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Stability and Hopf bifurcation of a producer-scrounger model with age-structure

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Abstract

We derive a producer-scrounger model with age-structure in scrounger and looks into its dynamics. Using the methods of eigenvalue analysis and Lyapunov function, we find sufficient and necessary conditions for globally asymptotical stability of extinction equilibrium and scrounger-free equilibrium. A so-called basic reproduction ratio R_0 was established to determine whether the scrounger is extinct or uniformly persistent. It is found that if $R_0 > 1$, the mature time τ does change the dynamical behavior of the model. We confirm that Hopf bifurcation happens if the mature time τ increases.

Keywords: producer-scrounger model; age-structure; stability; uniform persistence; Hopf bifurcation

1 Introduction

There are three forms of basic interaction between two species: cooperation, competition, and predator-prey, which has been extensively investigated (*e.g.*, see [1, 2] and the references therein). However, interaction forms between species in nature are complex and diverse. To forage foods, some species not only catch and feed on prey, but also can scrounge foods from others. For example, Bugnyar and Kotrschal [3] found that the free-ranging ravens steal wolves' food in a game park and the wolves prevent their food from being stolen. This phenomenon is called kleptoparasitism and describes an interaction form between two species, scrounger and producer. Here, scrounger steals food from producer.

To describe the kleptoparasitism interaction, Cosner and Nevai [4] recently established the following diffusive model:

$$\begin{cases} \frac{\partial P}{\partial t} = d_1 \Delta P + (-b_1 - a_1 P)P + m(x)\frac{dP}{S+d}, & t \geq 0, \\ \frac{\partial S}{\partial t} = d_2 \Delta S + (-b_2 - a_2 S)S + \theta m(x)\frac{PS}{S+d}, & t \geq 0. \end{cases} \tag{1.1}$$

Here $x \in \Omega$, Ω is a bounded domain in $\mathbb{R}^n$ with smooth boundary, P and S are the densities of producer and scrounger, respectively, $m(x)$ denotes the producer's ability to discover food at $x \in \Omega$, and $d > 0$ represents the producer's ability to avoid food to be stolen, b_i is the natural mortality rate, a_i is the death rate caused by intraspecies competition, $d_i > 0$ is

the spatial diffusive rate, and θ is the energy transition rate. Note that letting $S = 0$ in the first equation of (1.1), we have

$$\frac{\partial P}{\partial t} = d_1 \Delta P + \left[m(x) - b_1 - a_1 P \right] P,$$

and thus we can regard $m(x)$ as the birth rate of producer without scourging. Furthermore, $m(x)\frac{d}{S+d}$ is the birth rate of producer with scounging.

General speaking, all individuals always have two stages, immature and mature, and they perform very differently in some aspects. For example, the immature ravens are incapable to fly and have to stay in the nest while the mature ravens undertake the task of searching for food. In mathematics, a model with delay τ (being the maturation period) can be established to describe the population dynamics with age-structure (*e.g.*, see [5–13]). In the current paper, we try to establish a producer-scrounger model with age-structure in scrounger, and study the dynamics and the influence of maturation period in the scrounge interaction.

The paper is organized as follows. In Section 2, a producer-scrounger model with age-structure in scrounger is derived. In Section 3, the basic theory, including existence, uniqueness, positivity and boundedness of solutions for the model are discussed. The stability of equilibriums, uniform persistence, and Hopf bifurcation are investigated in Section 4. Some numerical simulations and concluding discussions are given in the last section.

2 Model derivation

Let $P(t)$ remain the density of producer at time $t \geq 0$, and positive numbers b_1, a_1, m, d, and θ be of the same meaning as in system (1.1). Assume that $S(t)$ and $I(t)$ express the densities of mature scrounger and immature scrounger, respectively, b_2 (b_3) is the natural mortality rate of mature (immature) scrounger, a_2 (a_3) is the death rate of mature (immature) scrounger caused by intraspecies competition. Furthermore, assume that there exists neither competition between the immature scrounger and mature scrounger nor intraspecies competition between the immature scroungers (*i.e.*, $a_3 = 0$). For simplicity, we assume that the spatial environment is homogeneous, and thus $m(x) \equiv m$ is a constant.

Firstly, we see that the producer fits an equation as follows:

$$\frac{dP(t)}{dt} = -b_1 P(t) - a_1 P^2(t) + m\frac{dP(t)}{S(t) + d}.$$

Now we derive equations for scrounger. Let $i(t, a)$ be the density of immature scrounger at time t and age a. Then $i(t, a)$ satisfies

$$\frac{\partial i(t, a)}{\partial t} + \frac{\partial i(t, a)}{\partial a} = -b_3 i(t, a). \tag{2.1}$$

Let $I(t) = \int_0^\tau i(t, a)\, da$, where $\tau \geq 0$ is a constant number that denotes the time period for an immature to become mature from its birth. Integrating equation (2.1) from 0 to τ with respect to the variable a, we get

$$\frac{dI(t)}{dt} = i(t, 0) - i(t, \tau) - b_3 I(t). \tag{2.2}$$

Here, $i(t, 0)$ denotes the density of new-born scrounger at time t, and $i(t, \tau)$ is the recruitment term, coinciding with those of maturation age.

Suppose that there is a resource of one. If the proportion of this resource ultimately acquired by the producers is $\frac{d}{S(t)+d}$, and the mature scroungers have resource accounted for $1 - \frac{d}{S(t)+d} = \frac{S(t)}{S(t)+d}$. Considering the producer's ability to discover food, the number of producers, and the energy transition rate, we can regard $\theta m \frac{P(t)}{S(t)+d}$ as the birth rate of mature scrounger, and then $i(t, 0) = \theta m \frac{P(t)}{S(t)+d} S(t)$.

To calculate $i(t, \tau)$, denote $i^{\xi}(a) = i(a + \xi, a)$. Then

$$\frac{di^{\xi}(a)}{da} = -b_3 i^{\xi}(a). \tag{2.3}$$

Solving (2.3), we get

$$i^{\xi}(a) = i^{\xi}(0)e^{-b_3 a}. \tag{2.4}$$

Let $a = \tau$ and $\xi = t - \tau$ in (2.4). Then

$$i(t, \tau) = i(t - \tau, 0)e^{-b_3 \tau} = \theta m \frac{P(t - \tau)S(t - \tau)}{S(t - \tau) + d} e^{-b_3 \tau}.$$

Therefore, equation (2.2) can be rewritten as

$$\frac{dI(t)}{dt} = -b_3 I(t) + \theta m \frac{P(t)S(t)}{S(t) + d} - \theta m \frac{P(t - \tau)S(t - \tau)}{S(t - \tau) + d} e^{-b_3 \tau},$$

and further the equation about the mature scrounger follows:

$$\frac{dS(t)}{dt} = -b_2 S(t) - a_2 S^2(t) + \theta m \frac{P(t - \tau)S(t - \tau)}{S(t - \tau) + d} e^{-b_3 \tau}.$$

Summarizing the discussion, we obtain the following producer-scrounger model with age-structure:

$$\begin{cases} \frac{dP(t)}{dt} = -b_1 P(t) - a_1 P^2(t) + m \frac{dP(t)}{S(t)+d}, \\ \frac{dI(t)}{dt} = -b_3 I(t) + \theta m \frac{P(t)S(t)}{S(t)+d} - \theta m \frac{P(t-\tau)S(t-\tau)}{S(t-\tau)+d} e^{-b_3 \tau}, \\ \frac{dS(t)}{dt} = -b_2 S(t) - a_2 S^2(t) + \theta m \frac{P(t-\tau)S(t-\tau)}{S(t-\tau)+d} e^{-b_3 \tau}. \end{cases} \tag{2.5}$$

Note that in (2.5), $I(t)$ is independent of the first and third equations. Therefore, we only need to study the following system with two equations:

$$\begin{cases} \frac{dP(t)}{dt} = -b_1 P(t) - a_1 P^2(t) + m \frac{dP(t)}{S(t)+d}, \\ \frac{dS(t)}{dt} = -b_2 S(t) - a_2 S^2(t) + \theta m \frac{P(t-\tau)S(t-\tau)}{S(t-\tau)+d} e^{-b_3 \tau}. \end{cases} \tag{2.6}$$

Remark 2.1 If $\tau = 0$, then system (2.5) yields to (1.1) with homogeneous spatial environment.

Remark 2.2 If there exists competition between immature scroungers (*i.e.*, $a_3 > 0$), then (2.1) is replaced by

$$\frac{\partial i(t,a)}{\partial t} + \frac{\partial i(t,a)}{\partial a} = -b_3 i(t,a) - a_3 i(t,a) I(t).$$

Similar analysis leads to a model

$$\begin{cases} \frac{dP(t)}{dt} = -b_1 P(t) - a_1 P^2(t) + m\frac{dP(t)}{S(t)+d}, \\ \frac{dI(t)}{dt} = -b_3 I(t) - a_3 I^2(t) + \theta m\frac{P(t)S(t)}{S(t)+d} \\ \qquad - \theta m\frac{P(t-\tau)S(t-\tau)}{S(t-\tau)+d} \exp[-\int_{t-\tau}^{t}(b_3 + a_3 I(\eta))\,d\eta], \\ \frac{dS(t)}{dt} = -b_2 S(t) - a_2 S^2(t) + \theta m\frac{P(t-\tau)(t-\tau)}{S(t-\tau)+d} \exp[-\int_{t-\tau}^{t}(b_3 + a_3 I(\eta))\,d\eta]. \end{cases} \tag{2.7}$$

3 Basic theory of solutions

In this section, we study the existence, uniqueness, positivity, and boundedness of solutions of (2.6).

Denote $X = C([-\tau, 0], \mathbb{R}_+^2)$, $\mathbb{R}_+^2 = \{(x,y)^T : x \geq 0, y \geq 0\}$. Then X is a Banach space with norm $\|\phi\| = \max\{|\phi(\xi)| : \xi \in [-\tau, 0]\}$, where $|\cdot|$ is the standard norm in $\mathbb{R}^2$. For $\sigma > 0$ and $\phi \in C([-\tau, \sigma), \mathbb{R}^2)$, define $\phi_t \in X$ as $\phi_t(\xi) = \phi(t + \xi)$ for $t \in [0, \sigma)$ and $\xi \in [-\tau, 0]$.

Define $f : X \to \mathbb{R}^2$ by

$$f(\phi) = \begin{pmatrix} -b_1 \phi_1(0) - a_1 \phi_1^2(0) + m\frac{d\phi_1(0)}{\phi_2(0)+d} \\ -b_2 \phi_2(0) - a_2 \phi_2^2(0) + \theta m\frac{\phi_1(-\tau)\phi_2(-\tau)}{\phi_2(-\tau)+d} e^{-b_3 \tau} \end{pmatrix},$$

where $\phi = (\phi_1, \phi_2)^T \in X$. It is easy to see that f is continuous and Lipschitz on ϕ in every compact set of X. In view of the basic theory of functional differential equations ([14], Theorem 2.2.3), we know that for any initial function $\phi = (\phi_1, \phi_2)^T \in X$, there exists a unique local solution $(P(t), S(t))^T = (P(t; \phi), S(t; \phi))^T$ of (2.6).

For biological significance, we consider the initial function satisfying

$$P(\xi) = \phi_1(\xi) \geq 0, \qquad S(\xi) = \phi_2(\xi) \geq 0, \quad \xi \in [-\tau, 0],$$

$$\phi_1(0) > 0, \qquad \phi_2(0) > 0. \tag{3.1}$$

In the discussion of boundedness of solutions, we need the positivity of the immature scrounger. Therefore, in the following, to express the initial value condition of immature scrounger, we use

$$I(\xi) = \phi_3(\xi) \geq 0, \quad \xi \in [-\tau, 0], \qquad \phi_3(0) > 0.$$

Then we have the following conclusion.

Lemma 3.1 (Positivity) *The solution* $(P(t), S(t), I(t))^T$ *of* (2.5) *with initial function* $\phi \geq 0$ *is nonnegative on its existence interval. Furthermore, if* $\phi_1(0) > 0$, $\phi_2(0) > 0$, *then* $(P(t), S(t)) > (0, 0)$ *as long as the solution* $(P(t), S(t))$ *exists.*

Proof Assume that the maximal existing interval of $(P(t), S(t), I(t))$ is $[0, T]$. Without loss of generality, we may assume that $\tau < T$. For $t \in [0, \tau]$, we have $P(t-\tau) \geq 0$ and $S(t-\tau) \geq 0$.

Thus, for $t \in [0, \tau]$, we have

$$\frac{dS(t)}{dt} = -b_2 S(t) - a_2 S^2(t) + \theta m \frac{P(t-\tau)S(t-\tau)}{S(t-\tau) + d} e^{-b_3 \tau} \geq -b_2 S(t) - a_2 S^2(t).$$

Comparing $S(t)$ with the solution $V(t)$ of the initial problem

$$\frac{dV(t)}{dt} \geq -b_2 V(t) - a_2 V^2(t), \qquad V(0) = S(0) \geq 0,$$

we have $S(t) \geq 0$ for $t \in [0, \tau]$. By using the induction argument, $S(t) \geq 0$ holds as long as it exists.

Assume that there exists t_0 such that $P(t_0) < 0$. Since $P(0) \geq 0$, by continuity and without loss of generality, we can find some $t_1 < t_o$ with $P(t) \geq 0$ for $t \in [0, t_1]$ and $P(t) < 0$ for $t \in (t_1, t_0)$. From the fact $S(t) \geq 0$ and the first equation of (2.6) we have

$$\frac{dP(t)}{dt} \geq -b_1 P(t) - a_1 P^2(t) + m P(t), \quad t \in (t_1, t_0).$$

Actually, the solution of $\frac{dZ(t)}{dt} = -b_1 Z(t) - a_1 Z^2(t) + m Z(t)$ with $Z(t_1) = 0$ is the zero solution. Then the comparison principle leads to $P(t) \geq 0$ for $t \geq t_1$, in contradiction with $P(t) < 0$, $t \in (t_1, t_0)$, that is, $P(t) \geq 0$ if $P(0) \geq 0$, also on its maximal existence interval.

Note that the second equation in (2.5) can be rewritten as

$$\frac{d}{dt}\left[I(t)e^{b_3 t}\right] = \frac{d}{dt}\left[\theta m \int_t^{t+\tau} \frac{P(\xi-\tau)S(\xi-\tau)}{S(\xi-\tau)+d} e^{b_3(\xi-\tau)} d\xi\right],$$

$$I(t)e^{b_3 t} = I(0) + \theta m \int_0^t \left[\int_s^{s+\tau} \frac{P(\xi-\tau)S(\xi-\tau)}{S(\xi-\tau)+d} e^{b_3(\xi-\tau)} d\xi\right] ds.$$

Thus, the nonnegativity of $P(t)$ and $S(t)$ leads to the nonnegativity of $I(t)$. Furthermore, $I(t) \geq 0$ if $I(0) \geq 0$.

If $\phi_1(0) > 0$ and $\phi_2(0) > 0$, then a similar argument leads to $(P(t), S(t)) > (0, 0)$ on its maximal existence interval. The proof is complete. □

The following lemma will lead to the global existence of solution $(P(t; \phi), S(t; \phi))$.

Lemma 3.2 (*Boundedness*) *The solution* $(P(t), S(t))^T$ *of* (2.6) *satisfying the initial condition* (3.1) *is bounded as long as it exists.*

Proof We consider (2.5) with the initial conditions (3.1), where $(\phi_1, \phi_2, \phi_3)^T \in C([\tau, 0], \mathbb{R}_+^3)$. In view of Lemma 3.1, we can obtain the existence of a unique local positive solution of (2.5), defined on its maximal interval $[0, T)$. Note that

$$\theta \frac{dP(t)}{dt} + \frac{dI(t)}{dt} + \frac{dS(t)}{dt}$$

$$= -\theta b_1 P(t) - \theta a_1 P^2(t) + \theta m \frac{dP(t)}{S(t)+d} - b_3 I(t) + \theta m \frac{P(t)S(t)}{S(t)+d} - b_2 S(t) - a_2 S^2(t)$$

$$= \theta(m - b_1)P(t) - \theta a_1 P^2(t) - b_3 I(t) - b_2 S(t) - a_2 S^2(t).$$

Then, for any positive constant number $\beta < \min\{b_2, b_3\}$, by the positivity of solution we have

$$
\theta \frac{dP(t)}{dt} + \frac{dI(t)}{dt} + \frac{dS(t)}{dt} + \beta\big(\theta P(t) + I(t) + S(t)\big)
$$

$$
\leq \theta(\beta + m - b_1)P(t) - \theta a_1 P^2(t)
$$

$$
= -\theta a_1 \left(P(t) - \frac{\beta + m - b_1}{2a_1} \right)^2 + \frac{\theta(\beta + m - b_1)^2}{4a_1}
$$

$$
\leq \frac{\theta(\beta + m - b_1)^2}{4a_1} := C_0.
$$

Furthermore, we have

$$
\theta P(t) + S(t) + I(t) < \frac{C_0}{\beta} + \left(\theta P(0) + S(0) + I(0) - \frac{C_0}{\beta} \right)e^{-\beta t},
$$

which implies that $(P(t), S(t))$ is bounded as long as it exists. $\qquad \square$

In view of Lemmas 3.1 and 3.2, we can draw the following conclusion.

Theorem 3.1 *There exists a positive solution of* (2.6) *defined on* $[0, \infty)$ *with the initial condition* (3.1), *which is unique. Furthermore, the solution semiflow* $\Phi(t)$ *of* (2.6), *defined by* $[\Phi(t)\phi](\xi) = (P_t(\xi), S_t(\xi))^T$, *is well defined and has a global attractor in* X.

4 Global dynamical properties

In this section, we look into the stability and Hopf bifurcation of system (2.6). Firstly, we investigate the existence of equilibria.

Lemma 4.1 *The following conclusions for* (2.6) *hold.*

(1) *The zero equilibrium* (*extinction equilibrium*) $E_0 = (0, 0)$ *always exists.*

(2) *A unique nonzero boundary equilibrium* (*scrounger-free equilibrium*)
    $E_1 = (\frac{m-b_1}{a_1}, 0) := (p_1, 0)$ *exists if and only if* $m > b_1$.

(3) *A unique positive equilibrium* (*coexistence equilibrium*) $E_* = (p^*, s^*)$ *exists if and only if*

$$
\theta m e^{-b_3 \tau}(m - b_1) > d a_1 b_2,
$$

where $E_* = (p^*, s^*)$ *satisfies*

$$
-b_1 - a_1 p^* + m \frac{d}{s^* + d} = 0, \qquad -b_2 - a_2 s^* + \theta m \frac{p^*}{s^* + d} e^{-b_3 \tau} = 0.
$$

In addition, if E_* *exists, then* E_1 *also exists.*

Proof The proof of (1) and (2) is obvious, so we omit it here. Now we prove (3). A coexistence equilibrium E_* exists if and only if the following algebraic system (4.1) has a pair of positive roots:

$$
-b_1 - a_1 p + m \frac{d}{s + d} = 0, \qquad -b_2 - a_2 s + \theta m \frac{p}{s + d} e^{-b_3 \tau} = 0. \tag{4.1}
$$

Solving (4.1) is equivalent to that two curves have a cross-point in the first quadrant of $\mathbb{R}^2$. Note that the curve $p = \frac{1}{a_1}(-b_1 + m\frac{d}{s+d})$ decreases as $s \geq 0$ increases and has a unique cross-point $(\frac{m-b_1}{a_1}, 0)$ with the p-axis. We know that $p = \frac{e^{b_3\tau}}{\theta m}(b_2 + a_2 s)(s + d)$ increases to $+\infty$ as s increases to $+\infty$ and also has a unique cross-point $(\frac{e^{b_3\tau}}{\theta m}b_2 d, 0)$ with the p-axis. Thus, their p-intercepts are $\frac{m-b_1}{a_1}$ and $\frac{e^{b_3\tau}}{\theta m}b_2 d$, respectively. Thus, a unique positive cross-point of the two curves exists if and only if their p-intercepts satisfy $\frac{m-b_1}{a_1} > \frac{e^{b_3\tau}}{\theta m}b_2 d$, that is, $\theta m e^{-b_3\tau}(m - b_1) > da_1 b_2$. The proof is complete. $\qquad\square$

4.1 Basic reproduction ratio and stability of boundary equilibria

The following theorem describes the stability of extinction equilibrium E_0.

Theorem 4.1 *If $m \leq b_1$, then the extinction equilibrium $E_0 = (0, 0)$ is globally asymptotically stable; if $m > b_1$, then the extinction equilibrium E_0 is unstable.*

Proof The linearized system of (2.6) at E_0 is

$$
\begin{cases}
\frac{dP(t)}{dt} = -b_1 P(t) + mP(t), \\
\frac{dS(t)}{dt} = -b_2 S(t),
\end{cases}
\tag{4.2}
$$

and the corresponding characteristic equation takes the form

$$
(\lambda - m + b_1)(\lambda + b_2) = 0.
\tag{4.3}
$$

It easy to see that (4.3) has and only has two roots, $-b_1 + m$ and $-b_2$. If $m > b_1$, then $-b_1 + m$ is positive. Thus, E_0 is unstable if $m > b_1$.

Now assume that $m \leq b_1$. Let

$$
V_1(P, S)(t) = \theta e^{-b_3\tau} P(t) + S(t) + \theta m e^{-b_3\tau} \int_0^\tau \frac{P(t - \eta)S(t - \eta)}{S(t - \eta) + d} \, d\eta.
$$

Note that

$$
\begin{aligned}
\frac{d}{dt} \int_0^\tau \frac{P(t - \eta)S(t - \eta)}{S(t - \eta) + d} \, d\eta &= \int_0^\tau \frac{d}{dt} \frac{P(t - \eta)S(t - \eta)}{S(t - \eta) + d} \, d\eta \\
&= -\int_0^\tau \frac{d}{d\eta} \frac{P(t - \eta)S(t - \eta)}{S(t - \eta) + d} \, d\eta \\
&= -\frac{P(t - \tau)S(t - \tau)}{S(t - \tau) + d} + \frac{P(t)S(t)}{S(t) + d}.
\end{aligned}
\tag{4.4}
$$

Then

$$
\begin{aligned}
\frac{dV_1(P, S)(t)}{dt} &= \theta e^{-b_3\tau} P'(t) + S'(t) + \theta m e^{-b_3\tau} \left(\frac{P(t)S(t)}{S(t) + d} - \frac{P(t - \tau)S(t - \tau)}{S(t - \tau) + d} \right) \\
&= \theta e^{-b_3\tau} \left(-b_1 P(t) - a_1 P^2(t) + m\frac{dP(t)}{S(t) + d} \right) \\
&\quad + \left(-b_2 S(t) - a_2 S^2(t) + \theta m \frac{P(t - \tau)S(t - \tau)}{S(t - \tau) + d} e^{-b_3\tau} \right)
\end{aligned}
$$

$$+ \theta m e^{-b_3\tau} \left(-\frac{P(t-\tau)S(t-\tau)}{S(t-\tau)+d} + \frac{P(t)S(t)}{S(t)+d} \right)$$

$$= -a_1\theta e^{-b_3\tau} P^2(t) - b_2 S(t) - a_2 S^2(t) + \theta e^{-b_3\tau}(m-b_1)P(t).$$

Since $m \le b_1$, it follows that $\frac{dV_1(P,S)(t)}{dt} \le 0$, and $\frac{dV_1(P,S)(t)}{dt} = 0$ if and only if $(P,S)(t) \equiv (0,0)$. The proof is complete. □

Now, we define a basic reproduction ratio R_0 for (2.6) (see [15]). Linearizing the second equation at the scrounger-free equilibrium $E_1 = (p_1, 0)$, we obtain

$$\frac{dS(t)}{dt} = \theta m e^{-b_3\tau} \frac{p_1}{d} S(t-\tau) - b_2 S(t) = \theta m e^{-b_3\tau} \frac{p_1}{d} S_t(-\tau) - b_2 S(t).$$

We then separate the last equation into two parts: $\frac{dS(t)}{dt} = F(S_t) - VS(t)$. The first part $F(S_t)$ describes the newly growth mature scroungers at time t depending linearly on the scrounging interaction over $[t-\tau, t]$, and the second part $-VS(t)$ describes the internal evolution of mature scroungers. Here, we define the function F mapping $C([-\tau, 0], \mathbb{R})$ into $\mathbb{R}$ by $F(\phi) = \theta m e^{-b_3\tau} \frac{p_1}{d} \phi(-\tau)$ and use $VS(t) = b_2 S(t)$. It is easy to see F is a nonnegative operator and the one-dimensional matrix $-V$ is cooperative. Denote $\hat{F}$ mapping $\mathbb{R}$ in $\mathbb{R}$ by $\hat{F}u = F(\hat{u})$, where $\hat{u}(\theta) \equiv u$ for $\forall \theta \in [-\tau, 0]$. Thus, $\hat{F} = \theta m e^{-b_3\tau} \frac{p_1}{d}$. Then, according to [15], Corollary 2.1, we have

$$R_0 = r(\hat{F}V^{-1}) = \theta m e^{-b_3\tau} \frac{p_1}{d} \cdot \frac{1}{b_2},$$

where $r(M)$ denotes the spectral radius of matrix M, and M^{-1} denotes the inverse matrix of M.

Remark 4.1 With R_0 defined as before, we see that $R_0 > 1$ is consistent with the condition for the existence of a unique coexistence equilibrium. Further, R_0 is in proportion to the birth rate of producer without mature scrounger's effect ($\theta m \frac{p_1}{d}$), the survival rate for immature scrounger ($e^{-b_3\tau}$), and the average lifetime of mature scrounger ($\frac{1}{b_2}$).

Theorem 4.2 *Assume that $m > b_1$. If $R_0 \le 1$, then the scrounger-free equilibrium $E_1 = (p_1, 0)$ is globally asymptotically stable; if $R_0 > 1$, then the scrounger-free equilibrium is unstable.*

Proof The linearized system of (2.6) at E_1 is

$$\begin{cases} \frac{dP(t)}{dt} = -a_1 p_1 P(t) - m\frac{p_1}{d}S(t), \\ \frac{dS(t)}{dt} = -b_2 S(t) + \theta m \frac{p_1 S(t-\tau)}{d} e^{-b_3\tau}, \end{cases} \tag{4.5}$$

and the corresponding characteristic equation takes the form

$$(\lambda + a_1 p_1)\left(\lambda + b_2 - \theta m\frac{p_1}{d} e^{-b_3\tau} e^{-\lambda\tau}\right) = 0. \tag{4.6}$$

Note that $g(\lambda) := \lambda + b_2 - \theta m\frac{p_1}{d} e^{-b_3\tau} e^{-\lambda\tau} \to \infty$ as $\lambda \to \infty$. If $R_0 > 1$, that is, $g(0) = b_2 - \theta m\frac{p_1}{d} e^{-b_3\tau} < 0$, then we can confirm that $g(\lambda) = 0$ has a positive root. Thus, E_1 is unstable.

Now assume that $R_0 \leq 1$. Let

$$V_2(P,S)(t) = \theta e^{-b_3\tau}\left(P(t) - p_1 - p_1 \ln \frac{P(t)}{p_1}\right) + S(t) + \theta m e^{-b_3\tau}\int_0^\tau \frac{P(t-\eta)S(t-\eta)}{S(t-\eta)+d}\,d\eta.$$

We have from (4.4) that

$$
\begin{aligned}
\frac{dV_2(P,S)(t)}{dt} &= \theta e^{-b_3\tau}P'(t)\left(1-\frac{p_1}{P(t)}\right) + S'(t) \\
&\quad + \theta m e^{-b_3\tau}\left(-\frac{P(t-\tau)S(t-\tau)}{S(t-\tau)+d} + \frac{P(t)S(t)}{S(t)+d}\right) \\
&= \theta e^{-b_3\tau}\left(-b_1 P(t) - a_1 P^2(t) + m\frac{dP(t)}{S(t)+d}\right)\left(1-\frac{p_1}{P(t)}\right) \\
&\quad + \left(-b_2 S(t) - a_2 S^2(t) + \theta m\frac{P(t-\tau)S(t-\tau)}{S(t-\tau)+d}e^{-b_3\tau}\right) \\
&\quad + \theta m e^{-b_3\tau}\left(-\frac{P(t-\tau)S(t-\tau)}{S(t-\tau)+d} + \frac{P(t)S(t)}{S(t)+d}\right) \\
&= \theta e^{-b_3\tau}\left(-m + m\frac{d}{S(t)+d}\right)(P(t)-p_1) - a_1\theta e^{-b_3\tau}(P(t)-p_1)^2 \\
&\quad + \left(-b_2 + \theta m\frac{P(t)}{S(t)+d}e^{-b_3\tau}\right)S(t) - a_2 S^2(t) \\
&= -\theta m e^{-b_3\tau}\frac{S(t)(P(t)-p_1)}{S(t)+d} - a_1\theta e^{-b_3\tau}(P(t)-p_1)^2 \\
&\quad + \theta m e^{-b_3\tau}\left(-\frac{p_1}{R_0 d} + \frac{p_1}{d} - \frac{p_1}{d} + \frac{P(t)}{S(t)+d}\right)S(t) - a_2 S^2(t) \\
&= -\theta m e^{-b_3\tau}\frac{S(t)(P(t)-p_1)}{S(t)+d} - a_1\theta e^{-b_3\tau}(P(t)-p_1)^2 - a_2 S^2(t) \\
&\quad + \theta m e^{-b_3\tau}\frac{p_1}{R_0 d}(R_0-1)S(t) + \theta m e^{-b_3\tau}\frac{(P(t)-p_1)d - p_1 S(t)}{d(S(t)+d)}S(t) \\
&= -a_1\theta e^{-b_3\tau}(P(t)-p_1)^2 - a_2 S^2(t) \\
&\quad + \frac{\theta m e^{-b_3\tau}p_1}{R_0 d}(R_0-1)S(t) - \frac{\theta m e^{-b_3\tau}p_1}{d(S(t)+d)}S^2(t).
\end{aligned}
$$

Since $R_0 \leq 1$, it follows that $\frac{dV_2(P,S)(t)}{dt} \leq 0$, and $\frac{dV_2(P,S)(t)}{dt} = 0$ if and only if $(P,S)(t) \equiv (p_1,0)$. The proof is complete. □

4.2 Persistence

Now we study the uniform persistence of system (2.6) (see [16]). Denote $X_0 = \{\phi = (\phi_1,\phi_2) \in X : \phi_1(0) > 0, \phi_2(0) > 0\}$ and $\partial X_0 = X\backslash X_0$. Obviously, X_0 is an open set in X. Let $\Phi(t)\phi = (P_t,S_t)(\phi)$ be the solution semiflow of (2.6) defined in Theorem 3.1. Furthermore, (2.6) and the boundedness of $(P(t),S(t))$ yield the boundedness of $(P'(t),S'(t))$ for $t \geq 0$. Now, by the Arzéla-Ascoli theorem we know that every positive half-orbit of Φ: $\gamma^+\phi = \{\Phi(t)\phi : t \geq 0\}$ is precompact. As usual, for every equilibrium E of (2.6), we call

$$W^s(E) = \left\{\phi \in X : \lim_{t\to\infty}\left\|\Phi(t)\phi - E\right\| = 0\right\}$$

'the stable set of E'.

Theorem 4.3 *Assume that $R_0 > 1$. Then system (2.6) is uniformly persistent. That is, there exists a positive number ε such that $\liminf_{t\to\infty} P(t) > \varepsilon$ and $\liminf_{t\to\infty} S(t) > \varepsilon$.*

Proof Denote by $\omega(\phi)$ the omega limit set of the positive half-orbit $\gamma^+\phi = \{\Phi(t)\phi : t \geq 0\}$ and $X_\partial = \{\phi \in \partial X_0 : \Phi(t)\phi \in \partial X_0, t \geq 0\}$.

For all $\phi \in X_\partial$, we have $\Phi(t)\phi \in \partial X_0 = X\backslash X_0 = \{\phi = (\phi_1, \phi_2) \in X : \phi_1(0) = 0 \text{ or } \phi_2(0) = 0\}$ for any $t \geq 0$. This implies that either $P(t) = 0$ or $S(t) = 0$ for $t \geq 0$. If $P(t) = 0$ for some t_0, then for $t \geq 0$, $P(t) \equiv 0$, and further we have $\omega(\phi) = E_0$. Otherwise, $P(t) > 0$ and $S(t) \equiv 0$ for any $t \geq 0$, and then $\omega(\phi) = E_1$. Thus, $\bigcup_{\phi \in X_\partial} \omega(\phi) \subset M := \{E_0, E_1\}$, and no subset of M forms a cycle in ∂X_0.

We now prove that there exists $\delta > 0$ such that $\limsup_{t\to\infty} S(t) \geq \delta$ for all solutions $(P(t), S(t))$. If it is false, then for any $\delta > 0$, there exists a solution $(P(t), S(t))$ such that $\limsup_{t\to\infty} S(t) < \delta$. This leads to $S(t) < \delta$ for sufficiently large t. By the first equation of (2.6), for sufficiently large t, we have

$$\frac{dP(t)}{dt} = -b_1 P(t) - a_1 P^2(t) + m\frac{dP(t)}{S(t) + d} > -b_1 P(t) - a_1 P^2(t) + m\frac{dP(t)}{\delta + d}.$$

Therefore, $\liminf_{t\to\infty} P(t) \geq \frac{1}{a_1}(-b_1 + m\frac{d}{\delta+d})$ and $P(t) \geq \frac{1}{a_1}(-b_1 + m\frac{d}{\delta+d}) - \delta$ for sufficiently large t.

From the second equation of (2.6), for sufficiently large t, we have

$$\frac{dS(t)}{dt} = -b_2 S(t) - a_2 S^2(t) + \theta m\frac{P(t-\tau)S(t-\tau)}{S(t-\tau) + d}e^{-b_3\tau}$$

$$\geq -b_2 S(t) - a_2 S^2(t) + \theta m\frac{(\frac{1}{a_1}(-b_1 + m\frac{d}{\delta+d}) - \delta)S(t-\tau)}{S(t-\tau) + d}e^{-b_3\tau}.$$

Note the characteristic equation of

$$\frac{dV(t)}{dt} = -b_2 V(t) - a_2 V^2(t) + \theta m\frac{(\frac{1}{a_1}(-b_1 + m\frac{d}{\delta+d}) - \delta)V(t-\tau)}{V(t-\tau) + d}e^{-b_3\tau} \tag{4.7}$$

is

$$\lambda = -b_2 + \theta m\frac{(\frac{1}{a_1}(-b_1 + m\frac{d}{\delta+d}) - \delta)}{d}e^{-\lambda\tau}e^{-b_3\tau}. \tag{4.8}$$

In view of the assumption $\theta m e^{-b_3\tau}(m - b_1) > da_1 b_2$, we can choose δ small enough such that $\theta m e^{-b_3\tau}(\frac{m-b_1}{a_1} - \frac{m\delta}{a_1(\delta+d)} - \delta) > db_2$. This implies that (4.8) has a positive root and the solution $V(t)$ of (4.7) grows exponentially. Furthermore, by comparison argument, $S(t)$ can also grow exponentially, in contradiction with the boundedness of $S(t)$. Therefore, $\limsup_{t\to\infty} S(t) \geq \delta$ for all solutions $(P(t), S(t))$. This leads to

$$\limsup_{t\to\infty} \|\Phi(t)\phi - E_0\| \geq \delta, \qquad \limsup_{t\to\infty} \|\Phi(t)\phi - E_1\| \geq \delta.$$

For any $\phi = (\phi_1, \phi_2) \in X$, define the generalized distance function d mapping X into $\mathbb{R}_+$ by

$$d(\phi) = \min\{\phi_1(0), \phi_2(0)\}.$$

Then it follows that E_0 and E_1 are both isolated in X and

$$W^s(E_0) \cap d^{-1}(0,\infty) = \emptyset, \qquad W^s(E_1) \cap d^{-1}(0,\infty) = \emptyset,$$

where $d^{-1}(0,\infty) = \{\phi \in X : d(\phi) > 0\}$.

According to [16], Theorem 3, there exists a positive number ε such that $\liminf_{t\to\infty} P(t) > \varepsilon$ and $\liminf_{t\to\infty} S(t) > \varepsilon$. The proof is complete. □

4.3 Stability of coexistence equilibrium and Hopf bifurcation

In this section, we need some notation:

$$u_1 := a_1 p^* + a_2 s^* + \theta m \frac{p^*}{s^* + d} e^{-b_3\tau}, \qquad u_0 := a_1 p^* \left(a_2 s^* + \theta m \frac{p^*}{s^* + d} e^{-b_3\tau} \right),$$

$$v_1 := -\theta m \frac{dp^*}{(s^* + d)^2} e^{-b_3\tau}, \qquad v_0 := -\theta m \frac{a_1 d(p^*)^2}{(s^* + d)^2} e^{-b_3\tau} + \theta m^2 \frac{dp^* s^*}{(s^* + d)^3} e^{-b_3\tau},$$

$$\omega_0 := \sqrt{\frac{-(u_1^2 - v_1^2 - 2u_0) + \sqrt{(u_1^2 - v_1^2 - 2u_0)^2 - 4(u_0^2 - v_0^2)}}{2}},$$

$$\tau_0 := \frac{1}{\omega_0} \arccos \frac{v_0(\omega_0^2 - u_0) - u_1 v_1 \omega_0^2}{v_0^2 + v_1^2 \omega_0^2}.$$

Our main results in this subsection are described in the following theorem concerning the stability of coexistence equilibrium and Hopf bifurcation.

Theorem 4.4 *Assume that $R_0 > 1$. Then we have the following conclusions.*
  (1) *The coexistence equilibrium E_* is globally asymptotic stable for $\tau = 0$.*
  (2) *If $u_0 > v_0$, then the coexistence equilibrium E_* is locally asymptotic stable for any $\tau \geq 0$.*
  (3) *If $u_0 < v_0$, then the coexistence equilibrium E_* is locally asymptotic stable for $0 \leq \tau < \tau_0$ and unstable for $\tau > \tau_0$. Furthermore, (2.6) undergoes a Hopf bifurcation at E_* when $\tau = \tau_0$. Here u_0, v_0, τ_0 are constants defined previously.*

Proof The linearized system of (2.6) at E_* is

$$\begin{cases} \frac{dP(t)}{dt} = -b_1 P(t) - 2a_1 p^* P(t) + m\frac{dP(t)}{s^*+d} - m\frac{dp^* S(t)}{(s^*+d)^2}, \\ \frac{dS(t)}{dt} = -b_2 S(t) - 2a_2 s^* S(t) + \theta m\frac{s^* P(t-\tau)}{s^*+d} e^{-b_3\tau} + \theta m\frac{dp^* S(t-\tau)}{(s^*+d)^2} e^{-b_3\tau}, \end{cases} \tag{4.9}$$

and the characteristic equation of (4.9) takes the form

$$\left(\lambda + a_1 p^*\right) \left[\lambda + a_2 s^* + \theta m \left(\frac{p^*}{s^* + d} - \frac{dp^* e^{-\lambda\tau}}{(s^* + d)^2} \right) e^{-b_3\tau} \right]$$

$$+ \theta m^2 \frac{dp^* s^*}{(s^* + d)^3} e^{-b_3\tau} e^{-\lambda\tau} = 0. \tag{4.10}$$

Case 1. If $\tau = 0$, then (4.10) becomes

$$\left(\lambda + a_1 p^*\right) \left(\lambda + a_2 s^* + \theta m \frac{p^* s^*}{(s^* + d)^2} \right) + \theta m^2 \frac{dp^* s^*}{(s^* + d)^3} = 0.$$

It is easy to see this equation has exactly two negative roots, and thus the coexistence equilibrium E_* is locally asymptotic stable.

Define the Lyapunov function

$$V_3(P,S)(t) = \theta\left(P(t) - p^* - p^* \ln \frac{P(t)}{p^*}\right) + \frac{d}{s^* + d}\left(S(t) - s^* - s^* \ln \frac{S(t)}{s^*}\right).$$

Then the derivative along system (2.6) is

$$
\begin{aligned}
\frac{dV_3(P,S)(t)}{dt} &= \theta P'(t)\left(1 - \frac{p^*}{P(t)}\right) + \frac{d}{s^* + d}S'(t)\left(1 - \frac{s^*}{S(t)}\right) \\
&= \theta\left(-b_1 P(t) - a_1 P^2(t) + m\frac{dP(t)}{S(t) + d}\right)\left(1 - \frac{p^*}{P(t)}\right) \\
&\quad + \frac{d}{s^* + d}\left(-b_2 S(t) - a_2 S^2(t) + \theta m\frac{P(t)S(t)}{S(t) + d}\right)\left(1 - \frac{s^*}{S(t)}\right) \\
&= -\theta a_1\left(P(t) - p^*\right)^2 - \frac{a_2 d}{s^* + d}\left(S(t) - s^*\right)^2 \\
&\quad + \theta md\left(\frac{1}{S(t) + d} - \frac{1}{s^* + d}\right)\left(P(t) - p^*\right) \\
&\quad - \frac{\theta md}{s^* + d}\left(\frac{p^*}{s^* + d} - \frac{P(t)}{S(t) + d}\right)\left(S(t) - s^*\right) \\
&= -\theta a_1\left(P(t) - p^*\right)^2 - \frac{a_2 d}{s^* + d}\left(S(t) - s^*\right)^2 \\
&\quad + \theta md\frac{s^* - S(t)}{(s^* + d)(S(t) + d)}\left(P(t) - p^*\right) \\
&\quad - \frac{\theta md}{s^* + d}\frac{p^*(S(t) - s^*) + (s^* + d)(p^* - P(t))}{(s^* + d)(S(t) + d)}\left(S(t) - s^*\right) \\
&= -\theta a_1\left(P(t) - p^*\right)^2 - \frac{a_2 d}{s^* + d}\left(S(t) - s^*\right)^2 - \frac{\theta md}{s^* + d}\frac{p^*(S(t) - s^*)^2}{(s^* + d)(S(t) + d)} \le 0.
\end{aligned}
$$

Furthermore, $\frac{dV_3(P,S)(t)}{dt} = 0$ if and only if $(P,S)(t) \equiv (p^*, s^*)$. Thus, E_* is globally asymptotically stable when $\tau = 0$.

Case 2. If $\tau > 0$, denote

$$u(\lambda) = \lambda^2 + u_1\lambda + u_0, \qquad v(\lambda) = v_1\lambda + v_0.$$

Then (4.10) can be rewritten as $g(\lambda, \tau) = 0$, where

$$g(\lambda, \tau) := u(\lambda) + v(\lambda)e^{-\lambda\tau} = \left(\lambda^2 + u_1\lambda + u_0\right) + (v_1\lambda + v_0)e^{-\lambda\tau}.$$

By calculation we have

$$
\begin{aligned}
&u_1^2 - v_1^2 - 2u_0 \\
&= \left(a_1 p^*\right)^2 + \left(a_2 s^* + \theta m\frac{p^*}{s^* + d}e^{-b_3\tau}\right)^2 - \left(\theta m\frac{dp^*}{(s^* + d)^2}e^{-b_3\tau}\right)^2
\end{aligned}
$$

$$= \left(a_1 p^*\right)^2 + \left(a_2 s^* + \theta m \frac{p^*}{s^* + d} e^{-b_3 \tau} + \theta m \frac{dp^*}{(s^* + d)^2} e^{-b_3 \tau}\right)\left(a_2 s^* + \theta m \frac{p^* s^*}{(s^* + d)^2} e^{-b_3 \tau}\right)$$

$$> 0$$

and

$$u_0 + v_0 = a_1 a_2 p^* s^* + \theta m \frac{a_1 (p^*)^2}{s^* + d} e^{-b_3 \tau} - \theta m \frac{a_1 d (p^*)^2}{(s^* + d)^2} e^{-b_3 \tau} + \theta m^2 \frac{dp^* s^*}{(s^* + d)^3} e^{-b_3 \tau}$$

$$= a_1 a_2 p^* s^* + \theta m \frac{a_1 s^* (p^*)^2}{(s^* + d)^2} e^{-b_3 \tau} + \theta m^2 \frac{dp^* s^*}{(s^* + d)^3} e^{-b_3 \tau}$$

$$> 0.$$

This leads to that the sign of $u_0^2 - v_0^2$ is consistent with the sign of $u_0 - v_0$.

Assuming that $\pm i\omega$ is a pair of pure imaginary roots of (4.10) such that

$$g(i\omega, \tau) = u(i\omega) + v(i\omega)e^{-i\omega\tau} = 0,$$

which yields $u(i\omega) = -v(i\omega)e^{-i\omega\tau}$, and thus $|u(i\omega)|^2 - |v(i\omega)|^2 = 0$. Now there exist two sub-cases, $u_0 > v_0$ and $u_0 < v_0$.

Subcase 2a. If $u_0 > v_0$, according to [17] (also see [18], Theorem 4.1),

$$G(\omega) := \left|u(i\omega)\right|^2 - \left|v(i\omega)\right|^2 = \omega^4 + \left(u_1^2 - v_1^2 - 2u_0\right)\omega^2 + u_0^2 - v_0^2$$

has no positive roots, and thus no stability switch occurs, that is, the coexistence equilibrium E_* is locally asymptotic stable for any $\tau \geq 0$ from its stability for $\tau = 0$.

Subcase 2b. If $u_0 < v_0$, $G(\omega)$ has a unique simple positive root

$$\omega_0 = \sqrt{\frac{-(u_1^2 - v_1^2 - 2u_0) + \sqrt{(u_1^2 - v_1^2 - 2u_0)^2 - 4(u_0^2 - v_0^2)}}{2}},$$

and as τ increases, stability switch occurs. Eventually the coexistence equilibrium E_* becomes unstable. In detail, $\pm i\omega_0$ is a pair of pure imaginary roots of (4.10) such that

$$g(i\omega_0, \tau) = \left(-\omega_0^2 + iu_1\omega_0 + u_0\right) + (iv_1\omega_0 + v_0)e^{-i\omega_0\tau} = 0.$$

Separating its real and imaginary parts, we have

$$u_0 - \omega_0^2 + v_1\omega_0 \sin\omega_0\tau + v_0 \cos\omega_0\tau = 0,$$

$$u_1\omega_0 + v_1\omega_0 \cos\omega_0\tau - v_0 \sin\omega_0\tau = 0.$$

Thus we obtain the following critical values for delay τ:

$$\tau_k = \frac{1}{\omega_0} \arccos \frac{v_0(\omega_0^2 - u_0) - u_1 v_1 \omega_0^2}{v_0^2 + v_1^2 \omega_0^2} + \frac{2k\pi}{\omega_0}, \quad k = 0, 1, 2, \ldots.$$

By the differentiation method of implicit functions we obtain from $g(\lambda, \tau) = 0$ that

$$
\begin{aligned}
\frac{d\tau}{d\lambda} &= \left(\frac{d\lambda}{d\tau}\right)^{-1} \\
&= \frac{2\lambda + u_1}{\lambda(v_1\lambda + v_0)e^{-\lambda\tau}} + \frac{v_1}{\lambda(v_1\lambda + v_0)} - \frac{\tau}{\lambda} \\
&= -\frac{2\lambda + u_1}{\lambda(\lambda^2 + u_1\lambda + u_0)} + \frac{v_1}{\lambda(v_1\lambda + v_0)} - \frac{\tau}{\lambda}.
\end{aligned}
$$

Note that

$$
G(\omega_0) = \omega_0^4 + (u_1^2 - v_1^2 - 2u_0)\omega_0^2 + u_0^2 - v_0^2 = u_1^2\omega_0^2 + (u_0 - \omega_0^2)^2 - (v_1^2\omega_0^2 + v_0^2) = 0,
$$

and then we have

$$
\begin{aligned}
\operatorname{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1}\bigg|_{\tau=\tau_k, \lambda=i\omega_0} &= \operatorname{Re}\left(-\frac{2i\omega_0 + u_1}{i\omega_0(-\omega_0^2 + i\omega_0 u_1 + u_0)} + \frac{v_1}{i\omega_0(i\omega_0 v_1 + v_0)}\right) \\
&= -\frac{-u_1^2 + 2(u_0 - w_0^2)}{u_1^2\omega_0^2 + (u_0 - \omega_0^2)^2} - \frac{v_1^2}{v_1^2\omega_0^2 + v_0^2} \\
&= \frac{(2\omega_0^2 + u_1^2 - v_1^2 - 2u_0)(v_1^2\omega_0^2 + v_0^2) - v_1^2 G(\omega_0)}{[u_1^2\omega_0^2 + (u_0 - \omega_0^2)^2](v_1^2\omega_0^2 + v_0^2)} \\
&= \frac{2\omega_0^2 + u_1^2 - v_1^2 - 2u_0}{u_1^2\omega_0^2 + (u_0 - \omega_0^2)^2} = \frac{\sqrt{(u_1^2 - v_1^2 - 2u_0)^2 - 4(u_0^2 - v_0^2)}}{u_1^2\omega_0^2 + (u_0 - \omega_0^2)^2} > 0.
\end{aligned}
$$

Combining the stability of E_* for $\tau = 0$, this implies that the transversal condition for Hopf bifurcation holds at $\tau = \tau_0$. The proof is complete.   □

In fact, we could discuss the direction and stability of the Hopf bifurcation by using the normal form theory and the center manifold reduction introduced by Hassard *et al.* [19]. However, the algorithm is standard, and the application of the result needs complex computations. Therefore, we just do some numerical simulations in the next section instead.
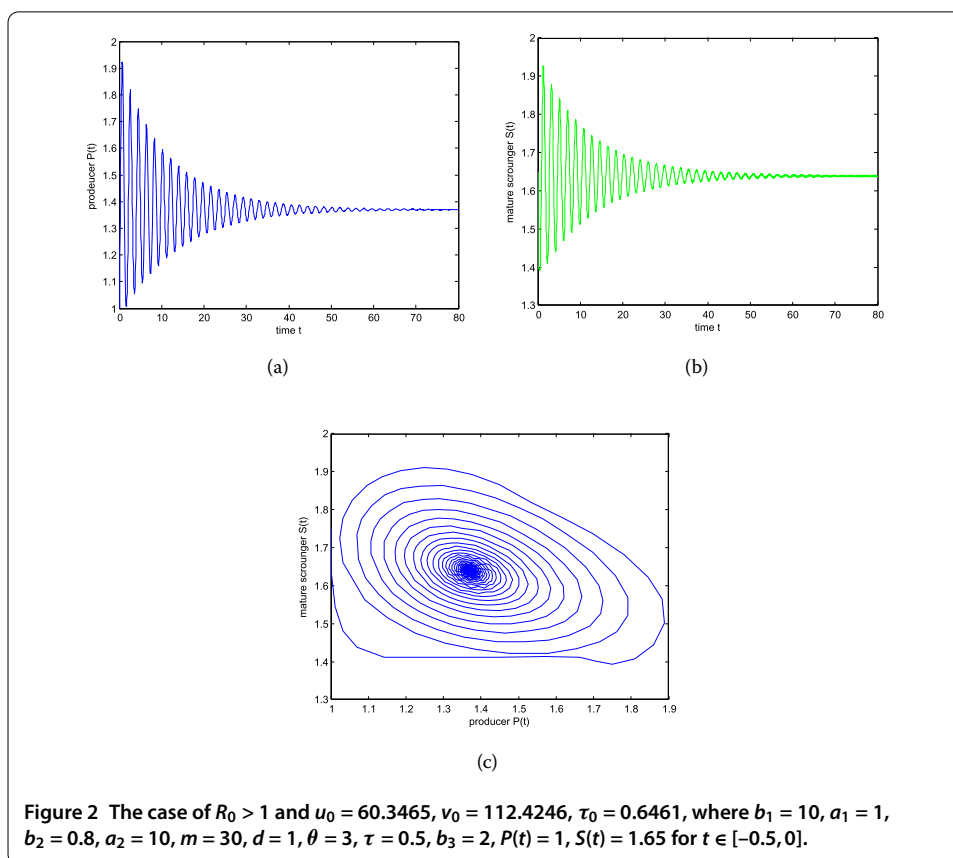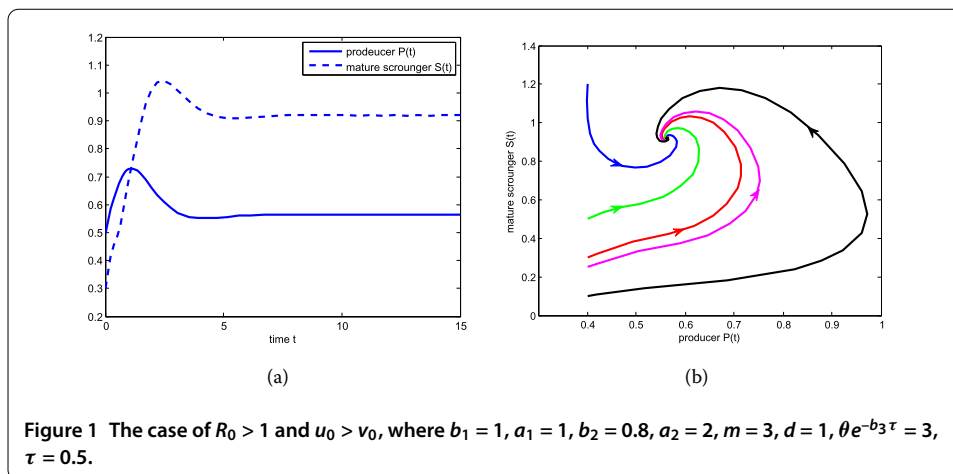
5 Numerical simulations and concluding discussions
We now give numerical simulations as $R_0 > 1$ for (2.6) with some different values of parameters (see Figures 1-5). We can see from Figures 4 and 5 that the dynamical behavior would be very complex when $R_0 > 1$ and $u_0 < v_0$ with large τ. That is, the time delay τ has really a huge impact on the dynamical behavior of (2.6).

In the following, we give some discussion on the influence of maturation period τ in the scrounge interaction.

The existence of producer. The existence of producer is just determined by their ability to discover food (m) and the natural mortality rate b_1. However, the mature time τ does not determine the existence of producer.

The existence of scrounger. The basic reproduction ratio R_0 determines the existence of scrounger. Note that $R_0 = \theta m \frac{p_1}{db_2} e^{-b_3\tau}$ decreases as τ increases, and it is a bounded function of variable τ. We find that (i) if $\theta m p_1 < db_2$, no matter how long the mature time

Figure 1 The case of $R_0 > 1$ and $u_0 > v_0$, where $b_1 = 1$, $a_1 = 1$, $b_2 = 0.8$, $a_2 = 2$, $m = 3$, $d = 1$, $\theta e^{-b_3 \tau} = 3$, $\tau = 0.5$.


Figure 2 The case of $R_0 > 1$ and $u_0 = 60.3465$, $v_0 = 112.4246$, $\tau_0 = 0.6461$, where $b_1 = 10$, $a_1 = 1$, $b_2 = 0.8$, $a_2 = 10$, $m = 30$, $d = 1$, $\theta = 3$, $\tau = 0.5$, $b_3 = 2$, $P(t) = 1$, $S(t) = 1.65$ for $t \in [-0.5, 0]$.

is, the scrounger finally extincts; (ii) if $\theta m p_1 > d b_2$, shorter mature time is in favor of the existence of scrounger.

Global behaviors for $R_0 > 1$. In the case $R_0 > 1$, we have no results of the global stability for $\tau > 0$. But in view of the global convergence to the coexistence equilibrium E_* at $\tau = 0$ and numerical simulations, we found that the mature time τ does change the dynamical behavior of the model. We conjecture that (i) when $u_0 > v_0$, the coexistence equilibrium is globally asymptotically stable for $\tau > 0$; (ii) when $u_0 < v_0$, the coexistence equilibrium
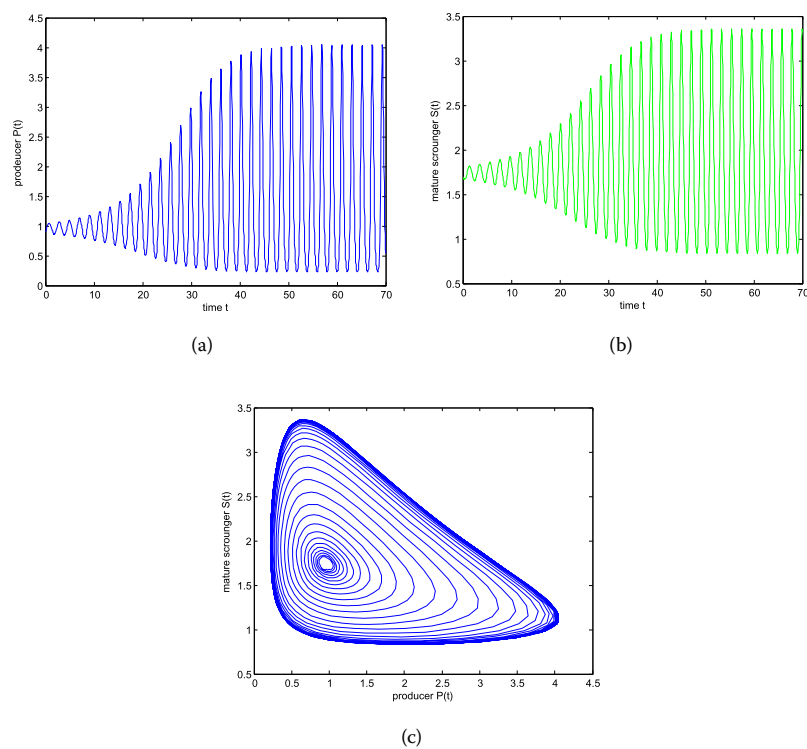
Figure 3 The case of $R_0 > 1$ and $u_0 = 44.0951$, $v_0 = 120.0637$, $\tau_0 = 0.5223$, where $b_1 = 10$, $a_1 = 1$, $b_2 = 0.8$, $a_2 = 10$, $m = 30$, $d = 1$, $\theta = 3$, $\tau = 0.55$, $b_3 = 1$, $P(t) = 0.9$, $S(t) = 1.7$ for $t \in [-0.55, 0]$.
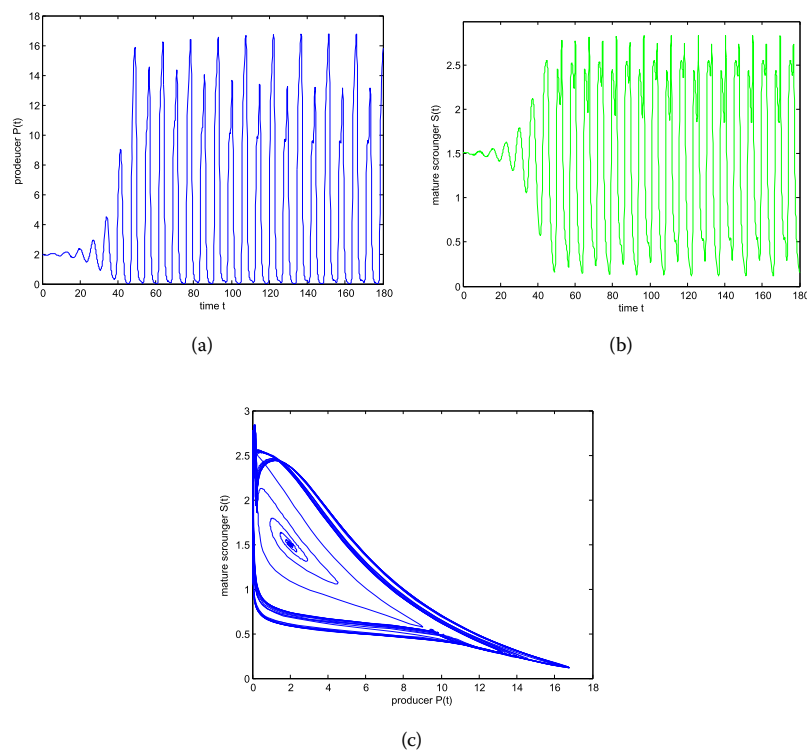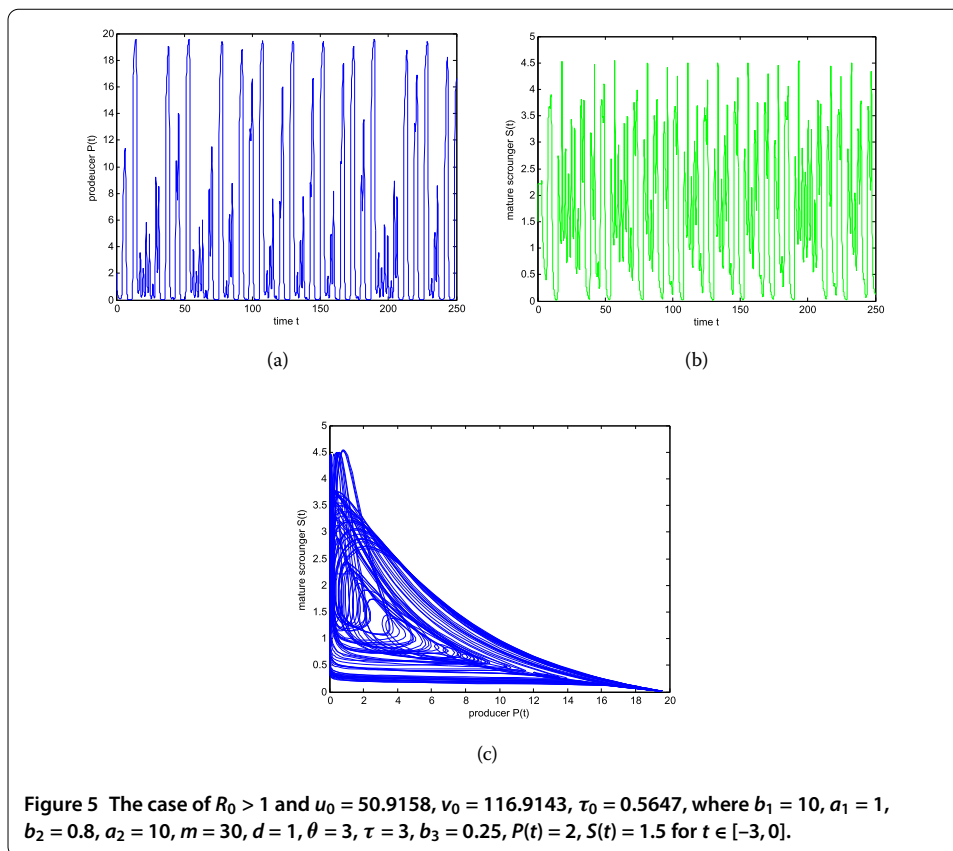

Figure 4 The case of $R_0 > 1$ and $u_0 = 81.8961$, $v_0 = 101.5272$, $\tau_0 = 1.1423$, where $b_1 = 10$, $a_1 = 1$, $b_2 = 0.8$, $a_2 = 10$, $m = 30$, $d = 1$, $\theta = 3$, $\tau = 3$, $b_3 = 0.5$, $P(t) = 2$, $S(t) = 1.5$ for $t \in [-3, 0]$.

Figure 5 The case of $R_0 > 1$ and $u_0 = 50.9158$, $v_0 = 116.9143$, $\tau_0 = 0.5647$, where $b_1 = 10$, $a_1 = 1$, $b_2 = 0.8$, $a_2 = 10$, $m = 30$, $d = 1$, $\theta = 3$, $\tau = 3$, $b_3 = 0.25$, $P(t) = 2$, $S(t) = 1.5$ for $t \in [-3, 0]$.

remains globally asymptotically stable for small $\tau > 0$; (iii) when $u_0 < v_0$, the positive solutions convergence to a periodic solution for large τ.

Note that we also derived another model (2.7) in Section 2, whereas there exists competition between immature scroungers. The investigation of this model seems challenging. We leave it as an open problem.

We want to make some more comments on open problems. In this article and [4], we both assume that the proportion of the resource ultimately acquired by producer after the interaction is $\frac{d}{S+d}$, where S is the number of scroungers. However, there may be some other models for different species groups by using different proportion functions. In this meaning, we can consider the following more general model for (1.1) with homogenous spatial environment:

$$\begin{cases} \frac{dP(t)}{dt} = -b_1 P(t) - a_1 P^2(t) + mg(P, S, d)P(t), \\ \frac{dS(t)}{dt} - b_2 S(t) - a_2 S^2(t) + \theta m(1 - g(P, S, d))P(t). \end{cases} \tag{5.1}$$

If $g(P, S, d) \equiv 1$, that is, the scrounger is incapable of stealing food from producer, (5.1) becomes

$$\begin{cases} \frac{dP(t)}{dt} = (m - b_1)P(t) - a_1 P^2(t), \\ \frac{dS(t)}{dt} - b_2 S(t) - a_2 S^2(t). \end{cases} \tag{5.2}$$

If $g(P, S, d) = \frac{d}{S+d}$, (5.1) becomes (1.1) with homogenous spatial environment.

We can also consider other cases such as $g(P, S, d) = \frac{d^2}{S+d^2}$ for different species and such that even g actually depends on the producer P. Furthermore, one can derive a new model that involves a continuous immature age structure. We leave these problems for future research.

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