Dynamic behavior of a parasite–host model with general incidence ☆

Guihua Li [a,b,c], Wendi Wang [b,*], Kaifa Wang [b], Zhen Jin [c]

[a] *Key Laboratory of Eco-environments in Three Gorges Reservoir Region (Ministry of Education),
Faculty of Life Science, Southwest University, Chongqing 400715, PR China*
[b] *School of Mathematics and Statistics, Southwest University, Chongqing 400715, PR China*
[c] *Department of Mathematics, North University of China, Taiyuan, Shanxi 030051, PR China*

Abstract

In this paper, we consider the global dynamics of a microparasite model with more general incidences. For the model with the bilinear incidence, Ebert et al. [D. Ebert, M. Lipsitch, K.L. Mangin, The effect of parasites on host population density and extinction: Experimental epidemiology with Daphnia and six microparasites, American Naturalist 156 (2000) 459–477] observed that parasites can reduce host density, but the extinction of both host population and parasite population occurs only under stochastic perturbations. Hwang and Kuang [T.W. Hwang, Y. Kuang, Deterministic extinction effect of parasites on host populations, J. Math. Biol. 46 (2003) 17–30] studied the model with the standard incidence and found that the host population may be extinct in the absence of random disturbance. We consider more general incidences that characterize transitions from the bilinear incidence to the standard incidence to simulate behavior changes of populations from random mobility in a fixed area to the mobility with a fixed population density. Using the techniques of Xiao and Ruan [D. Xiao, S. Ruan, Global dynamics of a ratio-dependent predator–prey system, J. Math. Biol. 43 (2001) 268–290], it is shown that parasites can drive the host to extinction only by the standard incidence. The complete classifications of dynamical behaviors of the model are obtained by a qualitative analysis.
© 2006 Elsevier Inc. All rights reserved.

Keywords: General incidence; Microparasite model; Host extinction; Global stability

1. Introduction

In practice, parasites may be used to control pest species instead of chemical pesticides. This is based on the fact that parasites can reduce host density and even drive host populations to extinction [1–6,11,14]. Theory on the effects of parasites on host population dynamics has been extensively developed, with the aim of understanding whether variability in the effects of parasites on host fecundity and survival is reflected in host population dynamics.

In an effort to understand the ability of six microparasites to regulate Daphnia populations and drive the populations to extinction, Ebert et al. [7] formulated the following microparasite model with horizontal transmission:

$$\begin{cases} \dfrac{dS}{dt} = r(S + \sigma I)\left(1 - \dfrac{S + I}{K}\right) - dS - \beta SI, \\ \dfrac{dI}{dt} = \lambda SI - (d + \epsilon)I, \end{cases} \tag{1.1}$$

where $S(t)$ and $I(t)$ represent the densities of uninfected (susceptible) and infected (infective) hosts at time t, respectively, r is the per capita growth rate of uninfected hosts, σ is the relative fecundity of an infected host with $0 \leqslant \sigma \leqslant 1$, K is the carrying capacity of the environment for the host population, d is the parasite mortality rate, β is the infection rate coefficient, and ϵ is the infection-induced death rate.

This deterministic model predicts the existence of a globally stable steady state and the host density will decrease monotonically as a function of parasite-induced reductions in fecundity. Whereas in the population experiments, Ebert et al. [7] found that the time series from the infection treatment fell into three categories. First, host and parasite coexisted throughout the experiment. Second, the parasite went extinct. Third, the Daphnia population and the parasites went extinct together. This means that the model cannot predict the extinction of both host population and parasites. However, they found, by computer simulations, that the extinction of both the host population and parasite population occurs under suitable stochastic perturbations. In [9], Hwang and Kuang changed the mass action incidence βSI to the standard incidence $\beta \frac{S}{S+I} I$. Significantly, this revised parasite–host model can exhibit the observed parasite-induced host extinction. This means that the extinction of the host population may be due to deterministic factors instead of stochastic factors. Note that the mass action incidence implies that individuals of the population occupy a fixed area so that the contact rate is proportional to the population density. Note also that the standard incidence implies that the occupied area is proportional to its population size so that the contact rate is a constant. This means that the two incidences are two extreme cases.

Now, it is natural to ask what is the evolutionary consequence of the host population and parasites if the incidence lies between these two extreme cases. Especially, can parasites drive host population to extinction now? In order to understand the mechanism, we consider a more general incidence $\beta N^\alpha \frac{S}{N} I$ (where $0 \leqslant \alpha \leqslant 1$) that characterizes continuous transitions from the bilinear incidence $\beta N \frac{S}{N} I$ to the standard incidence $\beta \frac{S}{N} I$. Indeed, it reduces to the bilinear incidence if $\alpha = 1$ and the standard incidence if $\alpha = 0$. Furthermore, if the occupied area of population is given by $\frac{k_1}{N^{1-\alpha}}$, which implies that the population density is $k_1 N^\alpha$, and population movement is random in the occupied area, then the valid contact rate can be in the form of βN^α. In this case, when α is decreased from 1 to 0, the occupied area varies from the constant k_1 to $\frac{k_1}{N}$, which corresponds to the changes from a fixed occupied area to the area with a fixed contact rate. With the given incidence, the model to be studied is

$$\begin{cases} \dfrac{dS}{dt} = \left(b - \dfrac{rN}{K}\right)(S + \sigma I) - dS - \beta N^{\alpha-1} SI, \\ \dfrac{dI}{dt} = \beta N^{\alpha-1} SI - (d + \epsilon)I, \end{cases} \tag{1.2}$$

where $N = S + I$. From (1.2), we obtain

$$\frac{dN}{dt} = r\left[N - (1 - \sigma)I\right]\left(1 - \frac{N}{K}\right) - \epsilon I + d(\sigma - 1)I, \tag{1.3}$$

where $r = b - d$. Thus, in the absence of the disease, (1.3) leads to

$$\frac{dN}{dt} = r(1 - N/K)N.$$

Hence, $N \to K$ as $t \to \infty$. The advantage of the model (1.2) is that the original meanings of parameters r and K in the logistic differential equation are maintained, in the sense that r is the intrinsic growth rate of the population and K is the carrying capacity of environment. For biological reasons, we will restrict out attention on the region $\{(S, I): 0 \leqslant S + I \leqslant K\}$.

In this paper we shall show that parasites could drive the host population to extinction only by the standard incidence. This means that a little expansion of the habitat for individuals in saturation level implies the survival of the host population. The key point is that the origin $(0, 0)$ is a highly degenerate equilibrium for system (1.2). Following the techniques of Xiao and Ruan [17], we shall give a complete analysis for dynamic behaviors of the solutions of system (1.2). The results extend the work in [7] where $\alpha = 1$ and the work in [9] where $\alpha = 0$. The rest of this paper is organized as follows. In Section 2, the conditions for the extinction of host populations are analyzed. Section 3 is devoted to the existence and uniqueness of positive equilibrium, and its global stability. The paper ends with brief discussions.

2. Asymptotic behavior at $(0, 0)$

For simplicity, we non-dimensionalise system (1.2) with the following scaling

$$S = \frac{d + \epsilon}{\beta}x, \qquad I = \frac{d + \epsilon}{\beta}y, \qquad \tau = (d + \epsilon)t.$$

If t is used to represent τ, we obtain

$$\begin{cases} \dfrac{dx}{dt} = ax + \sigma(a + c)y - hx^2 - h(\sigma + 1)xy - h\sigma y^2 - p(x + y)^{\alpha-1}xy, \\ \dfrac{dy}{dt} = p(x + y)^{\alpha-1}xy - y, \end{cases} \tag{2.1}$$

where

$$a = \frac{r}{d + \epsilon}, \qquad c = \frac{d}{d + \epsilon}, \qquad h = \frac{r}{\beta K}, \qquad p = \left(\frac{d + \epsilon}{\beta}\right)^{\alpha-1}.$$

In this paper, we assume that r, β, d and ϵ are positive constants, σ and α are constants in $[0, 1]$. The feasible region of (2.1) is $\{(x, y): x \geqslant 0, \ y \geqslant 0, \ 0 \leqslant x + y \leqslant \frac{a}{h}\}$.

There are two equilibria $(0, 0)$ and $(a/h, 0)$ in (2.1). First, we study the local stability of $(0, 0)$ when $\alpha = 0$. If $\alpha = 0$, system (2.1) is reduced to

$$\begin{cases} \dfrac{dx}{dt} = ax + \sigma(a + c)y - hx^2 - h(\sigma + 1)xy - h\sigma\, y^2 - p\dfrac{xy}{x + y}, \\ \dfrac{dy}{dt} = p\dfrac{xy}{x + y} - y. \end{cases} \tag{2.2}$$

We make another time scale change $dt = (x + y)\,d\xi$ (for simplicity t is used to represent ξ) such that system (2.2) is equivalent to the following system:

$$\begin{cases} \dfrac{dx}{dt} = X_2(x, y) + \Phi(x, y), \\ \dfrac{dy}{dt} = Y_2(x, y), \end{cases} \tag{2.3}$$

where

$$X_2(x, y) = ax^2 + (\sigma a + \sigma c + a - p)xy + \sigma(a + c)y^2,$$
$$\Phi(x, y) = -hx^3 - h(\sigma + 2)x^2 y - h(2\sigma + 1)xy^2 - h\sigma y^3,$$
$$Y_2(x, y) = y(px - x - y) \equiv Y_2(x, y).$$

By [18], if an orbit of (2.3) tends to the origin then it must tend to it along a fixed direction. This corresponds to the extinction of both parasites and the host population. To find characteristic directions, we introduce the polar coordinates $x = r\cos\theta$, $y = r\sin\theta$ to obtain

$$\begin{cases} \dfrac{dr}{dt} = r^2\big(H(\theta) + o(1)\big), \\ \dfrac{d\theta}{dt} = r\big(G(\theta) + o(1)\big), \end{cases} \tag{2.4}$$

where

$$\begin{aligned} H(\theta) &= Y_2\sin\theta + X_2\cos\theta \\ &= a\cos^3\theta + (\sigma a + \sigma c + p - 1)\cos\theta\sin^2\theta \\ &\quad + (\sigma a + \sigma c + a - p)\cos^2\theta\sin\theta - \sin^3\theta, \\ G(\theta) &= Y_2\cos\theta - X_2\sin\theta \\ &= \sin\theta(\cos\theta + \sin\theta)\big[(p - a - 1)\cos\theta - \sigma(a + c)\sin\theta\big]. \end{aligned}$$

Then the characteristic equation of system (2.3) takes the form

$$G(\theta) = \sin\theta(\cos\theta + \sin\theta)\big[(p - a - 1)\cos\theta - \sigma(a + c)\sin\theta\big] = 0. \tag{2.5}$$

$\theta = 0$ is a trivial characteristic direction. In $\theta = 0$, infected hosts die out and the uninfected host population tends to its carrying capacity K. To determine if there exist orbits of system (2.3) which tend to the origin along the direction $\theta = 0$ as t tends to $+\infty$ or $-\infty$, we have to compute the derivatives of $G(\theta)$.

$$\begin{aligned} G'(\theta) &= \cos 2\theta\big((p - a - 1)\cos\theta - (\sigma a + \sigma c + a - p + 1)\sin\theta\big) \\ &\quad + \cos\theta\sin\theta\big((a + 1 - p)\sin\theta - (\sigma a + \sigma c + a - p + 1)\cos\theta\big), \\ G''(\theta) &= 2\cos 2\theta\big((a + 1 - p)\sin\theta - (\sigma a + \sigma c + a - p + 1)\cos\theta\big) \\ &\quad + 5\cos\theta\sin\theta\big((a + 1 - p)\cos\theta + (\sigma a + \sigma c + a - p + 1)\sin\theta\big). \end{aligned}$$

By means of techniques from [17,18], we can obtain the following theorems.

Theorem 2.1. *Suppose* $p - a - 1 > 0$. *Then there exist* $\epsilon_1 > 0$ *and* $r_1 > 0$ *such that all orbits of system* (2.3) *in*

$$\left\{(\theta, r): 0 \leqslant \theta < \epsilon_1, \ 0 < r < r_1\right\}$$

tend to $(0, 0)$ *along* $\theta_1 = 0$ *as* $t \to -\infty$.

Proof. When $p - a - 1 > 0$, $\theta_1 = 0$ is a simple root of (2.5). Since $G'(\theta_1) = p - a - 1$, $H(\theta_1) = a$, and $G'(\theta_1)H(\theta_1) > 0$, by Theorem 3.4 in [18, p. 68] there exist $\epsilon_1 > 0$ and $r_1 > 0$ such that all orbits of system (2.3) in $\{(\theta, r): 0 \leqslant \theta < \epsilon_1, \ 0 < r < r_1\}$ tend to $(0, 0)$ along $\theta_1 = 0$ as $t \to -\infty$. $\quad\square$

Theorem 2.2. *Suppose* $p - a - 1 = 0$ *and* $0 < \sigma \leqslant 1$. *Then there exist* $\epsilon_2 > 0$ *and* $r_2 > 0$ *such that all orbits of system* (2.3) *in*

$$\left\{(\theta, r): 0 \leqslant \theta < \epsilon_2, \ 0 < r < r_2\right\}$$

tend to $(0, 0)$ *along* $\theta_1 = 0$ *as* $t \to -\infty$.

Proof. When $p - a - 1 = 0$ and $0 < \sigma \leqslant 1$, $\theta_1 = 0$ is a root of (2.5) with multiplicity 2. Since $G'(0) = 0$ and $G''(0) = -2\sigma(a + c)$, we have $G''(0)H(0) \neq 0$. It follows from Theorem 3.8 in [18, p. 75] that there exist $\epsilon_2 > 0$ and $r_2 > 0$ such that all orbits of system (2.3) in

$$\left\{(\theta, r): 0 \leqslant \theta < \epsilon_2, \ 0 < r < r_2\right\}$$

tend to $(0, 0)$ along $\theta_1 = 0$ as $t \to -\infty$. $\quad\square$

If $p - a - 1 = 0$ and $\sigma = 0$, we have $G(\theta) \equiv 0$. This is a singular case. By performing the Briot–Bouquet transformation $y = ux$ to transform (2.3), we obtain

$$\begin{cases} \dfrac{dx}{dt} = x\left(a - u - hx(1 + u)^2\right), \\ \dfrac{du}{dt} = hxu(1 + u)^2. \end{cases} \tag{2.6}$$

In the (u, x)-plane system, (2.6) can be written as

$$\frac{dx}{du} = \frac{a - u - hx(1 + u)^2}{hu(1 + u)^2}. \tag{2.7}$$

Equation (2.7) has a general solution:

$$x = \frac{k}{u} - \frac{a + 1}{hu(1 + u)} - \frac{\ln(1 + u)}{hu},$$

where k is an arbitrary constant. Thus, the general solution of system (2.3) is

$$y = k - \frac{(a + 1)x}{h(x + y)} - \frac{1}{h}\ln\left(1 + \frac{y}{x}\right).$$

The topological structure of the orbits of system (2.2) in the interior of the first quadrant is sketched in Fig. 1, which consists of an elliptic sector and a parabolic sector.

We now consider the case of $p - a - 1 > 0$. In this case, Eq. (2.5) has a non-trivial characteristic direction: $\theta_2 = \arctan\frac{p - a - 1}{\sigma a + \sigma c}$.
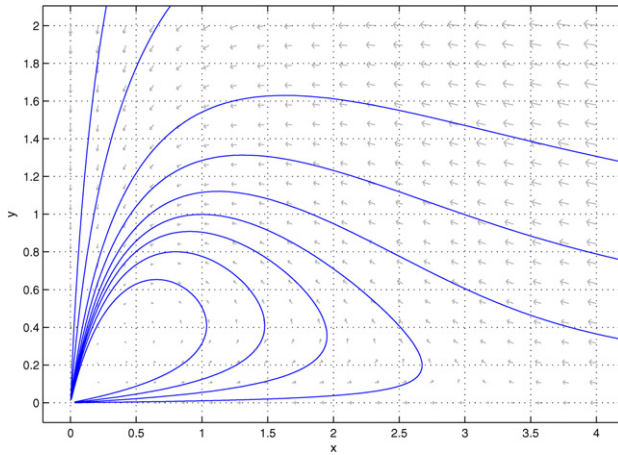
Fig. 1. Topological structure of the system (2.2) at $(0,0)$ when $p-a-1=0$ and $\sigma=0$, where $p=2, a=1, h=0.3$.

Theorem 2.3. *Assume* $p-a-1>0$. *Then*:

(a) *If* $\sigma(a+c)(p-1)<p-a-1$ *holds, there exist* $\epsilon_3>0$ *and* $r_3>0$ *such that all orbits of system* (2.3) *in*

$$\{(\theta,r):\ 0\leqslant|\theta-\theta_2|<\epsilon_3,\ 0<r<r_3\}$$

tend to $(0,0)$ *along* $\theta_2=\arctan\frac{p-a-1}{\sigma(a+c)}$ *as* $t\to+\infty$.

(b) *If* $\sigma(a+c)(p-1)>p-a-1$ *holds, there exist* $\epsilon_4>0$ *and* $r_4>0$ *such that there exists a unique orbit of system* (2.3) *in*

$$\{(\theta,r):\ 0\leqslant|\theta-\theta_2|<\epsilon_4,\ 0<r<r_4\}$$

which tends to $(0,0)$ *along* $\theta_2=\arctan\frac{p-a-1}{\sigma(a+c)}$ *as* $t\to-\infty$.

Proof. We apply the Briot–Bouquet transformation

$$x=x,\qquad y=ux,\qquad d\tau=x\,dt$$

to transform (2.3) into

$$\begin{cases}
\dfrac{dx}{dt}=-x\big[-a+hx-(\sigma a+\sigma c+a-p)u+h(\sigma+2)xu\\
\qquad\quad+h(2\sigma+1)xu^2+\sigma hxu^3\big],\\
\dfrac{du}{dt}=u(1+u)\big[p-a-1+hx-\sigma(a+c)u+h(\sigma+1)xu+\sigma hxu^2\big],
\end{cases}\tag{2.8}$$

where t is used to represent τ. On the u-axis system (2.8) has two equilibria $(0,0)$ and $(0,z_0)$ where $z_0=\frac{p-a-1}{\sigma(a+c)}$. Obviously, $(0,0)$ is an unstable node. To analyze equilibrium $(0,z_0)$, we make the change of variables $x_1=x, x_2=u-z_0$ to transform (2.8) to

$$\begin{cases}
\dfrac{dx_1}{dt}=g_1(z_0)x_1+o\big(\|(x_1,x_2)\|\big),\\
\dfrac{dx_2}{dt}=hz_0(z_0+1)^2(\sigma z_0+1)x_1+g_2(z_0)x_2+o\big(\|(x_1,x_2)\|\big),
\end{cases}\tag{2.9}$$

where

$$g_1(z_0) = \sigma(a+c)z_0^2 + (\sigma a + \sigma c + a - p)z_0 + a$$
$$= \sigma(a+c)(p-1) - p + a + 1,$$
$$g_2(z_0) = -3\sigma(a+c)z_0^2 - 2(\sigma a + \sigma c + a + 1 - p)z_0 + p - a - 1$$
$$= -(p-a-1)(\sigma a + \sigma c + p - a - 1).$$

If $p - a - 1 > 0$ and $\sigma(a+c)(p-1) < p - a - 1$, then $g_1(z_0) < 0$ and $g_2(z_0) < 0$. The equilibrium $(0,0)$ of system (2.9) is a stable node. Thus, $(0, z_0)$ of system (2.8) is a stable node in the interior of the first quadrant. We use the inverse Briot–Bouquet transformation to obtain the result: there exist $\epsilon_3 > 0$ and $r_3 > 0$ such that all orbits of system (2.3) in

$$\left\{ (\theta, r): 0 \leqslant |\theta - \theta_2| < \epsilon_3, \ 0 < r < r_3 \right\}$$

tend to $(0,0)$ along $\theta_2 = \arctan \frac{p-a-1}{\sigma(a+c)}$ as $t \to +\infty$.

If $p - a - 1 > 0$ and $\sigma(a+c)(p-1) > p - a - 1$, then $g_1(z_0) > 0$, $g_2(z_0) < 0$. Equilibrium $(0,0)$ of system (2.9) is a saddle. Therefore, the equilibrium $(0, z_0)$ of system (2.8) is a saddle, and there exists a unique separatrix of this equilibrium in the interior of the first quadrant of system (2.8), which tends to $(0, z_0)$ as $t \to -\infty$. By the inverse Briot–Bouquet transformation, there exist $\epsilon_4 > 0$ and $r_4 > 0$ such that there exists a unique orbit of system (2.3) in

$$\left\{ (\theta, r): 0 \leqslant |\theta - \theta_2| < \epsilon_4, \ 0 < r < r_4 \right\}$$

which tends to $(0,0)$ along $\theta_2 = \arctan \frac{p-a-1}{\sigma(a+c)}$ as $t \to -\infty$. $\square$

When $p - a - 1 < 0$, $\theta_1 = 0$ is a simple root of (2.5). By similar discussions to those in the proof of Theorem 2.1, we have

Theorem 2.4. *Suppose $p - a - 1 < 0$. Then there exist $\epsilon_5 > 0$ and $r_5 > 0$ such that a unique orbit of system* (2.3) *in*

$$\left\{ (\theta, r): 0 \leqslant \theta < \epsilon_5, \ 0 < r < r_5 \right\}$$

tends to $(0,0)$ along $\theta_1 = 0$ as $t \to -\infty$.

Let us now consider the case where $0 < \alpha \leqslant 1$. We make a time scale change $dt = (x+y)\,d\eta$ for system (2.1) such that system (2.1) is equivalent to the following system:

$$\begin{cases} \dfrac{dx}{dt} = X_2(x,y) + \Phi(x,y), \\ \dfrac{dy}{dt} = Y_2(x,y) + \Psi(x,y), \end{cases}$$

where t is used to represent η for simplicity, and

$$X_2(x,y) = ax^2 + (\sigma a + \sigma c + a)xy + \sigma(a+c)y^2,$$
$$\Phi(x,y) = -hx^3 - h(\sigma+2)x^2y - h(2\sigma+1)xy^2 - \sigma h y^3 - p(x+y)^\alpha xy,$$
$$Y_2(x,y) = -xy + y^2,$$
$$\Psi(x,y) = p(x+y)^\alpha xy.$$

We use the change of variables $x = r\cos\theta$, $y = r\sin\theta$ to obtain

$$\begin{cases} \dfrac{dr}{dt} = r^2\big(H(\theta) + o(1)\big), \\ \dfrac{d\theta}{dt} = r\big(G(\theta) + o(1)\big), \end{cases}$$

where

$$\begin{aligned} H(\theta) &= Y_2\sin\theta + X_2\cos\theta \\ &= (\cos\theta + \sin\theta)\big[a\cos^2\theta + \sigma(a+c)\sin\theta\cos\theta - \sin^2\theta\big], \\ G(\theta) &= Y_2\cos\theta - X_2\sin\theta \\ &= -\sin\theta(\cos\theta + \sin\theta)\big[(a+1)\cos\theta + \sigma(a+c)\sin\theta\big]. \end{aligned}$$

Then the characteristic equation of system (2.1) takes form

$$G(\theta) = -\sin\theta(\cos\theta + \sin\theta)\big[\sigma(a+c)\sin\theta + (a+1)\cos\theta\big] = 0.$$

Since $\sigma(a+c)$ and $a+1$ are always greater than zero, there is no characteristic direction in $(0, \pi/2)$. By similar discussions as above, we have the following theorem:

Theorem 2.5. *There are $\epsilon_6 > 0$ and $r_6 > 0$ such that (2.1) admits a unique orbit in $\{(\theta, r): 0 \leqslant \theta < \epsilon_6,\ 0 < r < r_6\}$ that tends to $(0, 0)$ along $\theta = 0$ as $t \to -\infty$.*

We have shown, in Theorems 2.1–2.4, that parasites can drive the host to extinction only by the standard incidence. In other situations the host population and parasites cannot die out together because $(0, 0)$ is a repeller. Computer simulations are given to show that parasites and the host population die out together when $\alpha = 0$ in Fig. 2 and parasites reduce only the host density when $\alpha \neq 0$ in Fig. 3. In addition, it is easy to see that the equilibrium $(a/h, 0)$ is a saddle, and the positive x-axis is divided by the point $(a/h, 0)$ into two parts. They are two separatrices of the equilibrium and both of them asymptotically approach the equilibrium as $t \to +\infty$. There also exists a unique separatrix in the closed first quadrant which tends to $(a/h, 0)$.
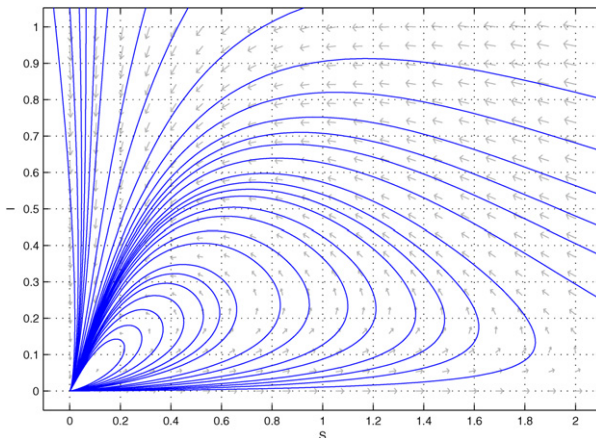

Fig. 2. Topological structure of the system (1.2) at $(0, 0)$ when $\alpha = 0$, $r = 0.5$, $d = 0.4$, $\epsilon = 0.5$, $K = 2$, $\sigma = 0.1$, $\beta = 1.6$.
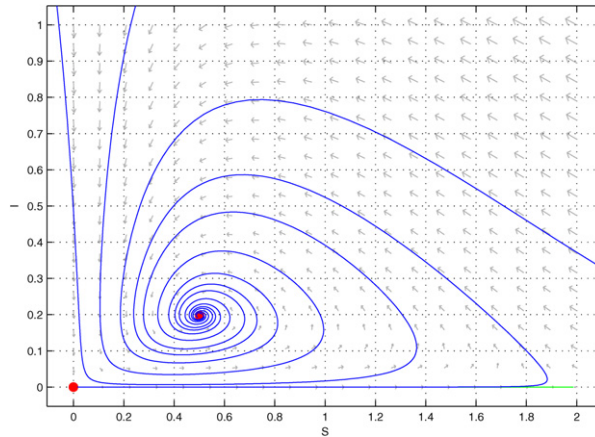
Fig. 3. Topological structure of the system (1.2) at $(0, 0)$ when $\alpha = 0.5$ with $r = 0.5$, $d = 0.4$, $\epsilon = 0.5$, $K = 2$, $\sigma = 0.1$, $\beta = 1.5$.

3. Existence and stability of positive equilibrium

We now consider positive equilibria of (2.1). Roughly speaking, the existence of these equilibria is necessary for the coexistence of the host population and parasites. First, we perform a topological transformation to (3.1) so that positive equilibria can be easily found. Set $u = x + y$, $v = y/(x + y)$. Substituting them into (2.1) and then replacing u by x, v by y, for the simplicity of notations, we obtain

$$\begin{cases} \dfrac{dx}{dt} = x\big[-hx + h(1 - \sigma)xy + (\sigma a + \sigma c - a - 1)y + a\big], \\ \dfrac{dy}{dt} = -y\big[-px^\alpha + px^\alpha y - hx + h(1 - \sigma)xy + (\sigma a + \sigma c - a - 1)y + a + 1\big]. \end{cases} \tag{3.1}$$

Evidently, we should consider this system in the region

$$D = \big\{(x, y): 0 < x < a/h, \ 0 < y < 1\big\}.$$

Setting the right-hand side of system (3.1) to zero, we obtain

$$-hx + h(1 - \sigma)xy + (\sigma a + \sigma c - a - 1)y + a = 0, \tag{3.2}$$
$$-px^\alpha + px^\alpha y - hx + h(1 - \sigma)xy + (\sigma a + \sigma c - a - 1)y + a + 1 = 0. \tag{3.3}$$

From (3.2) we obtain

$$x = \frac{(\sigma a + \sigma c - a - 1)y + a}{h(\sigma - 1)y + h}. \tag{3.4}$$

Substituting (3.2) into Eq. (3.3), we obtain

$$-px^\alpha + px^\alpha y + 1 = 0. \tag{3.5}$$

From (3.4) we see that $0 < y < \frac{-a}{\sigma a + \sigma c - a - 1}$ to have a positive x. If $\sigma a + \sigma c - 1 < 0$, we find the positive equilibrium of (3.1) in $0 < y < \frac{-a}{\sigma a + \sigma c - a - 1} < 1$. If $\sigma a + \sigma c - 1 > 0$, it suffices to consider $0 < y < 1$ because $\frac{-a}{\sigma a + \sigma c - a - 1} > 1$.

In the following, we consider two cases according to α.

(1) $\alpha = 0$. Then it is easy to see $y = \frac{p-1}{p}$. Assume $\sigma a + \sigma c - 1 < 0$. If

$$1 < p < \frac{\sigma a + \sigma c - a - 1}{\sigma a + \sigma c - 1},$$

it follows from (3.4) and (3.5) that system (3.1) has a unique positive equilibrium (x^*, y^*) where

$$x^* = \frac{(\sigma a + \sigma c - a - 1)(p - 1) + ap}{h(\sigma - 1)(p - 1) + ph}, \qquad y^* = \frac{p - 1}{p}. \tag{3.6}$$

Similarly, if $\sigma a + \sigma c - 1 > 0$ and $p > 1$, system (3.1) has a unique positive equilibrium (x^*, y^*) defined in (3.6).

(2) $\alpha \neq 0$. Then we solve (3.5) to obtain

$$x = \left(\frac{1}{p(1 - y)}\right)^{\frac{1}{\alpha}}.$$

By (3.4) we have

$$\left(\frac{1}{p(1 - y)}\right)^{\frac{1}{\alpha}} = \frac{(\sigma a + \sigma c - a - 1)y + a}{h(\sigma - 1)y + h}. \tag{3.7}$$

If $u = 1 - y$, it leads to

$$p^{\frac{1}{\alpha}} u^{\frac{1}{\alpha}} = \frac{h(1 - \sigma)u + h\sigma}{-(\sigma a + \sigma c - a - 1)u + \sigma a + \sigma c - 1}.$$

Define

$$f(u) = p^{\frac{1}{\alpha}} u^{\frac{1}{\alpha}},$$
$$g(u) = \frac{h(1 - \sigma)u + h\sigma}{-(\sigma a + \sigma c - a - 1)u + \sigma a + \sigma c - 1}.$$

Then the existence of positive equilibria of system (3.1) is changed into the existence of intersection points of $f(u)$ with $g(u)$ in the given region. Evidently, $f(u)$ is an increasing function. By calculations, we obtain

$$g'(u) = \frac{h(\sigma c - 1)}{(-u - au + u\sigma a + u\sigma c - \sigma a - \sigma c + 1)^2} < 0,$$

which means that $g(u)$ is a decreasing function.

When $\sigma a + \sigma c - 1 < 0$, since a feasible positive equilibrium satisfies

$$0 < y < \frac{-a}{\sigma a + \sigma c - a - 1} < 1,$$

we consider an intersection point of $f(u)$ with $g(u)$ in the interval:

$$u_0 := \frac{\sigma a + \sigma c - 1}{\sigma a + \sigma c - a - 1} < u < 1. \tag{3.8}$$

Note that

$$\lim_{u \to u_0 + 0} g(u) = +\infty.$$

If $g(1) < f(1)$, i.e., $\frac{h}{a} < p^{\frac{1}{\alpha}}$, it is easy to see that there is a unique intersection point of $f(u)$ with $g(u)$ in $(u_0, 1)$. If $g(1) > f(1)$, i.e., $\frac{h}{a} > p^{\frac{1}{\alpha}}$, there is no intersection point of $f(u)$ with $g(u)$ in $(u_0, 1)$.

When $\sigma a + \sigma c - 1 > 0$, we consider an intersection point of $f(u)$ with $g(u)$ in $0 < u < 1$. Note that

$$g(0) = \frac{\sigma h}{\sigma a + \sigma c - 1} > f(0) = 0.$$

If $g(1) < f(1)$, i.e., $\frac{h}{a} < p^{\frac{1}{\alpha}}$, there is a unique intersection point of $f(u)$ with $g(u)$ in $(0, 1)$. If $g(1) > f(1)$, i.e., $\frac{h}{a} > p^{\frac{1}{\alpha}}$, there is no intersection point of $f(u)$ with $g(u)$ in $(0, 1)$.

Note that $0 < y < 1$ implies

$$\frac{(\sigma a + \sigma c - a - 1)y + a}{h(\sigma - 1)y + h} = \frac{a}{h} + \frac{(\sigma c - 1)y}{h(\sigma - 1)y + h} < \frac{a}{h}.$$

Therefore, if y is a solution of (3.7) in $(0, 1)$, $x < a/h$ is automatically satisfied.

Summarizing above discussions, we have the following theorem:

Theorem 3.1. *For system* (3.1)*, the following statements are true.*

(a) *Assume $\alpha = 0$. Then system* (3.1) *has a positive equilibrium if one of the following conditions holds*:
    (1) *$\sigma a + \sigma c - 1 > 0$ and $p > 1$,*
    (2) *$\sigma a + \sigma c - 1 < 0$ and $1 < p < \frac{\sigma a + \sigma c - a - 1}{\sigma a + \sigma c - 1}$.*
(b) *Suppose $\alpha \neq 0$. Then we have*
    (i) *if $\frac{h}{a} < p^{\frac{1}{\alpha}}$, then system* (3.1) *has a positive equilibrium,*
    (ii) *if $\frac{h}{a} > p^{\frac{1}{\alpha}}$, then system* (3.1) *has no positive equilibrium.*

Now we consider the stability of the positive equilibrium. The Jacobian matrix at a positive equilibrium (x, y) is

$$J = \begin{pmatrix} -(\sigma a + \sigma c - a - 1)y - a & \frac{x}{y}(hx - a) \\ \frac{y}{x}(\alpha + a + (\sigma a + \sigma c - a - 1)y) & -px^{\alpha}y - hx + a \end{pmatrix}.$$

Its characteristic equation is

$$\lambda^2 + \left(px^{\alpha}y + hx - a + (\sigma a + \sigma c - a - 1)y + a \right)\lambda$$
$$+ \left((\sigma a + \sigma c - a - 1)y + a \right)\frac{y}{1 - y} - \frac{(\sigma c - 1)\alpha y}{(\sigma - 1)y + 1} = 0.$$

Since $1 - y < (\sigma - 1)y + 1$, we have

$$\det(J) = \left[(\sigma a + \sigma c - a - 1)y + a \right]\frac{y}{1 - y} - \frac{(\sigma c - 1)\alpha y}{(\sigma - 1)y + 1}$$
$$> \frac{\left[(\sigma a + \sigma c - a - 1)y + a \right]y - (\sigma c - 1)\alpha y}{(\sigma - 1)y + 1}.$$

Since a positive equilibrium (x, y) satisfies

$$0 < y < \frac{-a}{\sigma a + \sigma c - a - 1} < \frac{(\sigma c - 1)\alpha - a}{\sigma a + \sigma c - a - 1},$$

it is easy to see $\det(J) > 0$. In addition,

$$\text{tr } J = -px^\alpha y - hx - (\sigma a + \sigma c - a - 1)y.$$

Using (3.2) and (3.5), we have

$$
\begin{aligned}
\text{tr } J &= -\frac{y}{1-y} - \frac{(\sigma c - 1)y}{(\sigma - 1)y + 1} - (\sigma a + \sigma c - a - 1)y - a \\
&< -\frac{y}{1-y} - \frac{(\sigma c - 1)y}{(\sigma - 1)y + 1} \\
&< \frac{-\sigma c y}{1 + (\sigma - 1)y} < 0.
\end{aligned}
$$

Therefore, we can state the following theorem.

Theorem 3.2. *The unique interior equilibrium* (x^*, y^*), *whenever it exists, is locally asymptotically stable.*

In order to consider its global stability, we now return to the original system (2.1).

Theorem 3.3. *If system* (2.1) *has a unique interior equilibrium* (x_1^*, y_1^*), *then it is globally stable.*

Proof. It suffices to exclude the existence of a limit cycle in (2.1). Take a Dulac function $D = \frac{1}{xy}$ and denote the right-hand sides of (2.1) by P and Q, respectively. Then we have

$$
\begin{aligned}
\frac{\partial (DP)}{\partial x} + \frac{\partial (DQ)}{\partial y} &= -\frac{\sigma(a+c)}{x^2} - \frac{h}{y} + \frac{h\sigma y}{x^2} \\
&< -\frac{\sigma(a+c)}{x^2} - \frac{h}{y} + \frac{\sigma a}{x^2} \\
&= -\frac{\sigma c}{x^2} - \frac{h}{y} < 0.
\end{aligned}
$$

By the Bendixson–Dulac Theorem, there is no limit cycle in (2.1). Consequently, the positive equilibrium is globally stable. □

Remark 3.1. The global stability of the positive equilibrium is completely proved when $0 \leqslant \alpha \leqslant 1$. This extends the work of [9] where $\alpha = 0$ and the work of [7] where $\alpha = 1$.

4. Discussion

Epidemic models have been proposed and studied in many ways to understand mechanisms of disease transmissions (see, for example, [3,8,10,12,13,15,16] and the references cited therein). Ebert et al. [7] proposed a deterministic model with the bilinear incidence and found that parasites reduce the fecundity and survival of its host, which in turn is regulated both by density-dependent birth and by the parasite-induced mortality. They used a stochastic version of the model to simulate extinction probabilities. Hwang and Kuang [9] found that it is the deterministic model with the standard incidence that can exhibit the observed parasite-induced host extinction.

In the paper, we considered the model with a more general incidence $\beta N^\alpha \frac{S}{N} I$. This incidence mimics continuous transitions from the bilinear incidence $\beta N \frac{S}{N} I$ to the standard incidence $\beta \frac{S}{N} I$. By the qualitative theory of differential equations [18], we find that host may be extinct in some

conditions only for the standard incidence, i.e., $\alpha = 0$. If $0 < \alpha \leqslant 1$, parasites are shown only to reduce host density. Increasing of parasite-induced host mortality rate results in a greater degree of host population depression until the rate of loss of infected hosts begins to have a detrimental effect on the efficiency of disease transmission. When the level of pathogenicity is very high, infected hosts die before effective transmission is achieved and the disease is thus unable to persist within the host population. In brief, highly pathogenic organisms are likely to cause their own extinction but not that of their host. The application is to select highly pathogenic organisms for the biological control of pest species. Such pathogens may cause high initial mortality within the pest population in a manner analogous to a single application of a chemical pesticide [2]. Furthermore, we have obtained conditions for the existence of a positive equilibrium. Meanwhile, we have shown that a positive equilibrium, whenever it exists, is globally stable using the Bendixson–Dulac Theorem.

Acknowledgments

References

[1] R.M. May, R.M. Anderson, Population biology of infectious diseases: Part II, Nature 280 (1979) 455–461.
[2] R.M. Anderson, R.M. May, Population biology of infectious diseases: Part I, Nature 280 (1979) 361–367.
[3] F. Brauer, C. Castillo-Chavez, Mathematical Models in Population Biology and Epidemics, Springer-Verlag, Berlin, 2001.
[4] M.C.M. De Jong, O. Diekmann, J.A.P. Heesterbeek, How does transmission depend on population size?, in: D. Mollison (Ed.), Human Infectious Diseases, Epidemic Models, Cambridge Univ. Press, Cambridge, 1995, pp. 84–94.
[5] B.T. Grenfell, A.P. Dobson (Eds.), Ecology of Disease in Natural Populations, Cambridge Univ. Press, Cambridge, 1995.
[6] H. McCallum, Modelling wildlife–parasite interactions to help plan and interpret field studies, Wildlife Research 22 (1995) 21–29.
[7] D. Ebert, M. Lipsitch, K.L. Mangin, The effect of parasites on host population density and extinction: Experimental epidemiology with Daphnia and six microparasites, American Naturalist 156 (2000) 459–477.
[8] H.W. Hethcote, The mathematics of infectious diseases, SIAM Rev. 42 (2000) 599–653.
[9] T.W. Hwang, Y. Kuang, Deterministic extinction effect of parasites on host populations, J. Math. Biol. 46 (2003) 17–30.
[10] S. Ruan, Wendi Wang, S. Levin, The effect of global travel on the spread of SARS, Math. Biosci. Eng. 3 (2006) 205–218.
[11] H.R. Thieme, Stability change of the endemic equilibrium in age-structured models for the spread of $S \to I \to R$ type infectious diseases, in: Differential Equations Models in Biology, Epidemiology and Ecology, Claremont, CA, 1990, in: Lecture Notes in Biomath., vol. 92, Springer, Berlin, 1991, pp. 139–158.
[12] P. van den Driessche, James Watmough, Reproduction numbers and sub-threshold endemic equilibria for compartmental models of disease transmission, Math. Biosci. 180 (2002) 29–48.
[13] W. Wang, G. Mulone, Threshold of disease transmission on a patch environment, J. Math. Anal. Appl. 285 (2003) 321–335.
[14] W. Wang, Y. Li, H.W. Hethcote, Bifurcations in a host-parasite model with nonlinear incidence, Internat. J. Bifur. Chaos Appl. Sci. Engrg., in press.
[15] W. Wang, Xiao-Qiang Zhao, An age-structured epidemic model in a patchy environment, SIAM J. Appl. Math. 65 (2005) 1597–1614.
[16] W. Wang, Xiao-Qiang Zhao, An epidemic model with population dispersal and infection period, SIAM J. Appl. Math. 66 (2006) 1454–1472.
[17] D. Xiao, S. Ruan, Global dynamics of a ratio-dependent predator–prey system, J. Math. Biol. 43 (2001) 268–290.
[18] Z. Zhang, T. Ding, W. Huang, Z. Dong, Qualitative Theory of Differential Equations, Transl. Math. Monogr., vol. 101, Amer. Math. Soc., Providence, 1991.