

GLOBAL ANALYSIS OF A SIMPLE PARASITE-HOST MODEL WITH HOMOCLINIC ORBITS

JIANQUAN LI

Faculty of Science, Air Force Engineering University
Xi'an 710051, China

YANNI XIAO

Department of Applied Mathematics
Xi'an Jiaotong University
Xi'an 710049, China

YALI YANG

Faculty of Science, Air Force Engineering University
Xi'an 710051, China
and College of Mathematics and Information Sciences
Shaanxi Normal University
Xi'an 710062, China

(Communicated by Yang Kuang)

ABSTRACT. In this paper, a simple parasite-host model proposed by Ebert et al.(2000) is reconsidered. The basic epidemiological reproduction number of parasite infection (R_0) and the basic demographic reproduction number of infected hosts (R_1) are given. The global dynamics of the model is completely investigated, and the existence of heteroclinic and homoclinic orbits is theoretically proved, which implies that the outbreak of parasite infection may happen. The thresholds determining the host extinction in the presence of parasite infection and variation in the equilibrium level of the infected hosts with R_0 are found. The effects of R_0 and R_1 on dynamics of the model are considered and we show that the equilibrium level of the infected host may not be monotone with respect to R_0 . In particular, it is found that full loss of fecundity of infected hosts may lead to appearance of the singular case.

1. Introduction. Parasites can reduce host density and induce host population extinction in some cases. In order to understand how six microparasites regulate *Daphnia* populations and drive the populations to extinction, Ebert et al.[1] formulated the following epidemiological microparasite model

$$\begin{cases} \frac{dx}{dt} = a(x + \theta y) \left(1 - \frac{x+y}{K}\right) - dx - \beta xy, \\ \frac{dy}{dt} = \beta xy - (d + \alpha)y, \end{cases} \quad (1)$$

2000 *Mathematics Subject Classification.* 92D30, 34C37, 37G35.

Key words and phrases. Parasite-host model, global dynamics, homoclinic orbit, reproduction number.

The first author is supported by the China NSF Grant (No.11071256). The second author is supported in part by the China NSF Grant (No.11171268), the National Megaproject of Science Research of China (No.2012ZX10001-001), and the Fundamental Research Funds for the Central Universities (No. 08143042). The third author is supported by the Nature Science Foundation of Shaanxi Province of China (No. 2012JQ1019).

where $x(t)$ and $y(t)$ represent the densities of uninfected (susceptible) and infected (infective) hosts at time t , respectively; a is the maximum per capita birth rate of uninfected hosts; $\theta(0 \leq \theta \leq 1)$ is the relative fecundity of an infected host; K is the carrying capacity of the environment for the host population; d is the parasite-independent host background mortality; β is the constant infection rate, and α is the parasite-induced excess death rate.

In model (1), the microparasite transmission is assumed via a mass action process, the fecundity of uninfected host is density-dependent, and the fecundity of infected host may be reduced due to being infected compared with that of uninfected host. Here, $\theta = 0$ means that infected hosts completely lose fecundity; $\theta = 1$ means that the fecundity of infected hosts is not affected by parasite infection; $0 < \theta < 1$ means that the fecundity of infected hosts is reduced, but they still have certain fecundity. For model (1), there is always equilibrium $O(0, 0)$, which is a saddle when $a > d$. This implies that extinction of host is impossible when $a > d$, that is, host always persists when $a > d$. But, in [1], the simulation for the stochastic model indicates that extinction of host likely occurs in certain parameter regions.

By carefully examining the infection term βxy , Hwang and Kuang [2] replaced the mass action incidence function βxy with a standard incidence function $\beta xy/(x+y)$, and obtained the following model

$$\begin{cases} \frac{dx}{dt} = a(x + \theta y) \left(1 - \frac{x+y}{K}\right) - dx - \frac{\beta xy}{x+y}, \\ \frac{dy}{dt} = \frac{\beta xy}{x+y} - (d + \alpha)y, \end{cases} \quad (2)$$

where β represents the maximum number of infections that an infected host can cause per unit time. Subsequently, based on model (2), some higher dimensional epidemiological models were presented and analyzed[3, 4, 5].

Since model (2) is not differentiable at the origin, Hwang and Kuang [2] initially transformed model (2) into the form of a Gause-type predator-prey system by making the change of variables $(x, y) \rightarrow (u, y)$ with $u = x/y$, and then, by investigating the transformed system, they showed that the transformed system can exhibit the parasite induced host extinction. This theoretically complements the findings in [1]. However, Hwang and Kuang [2] did not consider dynamical behaviors of model (2) directly, some complicated and interesting dynamics of model (2) were missed.

In [6], Berezovsky et al. incorporated the emigration of uninfected hosts into model (2), and then obtained the following model

$$\begin{cases} \frac{dx}{dt} = a(x + \theta y) \left(1 - \frac{x+y}{K}\right) - (d + m)x - \frac{\beta xy}{x+y}, \\ \frac{dy}{dt} = \frac{\beta xy}{x+y} - (d + \alpha)y, \end{cases} \quad (3)$$

where m is the per capita emigration rate of uninfected hosts. They mathematically studied it as an epidemiological model, and found a family of homoclinic orbits by investigating the local dynamics of the model near the origin. But the effect of the related parameters on dynamical behaviors of the model is not discussed completely. In particular, the case $\theta = 0$ is not considered. Note that model (2) and model (3) are dynamically equivalent.

In this paper, we reconsider model (2) by rescaling it and completely analyzing the global dynamics of the rescaled model. The initial objective is to fully understand the asymptotic behavior of model (2) and theoretically prove the existence of its heteroclinic and homoclinic orbits. In particular, we investigate the effect of the basic epidemiological reproduction number of parasite (R_0) and the basic demographic reproduction number of infected hosts (R_1) on the survival of hosts,

and analyze the change of the level of infected hosts with the basic reproduction number of parasite infection (R_0).

The organization of this paper is as follows. In the next section, we initially rescale model (2) and then introduce the primary results on the rescaled system. In Sections 3 and 4, we theoretically analyze the rescaled system with cases $0 < \theta \leq 1$ and $\theta = 0$, respectively, and prove the existence of heteroclinic and homoclinic orbits of the rescaled system. Dynamic behaviors of system (2) are demonstrated in Section 5, where the effect of R_0 and R_1 on dynamics of the model is investigated. The effect of R_0 on the level of infected hosts is also considered in Section 6. We conclude with a discussion of the results in Section 7.

2. Rescaling and primary results. Rescaling model (2) by letting

$$\bar{x} = x/K, \quad \bar{y} = y/K, \quad \text{and} \quad \bar{t} = at,$$

and removing the bars leads to the rescaled system

$$\begin{cases} \frac{dx}{dt} = (x + \theta y)[1 - (x + y)] - \delta x - \frac{sx y}{x + y} =: P(x, y), \\ \frac{dy}{dt} = \frac{sx y}{x + y} - (\delta + r)y =: Q(x, y), \end{cases} \tag{4}$$

where

$$s = \beta/a, \delta = d/a, r = \alpha/a. \tag{5}$$

It follows from (4) that

$$\frac{d(x + y)}{dt} = (x + \theta y)[1 - (x + y)] - \delta(x + y) - ry.$$

Since $0 \leq \theta \leq 1$, then

$$\frac{d(x + y)}{dt} \leq (1 - \delta)(x + y) \quad \text{for } x \geq 0 \text{ and } y \geq 0,$$

which gives that $\lim_{t \rightarrow +\infty} (x(t), y(t)) = (0, 0)$ for $\delta \geq 1$. So, in the rest of this paper, we shall assume $\delta < 1$, which implies that $a > d$ for (2). For convenience of discussion hereafter, we give the following results about (4).

Lemma 2.1. (i) *The x-axis is an invariant set of (4). And $\lim_{t \rightarrow +\infty} x(t) = 1 - \delta$ for the initial value $(x(0), 0)$ with $x(0) > 0$; $\lim_{t \rightarrow -\infty} x(t) = 0$ for the initial value $(x(0), 0)$ (where $0 < x(0) < 1 - \delta$).*

(ii) *The set $D_1 = \{(x, y) \in R_+^2 : x + y \leq 1 - \delta\}$ is always positively invariant to (4).*

(iii) *The set $D_2 = \{(x, y) \in R_+^2 : \theta y \geq (s - r - 1)x, x + y \leq 1 - \delta\}$ is positively invariant to (4) when $s > r + 1$ and $\theta \neq 0$.*

Proof. Lemma 2.1 (i) and (ii) can be proved easily, so we omit it. To prove (iii) we get from (4),

$$\begin{aligned} \frac{d}{dt} \left(\frac{y}{x} \right) &= \frac{y}{x^2} \{[(s - r - 1)x - \theta y] + (x + \theta y)(x + y)\} \\ &> \frac{y}{x} \left[(s - r - 1) - \frac{\theta y}{x} \right], \quad \text{for } x > 0, y > 0, \end{aligned}$$

then $\liminf_{t \rightarrow +\infty} y(t)/x(t) \geq (s - r - 1)/\theta$ as $s > r + 1$. Hence, the set $\{(x, y) \in R_+^2 : \theta y > (s - r - 1)x\}$ is positively invariant to (4) when $s > r + 1$. Therefore, according to Lemma 2.1(ii), the set $D_2 = \{(x, y) \in R_+^2 : \theta y \geq (s - r - 1)x, x + y \leq 1 - \delta\}$ is positively invariant to (4) when $s > r + 1$. \square

According to Lemma 2.1, we henceforth do our mathematical analysis on the set D_1 . For the case $s > r + 1$, the feasible region may be limited on the set $D_2(D_2 \subset D_1)$.

On the other hand, if we choose $B(x, y) = 1/(xy)$ as a Dulac function, it follows from (4) that

$$\frac{\partial(BP)}{\partial x} + \frac{\partial(BQ)}{\partial y} = -\frac{1}{y} - \frac{\theta(1-y)}{x^2} < 0, \text{ for } (x, y) \in \text{int}D_1.$$

Therefore, we have

Lemma 2.2. *In the interior of the set D_1 , there is no closed orbit to (4).*

3. Mathematical analysis for system (4) with $0 < \theta \leq 1$. In this section, we consider dynamical behaviors of the rescaled system (4) with $0 < \theta \leq 1$, that is, the infected hosts have certain fecundity.

3.1. The existence and stability of equilibria. It is easy to see that $E_0(1-\delta, 0)$ is always an equilibrium of system (4). Direct calculation shows that, when $s > \delta + r$ and $\theta(s - \delta - r) > (\delta + r)(s - r - 1)$, system (4) has a unique positive equilibrium $E^*(x^*, y^*)$, where

$$x^* = \frac{(\delta+r)[\theta(s-\delta-r)-(\delta+r)(s-r-1)]}{s[\theta s+(1-\theta)(\delta+r)]},$$

$$y^* = \frac{[s-(\delta+r)][\theta(s-\delta-r)-(\delta+r)(s-r-1)]}{s[\theta s+(1-\theta)(\delta+r)]}.$$

Here, E_0 represents that host has not been infected, E^* implies that host is infected chronically. About the local stability of E_0 and E^* , we have

Theorem 3.1. *The boundary equilibrium E_0 is locally asymptotically stable on the set D_1 if $s \leq \delta + r$, and unstable if $s > \delta + r$. The positive equilibrium E^* is locally asymptotically stable if $s > \delta + r$ and $\theta(s - \delta - r) > (\delta + r)(s - r - 1)$.*

Proof. From the Jacobian matrices of (4) at E_0 and E^* , it is easy to know that E_0 is locally asymptotically stable on the set D_1 for $s < \delta + r$, and unstable for $s > \delta + r$. And the positive equilibrium E^* is locally asymptotically stable if it is feasible.

When $s = \delta + r$, equilibrium E_0 is a higher order one. To discuss its locally stability on the set D_1 , we make the change of variables: $u = x - (1 - \delta)$, $v = y$, which moves E_0 in the xy -plane to the origin in the uv -plane, then (4) becomes

$$\begin{cases} \frac{du}{dt} = -(1-\delta)u + [(1+\theta)\delta - 1 - s]v - (u + \theta v)(u + v) + \frac{sv^2}{(1-\delta)+u+v}, \\ \frac{dv}{dt} = -\frac{sv^2}{(1-\delta)+u+v}. \end{cases} \tag{6}$$

Letting $w = (1 - \delta)u - [(1 + \theta)\delta - 1 - s]v$, system (6) yields

$$\begin{cases} \frac{dw}{dt} = -(1-\delta) \left\{ w + \frac{[w+(\theta\delta-s)v][w+(\delta+\theta-1-s)v]}{(1-\delta)^2} - \frac{(s-\theta\delta)sv^2}{(1-\delta)^2+w+(\theta\delta-s)v} \right\}, \\ \frac{dv}{dt} = -\frac{(1-\delta)sv^2}{(1-\delta)^2+w+(\theta\delta-s)v}. \end{cases} \tag{7}$$

It follows from $\frac{dw}{dt} = 0$ that

$$w + \frac{[w + (\theta\delta - s)v][w + (\delta + \theta - 1 - s)v]}{(1 - \delta)^2} + \frac{(s - \theta\delta)sv^2}{(1 - \delta)^2 + w + (\theta\delta - s)v} = 0. \tag{8}$$

Direct calculation shows that, for the implicit function $w = w(v)$ defined by (8), $\frac{dw}{dv}|_{(0,0)} = 0$, which implies $w = o(v)$. Substituting it into the second equation of

(7) gives $dv/dt = -sv^2/(1 - \delta) + o(v^2)$. Thus, according to Theorem 7.1 in [7], $s/(1 - \delta) > 0$ implies that E_0 is locally asymptotically stable on the set D_1 for $s = \delta + r$. \square

To consider the global stability of E_0 and E^* of (4) on the positively invariant set D_1 , we first need to discuss the dynamical behaviors of (4) near the origin in the first quadrant since it may be complex.

Lemma 3.2. (i) When $s \leq r + 1$, orbits of system (4) starting from near the origin in the interior of D_1 move away from the origin as t increases;

(ii) When $s > r + 1$ and $\theta(s - \delta - r) > (\delta + r)(s - r - 1)$, orbits of system (4) initiating from near the origin in the interior of D_2 move away from the origin as t increases.

Proof. Let $dt = (x + y)d\tau$ then (4) becomes

$$\begin{cases} \frac{dx}{d\tau} = \{(x + y)[(1 - \delta)x + \theta y] - sxy\} - (x + \theta y)(x + y)^2, \\ \frac{dy}{d\tau} = y[(s - \delta - r)x - (\delta + r)y]. \end{cases} \tag{9}$$

Using the polar coordinates $x = \rho \cos \varphi, y = \rho \sin \varphi$, (9) becomes

$$\begin{cases} \frac{d\rho}{d\tau} = \rho^2 H(\varphi) - \rho^3 \cos \varphi (\cos \varphi + \theta \sin \varphi) (\cos \varphi + \sin \varphi)^2, \\ \frac{d\theta}{d\tau} = \rho G(\varphi) + \rho^2 \sin \varphi (\cos \varphi + \theta \sin \varphi) (\cos \varphi + \sin \varphi)^2, \end{cases} \tag{10}$$

where

$$\begin{aligned} H(\varphi) &= \cos \varphi \{(\cos \varphi + \sin \varphi)[(1 - \delta) \cos \varphi + \theta \sin \varphi] - s \cos \varphi \sin \varphi\} \\ &\quad + \sin^2 \varphi [(s - \delta - r) \cos \varphi - (\delta + r) \sin \varphi]. \\ G(\varphi) &= \rho \sin \varphi (\cos \varphi + \sin \varphi) [(s - r - 1) \cos \varphi - \theta \sin \varphi]. \end{aligned} \tag{11}$$

(i) When $s \leq r + 1$, $G(\varphi) < 0$ for $0 < \varphi < \frac{\pi}{2}$. So system (9) has no characteristic direction in the first quadrant, which implies that all orbits of (4) starting from near the origin move in the clockwise direction. Since $dx/d\tau|_{y=0} > 0$ for $0 < x < 1 - \delta$, then, according to the dependence of continuity of solutions on the initial conditions, all the orbits of (4) starting from near the origin in the interior of D_1 move away from the origin as t increases.

(ii) When $s > r + 1$ and $\theta(s - \delta - r) > (\delta + r)(s - r - 1)$, for (x, y) sufficiently close to the origin, we have

$$\frac{dx}{dt} \Big|_{\theta y = (s-r-1)x} = \frac{x \{[\theta(s - \delta - r) - (\delta + r)(s - r - 1)] - (s - r)(x + y)\}}{s + \theta - r - 1} > 0,$$

and

$$\frac{dy}{dt} \Big|_{\theta y = (s-r-1)x} = \frac{y}{s + \theta - r - 1} [\theta(s - \delta - r) - (\delta + r)(s - r - 1)] > 0.$$

Thus, according to dependence relationship of solutions of (4) on the initial values, orbits of (4) initiating from near the line $\theta y = (s - r - 1)x$ sufficiently close to the origin move away from the origin. And, for points in the interior of D_2 , the inequality $(s - r - 1) \cos \varphi < \theta \sin \varphi$ always holds, which implies $G(\varphi) < 0$. Similar to the case $s \leq r + 1$, (9) has no characteristic direction in the interior of D_2 for this case. Therefore, when $s > r + 1$ and $\theta(s - \delta - r) > (\delta + r)(s - r - 1)$, orbits of system (4) starting from near the origin in the interior of D_2 move away from the origin as t increases. \square

According to Lemma 3.2, when $s \leq r + 1$ or $s > r + 1$ and $\theta(s - \delta - r) > (\delta + r)(s - r - 1)$, no orbit of (4) starting from the first quadrant approaches the origin as $t \rightarrow +\infty$.

Notice that when $\delta + r < s \leq r + 1$, the inequality $\theta(s - \delta - r) > (\delta + r)(s - r - 1)$ holds. So equilibrium E^* exists when $\delta + r < s \leq r + 1$. Therefore, according to Lemma 2.2, we have the following conclusion about the global stability of E_0 and E^* .

Theorem 3.3. *For system (4), when $s \leq \delta + r$, equilibrium E_0 is globally stable on the set D_1 ; when $s > \delta + r$ and $\theta(s - \delta - r) > (\delta + r)(s - r - 1)$, equilibrium E^* is globally stable in the interior of the set D_1 .*

3.2. Heteroclinic and homoclinic orbits. According to the results obtained in Section 3.1, the global dynamical behaviors of (4) have been understood clearly for the following cases:

$$s \leq \delta + r; \quad s > \delta + r \text{ and } \theta(s - \delta - r) > (\delta + r)(s - r - 1).$$

Notice that the inequality $\theta(s - \delta - r) > (\delta + r)(s - r - 1)$ always holds for $\delta + r < s \leq r + 1$, then, in the following, we consider dynamics of (4) in a case of $s > r + 1$ and $\theta(s - \delta - r) \leq (\delta + r)(s - r - 1)$.

We initially discuss the vertical isocline L of (4). Denote

$$g(x, y) := (1 - \delta)x^2 + \theta y^2 + (\theta + 1 - \delta - s)xy,$$

then, it follows from $dx/dt = 0$ that the vertical isocline L of (4) is defined by equation

$$g(x, y) = (x + \theta y)(x + y)^2. \quad (12)$$

Obviously,

$$\theta(s - \delta - r) \leq (\delta + r)(s - r - 1) \Leftrightarrow f(r) := r^2 - (s + \theta - \delta - 1)r + [\delta(1 - \theta) - s(\delta - \theta)] \leq 0.$$

Since $f(r)$ is a quadratic function of r , then $f(r) \leq 0$ implies that the discriminant of equation $f(r) = 0$ is positive, that is, $\Delta := (\theta + 1 - \delta - s)^2 - 4\theta(1 - \delta) \geq 0$.

Notice that the discriminant of equation $g(1, u) = 0$ of u is also Δ . On the other hand, from $\theta(s - \delta - r) \leq (\delta + r)(s - r - 1)$ and $s - \delta - r > s - r - 1 > 0$, we easily have that $\theta < \delta + r$, i.e., $r > \theta - \delta$. So it follows from $s > r + 1$ that $s > \theta + 1 - \delta$, that is, $\theta + 1 - \delta - s < 0$. Thus, when $s > r + 1$ and $\theta(s - \delta - r) \leq (\delta + r)(s - r - 1)$, equation $g(1, u) = 0$ has two distinct positive roots,

$$k_{\pm} = \frac{(s + \delta - \theta - 1) \pm \sqrt{\Delta}}{2\theta}. \quad (13)$$

Therefore, for this case, $g(x, y)$ can be rewritten as $g(x, y) = \theta(y - k_+x)(y - k_-x)$. Furthermore, (12) can be rewritten as

$$(y - k_-x)(y - k_+x) = \left(y + \frac{1}{\theta}x\right)(y + x)^2. \quad (14)$$

By applying Lemma 7.1 in Appendix to (14), we have the following Lemma with respect to the vertical isocline L of system (4).

Lemma 3.4. *When $s > r + 1$ and $\theta(s - \delta - r) \leq (\delta + r)(s - r - 1)$, the vertical isocline L of (4) defined by (12) (or (14)) consists of two branches, which have the following properties:*

- (i) The two branches intersect with two coordinate axes at points $(1 - \delta, 0)$ and $(0, 1)$, respectively.
- (ii) The two branches are located in the regions $D_3 = \{(x, y) \in R_+^2 : y < k_-x\}$ and $D_4 = \{(x, y) \in R_+^2 : y > k_+x\}$, respectively.
- (iii) One of the two branches in the region D_3 is concave down, while the other in the region D_4 is concave left.

According to Lemma 3.4, the two branches of the vertical isocline L of (4) are shown in Figure 1.

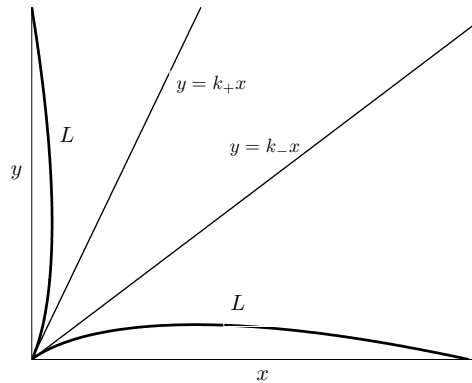


FIGURE 1. The vertical isocline L of (4) as $s > r + 1$ and $\theta(s - \delta - r) \leq (\delta + r)(s - r - 1)$.

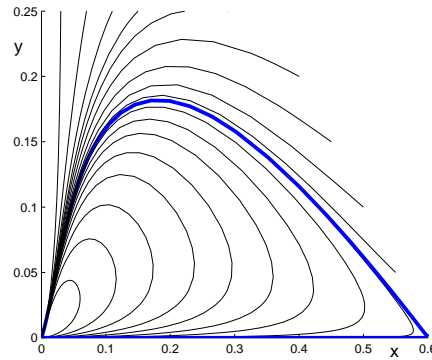


FIGURE 2. The heteroclinic and homoclinic orbits of (4). The thick closed curve is a heteroclinic closed orbit, the thin curves surrounded by the closed curve are all homoclinic orbits. Here, $\theta = 0.2, \delta = 0.4, r = 0.5$, and $s = 1.8$. All the orbits of (4) starting from the first quadrant approach the origin along the direction $\varphi = \arctan 1.5$ as t tends to positive infinity.

Theorem 3.5. *When $s > r + 1$ and $\theta(s - \delta - r) \leq (\delta + r)(s - r - 1)$, for (4) we have the following results:*

- (i) *There is a heteroclinic closed orbit of (4) on the set D_1 ;*
- (ii) *There is a family of homoclinic orbits of (4), which are full of the domain surrounded by the heteroclinic closed orbit (Fig. 2);*
- (iii) *All the orbits of (4) starting from the first quadrant approach the origin along the direction $\varphi = \arctan(s - r - 1)/\theta$ as t tends to positive infinity.*

Proof. (i) We initially prove that there is a heteroclinic orbit L_1 of (4) in the interior of D_1 , where $\lim_{t \rightarrow +\infty}(x(t), y(t)) = (0, 0)$ and $\lim_{t \rightarrow -\infty}(x(t), y(t)) = (1 - \delta, 0)$ for $(x(t), y(t)) \in L_1$.

Since $s > r + 1$ implies $s > \delta + r$, it follows from the Jacobian matrix of (4) at E_0 that E_0 is a saddle. Hence, there is a saddle separatrix L_1 of E_0 in the first quadrant, whose slope at E_0 is

$$k_1 = \frac{(1 - \delta) + (s - \delta - r)}{(1 + \theta)\delta - 1 - s}. \quad (15)$$

It is easy to know that L_1 is an unstable manifold of E_0 , that is, $\lim_{t \rightarrow -\infty}(x(t), y(t)) = E_0$ for $(x(t), y(t)) \in L_1$.

By Lemma 3.4, the vertical isocline L of (4) passes through E_0 . And direct calculation shows that the tangential slope of L at E_0 is

$$k_2 = \frac{1 - \delta}{(1 + \theta)\delta - 1 - s}. \quad (16)$$

Using $\theta(s - \delta - r) \leq (\delta + r)(s - r - 1)$ yields

$$(1 + \theta)\delta - 1 - s \leq -\frac{T}{s - \delta - r},$$

where $T = (s - r - 1)^2 + (1 - \delta)[(\delta + 3 + r)(s - r - 1) + (2 + r - \delta)]$. Obviously, $T > 0$ for $s > r + 1$. So $(1 + \theta)\delta - 1 - s < 0$. Thus, it follows from (15) and (16) that $-1 < k_1 < k_2 < 0$, which implies that the separatrix L_1 near E_0 is located between the line $x + y = 1 - \delta$ and the vertical isocline L .

According to Lemma 2.1, when $s > r + 1$, the separatrix L_1 must pass through the line $y = (s - r - 1)x/\theta$ and enter the region D_2 in a finite time. Again, $s > r + 1$ and $\theta(s - \delta - r) \leq (\delta + r)(s - r - 1)$ imply $0 < k_- < \frac{s - (\delta + r)}{\delta + r} \leq \frac{s - r - 1}{\theta} < k_+$, so it follows from Lemma 3.4 that system (4) has no equilibrium in the set $D_2 \setminus \{O\}$, then L_1 must approach the origin as t tends to positive infinity, that is, $\lim_{t \rightarrow +\infty}(x(t), y(t)) = O$ for $(x(t), y(t)) \in L_1$.

The above inference shows that $L_1 \subset D_1$ is a heteroclinic orbit of (4) connecting equilibrium E_0 and the origin O .

On the other hand, by Lemma 2.1 (i) the line segment $L_2 = \{(x, y) : 0 < x < 1 - \delta, y = 0\}$ is also a heteroclinic orbit of (4) connecting E_0 and O , and $\lim_{t \rightarrow -\infty}(x(t), y(t)) = O, \lim_{t \rightarrow +\infty}(x(t), y(t)) = E_0$. Therefore, the closed curve consisting L_1, L_2, E_0 and O is a closed heteroclinic orbit of (4) on the set D_1 .

(ii) Since (4) has no positive equilibrium in the set D_1 and $\varphi = 0$ is a characteristic direction of (4) according to expression (11), it is easy to know that there is a family of homoclinic orbits of (4) full of the interior of the heteroclinic closed orbit.

(iii) To further understand dynamics of (4) for $s > 1 + r$ and $\theta(s - \delta - r) \leq (\delta + r)(s - r - 1)$, by introducing the change of variables $(x, y) \rightarrow (x, u)$ for (4), where $u = y/x$, then (4) becomes

$$\begin{cases} x' = x \left\{ (1 + \theta u)[1 - x(1 + u)] - \delta - \frac{su}{1+u} \right\}, \\ u' = u \{s - r - (1 + \theta u)[1 - x(1 + u)]\}. \end{cases} \tag{17}$$

We claim that the set

$$\bar{D} = \{(x, u) : x \geq 0, u \geq 0, x(1 + u) \leq 1 - \delta, u \leq (s - \delta - r)/\theta\delta\}$$

is positively invariant to (17).

In fact, it follows from (17) that

$$\frac{d[x(1 + u)]}{dt} = x \{(1 + \theta u)[1 - x(1 + u)] - \delta - (\delta + r)u\}.$$

When $x(1 + u) > 1 - \delta$, $[x(1 + u)]' \leq -xu[(1 - \theta)\delta + r] < 0$ for $x > 0$ and $u > 0$. So any trajectory of system (17) starting from the set $R_+^2 \setminus \hat{D}$ will enter the set \hat{D} in a finite time, where $\hat{D} = \{(x, u) \in R_+^2 : x(1 + u) \leq 1 - \delta\}$.

Furthermore, from the first equation of (17), $u' \leq u[(s - \delta - r) - \theta\delta u]$ for $x(1 + u) \leq 1 - \delta$. Then it follows that $\limsup_{t \rightarrow +\infty} u(t) \leq (s - \delta - r)/\theta\delta$. Therefore, the claim holds.

Again, system (17) has three nonnegative equilibria: $\bar{O}(0, 0)$, $\bar{E}_0(1 - \delta, 0)$, and $\bar{E}_1(0, (s - r - 1)/\theta)$ for this case. They are all on the boundary of the region \bar{D} . From the Jacobian matrices of (17) at equilibria \bar{O} , \bar{E}_0 and \bar{E}_1 , it is easy to get that \bar{O} is an unstable node, \bar{E}_0 is a saddle, and \bar{E}_1 is a stable node. Since (17) has no equilibrium in the interior of the set \bar{D} , the equilibrium \bar{E}_1 is globally stable on the set \bar{D} for this case. Therefore, for (4), $\lim_{t \rightarrow +\infty} x(t) = 0$ and $\lim_{t \rightarrow +\infty} (y(t)/x(t)) = (s - r - 1)/\theta$. It implies that all the orbits of (4) starting from the first quadrant approach the origin along the direction $\varphi = \arctan(s - r - 1)/\theta$ as t tends to positive infinity. \square

4. Mathematical analysis for system (4) with $\theta = 0$. In this section, we consider dynamical behaviors of the rescaled system (4) in the case $\theta = 0$, which implies that the fecundity of infected hosts is completely lost.

When $\theta = 0$, system (4) becomes

$$\begin{cases} \frac{dx}{dt} = x \left[(1 - \delta) - (x + y) - \frac{sy}{x+y} \right], \\ \frac{dy}{dt} = y \left[\frac{sx}{x+y} - (\delta + r) \right]. \end{cases} \tag{18}$$

Similar to the previous argument for the case of $0 < \theta \leq 1$, for system (18) the first two items of Lemma 2.1 hold true, and so is Lemma 2.2. Wit respect to the existence and stability of equilibria of system (18), we have the following results.

Theorem 4.1. *System (18) always has the infection-free equilibrium $E_0(1 - \delta, 0)$, which is globally stable on the set D_1 when $s \leq \delta + r$; when $\delta + r < s < r + 1$, system (18) has a unique positive equilibrium $E_1^*(x_1^*, y_1^*)$, which is globally stable in the interior of the set D_1 , where*

$$x_1^* = \frac{(\delta + r)(r + 1 - s)}{s}, \quad y_1^* = \frac{(s - \delta - r)(r + 1 - s)}{s}.$$

In the following, we consider dynamics of system (18) for the case $s \geq r + 1$.

When $s \geq r + 1$, it is easy to know that, in the first quadrant, the vertical isocline of (18) defined by $1 - \delta = (x + y) + sy/(x + y)$ is above its horizontal isocline defined by $sx = (\delta + r)(x + y)$, and they intersect only at the origin. Especially for the case $s = r + 1$, they are tangent at the origin. So system (18) has no positive equilibrium as $s \geq r + 1$. And equilibrium E_0 is a saddle as $s \geq r + 1$.

Notice that both x -axis and y -axis are solution curves of system (18). For system (18) we can have the following results similar to Theorem 3.5.

Theorem 4.2. *When $s \geq r + 1$, system (18) has a heteroclinic closed orbit on the set D_1 , and a family of homoclinic orbits is full of the interior the heteroclinic closed orbit (Figure 3).*

For system (18), function $G(\varphi)$ defined in (11) becomes

$$G(\varphi) = \rho(s - r - 1) \sin \varphi \cos \varphi (\cos \varphi + \sin \varphi),$$

then, when $s > r + 1$, $\varphi = 0$ and $\varphi = \pi/2$ are the characteristic directions of system (18); when $s = r + 1$, $G(\varphi) \equiv 0$, which is the singular case. Therefore, for dynamics of system (18) near the origin O we have

Corollary 1. *When $s > r + 1$, any orbit of system (18) starting from the first quadrant approaches the origin along the y -axis as t tends to positive infinity, and any orbit leaving the origin moves along the x -axis as t increases (Figure 3(a)); however, when $s = r + 1$, along any direction except for $\varphi = \arctan \frac{s - (\delta + r)}{\delta + r}$, there is a unique orbit of system (18) which either tends to or leaves the origin (Figure 3(b)) as t increases.*

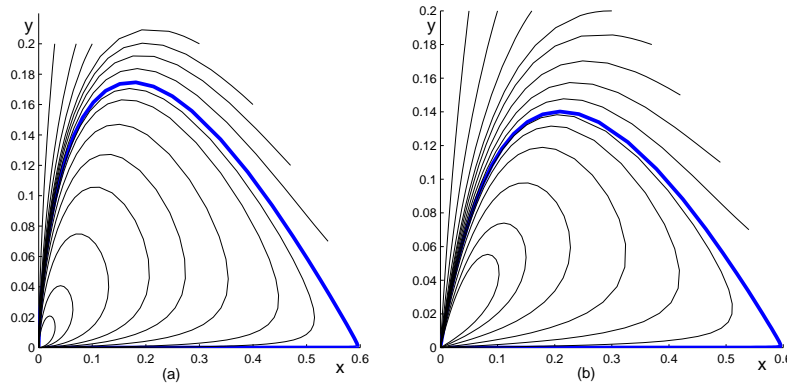


FIGURE 3. The heteroclinic and homoclinic orbits of (18). The thick closed curve is a heteroclinic closed orbit, the thin closed curves surrounded within the heteroclinic closed orbit are all homoclinic orbits. Figure 3(a) corresponds to the case $s > r + 1$, where $\delta = 0.4$, $r = 0.5$, and $s = 1.8$. Figure 3(b) corresponds to the case $s = r + 1$, where $\delta = 0.4$, $r = 0.5$, and $s = 1.5$.

5. Dynamic behaviors of system (2). In sections 3 and 4, we have completely analyzed the rescaled system (4). In this section, we will discuss dynamical behaviors of model (2) according to the above results, and explain these results epidemiologically.

We first summarize the main results on system (4) in Table 1, which shows that system (4) has four types of dynamical behaviors:

For Case (C1) defined in Table 1, the global stability of the origin O implies that hosts (including uninfected and infected hosts) go to extinction eventually. The host extinction in such case is not due to the parasite infection but demographic decline feature of hosts themselves.

For Case (C2), the global stability of E_0 implies that parasite infection dies out eventually in the host population, while uninfected host population approaches a positive constant as t tends to infinity.

For Case (C3), the parasite infection keeps present persistently. The sizes of both uninfected and infected hosts stabilize to positive constants eventually as t tends to infinity.

For Case (C4), the parasite infection leads to host extinction due to parasite regulation, whereas hosts do not extinct in the absence of parasite infection, which is different from Case (C1). Here, the existence of homoclinic orbits shows that the outbreak of parasite infection is possible. Whether the infected hosts can reproduce may lead to various phenomena. For $\theta \neq 0$, that is, the infected hosts can certainly reproduce, by Theorem 3.5 we have $\lim_{t \rightarrow \infty} y(t)/x(t) = (s - r - 1)/\theta$, which implies that in the process of host extinction the ratio between sizes of infected and uninfected hosts tends to a constant. However, for $\theta = 0$, that is, the infected hosts can not reproduce, the change of the ratio is complex according to Corollary 1.

To describe the obtained results with the original parameters in model (2) and demonstrate them epidemiologically, we introduce three new parameters with the original parameters:

$$R_0 = \frac{\beta}{d + \alpha}, \quad R_1 = \frac{\theta a}{d + \alpha}, \quad R_2 = \frac{a}{d}.$$

Since $1/d$ and $1/(d + \alpha)$ are the average periods that the uninfected and infected hosts stay in their compartments, respectively. a and θa are the per capita maximum birth rates of uninfected and infected hosts, respectively. Then R_0 is referred to as the basic epidemiological reproduction number of parasite infection, that is, average of number of secondary infections induced by a single infected host in a whole susceptibles during infectious period. Whereas, R_1 and R_2 are the basic demographic reproduction numbers of infected and uninfected hosts, respectively.

For simplicity, we define the following two parameters

$$\gamma = \frac{d}{d + \alpha}, \quad \bar{R}_0 = \begin{cases} 1 + \frac{\gamma(R_2 - 1)}{1 - R_1}, & \text{for } R_1 \neq 1; \\ +\infty, & \text{for } R_1 = 1, \end{cases}$$

where γ represents the ratio between the average life spans of infected and uninfected hosts, \bar{R}_0 is a threshold determining the existence of hosts in the presence of parasite, which will be understood in the following discussion.

By using expressions (5) and the new parameters defined above, the inequality $\theta(s - \delta - r) > (\delta + r)(s - r - 1)$ is equivalent to the inequality

$$(R_2 - 1)\gamma > (R_0 - 1)(1 - R_1). \tag{19}$$

Obviously, (19) holds true for $R_0 > 1$ and $R_2 > 1$ when $R_1 \geq 1$. However, when $R_1 < 1$, from (19) we have

$$R_0 < 1 + \frac{\gamma(R_2 - 1)}{1 - R_1} = \bar{R}_0.$$

Notice that, R_1 , $R_2\gamma$ and R_2 satisfy the relations $R_1 \leq R_2\gamma < R_2$ since $\theta \leq 1$. Thus, Table 1 can be re-expressed with Table 2, in which Case (C3) in Table 1 is

Cases	Conditions	Results
(C1)	$\delta \geq 1$	O is globally stable.
(C2)	$\delta < 1, s \leq \delta + r$	E_0 is globally stable.
(C3)	$\delta < 1, s > \delta + r,$ $\theta(s - \delta - r) > (\delta + r)(s - r - 1)$	E^* is globally stable.
(C4)	$\delta < 1, s > \delta + r,$ $\theta(s - \delta - r) \leq (\delta + r)(s - r - 1)$	O is globally attractive, and there are a family of homoclinic orbits of system (4).

TABLE 1. The complete global results of system (4).

Cases	Conditions	Results
(C1)	$R_2 \leq 1$	O is globally stable.
(C2)	$R_2 > 1, R_0 \leq 1$	E_0 is globally stable.
(C3)	(C3 ₁) $R_2 > 1, 1 \leq R_1 \leq R_2\gamma,$ $R_0 > 1$	E^* is globally stable.
	(C3 ₂) $R_2 > 1 > R_1, R_1 \leq R_2\gamma,$ $1 < R_0 < \bar{R}_0$	
(C4)	$R_2 > 1 > R_1, R_1 \leq R_2\gamma,$ $R_0 \geq \bar{R}_0$	O is globally attractive, and there are a family of homoclinic orbits of model (2).

TABLE 2. The complete global results of model (2)

Cases	Conditions	Results
(C1)	$R_2 \leq 1$	O is globally stable.
(C2)	$R_2 > 1, R_0 \leq 1$	E_0 is globally stable.
(C3)	$R_2 > 1, 1 < R_0 < 1 + \gamma(R_2 - 1)$	E^* is globally stable.
(C4)	$R_2 > 1, R_0 \geq 1 + \gamma(R_2 - 1)$	O is globally attractive, and there are a family of homoclinic orbits of system (18).

TABLE 3. The complete global results of system (18).

then divided into two subcases, and accordingly,

$$x^* = \frac{K(R_1 - 1)(R_0 - \bar{R}_0)}{R_0[R_1(R_0 - 1) + R_2\gamma]}, \quad y^* = K \left(1 - \frac{1}{R_0}\right) \frac{(R_1 - 1)(R_0 - \bar{R}_0)}{R_1(R_0 - 1) + R_2\gamma}.$$

Especially, when $\theta = 0$, that is, $R_1 = 0$, Table 2 can become Table 3, where

$$x^* = \frac{K[\gamma(R_2 - 1) + 1 - R_0]}{R_0R_2\gamma}, \quad y^* = \frac{K(R_0 - 1)[\gamma(R_2 - 1) + 1 - R_0]}{R_0R_2\gamma}.$$

Since $R_2 \leq 1$ implies that the basic demographic reproduction number of uninfected hosts is not greater than 1, then, corresponding to Case (C1), the extinction of hosts is natural in the absence of parasite infection. Therefore, in the following we only discuss the case $R_2 > 1$, which implies that hosts can persist forever in the absence of parasite infection.

In order to understand the dependence of dynamics of model (2) on the parameters R_0 and R_1 for the given parameters R_2 ($R_2 > 1$) and γ ($\gamma < 1$), we partition the feasible regions of R_0 and R_1 into some subregions according to Table 2. These

regions are shown in Figure 4. Figure 4(a) and (b) correspond to two cases: $R_2\gamma \geq 1$ and $R_2\gamma < 1$, respectively.

In Figure 4(a) we define the region $\Omega_2 = \{(R_1, R_0) : 0 \leq R_1 \leq R_2\gamma, 0 < R_0 \leq 1\}$ corresponding to Case (C2), the region $\Omega_{31} = \{(R_1, R_0) : 1 \leq R_1 \leq R_2\gamma, R_0 > 1\}$ corresponding to Case (C3₁), the region $\Omega_{32} = \{(R_1, R_0) : 0 \leq R_1 < 1, 1 < R_0 < \bar{R}_0\}$ corresponding to Case (C3₂), and the region $\Omega_4 = \{(R_1, R_0) : 0 \leq R_1 < 1, R_0 \geq \bar{R}_0\}$ corresponding to Case (C4). In Figure 4(b), Case (C3₁) does not exist for $R_1 \leq R_2\gamma < 1$. The region $\Omega'_2 = \{(R_1, R_0) : 0 \leq R_1 \leq R_2\gamma, 0 < R_0 \leq 1\}$ is associate with Case (C2), the region $\Omega'_{32} = \{(R_1, R_0) : 0 \leq R_1 \leq R_2\gamma, 1 < R_0 < \bar{R}_0\}$ is associated with Case (C3₂), and the region $\Omega'_4 = \{(R_1, R_0) : 0 \leq R_1 \leq R_2\gamma, R_0 \geq \bar{R}_0\}$ is related to Case (C4).

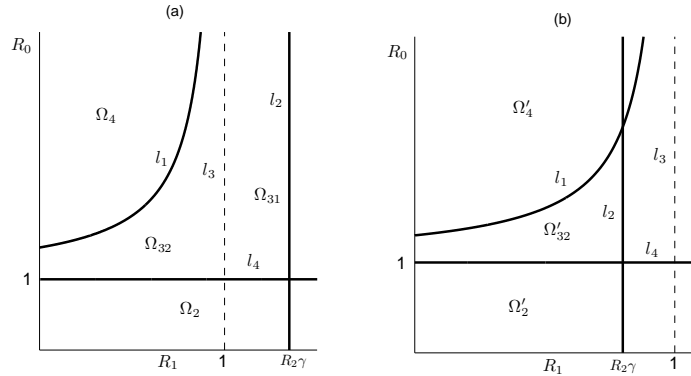


FIGURE 4. The division of the feasible region of R_0 and R_1 corresponding to the different dynamics of model (2), where the curve $l_1 : R_0 = 1 + \gamma(R_2 - 1)/(1 - R_1) (= \bar{R}_0)$; $l_2 : R_1 = R_2\gamma$; $l_3 : R_1 = 1$; and $l_4 : R_0 = 1$. Here, Figure 4(a) corresponds to the case $R_2\gamma \geq 1$; Figure 4(b) corresponds to the case $R_2\gamma < 1$.

In the region Ω_2 (or Ω'_2), the basic reproduction number of parasite infection R_0 is less than unity, which implies the parasite infection dies out eventually in the host population. The uninfected host population tends to $K(a - d)/a$ as t tends to infinity.

In the regions Ω_{31}, Ω_{32} and Ω_4 (or Ω'_{32} and Ω'_4), the basic reproduction number of parasite infection is greater than 1, which indicates that the parasite infection keeps persistently. However, for the different values of R_1 , there are some essential differences between the associated dynamical behaviors of (2).

In the region Ω_{31} , $R_1 \geq 1$ implies that infected hosts can reproduce sufficient uninfected hosts to maintain the supply of uninfected hosts being infected. In such case, parasite infection can not regulate the host population even if R_0 is sufficiently large. Whereas, in Ω_{32} (or Ω'_{32}), $R_1 < 1$ implies that infected hosts' reproduction is not large enough to induce various dynamics, depending on relation of R_0 and R_1 . In such scenario, parasite infection can not regulate the host population unless $R_0 \geq \bar{R}_0$.

In the region Ω_4 (or Ω'_4) where $R_0 \geq \bar{R}_0$ and $R_1 < 1$, a combination of large epidemiological reproduction number and small demographic reproduction number

of infected hosts results in ultimate extinction of both uninfected and infected hosts due to parasite regulation. However, according to Theorem 3.5 and Corollary 1, the trend of the extinction of uninfected and infected hosts is different for the cases $R_1 \neq 0$ and $R_1 = 0$. When $R_1 \neq 0$,

$$\lim_{t \rightarrow \infty} \frac{y(t)}{x(t)} = \frac{1}{R_1} [R_0 - 1 - \gamma(R_2 - 1)],$$

which implies that the extinction of uninfected and infected hosts is along certain direction. Whereas, when $R_1 = 0$, the limit (i.e., the direction of extinction) depends on the initial values of (2).

We initially consider the effect of R_0 on dynamics of the system for various R_1 . When $R_1 < 1$, the dynamics of system (2) go through extinction of parasite infection (i.e., global stability of disease-free equilibrium for $R_0 \leq 1$), persistence of both parasite infection and host population (i.e., global stability of the endemic state for $1 < R_0 < \bar{R}_0$), and hosts extinction while infection persistence (i.e., global attractiveness of the origin for $R_0 \geq \bar{R}_0$) as the epidemiological reproduction number R_0 increases. Whilst $R_1 \geq 1$, the first two kinds of dynamics of system (2) certainly occur, but the third kind - parasite regulation does not happen. For fixed R_0 (either $R_0 < 1$ or $1 < R_0 < 1 + \gamma(R_2 - 1)$), global extinction or persistence of parasite infection is independent on R_1 . However, for relatively large R_0 ($R_0 \geq 1 + \gamma(R_2 - 1)$), increasing R_1 would change the dynamics of system (2) from host extinction to host persistence while keeping infection present.

6. The effect of R_0 on the equilibrium level of infected hosts. For classical parasite-host models, virus dynamical models and epidemic models, the level of infected hosts (virus, individuals) often increases with increase of the associated basic reproduction number when the positive equilibrium is feasible. But, for system (2) the dependence of the level of infected hosts on the associated basic reproduction number is not such simple. In the following we consider the change of the equilibrium level of infected hosts with the basic reproduction number of parasite infection (R_0).

To show the dependence of the level of infected hosts y^* on R_0 , we denote $y^* = y^*(R_0)$, then direct calculation shows that

$$\frac{dy^*}{dR_0} = \frac{K\phi(R_0)}{R_0^2 [R_1(R_0 - 1) + R_2\gamma]^2},$$

where

$$\begin{aligned} \phi(R_0) &= c_0(R_1)R_0^2 + c_1(R_1)R_0 + c_2(R_1), \\ c_0(R_1) &= R_1^2 - (1 - \gamma)R_1 - \gamma R_2, \\ c_1(R_1) &= 2R_1 [(1 - \gamma) + (R_2\gamma - R_1)] > 0, \\ c_2(R_1) &= (\gamma R_2 - R_1) [(1 - \gamma) + (R_2\gamma - R_1)] > 0, \end{aligned}$$

with $R_1 \leq R_2\gamma$ and $\gamma < 1$ being used. It is easy to see that there exists a unique positive zero of quadratic function $c_0(R_1)$, $\bar{R}_1 = [(1 - \gamma) + \sqrt{(1 - \gamma)^2 + 4R_2\gamma}]/2$, such that $c_0(R_1) < 0$ as $0 \leq R_1 < \bar{R}_1$ and $c_0(R_1) > 0$ as $R_1 > \bar{R}_1$. Since $c_0(1) = \gamma(1 - R_2) < 0$ for $R_2 > 1$, it follows that $\bar{R}_1 > 1$.

Further, $c_1(R_1) > 0$, $c_2(R_1) > 0$, and $\phi(R_0)$ is a quadratic function of R_0 , then, when $c_0(R_1) \geq 0$, $\phi(R_0) > 0$ for $R_0 > 1$; when $c_0(R_1) < 0$, function $\phi(R_0)$ has a unique zero \bar{R}'_0 greater than 1 since $\phi(1) = (R_2 - 1)R_2\gamma^2 > 0$ for $R_2 > 1$, which implies that $\phi(R_0) > 0$ for $1 < R_0 < \bar{R}'_0$ and $\phi(R_0) < 0$ for $R_0 > \bar{R}'_0$. Therefore, according to the sign of function $c_0(R_1)$, we have that, when $R_1 \geq \bar{R}_1$, $dy^*/dR_0 > 0$

regions of parameters		existence of y^*	effect of R_0 on y^*
$R_1 \leq R_2\gamma < 1$		Case (C3 ₂)	Figure 5(a)
$1 \leq R_2\gamma < 2 - \gamma$	$R_1 < 1$	Case (C3 ₂)	Figure 5(a)
	$1 \leq R_1 \leq R_2\gamma$	Case (C3 ₁)	Figure 5(b)
$R_2\gamma \geq 2 - \gamma$	$R_1 < 1$	Case (C3 ₂)	Figure 5(a)
	$1 \leq R_1 < \bar{R}_1$	Case (C3 ₁)	Figure 5(b)
	$R_1 \leq R_1 \leq R_2\gamma$	Case (C3 ₁)	Figure 5(c)

TABLE 4. Classification of the existence of $E^*(x^*, y^*)$ and the effect of R_0 on y^* .

for $R_0 > 1$; when $0 \leq R_1 < \bar{R}_1$, $dy^*/dR_0 > 0$ for $1 < R_0 < \bar{R}'_0$, and $dy^*/dR_0 < 0$ for $R_0 > \bar{R}'_0$.

On the other hand, $c_0(R_2\gamma) = R_2\gamma(R_2\gamma + \gamma - 2)$, then $\bar{R}_1 \leq R_2\gamma$ as $R_2\gamma + \gamma - 2 \geq 0$, and $\bar{R}_1 > R_2\gamma$ as $R_2\gamma + \gamma - 2 < 0$. Since the existence of the positive equilibrium E^* corresponds to cases (C3₁) and (C3₂) in Table 2, then, for $R_0 > 1$ and $R_2 > 1$, we list a table (Table 4) to classify the feasible regions of parameters and the associated effect of R_0 on the level of infected hosts which are shown in Figure 5. Figure 5(a) shows the fact that y^* increases for $1 < R_0 < \bar{R}'_0$ and decreases for $\bar{R}'_0 < R_0 < \bar{R}_0 < +\infty$, and $\lim_{R_0 \rightarrow \bar{R}_0} y^* = 0$; Figure 5(b) is similar to Figure 5(a), but the limit of y^* as $R_0 \rightarrow \bar{R}_0$ is $K(R_1 - 1)/R_1$; Figure 5(c) represents that y^* increases monotonously, and $\lim_{R_0 \rightarrow \infty} y^* = K(R_1 - 1)/R_1$.

Comparing Figures 5 (a), (b) and (c) suggests the common feature is that the equilibrium level of the infected host (y^*) increases monotonously as R_0 increases initially. This can be easily understood epidemiologically. However, as R_0 keeps increasing various trends of y^* can observed, depending on R_1 . In fact, Figures 5 (a), corresponding to $R_1 < 1$, shows the more R_0 and the less the equilibrium level of the infected hosts. That is because the size of uninfected hosts reproduced by infected ones is small, which leads to the shortage of uninfected hosts. Then large R_0 causes more infected hosts and consequently more disease-induced death, and hence host extinction due to parasite infection may happen. For large R_1 ($R_1 \geq \bar{R}_1$), the infected hosts can reproduce sufficient uninfected ones to not only maintain supply of resource being infected but also balance disease-induced death, which suggests that y^* persistently increases and stabilizes at a fixed level with increasing R_0 , as shown in Figures 5 (c). For middle values of R_1 ($1 \leq R_1 \leq \min\{R_2\gamma, \bar{R}_1\}$), the equilibrium level of the infected hosts initially reaches a maximum and then decline to a certain level as R_0 increases. In addition, it follows from Figure 5 (a) and (b) that \bar{R}_0 is a threshold in the sense of monotonicity of y^* .

7. Conclusion and discussion. In this paper, by rescaling parasite-host model (2), we mathematically analyzed the global dynamics on the feasible region, and theoretically proved the existence of heteroclinic and homoclinic orbits which implies that the infection may break out in the process of host extinction.

According to the obtained results on model (2), we demonstrated the effect of the basic epidemiological reproduction number (R_0) and the demographic reproduction number of infected hosts (R_1) on the dynamics of the model and the level of infected hosts. Here, we obtained two new findings: one is that a combination of R_0 and R_1 may cause the complexity of dynamics of the model, the other is that, for the different range of R_1 , variation in the equilibrium level of the infected host (y^*) with

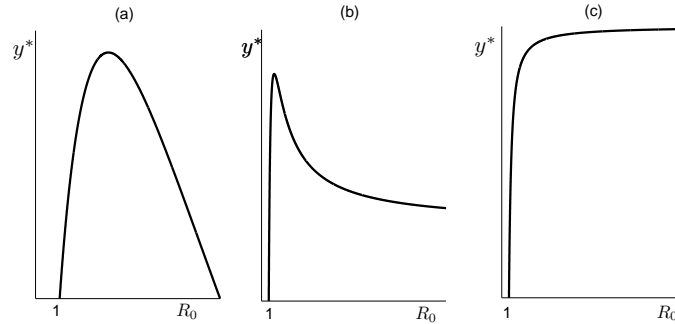


FIGURE 5. Variation in the equilibrium level of the infected hosts y^* with R_0 for (a): $R_1 < 1$; (b): $1 \leq R_1 < \min\{R_2\gamma, \bar{R}_1\}$; (c): $R_1 \geq \bar{R}_1$.

R_0 may not be monotone, which is different from the classical models accepted by mathematicians and epidemiologists. In addition, when the fecundity of infected hosts is lost fully (i.e., $\theta = 0$), the appearance of the singular case implies that the trends of host extinction may depend on the initial state of the model.

Note that in our model the standard incidence function $\beta xy/(x+y)$ plays an important role in coming up with rich dynamics from the point view of mathematics. In fact, standard incidence is indeed based on the epidemiological meanings, where finite contacts of an individual making in a unit time are observed due to finite and often slow movement in large populations, and more details can be found in [2]. We model the growth of host population with logistic growth function to describe the density-constraint growth within host population (or intra-species competition for resources). Hence, our model is reasonable to describe the realities in both biology and epidemiology. Further, our main results show that parasite infection could die out or persist in certain conditions, which is similar to those for other simple models [8]. However, it is interesting to note that our model (2) exhibits some novelties because of introduction of standard incidence. In particular, host extinction can be induced by either demographic decline feature of hosts themselves or parasite regulations. During host going to extinction parasite infection may outbreak and persist eventually, which is different from that for the models with bilinear incidence. Hence, the model examined here describes biological/epidemiological phenomena more reasonably and our conclusions show the dynamics and the biological implications more extensively.

Appendix.

Lemma 7.1. For $m > n > 0$ and $p > 0$, the part of curve \bar{L} in the first quadrant defined by equation

$$(y - mx)(y - nx) = (y + px)(y + x)^2 \quad (20)$$

consists of two branches, which are in the regions $\bar{D}_1 = \{(x, y) \in R_+^2 : y < nx\}$ and $\bar{D}_2 = \{(x, y) \in R_+^2 : y > mx\}$, respectively. Except for the origin, the two branches intersect with two coordinate axes at points $(mn/p, 0)$ and $(0, 1)$, respectively. One

of the two branches in the region \bar{D}_1 is concave downwards, the other in the region \bar{D}_2 is concave leftwards.

Proof. From (20), the polar coordinates equation of the curve \bar{L} is given by

$$\rho = \frac{(\sin \varphi - m \cos \varphi)(\sin \varphi - n \cos \varphi)}{(\sin \varphi + p \sin \varphi)(\sin \varphi + \cos \varphi)^2}.$$

Since polar radius is nonnegative, then, it is easy to see that in the first quadrant \bar{L} consists of two branches, which correspond to $0 < \varphi < \arctan n$ and $\arctan m < \varphi < \pi/2$, respectively. $\varphi = \arctan n$ and $\varphi = \arctan m$ represent two straight lines $y = nx$ and $y = mx$, respectively, so the two branches are located in the regions \bar{D}_1 and \bar{D}_2 , respectively.

Direct calculation shows that, except for the origin, the two branches intersect with two coordinate axes at points $(mn/p, 0)$ and $(0, 1)$, respectively.

Using Maple software, the second derivative of implicit function $y = y(x)$ defined by (20) is given by

$$\begin{aligned} \frac{d^2y}{dx^2} = & -\frac{2mn-2y-2px-4(y+x)p}{2y-nx-mx-2(y+x)(y+px)-(y+x)^2} \\ & + \frac{2[m(y-nx)+(y-mx)n+2(y+x)(y+px)+(y+x)^2p][m+n+4y+2px+2(y+x)p-2x]}{[2y-nx-mx-2(y+x)(y+px)-(y+x)^2]^2} \\ & - \frac{2[m(y-nx)+(y-mx)n+2(y+x)(y+px)+(y+x)^2p]^2(1-3y-px-2x)}{[2y-nx-mx-2(y+x)(y+px)-(y+x)^2]^3}. \end{aligned}$$

From (20), we have

$$p = \frac{1}{x} \left[\frac{(y - mx)(y - nx)}{(y + x)^2} - y \right].$$

Substituting it into the second derivative yields

$$\frac{d^2y}{dx^2} = \frac{2(y + x)(y - mx)(y - nx)T_2}{x^2T_1^3},$$

where

$$\begin{aligned} T_1 &= (y + x)^3 - x[(1 + m)(y - nx) + (1 + n)(y - mx)], \\ T_2 &= x(y + x)^3 [(1 + m)(y - nx) + (1 + n)(y - mx)] \\ &\quad - (y - mx)(y - nx) [(1 + m)(1 + n)x^2 - (y + x)(2y - mx - nx)] \\ &\quad - (y + x)^2 [(y - mx)^2 + (y - nx)^2]. \end{aligned}$$

$n < m$ implies that $y < mx$ as $y < nx$, so $T_1 > 0$ and $T_2 < 0$ for $y < nx$. Hence, $d^2y/dx^2 < 0$ for $y < nx$. This implies that the part of the curve \bar{L} in the region \bar{D}_1 is concave downwards.

To show that the part of the curve \bar{L} in the region \bar{D}_2 is concave leftwards, we make the change of variables:

$$x = \frac{mn}{p}v, \quad y = \frac{mn}{p}u,$$

then (20) becomes

$$\left(v - \frac{u}{m}\right) \left(v - \frac{u}{n}\right) = \left(v + \frac{u}{p}\right) (v + u)^2. \tag{21}$$

Since $1/n > 1/m$, then, according to the above inference for the case $y < nx$, the part of the curve \bar{L}' defined by (21) in the region $D'_2 = \{(u, v) \in R_+^2 : v < u/m\}$ is concave towards the u -axis.

Notice that $v < u/m$ is equivalent to $y > mx$, then the region D'_2 on the (u, v) -plane corresponds to the region \bar{D}_2 on the (x, y) -plane. Thus, the part of the curve \bar{L} in the region \bar{D}_2 is concave leftwards. \square

REFERENCES

- [1] D. Ebert, M. Lipsitch and 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.
- [2] T.-W. Hwang and Y. Kuang, *Deterministic extinction effect of parasites on host populations*, J. Math. Biol., **46** (2003), 17–30.
- [3] Kaifa Wang and Y. Kuang, *Fluctuation and extinction dynamics in host-microparasite systems*, Comm. Pure Appl. Anal., **10** (2011), 1537–1548.
- [4] S. Hews, S. Eikenberry, J. D. Nagy and Y. Kuang, *Rich dynamics of a hepatitis B viral infection model with logistic hepatocyte growth*, J. Math. Biol., **60** (2010), 573–590.
- [5] S. Eikenberry, S. Hews, J. D. Nagy and Y. Kuang, *The dynamics of a delay model of HBV infection with logistic hepatocyte growth*, Math. Biosci. Eng., **6** (2009), 283–299.
- [6] F. Berezovsky, G. Karev, B. Song and C. Castillo-Chavez, *A simple epidemic model with surprising dynamics*, Math. Biosci. Eng., **2** (2005), 133–152.
- [7] Z. Zhang, T. Ding, et al., “Qualitative Theory of Differential Equations,” Translations of Mathematical Monographs, Vol. 101, Amer. Math. Soc., Providence, Rhode Island, 1992.
- [8] Zhien Ma and Jia Li, “Dynamical Modeling and Analysis of Epidemics,” Singapore, 2009.

Received January 19, 2012; Accepted May 14, 2012.

E-mail address: jianq_li@263.net

E-mail address: yxiao@mail.xjtu.edu.cn

E-mail address: yylhgr@126.com