PERIODICALLY FORCED DISCRETE-TIME SIS EPIDEMIC MODEL WITH DISEASE INDUCED MORTALITY

JOHN E. FRANKE

Department of Mathematics
North Carolina State University
Raleigh, NC 27695-8205, USA

ABDUL-AZIZ YAKUBU

Department of Mathematics, Howard University
Washington, DC 20059, USA

ABSTRACT. We use a periodically forced SIS epidemic model with disease induced mortality to study the combined effects of seasonal trends and death on the extinction and persistence of discretely reproducing populations. We introduce the epidemic threshold parameter, $\mathcal{R}_0$, for predicting disease dynamics in periodic environments. Typically, $\mathcal{R}_0 < 1$ implies disease extinction. However, in the presence of disease induced mortality, we extend the results of Franke and Yakubu to periodic environments and show that a small number of infectives can drive an otherwise persistent population with $\mathcal{R}_0 > 1$ to extinction. Furthermore, we obtain conditions for the persistence of the total population. In addition, we use the Beverton-Holt recruitment function to show that the infective population exhibits period-doubling bifurcations route to chaos where the disease-free susceptible population lives on a 2-cycle (non-chaotic) attractor.

1. **Introduction.** The complexity of a fatal disease epidemic process is often obscured by neglecting seasonal factors [45]. In periodic environments, it is known that population sizes are often either enhanced via *resonance* or diminished via *attenuance* [5, 12, 13, 15, 16, 17, 18, 19, 20, 21, 22, 26, 27, 28, 31, 32, 33, 35, 36, 38]. However, most disease epidemic models in the literature (with a few exceptions) neglect seasonal factors [3, 4, 14]. For example, Allen and Burgin [1], Allen [2], and Castillo-Chavez and Yakubu [9, 10, 11] studied disease invasions in discretely reproducing populations that live on attractors in constant (nonperiodic) environments. Cushing and Henson [16], Elaydi and Sacker [19, 20, 21, 22], Franke and Yakubu [26, 27], Kocic [36], Kocic and Ladas [37], Kon [38], and others have studied the effects of periodic environments on ecological models with no explicit disease dynamics [47].

In this paper, we focus on the impact of seasonal factors on a discrete-time SIS (susceptible-infected-susceptible) epidemic model with disease induced mortality.

When the environment is constant and the disease is not fatal our model reduces to the SIS epidemic model of Castillo-Chavez and Yakubu [9, 10, 11]. However, when the environment is constant and the disease is fatal, our model reduces to that of Franke and Yakubu [25]. Hwang and Kuang [34, 39] as well as Berezovsky *et al* [6, 7] illustrated surprising dynamics in a simple continuous-time susceptible-infected (SI) model with variable population size and disease-induced mortality. In particular, in the continuous-time SI model, Berezovsky *et al* [6, 7] showed the existence of homoclinic trajectories that allow the possibility of outbreak of the disease at very low levels of infection. In this paper, we use a periodically forced discrete-time SIS model with disease induced mortality to show that a small number of infectives may cause the total population to go extinct although $\mathcal{R}_0 > 1$.

To construct our compartmental model, we assume that a disease invades and subdivides the target population into two classes: susceptibles (noninfectives) and infectives. Prior to the time of disease invasion, the population is assumed to be governed by a periodically forced demographic equation with a periodic recruitment function. Hence, the population is assumed to be either at a demographic "steady state" (an attracting cycle or a chaotic attractor) or at a periodic geometric growth rate. The transition from susceptible to infective is a function of the contact rate α (between individuals) and the proportion of infectives (prevalence) in the population.

We derive the epidemic threshold parameter, $\mathcal{R}_0$, for predicting disease persistence or extinction in periodic environments. Franke and Yakubu, in [25], showed that in constant environments, when $\mathcal{R}_0 > 1$ a tiny number of infected individuals can drive an otherwise persistent population to extinction. We extend this result to include periodic (non-constant) environments. In particular, we use numerical simulations and a periodically forced Beverton-Holt recruitment function to illustrate this in a specific example [8]. In addition, we show that it is possible for the infective population to exhibit period-doubling bifurcations route to chaos while the disease-free (susceptible) demographic dynamics is cyclic but nonchaotic [30].

The paper is organized as follows. In Section 2, we introduce the periodically forced demographic equation with disease induced mortality and the main model, a periodically forced discrete-time SIS epidemic model with disease-induced mortality. We extend, in Section 3, the results of Franke and Yakubu on periodically forced SIS epidemic models without disease-induced mortality. The demographic threshold parameter $\mathcal{R}_{D_i}$ and the basic reproductive number $\mathcal{R}_0$ are introduced in Section 4. These are used to predict the (uniform) persistence or extinction of the infective population in the SIS model. Section 5 concerns applications of the persistence and extinction results to an SIS model with the Beverton-Holt recruitment function. Also in Section 5, we illustrate period-doubling bifurcations in the epidemic model where the disease-free susceptible dynamics is cyclic and non-chaotic [41]. The implications of our results are discussed in Section 6.

2. **Demographic equations with seasonality.** In constant environments, theoretical discrete-time epidemic models with disease-induced mortality are usually formulated under the assumption that the dynamics of the total population size in generation t, denoted by $N(t)$, is governed by equations of the form

$$N(t + 1) = f(N(t)) + \gamma_1 S(t) + \gamma_2 I(t), \tag{1}$$

where γ_1 and $\gamma_2 \in (0,1)$ are respectively the constant "probabilities" of surviving of the susceptibles and infectives per generation and $f : \mathbb{R}_+ \to \mathbb{R}_+$ models the birth or recruitment process; where $\gamma_1 \geq \gamma_2$ [25].

To introduce seasonality into (1), we p-periodically force the recruitment function and the survival rates. This is modeled with the *p-periodic demographic equation*

$$N(t+1) = f(t, N(t)) + \gamma_{1t}S(t) + \gamma_{2t}I(t), \tag{2}$$

where $\exists \, p \in \mathbb{N}$ such that

$$f(t, N(t)) = f(t+p, N(t)) \quad \forall t \in \mathbb{Z}_+,$$

and for each $i \in \{1, 2\}$

$$\gamma_{i(t+p)} = \gamma_{it} \quad \forall t \in \mathbb{Z}_+,$$

where $\gamma_{it} \in (0,1)$. We assume throughout that $f(t, N) \in C^2(\mathbb{Z}_+ \times \mathbb{R}_+, \mathbb{R}_+)$ and $\gamma_{1t} \geq \gamma_{2t} \; \forall t \in \mathbb{Z}_+$.

In the absence of disease, $I(t) = 0$, Model (2) reduces to the disease-free demographic equation

$$S(t+1) = f(t, S(t)) + \gamma_{1t}S(t). \tag{3}$$

Franke and Yakubu, in [28], studied model (3) with periodic constant recruitment function

$$f(t, S(t)) = k_t(1 - \gamma_{1t}),$$

with periodic Beverton–Holt recruitment function

$$f(t, S(t)) = \frac{(1 - \gamma_{1t})\mu k_t S(t)}{(1 - \gamma_{1t})k_t + (\mu - 1 + \gamma_{1t})S(t)},$$

and with periodic Ricker function [42]

$$f(t, S(t)) = (1 - \gamma_{1t})S(t)e^{r\left(1 - \frac{S(t)}{k_t}\right)},$$

where the carrying capacity k_t and the survival rate of the susceptibles γ_{1t} are p-periodic, $k_{t+p} = k_t$ and $\gamma_{1(t+p)} = \gamma_{1t}$ for all $t \in \mathbb{Z}_+$ [16, 28]. Franke and Yakubu proved that periodically forced recruitment functions can generate globally attracting cycles in Model (3) [28]. In the following result, Franke and Yakubu obtained a globally attracting cycle for the periodic constant recruitment function.

Theorem 2.1. *Let*

$$f(t, S(t)) = k_t(1 - \gamma_{1t}).$$

Then Model (3) has a globally attracting q - periodic cycle that starts at

$$\overline{x}_0 = \frac{k_{p-1}(1 - \gamma_{1p-1}) + \gamma_{1p-1}k_{p-2}(1 - \gamma_{1p-2}) + ... + k_0(1 - \gamma_{10})\displaystyle\prod_{J=1}^{p-1}\gamma_{1J}}{1 - \displaystyle\prod_{J=0}^{p-1}\gamma_{1J}},$$

where q divides p.

Next, we state the result of Franke and Yakubu on globally attracting cycles for convex monotone recruitment functions [28].

Theorem 2.2. *If the recruitment functions of x for each t, $f(t, x)$, are increasing, concave down, bounded, pioneer functions, then the $p-$ periodic demographic system, Model (3), has a globally attracting positive q - cycle, where q divides p.*

By Theorem 2.2, Model (3) has a globally attracting cycle whenever the recruitment function is the periodically forced Beverton-Holt model.

Theorems 2.1 and 2.2 imply that in the absence of the disease, the susceptible population is asymptotically periodic (bounded) and lives on a cyclic attractor when the recruitment function is either a periodic constant or the periodic Beverton–Holt model. Denote this cycle by

$$\{\overline{S}_0, \overline{S}_1, \ldots, \overline{S}_{q-1}\}.$$

When new recruits arrive at the periodic positive per-capita growth rate λ_t, then

$$f(t, N(t)) = \lambda_t N(t),$$

where $\lambda_{t+p} = \lambda_t$ for all $t \in \mathbb{Z}_+$. The solution to the disease-free equation, Model (3), is

$$S(t) = \left(\prod_{J=0}^{t-1} (\lambda_J + \gamma_{1J}) \right) S(0),$$

and the demographic basic reproductive number is

$$\mathcal{R}_D = \frac{\prod_{J=0}^{p-1} (\lambda_J + \gamma_{1J}) - \prod_{J=0}^{p-1} \gamma_{1J}}{1 - \prod_{J=0}^{p-1} \gamma_{1J}}. \tag{4}$$

If $\mathcal{R}_D < 1$, the total population goes extinct at a geometric rate, and if $\mathcal{R}_D > 1$, the total population explodes at a geometric rate. In constant environments, $p = 1$, $\lambda_J = \lambda$, $\gamma_{1J} = \gamma_1$ and $\mathcal{R}_D$ reduces to

$$\mathcal{R}_{D_1} = \frac{\lambda}{1 - \gamma_1}.$$

In [25], Franke and Yakubu used $\mathcal{R}_{D_1} = \frac{\lambda}{1-\gamma_1}$ to study the long-term behavior of a geometrically growing disease-free state in constant environments.

To introduce our periodically forced SIS epidemic model with disease-induced mortality, we assume that infective individuals recover with constant probability $(1 - \sigma)$. Furthermore, we assume that

$$\phi : [0, \infty) \to [0, 1]$$

is a monotone convex probability function with $\phi(0) = 1, \phi'(x) < 0$ and $\phi''(x) \geq 0$ for all $x \in [0, \infty)$. Also, we assume that the susceptible individuals become infected with nonlinear probability $\left(1 - \phi \left(\alpha \frac{I}{N}\right)\right)$ per generation, where the transmission constant $\alpha > 0$. When infections are modeled as Poisson processes, for example, then

$$\phi \left(\alpha \frac{I}{N} \right) = e^{-\alpha \frac{I}{N}}$$

([10]).

Our assumptions and notation lead to the following periodically forced SIS epidemic model with disease induced mortality:

$$\left. \begin{aligned} S(t+1) &= f(t, N(t)) + \gamma_{1t}\phi \left(\alpha \frac{I(t)}{N(t)} \right) S(t) + \gamma_{2t}(1 - \sigma)I(t) \\ I(t+1) &= \gamma_{1t} \left(1 - \phi \left(\alpha \frac{I(t)}{N(t)} \right) \right) S(t) + \gamma_{2t}\sigma I(t) \end{aligned} \right\}. \tag{5}$$

We assume throughout that $\exists\, p \in \mathbb{N}$ such that

$$f(t, N(t)) = f(t + p, N(t)) \quad \forall t \in \mathbb{Z}_+,$$

and for each $i \in \{1, 2\}$

$$\gamma_{i(t+p)} = \gamma_{it} \quad \forall t \in \mathbb{Z}_+,$$

where $\gamma_{it}, \sigma \in (0, 1)$, $\gamma_{2t} \leq \gamma_{1t}$ and $f(t, N) \in C^2(\mathbb{Z}_+ \times \mathbb{R}_+, \mathbb{R}_+)$. Model (5) reduces to the SIS epidemic model of Franke and Yakubu when the environment is constant, $f(t, N(t)) = f(N(t))$ and $\gamma_{2t} = \gamma_2 \leq \gamma_{1t} = \gamma_1$ [25]. In Model (5), the total population in generation $t + 1$ ($N(t + 1) = S(t + 1) + I(t + 1)$), the sum of the two equations of the model, is Equation (2).

If the disease is not present ($I(t) = 0$), then $N(t) = S(t)$ and our SIS model reduces to Equation (3). When this reduced equation has the $q-$cycle attractor

$$\{\overline{S}_0, \overline{S}_1, \ldots, \overline{S}_{q-1}\},$$

then

$$\{(\overline{S}_0, 0), (\overline{S}_1, 0), \ldots, (\overline{S}_{q-1}, 0)\}$$

is a disease-free cycle of Model (5).

3. **Preliminary results.** Here, we obtain some auxiliary results that will be used to study disease persistence and extinction in our periodically forced SIS model. In the following result, we obtain one-variable bounds on the total population of the model.

Lemma 3.1. *In Model (5),*

$$f(t, N(t)) + \gamma_{2t} N(t) \leq N(t + 1) \leq f(t, N(t)) + \gamma_{1t} N(t).$$

Proof. Since $\gamma_{2t} \leq \gamma_{1t}$,
$$f(t, N(t)) + \gamma_{2t} N(t) = f(t, N(t)) + \gamma_{2t}(S(t) + I(t)) \leq f(t, N(t)) + \gamma_{1t} S(t) + \gamma_{2t} I(t)$$
$$= N(t + 1) \leq f(t, N(t)) + \gamma_{1t}(S(t) + I(t)) = f(t, N(t)) + \gamma_{1t} N(t). \qquad \square$$

Using the substitution $S(t) = N(t) - I(t)$, the I-equation and the N-equation in Model (5) become

$$I(t + 1) = \gamma_{1t} \left(1 - \phi \left(\alpha \frac{I(t)}{N(t)} \right) \right) (N(t) - I(t)) + \gamma_{2t} \sigma I(t)$$

and

$$N(t + 1) = f(t, N(t)) + \gamma_{1t}(N(t) - I(t)) + \gamma_{2t} I(t),$$

respectively.

On the closed interval $[0, N]$, let

$$F_{N,t}(I) = \gamma_{1t} \left(1 - \phi \left(\alpha \frac{I}{N} \right) \right) (N - I) + \gamma_{2t} \sigma I$$

and

$$G_{N,t}(I) = f(t, N) + \gamma_{1t}(N - I) + \gamma_{2t} I.$$

When $F_{N,t}$ has a unique positive fixed point and a unique critical point, we denote them by $I_{N,t}$ and $C_{N,t}$, respectively. The sets of sequences generated by

$$I(t + 1) = F_{N(t),t}(I(t))$$

and

$$N(t + 1) = G_{N(t),t}(I(t))$$

are the sets of density sequences generated by the infective and the total population equations, respectively.

To study Model (5), we need the following results on the properties of $F_{N,t}$ and $G_{N,t}$.

Lemma 3.2. $F_{N,t}(I)$ and $G_{N,t}(I)$ satisfy the following conditions.

(a) If $0 \leq I \leq N$, then $F_{N,t}(I) \leq \min\{N, G_{N,t}(I)\}$ with equality if and only if $(N, I) = (0, 0)$.

(b) $F'_{N,t}(0) = -\alpha\gamma_{1t}\phi'(0) + \gamma_{2t}\sigma$ and $F'_{N,t}(N) > -1$.

(c) $F_{N,t}(I)$ is concave down on $[0, N]$.

(d) $F_{N,t}(I) < F'_{N,t}(0)I$ on $(0, N]$.

(e) If $F'_{N,t}(0) > 1$, then $F_{N,t}$ has a unique positive fixed point $I_{N,t}$ in $[0, N]$.

(f) Let $\Psi_N(I) = \frac{I}{N}$. Then $F_{1,t}(\Psi_N(I)) = \Psi_N(F_{N,t}(I))$. That is, Ψ_N is a topological conjugacy between $F_{1,t}$ and $F_{N,t}$.

(g) If $N_0 < N_1$ and $F'_{N,t}(0) > 1$, then $I_{N_0,t} < I_{N_1,t}$ where $I_{N_i,t}$ is the positive fixed point of $F_{N_i,t}$ in $[0, N_i]$. In general, the fixed point for $F_{N,t}$ is $NI_{1,t}$.

(h) If $C_{1,t}$ exists, then $C_{N,t} = NC_{1,t}$.

(i) If $N_0 < N_1$, then $F_{N_0,t}(I) < F_{N_1,t}(I)$ for all $I \in (0, N_0]$.

Proof. (a)
Since

$$F_{N,t}(I) = \gamma_{1t}\left(1 - \phi\left(\alpha\frac{I}{N}\right)\right)(N - I) + \gamma_{2t}\sigma I,$$

$$
\begin{aligned}
F_{N,t}(I) &= \gamma_{1t}\left(1 - \phi\left(\alpha\frac{I}{N}\right)\right)(N - I) + \gamma_{2t}\sigma I \\
&\leq \gamma_{1t}(N - I) + \gamma_{2t}I \leq N\max\{\gamma_{1t}, \gamma_{2t}\} \leq N.
\end{aligned}
$$

Since

$$
\begin{aligned}
G_{N,t}(I) &= f(t, N) + \gamma_{1t}(N - I) + \gamma_{2t}I, \\
G_{N,t}(I) - F_{N,t}(I) &= f(t, N) + \gamma_{1t}\phi\left(\alpha\frac{I}{N}\right)(N - I) + \gamma_{2t}(1 - \sigma)I \geq 0.
\end{aligned}
$$

Hence,

$$F_{N,t}(I) \leq \min\{N, G_{N,t}(I)\}.$$

It is easy to check that the equality holds if and only if $(N, I) = (0, 0)$.

(b)

$$F'_{N,t}(I) = -\frac{\alpha\gamma_{1t}}{N}\phi'\left(\alpha\frac{I}{N}\right)(N - I) - \gamma_{1t}\left(1 - \phi\left(\alpha\frac{I}{N}\right)\right) + \gamma_{2t}\sigma.$$

$$
\begin{aligned}
F'_{N,t}(0) &= -\frac{\alpha\gamma_{1t}}{N}\phi'(0)N - \gamma_{1t}(1 - \phi(0)) + \gamma_{2t}\sigma \\
&= -\alpha\gamma_{1t}\phi'(0) + \gamma_{2t}\sigma.
\end{aligned}
$$

$$
\begin{aligned}
F'_{N,t}(N) &= -\frac{\alpha\gamma_{1t}}{N}\phi'\left(\alpha\frac{N}{N}\right)(N - N) - \gamma_{1t}\left(1 - \phi\left(\alpha\frac{N}{N}\right)\right) + \gamma_{2t}\sigma \\
&= -\gamma_{1t}(1 - \phi(\alpha)) + \gamma_{2t}\sigma > -\gamma_{1t} > -1.
\end{aligned}
$$

(c)

$$F''_{N,t}(I) = -\left(\frac{\alpha}{N}\right)^2\gamma_{1t}\phi''\left(\alpha\frac{I}{N}\right)(N - I) + 2\frac{\alpha\gamma_{1t}}{N}\phi'\left(\alpha\frac{I}{N}\right).$$

Since $\phi' < 0$ and $\phi'' \geq 0$ on $[0, \infty)$, we have

$$F''_{N,t}(I) < 0 \text{ on } [0, N].$$

(d)

$F_{N,t}(0) = 0$ implies that $y = F'_{N,t}(0)I$ is the tangent line to the graph of $F_{N,t}(I)$ at 0. Since $F_{N,t}$ is concave down on $[0, N]$, its graph is below the tangent line at the origin on $[0, N]$. Hence,

$$F_{N,t}(I) < F'_{N,t}(0)I \text{ on } (0, N].$$

(e)

$F_{N,t}(N) = \gamma_{2t}\sigma N < N$. Since $F'_{N,t}(0) > 1$, the graph of $F_{N,t}(I)$ starts out higher than the diagonal and must cross it before $I = N$. The concavity property of $F_{N,t}(I)$ (see (c)) implies that there is a unique positive fixed point.

(f)

$F_{1,t}(I) = \gamma_{1t}(1 - \phi(\alpha I))(1 - I) + \gamma_{2t}\sigma I$. Thus,

$$F_{1,t}(\Psi_N(I)) = \gamma_{1t}\left(1 - \phi\left(\alpha\frac{I}{N}\right)\right)(1 - \frac{I}{N}) + \gamma_{2t}\sigma\frac{I}{N} =$$

$$\frac{1}{N}F_{N,t}(I) = \Psi_N(F_{N,t}(I)).$$

(g)

Since

$$F'_{N_0,t}(0) = (-\alpha\gamma_{1t}\phi'(0) + \gamma_{2t}\sigma) > 1,$$

$I_{N_0,t}$ exists with $F_{N_0,t}(I_{N_0,t}) = I_{N_0,t}$. Thus,

$$\Psi_{N_0}(F_{N_0,t}(I_{N_0,t})) = \Psi_{N_0}(I_{N_0,t}) = F_{1,t}(\Psi_{N_0}(I_{N_0,t})).$$

That is. $\Psi_{N_0}(I_{N_0,t}) = I_{1,t}$, the unique positive fixed point of $F_{1,t}$ and $I_{N_0,t} = N_0 I_{1,t}$. Similarly, $I_{N_1,t} = N_1 I_{1,t}$. Hence, $N_0 < N_1$ implies $I_{N_0,t} < I_{N_1,t}$. In general, the fixed point for $F_{N,t}$ is $N I_{1,t}$.

(h)

Topological conjugacy preserves critical points. The result follows from (f).

(i)

Let $N_0 < N_1$ and $I \in (0, N_0]$. The topological conjugacy in Part (f) shows that

$$F_{N_0,t}(I) = N_0 F_{1,t}(\frac{I}{N_0})$$

and

$$F_{N_1,t}(I) = N_1 F_{1,t}(\frac{I}{N_1}).$$

Note that $\frac{I}{N_1} < \frac{I}{N_0}$. Since the graph of $F_{1,t}$ goes through the origin with positive slope and is concave down, the ray through the origin and $\left(\frac{I}{N_1}, F_{1,t}(\frac{I}{N_1})\right)$ has a larger slope than the ray through the origin and $\left(\frac{I}{N_0}, F_{1,t}(\frac{I}{N_0})\right)$. The first ray contains the point $\left(I, N_1 F_{1,t}(\frac{I}{N_1})\right)$, while the second ray contains $\left(I, N_0 F_{1,t}(\frac{I}{N_0})\right)$. Hence, $F_{N_1,t}(I) = N_1 F_{1,t}(\frac{I}{N_1}) > N_0 F_{1,t}(\frac{I}{N_0}) = F_{N_0,t}(I)$. $\square$

Next, we obtain the invariance of the positive quadrant.

Lemma 3.3. *In Model* (5),

$$(a) \text{ If } I(0) > 0 \text{ then } I(t) > 0 \ \forall \ t \in \mathbb{Z}_+.$$
$$(b) \text{ If } N(0) > 0 \text{ then } N(t) > 0 \ \forall \ t \in \mathbb{Z}_+.$$

Proof. (a)

$I(t+1) = \gamma_{1t}\left(1 - \phi\left(\alpha\frac{I(t)}{N(t)}\right)\right)(N(t) - I(t)) + \gamma_{2t}\sigma I(t)$. By Lemma 3.2$a$, $N(t) - I(t) \geq 0 \, \forall t \in \mathbb{Z}_+$. Therefore, $\gamma_{1t}\left(1 - \phi\left(\alpha\frac{I(t)}{N(t)}\right)\right)(N(t) - I(t)) \geq 0$. $I(0) > 0$ implies $\gamma_{2t}\sigma I(0) > 0$ and hence, $I(1) > 0$. By induction, assume $I(t) > 0$ and $\gamma_{2t}\sigma I(t) > 0$. Hence, $I(t+1) > 0$.

(b)

Use $N(t+1) = f(t, N(t)) + \gamma_{1t}(N(t) - I(t)) + \gamma_{2t}I(t)$ and proceed as in part (a). $\qquad\square$

4. **Disease extinction or persistence.** To study the qualitative dynamics of Model (5), we define the $p - periodic$ dynamical system

$$H_t : \Omega \to \Omega$$

by

$$H_t(N, I) = (G_{N,t}(I), F_{N,t}(I)),$$

where $H_t = H_{t+p}$ for all t and $\Omega = \{(N, I)|0 \leq I \leq N\}$. Since ϕ is a decreasing function and $0 \leq \frac{I}{N} \leq 1$, $\{H_t\}$ is a continuous $p - periodic$ dynamical system that is C^1 away from $(0, 0)$. We will study the behavior of solutions to Model (5) by analyzing H_t on the triangular region Ω.

Lemmas 3.2 and 3.3 show that the set of iterates of the $p - periodic$ dynamical system $\{H_t\}$ on $\{(N, I)|0 \leq I \leq N\}$ is equivalent to set of density sequences generated by Model (5), where

$$\pi_i \circ H_t \circ \cdots \circ H_1 \circ H_0(N, I)$$

denotes the $i - th$ component of the $(t + 1) - th$ iterate (under $\{H_t\}$) of the initial condition (N, I).

Definition 4.1. The total population is *uniformly persistent* under $\{H_t\}$ if there exists a constant $\eta > 0$ such that

$$\underline{lim}_{t \to \infty} \pi_1 \circ H_t \circ \cdots \circ H_1 \circ H_0(N, I) \geq \eta$$

for every nonzero initial condition.

The total population is said to be persistent under $\{H_t\}$ if $\underline{lim}_{t \to \infty} \pi_1 \circ H_t \circ \cdots \circ H_1 \circ H_0(N, I) > 0$ [48]. Consequently, uniform persistence implies the persistence of the total population.

Definition 4.2. The total population is driven to *extinction* under $\{H_t\}$ if

$$lim_{t \to \infty} \pi_1 \circ H_t \circ \cdots \circ H_1 \circ H_0(N, I) = 0$$

for every initial condition.

For each $i \in \{1, 2\}$, define the $p - periodic$ dynamical system

$$D_{i,t} : [0, \infty) \to [0, \infty)$$

by

$$D_{i,t}(N) = f(t, N) + \gamma_{it}N. \tag{6}$$

By Lemma 3.1,

$$D_{2,t}(N(t)) \leq N(t+1) \leq D_{1,t}(N(t)).$$

Now, we introduce the demographic threshold parameter

$$\mathcal{R}_{D_i} = \prod_{t=0}^{p-1} (f'(t, 0) + \gamma_{it}).$$

In the following lemma, we show that $\mathcal{R}_{D_1} > 1$ implies the uniform persistence of the susceptible population while $\mathcal{R}_{D_1} < 1$ implies local extinction of the total population.

Lemma 4.3. *Let $f(t, 0) = 0$ for all t. If $\mathcal{R}_{D_1} > 1$, then the disease-free susceptible population described by Model (3) is uniformly persistent. However, if $\mathcal{R}_{D_1} < 1$ then $\{(0, 0)\}$ is locally asymptotically stable in Model (5), and both the susceptible and infected populations go extinct at low values of initial population sizes.*

Proof. The disease-free susceptible population dynamics is given by the $p-periodic$ system $\{D_{1,t}\}$. $\mathcal{R}_{D_1} = \prod_{t=0}^{p-1} (f'(t, 0) + \gamma_{1t})$ is the derivative of

$D_{1,t+p-1} \circ \cdots \circ D_{1,t+1} \circ D_{1,t}$ at 0 for all t.

Since $D_{1,t}$ is continuous, $D_{1,t}(0) = 0$ and $D'_{1,t}(0) = f'(t, 0) + \gamma_{1t} > 0$, there is an interval containing 0 on which $D_{1,t}$ is increasing.

Since $\mathcal{R}_{D_1} > 1$, there is a $\kappa > 0$ such that $N \in (0, \kappa)$ implies that

$$N < D_{1,t+p-1} \circ \cdots \circ D_{1,t+1} \circ D_{1,t}(N)$$

for all t. By taking κ smaller if needed, we can assume that each $D_{1,t}$ is increasing on $(0, \kappa)$. Note that $D_{1,t}(N) \geq \gamma_{1t}N$. Furthermore, if $\kappa > D_{1,t}(N) \geq \gamma_{1t}N$, then $D_{1,t+1} \circ D_{1,t}(N) \geq D_{1,t+1}(\gamma_{1t}N) \geq \gamma_{1t+1}\gamma_{1t}N$. Let $\lfloor x \rfloor$ be the greatest integer less than or equal to x. If the jth image of N is N^* and if it and the next n images under the p-periodic dynamical system $\{D_{1,t}\}$ are in $(0, \kappa)$, then

$$D_{1,j+n-1} \circ \cdots \circ D_{1,j+1} \circ D_{1,j}(N^*) \geq (\mathcal{R}_{D_1})^{\lfloor n/p \rfloor} \left(\Pi_{t=j}^{(j+n-1) \mod p} \gamma_{1t} \right) N^* \geq$$

$(\mathcal{R}_{D_1})^{\lfloor n/p \rfloor} \left(\Pi_{t=0}^{p-1} \gamma_{1t} \right) N^*.$

Thus the orbit must leave $(0, \kappa)$ and $\left(\Pi_{t=0}^{p-1} \gamma_{1t} \right) N^*$ is a lower bound for these values.

If $N > \max_t \{ \frac{\kappa}{\gamma_{1t}} \}$, then $\kappa < D_{1,t}(N)$ for all t. Let

$$A_\kappa = \{ (N, I) | 0 \leq I \leq N, \kappa \leq N \leq \max_t \{ \frac{\kappa}{\gamma_{1t}} \} \}.$$

$D_{1,t}$ is positive on the compact set A_κ, and it has a minimum $\overline{\kappa}_t > 0$ on A_κ. Let $\overline{\kappa} = \min_t \{ \overline{\kappa}_t \}$. Consequently,

$$\underset{t \to \infty}{\lim} D_{1,t} \circ \cdots \circ D_{1,1} \circ D_{1,0}(N, I) \geq \min \{ \kappa, \left(\Pi_{t=0}^{p-1} \gamma_{1t} \right) \overline{\kappa} \} = \eta > 0.$$

Hence the disease-free susceptible population is uniformly persistent.

We now consider the case where $\mathcal{R}_{D_1} < 1$. Lemma 3.1 gives $\pi_1 \circ H_t(N, I) \leq D_{1t}(N)$ for all t. $D'_{1,t}(0) = f'(t, 0) + \gamma_{1t} > 0$, hence there is an interval containing 0 on which $D_{1,t}$ is increasing. So if N is small the continuity of H_t gives

$$D_{1,1} \circ D_{1,0}(N) \geq D_{1,1} \circ \pi_1 \circ H_0(N, I) \geq \pi_1 \circ H_1 \circ H_0(N, I).$$

Inductively, we obtain that if N is small then

$$D_{1,p-1} \circ \cdots \circ D_{1,1} \circ D_{1,0}(N) \geq \pi_1 \circ H_{p-1} \circ \cdots \circ H_1 \circ H_0(N, I).$$

$\mathcal{R}_{D_1} = \prod\limits_{t=0}^{p-1} (f'(t,0) + \gamma_{1t})$ is the derivative of

$D_{1,p-1} \circ \cdots \circ D_{1,1} \circ D_{1,0}$ with respect to N at 0. Thus $\mathcal{R}_{D_1} < 1$ implies that there is a δ such that $\mathcal{R}_{D_1} < \delta < 1$. Hence there is a $\kappa > 0$ such that

$$N > \delta N > D_{1,p-1} \circ \cdots \circ D_{1,1} \circ D_{1,0}(N) \geq \pi_1 \circ H_{p-1} \circ \cdots \circ H_1 \circ H_0(N,I).$$

whenever $N \in (0, \kappa)$. Therefore $\{(0,0)\}$ is locally asymptotically stable. $N = S + I$ implies the extinction of the susceptible and infected populations at positive small initial values of S and I. $\qquad\square$

Lemma 4.4. *If either $f(t,0) > 0$ for some t or $f(t,0) = 0$ for all t and $\mathcal{R}_{D_2} > 1$, then the total population is uniformly persistent.*

Proof. First, we consider the case $f(t^*,0) > 0$ for some t^*. Since $\lim\limits_{N \to \infty} f(t,N) + \gamma_{2t} N = \infty$, $D_{2,t^*}(N) = f(t^*,N) + \gamma_{2t^*} N$ has a positive minimum m^* on $[0,\infty)$. $D_{2,t^*+1}([m^*,\infty)) \subset [\gamma_{2t^*+1}m^*,\infty)$. Thus a nonzero initial condition gets above m^* and stays above $\left(\Pi_{t=0}^{p-1}\gamma_{2t}\right)m^*$. Lemma 3.1 gives $D_{2t}(N) \leq \pi_1 \circ H_t(N,I)$ for all t. Thus, $\pi_1 \circ H_{t^*} \circ (\cdots \circ H_1 \circ H_0(N,I))$ is larger than m^* and stays larger than $\left(\Pi_{t=0}^{p-1}\gamma_{2t}\right)m^*$ for every $t > 0$. Hence the total population is uniformly persistent.

Now, we consider the case $f(t,0) = 0$ for all t and $\mathcal{R}_{D_2} > 1$. Since $D_{2,t}$ is continuous and $D'_{2,t}(0) = f'(t,0) + \gamma_{2t} > 0$, there is an interval containing 0 on which $D_{2,t}$ is increasing. Lemma 3.1 gives $D_{2t}(N) \leq \pi_1 \circ H_t(N,I)$ for all t. So if N is small the continuity of H_t gives

$$D_{2,1} \circ D_{2,0}(N) \leq D_{2,1} \circ \pi_1 \circ H_0(N,I) \leq \pi_1 \circ H_1 \circ H_0(N,I).$$

Inductively, we obtain that if N is small then

$$D_{2,p-1} \circ \cdots \circ D_{2,1} \circ D_{2,0}(N) \leq \pi_1 \circ H_{p-1} \circ \cdots \circ H_1 \circ H_0(N,I).$$

$\mathcal{R}_{D_2} = \prod\limits_{t=0}^{p-1} (f'(t,0) + \gamma_{2t})$ is the derivative of $D_{2,p-1} \circ \cdots \circ D_{2,1} \circ D_{2,0}$ at 0. Since $\mathcal{R}_{D_2} > 1$, there is a $\kappa > 0$ such that $N \in (0, \kappa)$ implies that

$$N < D_{2,p-1} \circ \cdots \circ D_{2,1} \circ D_{2,0}(N) \leq \pi_1 \circ H_{p-1} \circ \cdots \circ H_1 \circ H_0(N,I).$$

If $N > \max\limits_{t}\{\frac{\kappa}{\gamma_{2t}}\}$, then $\kappa < D_{2,t}(N) \leq \pi_1 \circ H_t(N,I)$. Let

$$A_\kappa = \{(N,I) | 0 \leq I \leq N, \kappa \leq N \leq \max\limits_{t}\{\frac{\kappa}{\gamma_{2t}}\}\}.$$

H_1 is positive on the compact set A_κ, and it has a minimum $\overline{\kappa} > 0$ on A_κ. Consequently,

$$\lim\limits_{t \to \infty} \pi_1 \circ H_t \circ \cdots \circ H_1 \circ H_0(N,I) \geq \min\{\kappa, \overline{\kappa}\} = \eta > 0$$

for all nonzero initial conditions and the total population is uniformly persistent. $\quad\square$

By Lemma 4.4, the total population is uniformly persistent when the recruitment function is periodically constant,

$$f(t, N(t)) = k_t(1 - \gamma_{1t}).$$

When the recruitment function is the periodic Beverton–Holt function,

$$f(t, N(t)) = \frac{(1 - \gamma_{1t})\mu k_t N(t)}{(1 - \gamma_{1t})k_t + (\mu - 1 + \gamma_{1t})N(t)},$$

and

$$\Pi_{t=0}^{p-1}(\mu + \gamma_{2t}) > 1$$

then the total population is uniformly persistent. When the recruitment function is the periodic Ricker function

$$f(t, N) = (1 - \gamma_{1t})Ne^{r\left(1 - \frac{N}{k_t}\right)}$$

and

$$\Pi_{t=0}^{p-1}((1 - \gamma_{1t})e^r + \gamma_{2t}) > 1$$

then the total population is uniformly persistent.

Next, we obtain that all positive initial conditions are attracted to a trapping region of our epidemic model.

Lemma 4.5. *If*

$$\overline{\lim_{N \to \infty}} \max_t \left\{ \frac{f(t, N) + \gamma_{1t}N}{N} \right\} < 1,$$

then there is a compact subset, W, of cylinder space $\{(N, I)|0 \le I \le N\} \times \{0, 1, \cdots, p-1\}$ that attracts all initial conditions under $\{H_t\}$ iterations. That is, there is no population explosion.

Proof. Let

$$\delta = \overline{\lim_{N \to \infty}} \max_t \left\{ \frac{f(t, N) + \gamma_{1t}N}{N} \right\} < 1.$$

There is an $\overline{N} > 0$ such that $N \ge \overline{N}$ implies

$$\max_t \left\{ \frac{f(t, N) + \gamma_{1t}N}{N} \right\} = \max_t \left\{ \frac{D_{1,t}(N)}{N} \right\}$$

$$< \delta + \frac{1 - \delta}{2} = \frac{1 + \delta}{2} < 1.$$

Hence if $N \ge \overline{N}$ then $D_{1,t}(N) < \frac{1+\delta}{2}N$. Lemma 3.1 gives that, for all t, $\pi_1 \circ H_t(N, I) \le D_{1,t}(N)$. Thus if $N \ge \overline{N}$ then $\pi_1 \circ H_t(N, I) < \frac{1+\delta}{2}N$. Since each H_t is continuous on the compact set $\{(N, I)|0 \le I \le N \le \overline{N}\}$, each has a maximum $\overline{\eta}_t > 0$. Let $\overline{\eta} = \max\{\overline{\eta}_0, \overline{\eta}_1, \cdots, \overline{\eta}_{p-1}\}$. Then, the region

$$\{(N, I)|0 \le I \le N \le \max\{\overline{N}, \overline{\eta}\}\} \times \{0, 1, \cdots, p-1\}$$

is a compact subset of the cylinder space which attracts all initial conditions under $\{H_t\}$ iterations. Hence, all orbits are bounded. $\square$

To prevent population explosion in our $p - periodic$ epidemic model, we assume throughout that

$$\overline{\lim_{N \to \infty}} \max_t \left\{ \frac{f(t, N) + \gamma_{1t}N}{N} \right\} < 1.$$

Let

$$\mathcal{R}_{0,t} = -\alpha\gamma_{1t}\phi'(0) + \gamma_{2t}\sigma$$

and

$$\mathcal{R}_0 = \prod_{t=0}^{p-1} \mathcal{R}_{0,t}.$$

Next, we prove that $\mathcal{R}_0 < 1$ implies disease extinction whereas $\mathcal{R}_0 > 1$ together with the persistence of the total population implies persistence of the disease.

Theorem 4.6. *In Model (5), let $N(0) \geq I(0) > 0$.*

(a) *If $\mathcal{R}_0 < 1$, then $\lim\limits_{t \to \infty} I(t) = 0$.*
That is, the disease goes extinct.
(b) *If $\mathcal{R}_0 > 1$ and the total population is uniformly persistent,*
then $\lim\limits_{t \to \infty} \pi_2 \circ H_t \circ \cdots \circ H_1 \circ H_0(N, I) \geq \eta > 0$.
That is, the disease is uniformly persistent.

The proof of Theorem 4.6 is in the Appendix. In most epidemic models, $\mathcal{R}_0 > 1$ implies disease persistence. However, in our SIS epidemic model with disease induced mortality, we obtain sufficient conditions that guarantee total population extinction for some initial conditions, where $\mathcal{R}_0 > 1$.

Theorem 4.7. *Let $\mathcal{R}_0 > 1$, $f(t,0) = 0$ and $f(t,N) \leq f'(t,0)N$ for all t and $N > 0$. If $\gamma_{1t^*} > \gamma_{2t^*}$ for some t^*, then there is a $\varsigma > 1$, such that if $1 < \mathcal{R}_{D_1} < \varsigma$ then the total population goes extinct under $\{H_t\}$ iteration whenever $I(0) > 0$. The ς can be chosen so that it is independent of f.*

The proof of Theorem 4.7 is in the Appendix.

5. **Application.** In this section, we use the periodically forced Beverton-Holt model

with its specific recruitment function to illustrate the general results from the previous sections [43].

Consider Model (5) with the Beverton-Holt recruitment function [44],

$$f(t, N) = \frac{aN}{1 + b_t N},$$

and

$$\phi\left(\frac{\alpha I}{N}\right) = e^{-\frac{\alpha I}{N}},$$

where

$$0.11 \quad < \quad a < 0.15, \quad b_t = 1.2 + (-1)^t * 0.1, \quad \alpha = 5, \quad \gamma_{1t} = 0.9 + (-1)^t * 0.05,$$
$$\gamma_{2t} \quad = \quad 0.8 + (-1)^t * 0.05, \text{ and } \sigma = 0.9.$$

In this example, $\mathcal{R}_{D_i} = \prod\limits_{t=0}^{p-1} (f'(t,0) + \gamma_{it})$.

$$\mathcal{R}_{D_1} = (a + \gamma_{1,0})(a + \gamma_{1,1}) > (0.11 + 0.95)(.11 + 0.85) > 1.01 > 1$$

implies the persistence of the susceptible population in the absence of the disease (Lemma 4.3), where

$$\mathcal{R}_{D_2} = (a + \gamma_{2,0})(a + \gamma_{2,1}) < (0.15 + 0.85)(.15 + 0.75) = 0.9 < 1.$$

With our choice of parameters, the disease-free dynamics are governed by the Beverton-Holt model and the susceptible population persists. That is, in the absence of the disease, the susceptible population exhibits a globally attracting positive 2-cycle. Moreover, $\mathcal{R}_{0,t} = -\alpha\gamma_{1t}\phi'(0) + \gamma_{2t}\sigma$ and $\mathcal{R}_0 = \prod\limits_{t=0}^{p-1} \mathcal{R}_{0,t}$. Hence,

$$\mathcal{R}_0 = (-\alpha\gamma_{1,0}\phi'(0) + \gamma_{2,0}\sigma)(-\alpha\gamma_{1,1}\phi'(0) + \gamma_{2,1}\sigma)$$
$$> (5 * 0.95 + 0.85 * .9)(5 * 0.85 + 0.75 * .9) = 27.16 > 1,$$

$f'(t, 0) = a$, $f(t, 0) = 0$, and $f(t, x)$ is concave down so $f(t, N) \leq f'(t, 0)N$ for all N. Hence, all of the hypotheses of Theorem 4.7 are satisfied and our numerical results show that $0.11 < a < 0.15$ gives the extinction of the total population predicted by the theorem (see Figure (1)). In Figure 1, $a = 0.12$. The population without disease exhibits an attracting period 2 cycle from 1.589 to 1.513. However, adding a small number of infectives first increases the number of infectives and then drives the total population to extinction.
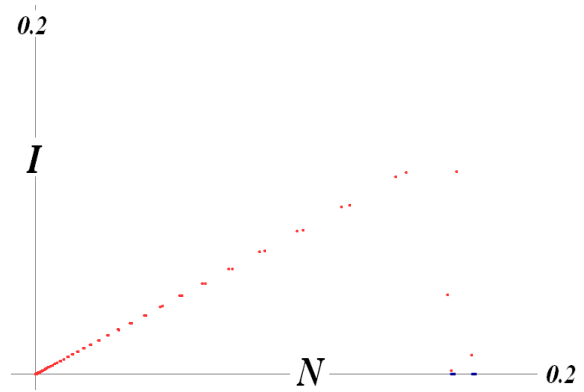

FIGURE 1. A small number of infectives drives an otherwise persistent total population to extinction.

The behavior of the orbit in Figure 1 is a bit surprising. By our simulations, as in Figure 1 most positive orbits seem to move along a line and then turn and crash. Understanding the basin of attraction of the origin is an interesting open problem.

5.1. **Bifurcation diagram.** Without infectives the total population in the example is governed by the Beverton-Holt model. So under 2-cycle survival rates, the population exhibits an attracting 2-cycle. However, the dynamics of the infective population can be much more complicated. In fact the infective population can exhibits a period doubling route to chaos. To illustrate this, we make the following choice of parameters in the example.
$a = 2$, $b_t = 1.3 + (-1)^t * 1.2995$, $\alpha \in [5, 300]$, $\gamma_{1t} = 0.45 + (-1)^t * 0.03$,
$\gamma_{2t} = 0.4 + (-1)^t * 0.02$, and $\sigma = 0.0002$.

To illustrate the structure of the chaotic attractor depicted in Figure 2, we let $\alpha = 250$ and keep all the other parameters fixed at the same values as in Figure 1. Figure 3 shows a complicated structure for a 4-piece chaotic attractor in the $(N, I) - plane$ [47].

To illustrate the region that leads to extinction, we let

$$\gamma_2 = \frac{\gamma_{2,1} + \gamma_{2,2}}{2}.$$

That is, γ_2 is the average of the $\gamma_{2,i}$. In the (a, γ_2) - parameter space of the Beverton–Holt model, we continuously vary the intrinsic growth rate a between 0 and 1, and γ_2 between 0 and 0.9 leaving $|\gamma_{2,1} - \gamma_{2,2}| = 0.1$, where all the other parameters are kept fixed at the same values as in Figure 1. Figure 4 shows that in (a, γ_2)-space, the species goes extinct at low values of the intrinsic growth rate whenever $\mathcal{R}_{D_2} < 1$.
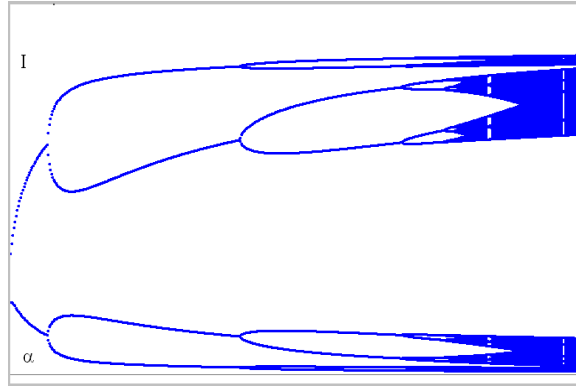
FIGURE 2.   Infective population undergoes period-doubling bi-
furcation route to chaos as α varies between 5 and 400. On the
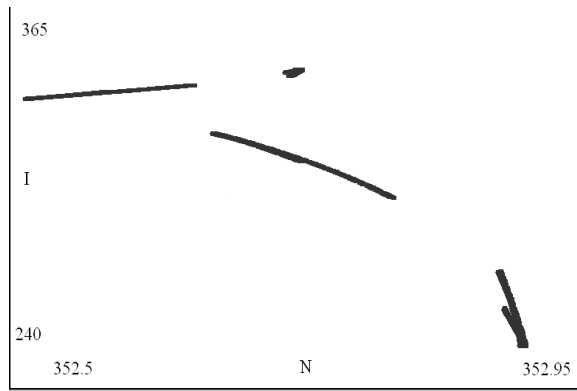$x - axis$, $\alpha \in [5, 300]$ and on the $y - axis$, $I \in [0, 400]$.

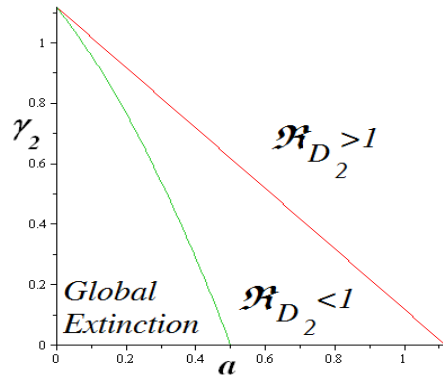FIGURE 3.   A chaotic attrator in the $(N, I) -space$.

FIGURE 4.   Regions of extinction versus persistence in the (a, γ_2)-space.

6. **Conclusion.** The study of the combined effects of disease induced mortality and seasonal trends on the control of diseases in discretely reproducing populations has received little attention. In this paper, we focus on the joint impact of periodic environments and disease induced mortality on the persistence or extinction of discretely reproducing populations. We formulated and analyzed a periodically forced discrete-time SIS epidemic model with disease induced mortality. For our model, we computed the basic reproduction number, $\mathcal{R}_0$, and used it to investigate the relationship between disease persistence and extinction. We showed that $\mathcal{R}_0 < 1$ implies the extinction of the infective population.

In constant (non-periodic) environments, Franke and Yakubu, in an earlier work, used a discrete-time SIS epidemic model with disease induced mortality to show that a tiny number of infectious individuals can drive an otherwise persistent (susceptible) population to extinction whenever $\mathcal{R}_0 > 1$. In this paper, we extend this result to include periodic (non-constant) environments. That is, in SIS models with diseases induced mortality, when the environment is either constant or periodic and $\mathcal{R}_0 > 1$, a tiny number of infective population can drive the total population to extinction. In addition, we obtained conditions that guarantee the persistence of the total population whenever $\mathcal{R}_0 > 1$ and the environment is periodic [25].

Periodically forced models are known to exhibit oscillatory and chaotic dynamics [25]. In this paper, we used a periodically forced Beverton–Holt model to illustrate period-doubling bifurcations route to chaos in SIS models with disease induced mortality where the disease-free susceptible population exhibits a cyclic and non-chaotic attractor. In addition, we use an example to highlight that the structure of the chaotic attractors can be very complicated. It is also possible that a continuous-time model with an infective period of fixed length might exhibit similar dynamical behaviors. Studies of analogous questions for SIR epidemic models are in the process and will be reported elsewhere.

7. **Appendix.**

Proof of Theorem 4.6. Since $I(0) \leq N(0)$, Lemma 3.2 implies that $I(t) \leq N(t)$ for all $t \in \mathbb{Z}_+$.

(a) Since

$$\mathcal{R}_0 = \prod_{t=0}^{p-1} \left(-\alpha \gamma_{1t} \phi'(0) + \gamma_{2t} \sigma \right) < 1,$$

Lemma 3.2 gives

$$F'_{N,t}(0) = -\alpha \gamma_{1t} \phi'(0) + \gamma_{2t} \sigma$$

and

$$I(1) = F_{N(0),0}(I(0)) \leq F'_{N(0),0}(0)I(0).$$

Thus,

$$I(2) = F_{N(1),1}(I(1)) \leq F'_{N(1),1}(0)I(1) \leq F'_{N(1),1}(0)F'_{N(0),0}(0)I(0)$$

and inductively

$$I(n) \leq \left(\prod_{t=0}^{n-1} F'_{N(t),t}(0) \right) I(0) \leq$$

$$(\mathcal{R}_0)^{\lfloor n/p \rfloor} \max_{j \in \{1,2,\cdots,p-1\}} \left\{ \prod_{t=0}^{j-1} F'_{N(t),t}(0) \right\} I(0).$$

The sequence $\{I(t)\}$ is dominated by the decreasing sequence

$$\left\{ (\mathcal{R}_0)^{\lfloor n/p \rfloor} \max_{j \in \{1,2,\cdots,p-1\}} \left\{ \prod_{t=0}^{j-1} F'_{N(t),t}(0) \right\} I(0) \right\}$$

which converges to 0. Hence,

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

(b) By Lemma 3.3, since $I(0) > 0$ we have $I(t) > 0$ for all $t \in \mathbb{Z}_+$. Lemma 3.2 gives

$$F'_{N,t}(0) = -\alpha \gamma_{1t} \phi'(0) + \gamma_{2t} \sigma$$

for all N and t. $\mathcal{R}_0 = \prod_{t=0}^{p-1} (-\alpha \gamma_{1t} \phi'(0) + \gamma_{2t} \sigma) > 1$ implies

$\prod_{t=0}^{p-1} F'_{N(t),t}(0) > 1$. Note that $F_{N,t}(N,0) = 0$ for all t and N. The derivative of
$\pi_2 \circ H_1 \circ H_0(N,I) = F_{\pi_1 \circ H_0(N,I),1} \circ F_{N,0}(N,I)$ with respect to I is
$\frac{\partial \pi_2 \circ H_1}{\partial N}(H_0(N,I)) \frac{\partial \pi_1 \circ H_0}{\partial I}(N,I) + \frac{\partial \pi_2 \circ H_1}{\partial I}(H_0(N,I)) \frac{\partial \pi_2 \circ H_0}{\partial I}(N,I)$. When $I = 0$, this
derivative becomes
$\frac{\partial \pi_2 \circ H_1}{\partial N}(H_0(N,0)) \frac{\partial \pi_1 \circ H_0}{\partial I}(N,0) + \frac{\partial \pi_2 \circ H_1}{\partial I}(H_0(N,0)) \frac{\partial \pi_2 \circ H_0}{\partial I}(N,0) =$
$\frac{\partial F_{N,1}}{\partial N}(\pi_1 \circ H_0(N,0),0) \frac{\partial \pi_1 \circ H_0}{\partial I}(N,0) + \frac{\partial F_{N,1}}{\partial I}(\pi_1 \circ H_0(N,0),0) \frac{\partial F_{N,0}}{\partial I}(N,0) =$
$0 * \frac{\partial \pi_1 \circ H_0}{\partial I}(N,0) + (-\alpha \gamma_{11} \phi'(0) + \gamma_{21} \sigma) * (-\alpha \gamma_{10} \phi'(0) + \gamma_{20} \sigma) =$

$$(-\alpha \gamma_{11} \phi'(0) + \gamma_{21} \sigma) * (-\alpha \gamma_{10} \phi'(0) + \gamma_{20} \sigma) = \prod_{t=0}^{1} F'_{N(t),t}(0).$$

Inductively, the derivative of
$\pi_2 \circ H_{p-1} \circ \cdots \circ H_1 \circ H_0(N,I)$ with respect to I at an arbitrary $(N,I) = (N,0)$ is
$\prod_{t=0}^{p-1} F'_{N(t),t}(0)$ which is independent of N. Similarly, if $\{\widehat{N}_t\}$ is a p- periodic sequence
of positive numbers, then derivative of
$\widehat{H}(\widehat{N}_0, \widehat{N}_1, \cdots, \widehat{N}_{p-1}, I) =$
$\pi_2 \circ H_{p-1}(\widehat{N}_{p-1}, \pi_2 \circ H_{p-2}(\cdots H_2(\widehat{N}_2, \pi_2 \circ H_1(\widehat{N}_1, \pi_2 \circ H_0(\widehat{N}_0,I))) \cdots))$ with re-
spect to I at $I = 0$ is $\prod_{t=0}^{p-1} F'_{1,t}(0)$. Now, consider $\widehat{H}(\widehat{N}_0, \widehat{N}_1, \cdots, \widehat{N}_{p-1}, I)$ as a function
of the one variable I. Since $\prod_{t=0}^{p-1} F'_{1,t}(0) > 1$ and $\widehat{H}$ is C^1 on a neighborhood U of
$\left(\widehat{N}_0, \widehat{N}_1, \cdots, \widehat{N}_{p-1}, I \right)$ there exist two positive numbers $\nu > 1$ and β and a neighbor-
hood W of $\left(\widehat{N}_0, \widehat{N}_1, \cdots, \widehat{N}_{p-1} \right)$ such that $\widehat{H}(x_0, x_1, \cdots, x_{p-1}, I) \geq \nu I$ on $W \times [0, \beta]$.

By uniform persistence of the total population there is a $\eta_* > 0$ such that even-
tually $\pi_1 \circ H_t \circ \cdots \circ H_1 \circ H_0(N,I) > \eta_*$ and it remains true for larger t values. By
Lemma 4.5 there is a $\eta^* > 0$ such that eventually $\pi_1 \circ H_t \circ \cdots \circ H_1 \circ H_0(N,I) < \eta^*$
and it remains true for larger t values. Since $C = \underbrace{[\eta_*, \eta^*] \times [\eta_*, \eta^*] \times \cdots \times [\eta_*, \eta^*]}_{p-fold}$
is compact, every open cover has a finite subcover. Let $(x_0, x_1, \cdots, x_{p-1}) \in C$.
Then there exist two positive numbers $\nu > 1$ and β and a neighborhood W of
$(x_0, x_1, \cdots, x_{p-1})$ such that $\widehat{H}(x_0, x_1, \cdots, x_{p-1}, I) \geq \nu I$ on $W \times [0, \beta]$. Since we can
do this for every point in C, the Ws give an open cover of C. A finite subcover
gives finite sequences of ν and β. Taking the minimum of these gives a $\overline{\nu} > 1$ and

$\overline{\beta} > 0$ such that $\widehat{H}(x_0, x_1, \cdots, x_{p-1}, I) \geq \overline{\nu}I$ on $C \times [0, \overline{\beta}]$. We may assume that $\overline{\beta} < \eta_*$.

Let $\xi_t = \min\{\pi_2 \circ H_t(N, I) : \overline{\beta} \leq I \leq N, \eta_* \leq N \leq \eta^*\}$ which is positive because H_t is positive on the compact set. Let $\xi^* = \min_t\{\xi_t\}$. The first components of the orbit of $(N(0), I(0))$, under $\{H_t\}$ eventually get into $[\eta_*, \eta^*]$ and stay there for all t bigger than or equal to some t^*. Let $\overline{\eta} = \min\{\overline{\beta}, \left(\prod_{t=0}^{p-1} (\gamma_{2t}\sigma)\right) \xi^*\}$. If $I(t^*) < \overline{\beta}$ then $I(t^* + p) \geq \overline{\nu}I(t^*)$ and $I(t^* + np) \geq \overline{\nu}^n I(t^*)$ as long as $I(t^* + (n-1)p) < \overline{\beta}$. Since $\overline{\nu} > 1$, $I(t)$ eventually gets larger than $\overline{\beta}$. The $I(t)$ could stay larger than $\overline{\beta}$, but if they get smaller, the first time they must be at least ξ^*. It is possible that the next $p-1$ iterations are smaller but they must stay larger than $\left(\prod_{t=0}^{p-1} (\gamma_{2t}\sigma)\right) \xi^*$ and they start increasing after p iterations. They then eventually get larger than $\overline{\beta}$. Hence $\lim_{t\to\infty} \pi_2 \circ H_t \circ \cdots \circ H_1 \circ H_0(N, I) \geq \overline{\eta} > 0$. That is, the disease is uniformly persistent. $\square$

Proof of Theorem 4.7. Let $0 < \beta \leq 1$. Now, we investigate the ray through the origin with slope β. If a point $(N(t), I(t))$ on the orbit of a positive initial condition $(N(0), I(0))$ is on this ray then $I(t) = \beta N(t)$. To calculate the slope of the ray that contains the image of this point under H_t, we have

$$F_{N,t}(I) = F_{N,t}(\beta N) = F_{1,t}(\beta)N,$$

and

$$G_{N,t}(I) = G_{N,t}(\beta N) = f(t, N) + (\gamma_{1t}(1 - \beta) + \gamma_{2t}\beta) N.$$

The new slope is

$$m_{N,t}(\beta) = \frac{F_{N,t}(\beta N)}{G_{N,t}(\beta N)} = \frac{F_{1,t}(\beta)N}{f(t, N) + (\gamma_{1t}(1 - \beta) + \gamma_{2t}\beta) N}.$$

Since $f(t, N) \leq f'(t, 0)N$ for all t and $N > 0$,

$$m_{N,t}(\beta) \quad \geq \quad \frac{F_{1,t}(\beta)}{f'(t, 0) + (\gamma_{1t}(1 - \beta) + \gamma_{2t}\beta)} \tag{7}$$

$$\geq \quad \frac{F_{1,t}(\beta)}{f'(t, 0) + \gamma_{1t}}. \tag{8}$$

Since $F_{1,t}(\beta)$ is differentiable, $F_{1,t}(0) = 0$, and $F'_{1,t}(0) = -\alpha\gamma_{1t}\phi'(0) + \gamma_{2t}\sigma$ for every $\varepsilon > 0$ there is a neighborhood $U_{1,t} = (-a, \beta_{0,t})$ of 0, such that if $0 < \beta \in U_{1,t}$ then

$$F_{1,t}(\beta) > (-\alpha\gamma_{1t}\phi'(0) + \gamma_{2t}\sigma - \varepsilon) \beta.$$

The limit, $\lim_{\varepsilon\to 0^+} \prod_{t=0}^{p-1} (-\alpha\gamma_{1t}\phi'(0) + \gamma_{2t}\sigma - \varepsilon) = \prod_{t=0}^{p-1} (-\alpha\gamma_{1t}\phi'(0) + \gamma_{2t}\sigma) = \mathcal{R}_0 > 1$. Thus there is an $\varepsilon_0 > 0$ such that

$$\varsigma_1 = \prod_{t=0}^{p-1} (-\alpha\gamma_{1t}\phi'(0) + \gamma_{2t}\sigma - \varepsilon_0) > 1.$$

By taking ε_0 even smaller, if necessary, we can assume that for each t

$$-\alpha\gamma_{1t}\phi'(0) + \gamma_{2t}\sigma - \varepsilon_0 > 0.$$

Also there is a $\beta_0 > 0$ such that for each $\beta \in (0, \beta_0]$ and for each t

$$F_{1,t}(\beta) > \left(-\alpha\gamma_{1t}\phi'(0) + \gamma_{2t}\sigma - \varepsilon_0\right)\beta$$

Note that β_0 and ς_1 are independent of f.

Note $m_{N,t}(0) = 0$ and

$$m'_{N,t}(0) = \frac{F'_{1,t}(0)N}{f(t,N) + \gamma_{1t}N} \geq \frac{F'_{1,t}(0)}{f'(t,0) + \gamma_{1t}} > 0.$$

Hence when β and $m_{N(0),0}(\beta) \in (0, \beta_0]$,

$$
\begin{aligned}
& m_{N(1),1}\left(m_{N(0),0}(\beta)\right) \\
&= \frac{F_{1,1}(m_{N(0),0}(\beta))N(1)}{f(1,N(1)) + \left(\gamma_{11}(1 - m_{N(0),0}(\beta)) + \gamma_{21}m_{N(0),0}(\beta)\right)N(1)} \\
&\geq \frac{F_{1,1}(m_{N(0),0}(\beta))}{f'(1,0) + \left(\gamma_{11}(1 - m_{N(0),0}(\beta)) + \gamma_{21}m_{N(0),0}(\beta)\right)} \\
&\geq \frac{F_{1,1}(m_{N(0),0}(\beta))}{f'(1,0) + \gamma_{11}} \geq \frac{\left(-\alpha\gamma_{11}\phi'(0) + \gamma_{21}\sigma - \varepsilon_0\right)\left(m_{N(0),0}(\beta)\right)}{f'(1,0) + \gamma_{11}} \\
&\geq \frac{\left(-\alpha\gamma_{11}\phi'(0) + \gamma_{21}\sigma - \varepsilon_0\right)\left(\frac{F_{10}(\beta)}{f'(0,0)+\gamma_{10}}\right)}{f'(1,0) + \gamma_{11}} \\
&\geq \frac{\left(-\alpha\gamma_{11}\phi'(0) + \gamma_{21}\sigma - \varepsilon_0\right)\left(-\alpha\gamma_{10}\phi'(0) + \gamma_{20}\sigma - \varepsilon_0\right)}{\left(f'(1,0) + \gamma_{11}\right)\left(f'(0,0) + \gamma_{10}\right)}\beta.
\end{aligned}
$$

Let j be a nonnegative integer. Inductively, as long as the iterations, $m_{N(t+j),t+j} \circ m_{N(t+j-1),t+j-1} \circ \cdots \circ m_{N(j),j}(\beta)$, remain in $(0, \beta_0]$,

$$
\begin{aligned}
& m_{N(t+j),t+j} \circ m_{N(t+j-1),t+j-1} \circ \cdots \circ m_{N(j),j}(\beta) \\
&\geq \frac{\prod\limits_{i=j}^{t+j}\left(-\alpha\gamma_{1i}\phi'(0) + \gamma_{2i}\sigma - \varepsilon_0\right)}{\prod\limits_{i=j}^{t+j}\left(f'(i,0) + \gamma_{1i}\right)}\beta.
\end{aligned}
$$

In particular

$$
\begin{aligned}
& m_{N(p-1+j),p-1+j} \circ m_{N(p-2+j),p-2+j} \circ \cdots \circ m_{N(j),j}(\beta) \\
&\geq \frac{\prod\limits_{i=0}^{p-1}\left(-\alpha\gamma_{1i}\phi'(0) + \gamma_{2i}\sigma - \varepsilon_0\right)}{\prod\limits_{i=0}^{p-1}\left(f'(i,0) + \gamma_{1i}\right)}\beta \\
&= \frac{\varsigma_1}{\mathcal{R}_{D_1}}\beta
\end{aligned}
$$

if the iterations, $m_{N(p-1+j),p-1+j} \circ m_{N(p-2+j),p-2+j} \circ \cdots \circ m_{N(j),j}(\beta)$, remain in $(0, \beta_0]$. Hence if $\mathcal{R}_{D_1} < \varsigma_1$, then β grows geometrically at a rate of at least $\frac{\varsigma_1}{\mathcal{R}_{D_1}} > 1$ after p iterations.

$$\varsigma_1 > \mathcal{R}_{D_1} = \prod_{t=0}^{p-1}\left(f'(t,0) + \gamma_{1t}\right) \geq \left(f'(t,0) + \gamma_{1t}\right)\prod_{\substack{i=0 \\ i\neq t}}^{p-1}\gamma_{1i}.$$

Hence,

$$f'(t,0) + \gamma_{1t} < \frac{\varsigma_1}{\prod\limits_{t=0}^{p-1} \gamma_{1t}},$$

and $\frac{\varsigma_1}{\prod\limits_{t=0}^{p-1} \gamma_{1t}}$ is independent of f.

The first p-1 iterates could decrease but they stay above

$$\left(\min_{j,t\in\{0,1,\cdots,p-1\}} \left\{ \frac{\left(\prod\limits_{t=0}^{p-1}\gamma_{1t}\right)^t \prod\limits_{i=0}^{t} \left(-\alpha\gamma_{1(i+j)}\phi'(0) + \gamma_{2(i+j)}\sigma - \varepsilon_0\right)}{\varsigma_1^t} \right\} \right) \beta > 0.$$

Thus, the slopes eventually get larger than $\beta_0 > 0$.

Each $m_t(\beta) \geq \frac{F_{1,t}(\beta)}{f'(t,0)+\gamma_{1t}} \geq \frac{F_{1,t}(\beta)}{\varsigma_1}\prod\limits_{t=0}^{p-1}\gamma_{1t}$. $F_{1,t}(\beta)$ is continuous and positive on $[\beta_0,1]$. Let $\overline{\beta}_t = \min\{\frac{F_{1,t}(\beta)}{\varsigma_1}\prod\limits_{t=0}^{p-1}\gamma_{1t} : \beta \in [\beta_0,1]\} > 0$ and $\overline{\beta} = \min\limits_t \{\overline{\beta}_t\}$. $\overline{\beta}$ is independent of f.

Thus, the slopes grow when they are small until they reach at least β_0. They can then decrease but not less than $\overline{\beta}$ in one step. The next few steps could take a slope lower before it starts increasing geometrically. The smallest it could get is

$$\left(\min_{j,t\in\{0,1,\cdots,p-1\}} \left\{ \frac{\left(\prod\limits_{t=0}^{p-1}\gamma_{1t}\right)^t \prod\limits_{i=0}^{t} \left(-\alpha\gamma_{1(i+j)}\phi'(0) + \gamma_{2(i+j)}\sigma - \varepsilon_0\right)}{\varsigma_1^t} \right\} \right) \overline{\beta} > 0.$$

Thus, the lim inf of the slopes is at least

$$\beta_\eta = \min\left\{ \beta_0, \left(\min_{j,t\in\{0,1,\cdots,p-1\}} \left\{ \frac{\left(\prod\limits_{t=0}^{p-1}\gamma_{1t}\right)^t \prod\limits_{i=0}^{t} \left(-\alpha\gamma_{1(i+j)}\phi'(0) + \gamma_{2(i+j)}\sigma - \varepsilon_0\right)}{\varsigma_1^t} \right\} \right) \overline{\beta} \right\}$$
$$> 0.$$

Note β_η is independent of f. We now need to show that the total population decreases when $\beta \geq \beta_\eta$. This will be accomplished by taking $1 < \mathcal{R}_{D_1} < \varsigma_2$ for some appropriate ς_2 that is independent of f.

Since the tth iterate of $(N(0), \beta N(0))$ is $(N(t), m_{N(t-1),t-1} \circ m_{N(t-2),t-2} \circ \cdots \circ m_{N(1),1} \circ m_{N(0),0}(\beta)N(t))$,

$$
\begin{aligned}
& N(t+1) \\
=\ & G_{N(t),t}(m_{N(t-1),t-1} \circ m_{N(t-2),t-2} \circ \cdots \circ m_{N(1),1} \circ m_{N(0),0}(\beta)N(t)) \\
=\ & f(t, N(t)) \\
& + \left(\begin{array}{c} \gamma_{1,t}(1 - m_{N(t-1),t-1} \circ m_{N(t-2),t-2} \circ \cdots \\ \circ m_{N(1),1} \circ m_{N(0),0}(\beta)) + \gamma_{2,t} m_{N(t-1),t-1} \circ m_{N(t-2),t-2} \circ \cdots \\ \circ m_{N(1),1} \circ m_{N(0),0}(\beta) \end{array} \right) N(t) \\
\leq\ & \left(f'(t,0) + \right. \\
& \left. \left(\begin{array}{c} \gamma_{1t}(1 - m_{N(t-1),t-1} \circ m_{N(t-2),t-2} \circ \cdots \\ \circ m_{N(1),1} \circ m_{N(0),0}(\beta)) + \gamma_{2,t} m_{N(t-1),t-1} \circ m_{N(t-2),t-2} \circ \cdots \\ \circ m_{N(1),1} \circ m_{N(0),0}(\beta) \end{array} \right) \right) N(t) \\
\leq\ & \left(f'(t,0) + \right. \\
& \left(\begin{array}{c} \gamma_{1t}(1 - m_{N(t-1),t-1} \circ m_{N(t-2),t-2} \circ \cdots \\ \circ m_{N(1),1} \circ m_{N(0),0}(\beta)) + \gamma_{2t} m_{N(t-1),t-1} \circ m_{N(t-2),t-2} \circ \cdots \\ \circ m_{N(1),1} \circ m_{N(0),0}(\beta) \end{array} \right) \cdot \\
& \left(f'(t-1,0) + \right. \\
& \left. \left. \left(\begin{array}{c} \gamma_{1(t-1)}(1 - m_{N(t-2),t-2} \circ m_{N(t-3),t-3} \circ \cdots \\ \circ m_{N(1),1} \circ m_{N(0),0}(\beta)) + \gamma_{2t} m_{N(t-2),t-2} \circ m_{N(t-3),t-3} \circ \cdots \\ \circ m_{N(1),1} \circ m_{N(0),0}(\beta) \end{array} \right) \right) \right) \right) \cdot \\
& N(t-1) \\
\leq\ & \left[\prod_{i=1}^{t} \left(f'(i,0) + \right. \right. \\
& \left. \left. \left(\begin{array}{c} \gamma_{1i}(1 - m_{N(i-1),i-1} \circ m_{N(i-2),i-2} \circ \cdots \\ \circ m_{N(1),1} \circ m_{N(0),0}(\beta)) + \gamma_{2i} m_{N(i-1),i-1} \circ m_{N(i-2),i-2} \circ \cdots \\ \circ m_{N(1),1} \circ m_{N(0),0}(\beta) \end{array} \right) \right) \right] \cdot \\
& \left(f'(0,0) + \gamma_{10}(1-\beta) + \gamma_{20}\beta \right) N(0).
\end{aligned}
$$

Recall that $\gamma_{1t^*} - \gamma_{2t^*} > 0$ and $f'(i,0) + \gamma_{1i}(1 - m_{N(i-1),i-1} \circ m_{N(i-2),i-2} \circ \cdots \circ m_{N(1),1} \circ m_{N(0),0}(\beta)) + \gamma_{2i} m_{N(i-1),i-1} \circ m_{N(i-2),i-2} \circ \cdots \circ m_{N(1),1} \circ m_{N(0),0}(\beta) > 0$. So $f'(i,0) + \gamma_{1i} > \gamma_{1i}(m_{N(i-1),i-1} \circ m_{N(i-2),i-2} \circ \cdots \circ m_{N(1),1} \circ m_{N(0),0}(\beta)) - \gamma_{2i} m_{N(i-1),i-1} \circ m_{N(i-2),i-2} \circ \cdots \circ m_{N(1),1} \circ m_{N(0),0}(\beta) \geq 0$.

Thus

$$N(t+1)$$

$$\leq \quad \left[\prod_{i=1}^{t} \left(f'(i,0) + \right. \right.$$

$$\left. \left(\begin{array}{c} \gamma_{1i}(1 - m_{N(i-1),i-1} \circ m_{N(i-2),i-2} \circ \cdots \\ \circ m_{N(1),1} \circ m_{N(0),0}(\beta)) + \gamma_{2,i} m_{N(i-1),i-1} \circ m_{N(i-2),i-2} \circ \cdots \\ \circ m_{N(1),1} \circ m_{N(0),0}(\beta) \end{array} \right) \right] \cdot$$

$$\left(f'(0,0) + \gamma_{10}(1-\beta) + \gamma_{20}\beta \right) N(0)$$

$$= \quad (f'(j,0) + \gamma_{1j}) \cdot$$

$$\left[\begin{array}{c} \prod_{\substack{i=1 \\ i \neq j}}^{t} \left(f'(i,0) + \right. \\ \left(\begin{array}{c} \gamma_{1i}(1 - m_{N(i-1),i-1} \circ m_{N(i-2),i-2} \circ \cdots \\ \circ m_{N(1),1} \circ m_{N(0),0}(\beta)) + \gamma_{2,i} m_{N(i-1),i-1} \circ m_{N(i-2),i-2} \circ \cdots \\ \circ m_{N(1),1} \circ m_{N(0),0}(\beta) \end{array} \right) \end{array} \right] \cdot$$

$$(f'(0,0) + \gamma_{10}(1-\beta) + \gamma_{20}\beta) N(0) -$$

$$\left[\begin{array}{c} \gamma_{1j} m_{N(j-1),j-1} \circ m_{N(j-2),j-2} \circ \cdots \\ \circ m_{N(1),1} \circ m_{N(0),0}(\beta) + \gamma_{2j} m_{N(j-1),j-1} \circ m_{N(j-2),j-2} \circ \cdots \\ \circ m_{N(1),1} \circ m_{N(0),0}(\beta) \end{array} \right] \cdot$$

$$\left[\begin{array}{c} \prod_{\substack{i=1 \\ i \neq j}}^{t} \left(f'(i,0) - \right. \\ \left(\begin{array}{c} \gamma_{1i}(1 - m_{N(i-1),i-1} \circ m_{N(i-2),i-2} \circ \cdots \\ \circ m_{N(1),1} \circ m_{N(0),0}(\beta)) + \gamma_{2i} m_{N(i-1),i-1} \circ m_{N(i-2),i-2} \circ \cdots \\ \circ m_{N(1),1} \circ m_{N(0),0}(\beta) \end{array} \right) \end{array} \right] \cdot$$

$$(f'(0,0) + \gamma_{10}(1-\beta) + \gamma_{20}\beta) N(0)$$

$$\leq \quad (f'(j,0) + \gamma_{1,j}) \cdot$$

$$\left[\begin{array}{c} \prod_{\substack{i=1 \\ i \neq j}}^{t} \left(f'(i,0) + \right. \\ \left(\begin{array}{c} \gamma_{1i}(1 - m_{N(i-1),i-1} \circ m_{N(i-2),i-2} \circ \cdots \\ \circ m_{N(1),1} \circ m_{N(0),0}(\beta)) + \gamma_{2i} m_{N(i-1),i-1} \circ m_{N(i-2),i-2} \circ \cdots \\ \circ m_{N(1),1} \circ m_{N(0),0}(\beta) \end{array} \right) \end{array} \right] \cdot$$

$$(f'(0,0) + \gamma_{10}(1-\beta) + \gamma_{20}\beta) N(0).$$

So if $t \geq t^*$, carrying out this procedure for all but the t^* term gives

$$N(t+1)$$

$$\leq \quad \left[\prod_{\substack{i=0 \\ i \neq t^*}}^{t} (f'(i,0) + \gamma_{1i}) \right] (f'(t^*,0) + \gamma_{1t^*}(1 - m_{N(t^*-1),t^*-1} \circ m_{N(t^*-2),t^*-2} \circ \cdots$$

$$\circ m_{N(1),1} \circ m_{N(0),0}(\beta)) + \gamma_{2t^*} m_{N(t^*-1),t^*-1} \circ m_{N(t^*-2),t^*-2} \circ \cdots$$

$$\circ m_{N(1),1} \circ m_{N(0),0}(\beta)) N(0)$$

$$
\begin{aligned}
&= \quad \left[\prod_{i=0}^{t} (f'(i,0) + \gamma_{1i}) \right] N(0) - [\gamma_{1t^*} m_{N(t^*-1),t^*-1} \circ m_{N(t^*-2),t^*-2} \circ \cdots \\
&\quad \circ m_{N(1),1} \circ m_{N(0),0}(\beta)) - \gamma_{2t^*} m_{N(t^*-1),t^*-1} \circ m_{N(t^*-2),t^*-2} \circ \cdots \\
&\quad \circ m_{N(1),1} \circ m_{N(0),0}(\beta))] N(0) \\
&< \quad \left(\left(\prod_{i=0}^{t} (f'(i,0) + \gamma_{1i}) \right) - (\gamma_{1t^*} - \gamma_{2t^*})\beta_\eta \right) N(0).
\end{aligned}
$$

Taking $t = p - 1$ gives

$$
\begin{aligned}
N(p) \quad &< \quad \left(\prod_{i=0}^{p-1} (f'(i,0) + \gamma_{1i}) - (\gamma_{1t^*} - \gamma_{2t^*})\beta_\eta \right) N(0). \\
&= \quad (\mathcal{R}_{D_1} - (\gamma_{1t^*} - \gamma_{2t^*})\beta_\eta) N(0).
\end{aligned}
$$

Note that for each nonnegative integer j

$$
\begin{aligned}
N(p+j) \quad &< \quad \left(\prod_{i=0}^{p-1} (f'(i,0) + \gamma_{1i}) - (\gamma_{1t^*} - \gamma_{2t^*})\beta_\eta \right) N(j). \\
&= \quad (\mathcal{R}_{D_1} - (\gamma_{1t^*} - \gamma_{2t^*})\beta_\eta) N(j).
\end{aligned}
$$

Thus, if $1 < \mathcal{R}_{D_1} < \varsigma_2 = 1 + (\gamma_{1t^*} - \gamma_{2t^*})\beta_\eta$ the total population decreases by a factor less than 1 after each p iterations. So if $I(0) > 0$, then the slopes of the iterates increase until in a finite number of iterations it is larger than β_η. Then the total population decreases at a rate less than 1 after each p iterations. Consequently, if $1 < \mathcal{R}_{D_1} < \varsigma = \min\{\varsigma_1, \varsigma_2\}$ all positive initial conditions converge to the origin and the total population is driven to extinction, where ς is independent of f. $\square$

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E-mail address: franke@math.ncsu.edu
E-mail address: ayakubu@howard.edu