)$ representing the densities of susceptible (healthy) and infected (infectious) hosts at time t, respectively; b is the maximum per capita birth rate of healthy hosts; f is the relative fecundity of a host after infection; c is the density dependent reduction of birth rate; d is the natural death rate;

β measures the infection proportionality constant; and α is the parasite-induced excess mortality rate. Notice that the birth rate of uninfected hosts is then equal to $b(S + fI)[1 - c(S + I)]$. The disease transmission is assumed here to be horizontal only: even births by infected individuals fall into the healthy category.

Several relevant observations are made regarding the biology of the system. The microparasites represented by this model are small unicellular parasites with direct reproduction within their hosts [8]. The host studied, *Daphnia magna*, in absence of parasites and with constant food supply, is reasonably described as logistic population growth, and produces their first eggs after 7-15 days, followed by a clutch of parthenogenic clutch every 3-4 days.

This SI deterministic model predicts the existence of a globally stable equilibrium, and precludes the existence of non-trivial host or parasite extinction. A stochastic model is then needed to simulate extinction possibilities.

The first stochastic modeling technique yields an SDE of the form:

$$\frac{d\vec{X}}{dt} = \vec{\mu} + B\frac{d\vec{W}(t)}{dt} \quad , \tag{3.2}$$

where $\vec{X} = (S, I)^T$,

$$\vec{\mu} = [b(S+fI)(1-c(S+I)) - dS - \beta SI, -(d+\alpha)I + \beta SI]^T,$$

$$B = \frac{1}{\sqrt{r+u+2s+2w}}\begin{bmatrix} r+s+w & -s \\ -s & u+s+w \end{bmatrix}, \tag{3.3}$$

as in (2.4), but with $r = b(S + fI)[1 - c(S + I)] + dS$,

$s = \beta SI$, $u = (d + \alpha)I$, $w = \sqrt{ru + rs + su}$, and $\vec{W}(t)$ is a two dimensional-Wiener process.

Using the second stochastic modeling technique, one obtains an SDE of the form:

$$\frac{d\vec{X}}{dt} = \vec{\mu} + G\frac{d\vec{W}(t)}{dt} \quad , \tag{3.4}$$

where $\vec{X}$ and $\vec{\mu}$ are the same as in (3.2)

$$G = \begin{bmatrix} G_1 & -G_2 & -G_3 & 0 \\ 0 & 0 & G_3 & -G_4 \end{bmatrix}, \tag{3.5}$$

where
$G_1 = \sqrt{b(S + fI)[1 - c(S + I)]}$, $G_2 = \sqrt{dS}$, $G_3 = \sqrt{\beta SI}$

and $G_4 = \sqrt{(d + \alpha)I}$.
Here $\vec{W}(t)$ is now a four-dimensional Wiener process.

While several methods exist for approximating solutions to stochastic differential equations (see for example [6, 10, 11] and the references therein), the models described in the present investigation may be readily approximated using Euler's Method.

4. AN SIR MODEL

The next model, developed in [17], provides a way to examine populations which may gain an immunity to the given parasite.

$$\begin{cases} \frac{dS}{dt} = bN - (d + cN)S - \beta SI + \lambda R \\ \frac{dI}{dt} = \beta SI - (d + cN + \alpha)I - \gamma I \\ \frac{dR}{dt} = \gamma I - (d + cN)R - \lambda R \\ S(0) = S_0 > 0, \\ I(0) = I_0 > 0 \\ R(0) = R_0 \geq 0 \end{cases} \tag{4.1}$$

This system of differential equations can be illustrated using the following compartmental model:

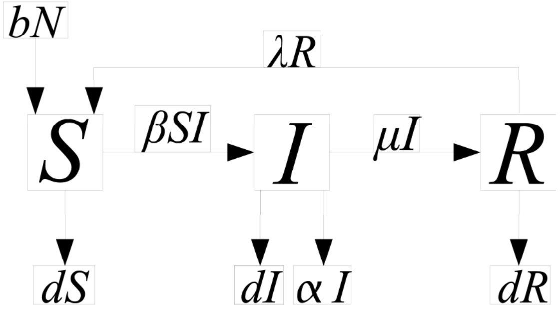

Figure 4.3: *SIR Model*

In this model, S and I are again the susceptible and infected populations, but R is introduced to accommodate the recovered and immune populations. This model has a simpler population growth rate of b, proportional to the size of the entire population N. The carrying capacity of the environment in this model, a rate c proportional to N, is mortality-inducing, rather than birth-restricting. Individuals now recover from this parasite at a rate γ and become temporarily immune, but that immunity is lost at a rate λ.

The first SDE equation is as in (3.2):

$$\frac{d\vec{X}}{dt} = \vec{\mu} + B\frac{d\vec{W}(t)}{dt} \quad , \tag{4.2}$$

where $\vec{X} = (S, I, R)^T$,

$$\vec{\mu} = \begin{bmatrix} bN - (d + cN)S - \beta SI + \lambda R \\ \beta SI - (d + cN + \alpha)I - \gamma I \\ \gamma I - (d + cN)R - \lambda R \end{bmatrix}, \tag{4.3}$$

$\vec{W}$ is a three dimensional Wiener process, and

$$B^2 = \begin{bmatrix} B_{11}^2 & B_{12}^2 & B_{13}^2 \\ B_{12}^2 & B_{22}^2 & B_{23}^2 \\ B_{13}^2 & B_{23}^2 & B_{33}^2 \end{bmatrix}, \tag{4.4}$$

where the entries in B^2 are given by

$B_{11}^2 = bN + (d + CN)S + \beta SI + \lambda R,$

$B_{12}^2 = -\beta SI,$

$$B_{13}^2 = -\lambda R,$$

$$B_{22}^2 = \beta SI + (d + cN + \alpha)I + \gamma I,$$

$$B_{23}^2 = -\gamma I,$$

$$B_{33}^2 = (d + cN)R + \lambda R.$$

The product $Bd\vec{W}(t)$ is approximated using the numerical methods in [3].

Using the second stochastic modeling technique, we obtain an SDE of the form:

$$\frac{d\vec{X}}{dt} = \vec{\mu} + G\frac{d\vec{W}(t)}{dt} \quad , \tag{4.5}$$

where $\vec{X}$ and $\vec{\mu}$ are the same as in (4.2), and

$$G = \begin{bmatrix} G_1 & -G_2 & -G_3 & 0 & 0 & 0 & G_7 \\ 0 & 0 & G_3 & -G_4 & -G_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & G_5 & -G_6 & -G_7 \end{bmatrix}, \tag{4.6}$$

where

$$G_1 = \sqrt{bN},$$

$$G_2 = \sqrt{(d + cN)S},$$

$$G_3 = \sqrt{\beta SI},$$

$$G_4 = \sqrt{(d + cN + \alpha)I},$$

$$G_5 = \sqrt{\gamma I},$$

$$G_6 = \sqrt{(d + cN)R},$$

$$G_7 = \sqrt{\lambda R}.$$

Here $\vec{W}$ is a seven dimensional Wiener process.

5. COMPUTATIONAL RESULTS

In this section, computational results are given for the models described in the previous sections. First consider the SI models considered in Section 3. Figure 5.4 illustrates the suseptible and infected individuals, together with the total population. Notice that parasite extinction is unlikely for this deterministic model.

Two simulations of the stochastic SI model are illustrated in Figure 5.5. Notice that for the stochastic model parasite extinction is possible.

The deterministic and stochastic SIR models discussed in Section 4 are illustrated in the next two figures. First, Figure 5.6 illustrates the deterministic model, and then, Firgure 5.7 illustrates the stochastic model. Again notice the posibility of parasite extinction in the stochastic model in contracst to deterministic model, where exticion is unlikely.

The next two figures illustrate the infected population for the SIR model deterministically and stochastically. Figure 5.8 illustrates the deterministic infected population. Figure 5.9 illustrates the mean of 100 simulations along with two simulations. Notice that the solution to the deterministic model is in agreement with the mean of the stochastic model.

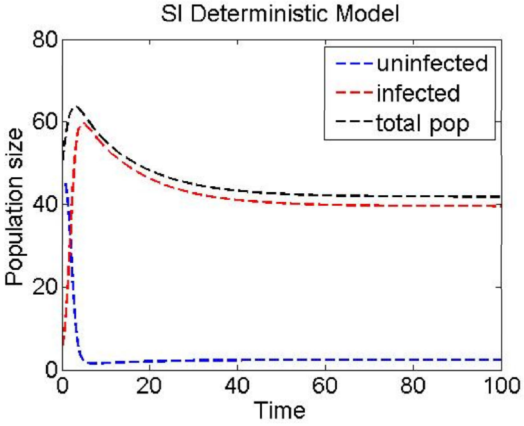

Figure 5.4: *SI Deterministic Model*

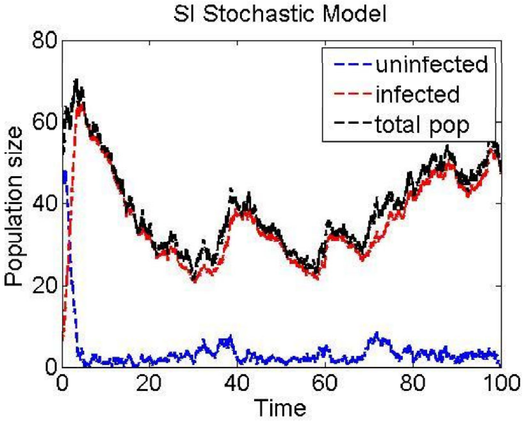

Figure 5.5: *SI Stochastic Model*

6. CONCLUSION

Existing mathematical models for parasite-host interaction that address the host density reduction scenario were studied. A new stochastic model was introduced. The two equivalent methods were compared. Computational simulations were presented.

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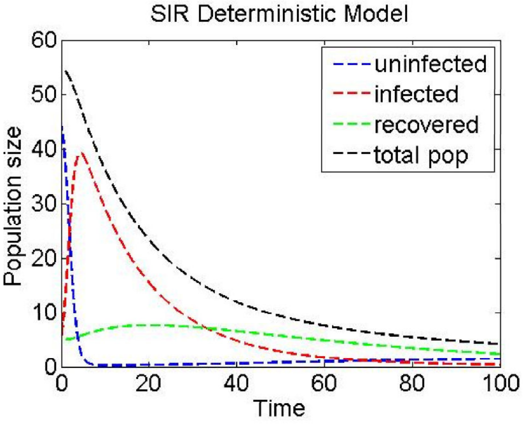

Figure 5.6: *SIR Deterministic Model*

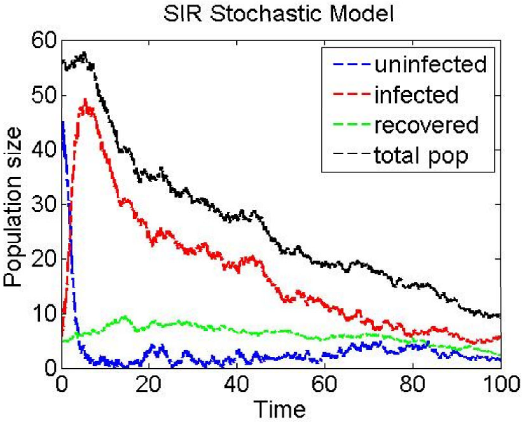

Figure 5.7: *SIR Stochastic Model*

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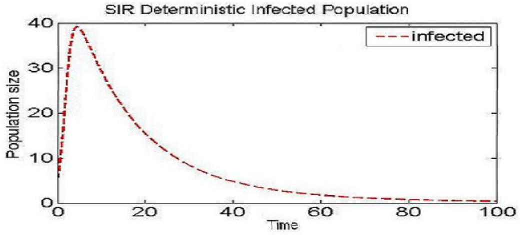

Figure 5.8: *SIR Deterministic Infected Population*

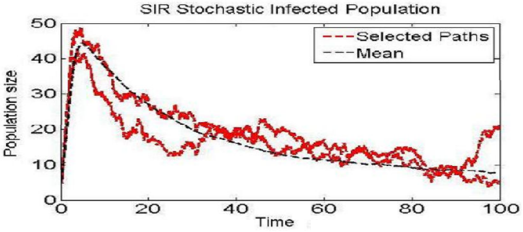

Figure 5.9: *SIR Stochastic Infected Population*

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