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SENSITIVITY ANALYSIS FOR A NONLINEAR SIZE-STRUCTURED POPULATION MODEL

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Abstract. In this paper, we consider a nonlinear size-structured population model with vital rates depending on the total population. We derive sensitivity partial differential equations for the sensitivities of the solution with respect to the reproduction and mortality rates. We also present numerical results to illustrate the use of these sensitivity equations.

1. Introduction. In this paper, we consider the following nonlinear size-structured population model:

$$\begin{aligned} &u_t + (g(x)u)_x + m(x, P(t))u = 0, && (x,t) \in (0,\bar{x}) \times (0,T), \\ &g(0)u(0,t) = C(t) + \textstyle\int_0^{\bar{x}} \beta(x, P(t))u(x,t)dx, && t \in (0,T), \\ &u(x,0) = u_0(x), && x \in [0,\bar{x}]. \end{aligned} \tag{1.1}$$

Here $u(x,t)$ is the population density of size x at time t, and $\bar{x}$ is the maximum size of individuals. $P(t) = \int_0^{\bar{x}} u(x,t)dx$ is the total population at time t. The function g is the growth rate of an individual. The functions m and β denote the mortality and reproduction rates, respectively. $C(t)$ represents the inflow of zero-size individuals from an external source.

Size-structured population models such as (1.1) have been extensively studied in recent years. Existence-uniqueness results have been established using the characteristic method with fixed point argument, the semigroup of linear operators theoretic approach, the finite-difference approximation, or the monotone scheme based on a comparison principle [3–5, 9, 10, 12]. Meanwhile, the asymptotic behavior of the model has been analyzed by

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semigroup and spectral methods [12, 13, 16]. In addition, computational methodologies for fitting parameters have been discussed for certain size-structured population models [1, 7, 11].

Our objective here is to conduct sensitivity analysis for model (1.1). The importance of sensitivity equations has been recognized, as they provide a measure of model response (output) to variation in the underlying model parameters (e.g., see [14, 17] and the references therein). The derivation of sensitivity equations for discrete structured population models (matrix models) has drawn a lot of attention in the past few decades (see [14] and the references therein). However, little work has been done on the derivation of sensitivity equations for continuous structured population models. Such equations are useful for computing variances of estimated model parameters from observation data (e.g., see [2, 6, 15]). Our direct motivation comes from the paper [8], wherein sensitivity partial differential equations were derived for the following linear size-structured population model:

$$\begin{aligned} &u_t + (g(x)u)_x + m(x)u = 0, && (x,t) \in (0,\bar{x}) \times (0,T), \\ &g(0)u(0,t) = \textstyle\int_0^{\bar{x}} \beta(x)u(x,t)dx, && t \in (0,T), \\ &u(x,0) = u_0(x), && x \in [0,\bar{x}]. \end{aligned} \tag{1.2}$$

There is a main difference between models (1.1) and (1.2). All vital rates in (1.2) are linear, but the mortality and reproduction rates in (1.1) are dependent on the total population. Due to the nonlinear structure of model (1.1), the situation becomes more complicated, and certain techniques used for (1.2) seem not applicable to (1.1).

The paper is organized as follows. In section 2, we establish an existence result for directional derivatives with respect to parameters. In section 3, we derive sensitivity partial differential equations for the sensitivities of the solution with respect to the reproduction and mortality rates. In section 4, we present numerical results to illustrate the use of these sensitivity equations.

2. Existence of the directional derivative. Throughout the discussion, we assume that the parameters in (1.1) satisfy the following:

(A1) $g(x)$ is continuously differentiable. Furthermore, $g(x) > 0$ for $x \in [0,\bar{x})$ and $g(\bar{x}) = 0$.

(A2) $m(x,P)$ is continuous with respect to x and continuously differentiable with respect to P. Furthermore, $m \geq 0$ and $m_P \geq 0$.

(A3) $\beta(x,P)$ is continuous with respect to x and continuously differentiable with respect to P. Furthermore, $\beta \geq 0$ and $\beta_P \leq 0$.

(A4) $C(t)$ is continuous and nonnegative.

(A5) $u_0(x)$ is integrable, bounded and nonnegative.

We first introduce the solution representation for problem (1.1) via the method of characteristics. For the equation in (1.1), the characteristic curves are given by

$$\begin{cases} \dfrac{d}{ds}t(s) = 1, \\ \dfrac{d}{ds}x(s) = g(x(s)). \end{cases} \tag{2.1}$$

Under assumption (A1), equation (2.1) has a unique solution for any initial point $(x(s_0), t(s_0))$. Parameterizing the characteristic curves with the variable t, a characteristic curve passing through $(\hat{x}, \hat{t})$ is given by $(X(t; \hat{x}, \hat{t}), t)$, where X satisfies

$$\frac{d}{dt} X(t; \hat{x}, \hat{t}) = g(X(t; \hat{x}, \hat{t}))$$

and $X(\hat{t}; \hat{x}, \hat{t}) = \hat{x}$. By (A1) the function X is strictly increasing, and therefore a unique inverse function $\Gamma(x; \hat{x}, \hat{t})$ exists. Let $z(t) = X(t; 0, 0)$; then $(z(t), t)$ represents the characteristic curve passing through $(0, 0)$, and this curve divides the (x, t)-plane into two parts. Hence, the solution of (1.1) can be represented as follows:

$$u(x,t) = \begin{cases} \frac{B(\Gamma(0))}{g(0)} \exp\left(-\int_{\Gamma(0)}^{t} (g_x(X(s)) + m(X(s), P(s)))ds\right), & \text{if } x < z(t), \\ u_0(X(0)) \exp\left(-\int_0^t (g_x(X(s)) + m(X(s), P(s)))ds\right), & \text{if } x \geq z(t), \end{cases} \tag{2.2}$$

where for simplicity $X(s) = X(s; x, t)$, $\Gamma(0) = \Gamma(0; x, t)$, and $B(t)$ is given by

$$B(t) = C(t) + \int_0^{\bar{x}} \beta(x, P(t)) u(x,t) dx, \tag{2.3}$$

the inflow of newborns in the population at time t.

Integrating (2.2) with respect to x, we obtain an integral equation for $P(t)$:

$$\begin{aligned} P(t) &= \int_0^{z(t)} \frac{B(\Gamma(0))}{g(0)} \exp\left(-\int_{\Gamma(0)}^{t} (g_x(X(s)) + m(X(s), P(s)))ds\right) dx \\ &\quad + \int_{z(t)}^{\bar{x}} u_0(X(0)) \exp\left(-\int_0^t (g_x(X(s)) + m(X(s), P(s)))ds\right) dx \\ &= \int_0^t B(\tau) \exp\left(-\int_\tau^t m(X(s; 0, \tau), P(s))ds\right) d\tau \\ &\quad + \int_0^{\bar{x}} u_0(\xi) \exp\left(-\int_0^t m(X(s; \xi, 0), P(s))ds\right) d\xi, \end{aligned} \tag{2.4}$$

where we have changed the variable x in the first integral on the right hand side by $\tau = \Gamma(0; x, t)$ and in the second integral by $\xi = X(0; x, t)$.

Substituting (2.2) into (2.3) and integrating with respect to x, we also obtain an integral equation for $B(t)$:

$$\begin{aligned} B(t) &= C(t) + \int_0^{z(t)} \beta(x, P(t)) \frac{B(\Gamma(0))}{g(0)} \exp\left(-\int_{\Gamma(0)}^{t} (g_x(X(s)) + m(X(s), P(s)))ds\right) dx \\ &\quad + \int_{z(t)}^{\bar{x}} \beta(x, P(t)) u_0(X(0)) \exp\left(-\int_0^t (g_x(X(s)) + m(X(s), P(s)))ds\right) dx \\ &= C(t) + \int_0^t \beta(X(t; 0, \tau), P(t)) B(\tau) \exp\left(-\int_\tau^t m(X(s; 0, \tau), P(s))ds\right) d\tau \\ &\quad + \int_0^{\bar{x}} \beta(X(t; \xi, 0), P(t)) u_0(\xi) \exp\left(-\int_0^t m(X(s; \xi, 0), P(s))ds\right) d\xi. \end{aligned} \tag{2.5}$$

Thus (2.4) and (2.5) form a system of integral equations.

As in [8], we then introduce the directional derivative of a function f with respect to a parameter θ.

Definition 2.1. Let Θ be a convex subset in some topological vector space, and let $f : \mathbb{R}_+ \times \Theta \to \mathbb{R}$. Given θ and $\hat{\theta}$ in Θ, we define the derivative $f_\theta(t; \theta, \hat{\theta} - \theta)$ of f at θ in the direction $\hat{\theta} - \theta$ to be

$$f_\theta(t; \theta, \hat{\theta} - \theta) = \lim_{\varepsilon \to 0^+} \frac{f(t; \theta + \varepsilon(\hat{\theta} - \theta)) - f(t; \theta)}{\varepsilon}, \tag{2.6}$$

provided this limit exists.

We now establish an existence result which will play an important role in our sensitivity analysis. To simplify our discussion, we may rewrite $P(t)$ and $B(t)$ as follows:

$$\begin{aligned} P(t) &= \int_0^t B(\tau)\varphi(\tau)d\tau + \int_0^{\bar{x}} u_0(\xi)\psi(\xi)d\xi, \\ B(t) &= C(t) + \int_0^t \beta(P(t))B(\tau)\varphi(\tau)d\tau + \int_0^{\bar{x}} \beta(P(t))u_0(\xi)\psi(\xi)d\xi, \end{aligned} \tag{2.7}$$

where $\varphi(\tau) = \exp\left(-\int_\tau^t m(X(s;0,\tau),P(s))ds\right)$, $\psi(\xi) = \exp\left(-\int_0^t m(X(s;\xi,0),P(s))ds\right)$, and since $X(t;0,\tau)$ and $X(t;\xi,0)$ are independent of the parameter θ, $\beta(P(t))$ is written in place of $\beta(X(t;0,\tau),P(t))$ and $\beta(X(t;\xi,0),P(t))$.

THEOREM 2.2. For θ and $\hat{\theta}$ in Θ, suppose that β and m each have a bounded directional derivative $\beta_\theta(x,P(t);\theta,\hat{\theta}-\theta)$ and $m_\theta(x,P(t);\theta,\hat{\theta}-\theta)$ on $[0,T]$, respectively, in the direction $\hat{\theta}-\theta$. Furthermore, we assume that β_P and m_P are continuously dependent on θ. Then the directional derivatives $P_\theta(t;\theta,\hat{\theta}-\theta)$ of P and $B_\theta(t;\theta,\hat{\theta}-\theta)$ of B in the direction $\hat{\theta}-\theta$ exist. Let $\Phi(t) = P_\theta(t;\theta,\hat{\theta}-\theta)$ and $\Psi(t) = B_\theta(t;\theta,\hat{\theta}-\theta)$. Φ and Ψ satisfy the following system of integral equations:

$$\Phi(t) = \int_0^t \Psi(\tau)\varphi(\tau;\theta)d\tau + \int_0^t B(\tau;\theta)\varphi_\theta(\tau;\theta)d\tau + \int_0^{\bar{x}} u_0(\xi)\psi_\theta(\xi;\theta)d\xi, \tag{2.8}$$

$$\begin{aligned} \Psi(t) = &\int_0^t \beta_P(P(t;\theta);\theta)\Phi(t)B(\tau;\theta)\varphi(\tau;\theta)d\tau + \int_0^t \beta_\theta(P(t;\theta);\theta)B(\tau;\theta)\varphi(\tau;\theta)d\tau \\ &+ \int_0^t \beta(P(t;\theta);\theta)\Psi(\tau)\varphi(\tau;\theta)d\tau + \int_0^t \beta(P(t;\theta);\theta)B(\tau;\theta)\varphi_\theta(\tau;\theta)d\tau \\ &+ \int_0^{\bar{x}} \beta_P(P(t;\theta);\theta)\Phi(t)u_0(\xi)\psi(\xi;\theta)d\xi + \int_0^{\bar{x}} \beta_\theta(P(t;\theta);\theta)u_0(\xi)\psi(\xi;\theta)d\xi \\ &+ \int_0^{\bar{x}} \beta(P(t;\theta);\theta)u_0(\xi)\psi_\theta(\xi;\theta)d\xi, \end{aligned} \tag{2.9}$$

where

$$\begin{aligned} \varphi_\theta(\tau;\theta) &= -\varphi(\tau;\theta)\int_\tau^t \left(m_\theta(X(s;0,\tau),P(s;\theta);\theta) + m_P(X(s;0,\tau),P(s;\theta);\theta)\Phi(s)\right)ds, \\ \psi_\theta(\xi;\theta) &= -\psi(\xi;\theta)\int_0^t \left(m_\theta(X(s;\xi,0),P(s;\theta);\theta) + m_P(X(s;\xi,0),P(s;\theta);\theta)\Phi(s)\right)ds. \end{aligned} \tag{2.10}$$

Proof. We first show that there exists a unique bounded solution $(\Phi(t),\Psi(t))$ of (2.8)-(2.9). By assumptions (A2)-(A3) and the fact that $P(t)$ is bounded on $[0,T]$, the vital rates β, m and their derivatives are bounded. Because m is nonnegative, φ and ψ are uniformly bounded. Moreover, by assumptions (A3)-(A4), $B(t)$ is bounded on $[0,T]$. Since (2.8)-(2.9) is a linear system of integral equations, it has a unique solution. Noticing (2.10), the boundedness of the solution follows from the application of Gronwall's inequality.

We then prove that $P(t;\theta)$ and $B(t;\theta)$ are continuously dependent on θ. Let $e_1(t;\theta,\hat{\theta},\varepsilon) = P(t;\theta+\varepsilon(\hat{\theta}-\theta)) - P(t;\theta)$ and $e_2(t;\theta,\hat{\theta},\varepsilon) = B(t;\theta+\varepsilon(\hat{\theta}-\theta)) - B(t;\theta)$. e_1 and e_2 satisfy

$$\begin{aligned} e_1(t;\theta,\hat{\theta},\varepsilon) = &\int_0^t (B(\tau;\theta+\varepsilon(\hat{\theta}-\theta))\varphi(\tau;\theta+\varepsilon(\hat{\theta}-\theta)) - B(\tau;\theta)\varphi(\tau;\theta))d\tau \\ &+ \int_0^{\bar{x}} u_0(\xi)(\psi(\xi;\theta+\varepsilon(\hat{\theta}-\theta)) - \psi(\xi;\theta))d\xi, \end{aligned} \tag{2.11}$$

$$
\begin{aligned}
e_2(t;\theta,\hat{\theta},\varepsilon) = \int_0^t &(\beta(P(t;\theta+\varepsilon(\hat{\theta}-\theta));\theta+\varepsilon(\hat{\theta}-\theta))B(\tau;\theta+\varepsilon(\hat{\theta}-\theta))\varphi(\tau;\theta+\varepsilon(\hat{\theta}-\theta)) \\
&-\beta(P(t;\theta);\theta)B(\tau;\theta)\varphi(\tau;\theta))d\tau \\
&+\int_0^{\bar{x}} u_0(\xi)(\beta(P(t;\theta+\varepsilon(\hat{\theta}-\theta));\theta+\varepsilon(\hat{\theta}-\theta))\psi(\xi;\theta+\varepsilon(\hat{\theta}-\theta)) \\
&\quad -\beta(P(t;\theta);\theta)\psi(\xi;\theta))d\xi.
\end{aligned}
\tag{2.12}
$$

Thus, by (2.11) there exists a positive constant K_1 such that

$$
\begin{aligned}
|e_1(t;\theta,\hat{\theta},\varepsilon)| &\le \int_0^t |e_2(\tau;\theta,\hat{\theta},\varepsilon)||\varphi(\tau;\theta+\varepsilon(\hat{\theta}-\theta))|d\tau \\
&\quad + \int_0^t |B(\tau;\theta)||\varphi(\tau;\theta+\varepsilon(\hat{\theta}-\theta)) - \varphi(\tau;\theta)|d\tau \\
&\quad + \int_0^{\bar{x}} |u_0(\xi)||\psi(\xi;\theta+\varepsilon(\hat{\theta}-\theta)) - \psi(\xi;\theta)|d\xi \\
&\le \int_0^t |e_2(\tau;\theta,\hat{\theta}-\theta)|d\tau \\
&\quad + K_1\int_0^t |\varphi(\tau;\theta+\varepsilon(\hat{\theta}-\theta)) - \varphi(\tau;\theta)|d\tau \\
&\quad + K_1\int_0^{\bar{x}} |\psi(\xi;\theta+\varepsilon(\hat{\theta}-\theta)) - \psi(\xi;\theta)|d\xi.
\end{aligned}
\tag{2.13}
$$

Further, by (2.12) and (2.13) there exists a positive constant K_2 such that

$$
\begin{aligned}
&|e_2(t;\theta,\hat{\theta},\varepsilon)| \\
&\quad \le \int_0^t |\beta_P(P_1(t;\theta);\theta+\varepsilon(\hat{\theta}-\theta))||e_1(t;\theta,\hat{\theta},\varepsilon)||B(\tau;\theta+\varepsilon(\hat{\theta}-\theta))||\varphi(\tau;\theta+\varepsilon(\hat{\theta}-\theta))|d\tau \\
&\qquad + \int_0^t |\beta(P(t;\theta);\theta+\varepsilon(\hat{\theta}-\theta)) - \beta(P(t;\theta);\theta)||B(\tau;\theta+\varepsilon(\hat{\theta}-\theta))| \\
&\qquad\qquad \cdot|\varphi(\tau;\theta+\varepsilon(\hat{\theta}-\theta))|d\tau \\
&\qquad + \int_0^t |\beta(P(t;\theta);\theta)||e_2(\tau;\theta,\hat{\theta},\varepsilon)||\varphi(\tau;\theta+\varepsilon(\hat{\theta}-\theta))|d\tau \\
&\qquad + \int_0^t |\beta(P(t;\theta);\theta)||B(\tau;\theta)||\varphi(\tau;\theta+\varepsilon(\hat{\theta}-\theta)) - \varphi(\tau;\theta)|d\tau \\
&\qquad + \int_0^{\bar{x}} |u_0(\xi)||\beta_P(P_2(t;\theta);\theta+\varepsilon(\hat{\theta}-\theta))||e_1(t;\theta,\hat{\theta},\varepsilon)||\psi(\xi;\theta+\varepsilon(\hat{\theta}-\theta))|d\xi \\
&\qquad + \int_0^{\bar{x}} |u_0(\xi)||\beta(P(t;\theta);\theta+\varepsilon(\hat{\theta}-\theta)) - \beta(P(t;\theta);\theta)||\psi(\xi;\theta+\varepsilon(\hat{\theta}-\theta))|d\xi \\
&\qquad + \int_0^{\bar{x}} |u_0(\xi)||\beta(P(t;\theta);\theta)||\psi(\xi;\theta+\varepsilon(\hat{\theta}-\theta)) - \psi(\xi;\theta)|d\xi \\
&\quad \le K_2\left(\int_0^t |e_2(\tau;\theta,\hat{\theta},\varepsilon)|d\tau + \int_0^t |\beta(P(t;\theta);\theta+\varepsilon(\hat{\theta}-\theta)) - \beta(P(t;\theta);\theta)|d\tau\right) \\
&\qquad + K_2\left(\int_0^t |\varphi(\tau;\theta+\varepsilon(\hat{\theta}-\theta)) - \varphi(\tau;\theta)|d\tau + \int_0^{\bar{x}} |\psi(\xi;\theta+\varepsilon(\hat{\theta}-\theta)) - \psi(\xi;\theta)|d\xi\right),
\end{aligned}
\tag{2.14}
$$

where $P_1(t;\theta), P_2(t;\theta)$ are between $P(t;\theta)$ and $P(t;\theta+\varepsilon(\hat{\theta}-\theta))$, and because β_θ is bounded on $[0,T]$, $\lim_{\varepsilon\to 0^+}\beta(P(t;\theta);\theta+\varepsilon(\hat{\theta}-\theta)) = \beta(P(t;\theta);\theta)$. In addition, there exists a positive constant K_3 such that

$$
\begin{aligned}
&|\varphi(\tau;\theta+\varepsilon(\hat{\theta}-\theta)) - \varphi(\tau;\theta)| \\
&\quad \le \int_\tau^t |m(X(s;0,\tau),P(s;\theta+\varepsilon(\hat{\theta}-\theta));\theta+\varepsilon(\hat{\theta}-\theta)) - m(X(s;0,\tau),P(s;\theta);\theta)|ds \\
&\quad \le K_3\int_\tau^t |e_1(s;\theta,\hat{\theta},\varepsilon)|ds \\
&\qquad + \int_\tau^t |m(X(s;0,\tau),P(s;\theta);\theta+\varepsilon(\hat{\theta}-\theta)) - m(X(s;0,\tau),P(s;\theta);\theta)|ds
\end{aligned}
\tag{2.15}
$$

and

$$
\begin{aligned}
&|\psi(\xi;\theta+\varepsilon(\hat{\theta}-\theta)) - \psi(\xi;\theta)| \\
&\quad \le \int_0^t |m(X(s;\xi,0),P(s;\theta+\varepsilon(\hat{\theta}-\theta));\theta+\varepsilon(\hat{\theta}-\theta)) - m(X(s;\xi,0),P(s;\theta);\theta)|ds \\
&\quad \le K_3\int_0^t |e_1(s;\theta,\hat{\theta},\varepsilon)|ds \\
&\qquad + \int_0^t |m(X(s;\xi,0),P(s;\theta);\theta+\varepsilon(\hat{\theta}-\theta)) - m(X(s;\xi,0),P(s;\theta);\theta)|ds,
\end{aligned}
\tag{2.16}
$$

where $\lim_{\varepsilon\to 0^+} m(X(s;\xi,0),P(s;\theta);\theta+\varepsilon(\hat\theta-\theta)) = m(X(s;\xi,0),P(s;\theta);\theta)$, since m_θ is bounded on $[0,T]$.

Adding (2.13) and (2.14), making use of (2.15)-(2.16), and applying Gronwall's inequality, we have $\lim_{\varepsilon\to 0^+}(|e_1(t;\theta,\hat\theta,\varepsilon)| + |e_2(t;\theta,\hat\theta,\varepsilon)|) = 0$.

We now show that $P_\theta(t;\theta,\hat\theta-\theta)$ and $B_\theta(t;\theta,\hat\theta-\theta)$ exist and satisfy equations (2.8)-(2.9). Let

$$D_1(t;\theta,\hat\theta,\varepsilon) = \frac{P(t;\theta+\varepsilon(\hat\theta-\theta)) - P(t;\theta)}{\varepsilon} - \Phi(t)$$

and

$$D_2(t;\theta,\hat\theta,\varepsilon) = \frac{B(t;\theta+\varepsilon(\hat\theta-\theta)) - B(t;\theta)}{\varepsilon} - \Psi(t).$$

In view of (2.8) and (2.11), we find that there exists a positive constant K_4 such that

$$\begin{aligned} D_1(t;\theta,\hat\theta,\varepsilon) &\le \textstyle\int_0^t |D_2(\tau;\theta,\hat\theta,\varepsilon)||\varphi(\tau;\theta+\varepsilon(\hat\theta-\theta))|d\tau \\ &\quad + \textstyle\int_0^t |B(\tau;\theta)| \left|\frac{\phi(\tau;\theta+\varepsilon(\hat\theta-\theta))-\varphi(\tau;\theta)}{\varepsilon} - \varphi_\theta(\tau;\theta)\right| d\tau \\ &\quad + \textstyle\int_0^{\bar x} |u_0(\xi)| \left|\frac{\psi(\xi;\theta+\varepsilon(\hat\theta-\theta))-\psi(\xi;\theta)}{\varepsilon} - \psi_\theta(\xi;\theta)\right| d\xi \\ &\le \textstyle\int_0^t |D_2(\tau;\theta,\hat\theta,\varepsilon)|d\tau \\ &\quad + K_4 \textstyle\int_0^t \left|\frac{\phi(\tau;\theta+\varepsilon(\hat\theta-\theta))-\varphi(\tau;\theta)}{\varepsilon} - \varphi_\theta(\tau;\theta)\right| d\tau \\ &\quad + K_4 \textstyle\int_0^{\bar x} \left|\frac{\psi(\xi;\theta+\varepsilon(\hat\theta-\theta))-\psi(\xi;\theta)}{\varepsilon} - \psi_\theta(\xi;\theta)\right| d\xi. \end{aligned} \tag{2.17}$$

On the other hand, by (2.9) and (2.12), we can see that

$$\begin{aligned} &|D_2(t;\theta,\hat\theta,\varepsilon)| \\ &\quad\le \textstyle\int_0^t |\beta_P(P_3(t;\theta);\theta+\varepsilon(\hat\theta-\theta))D_1(t;\theta,\hat\theta,\varepsilon)B(\tau;\theta+\varepsilon(\hat\theta-\theta))\varphi(\tau;\theta+\varepsilon(\hat\theta-\theta))|d\tau \\ &\qquad + \textstyle\int_0^t |\beta_P(P_3(t;\theta);\theta+\varepsilon(\hat\theta-\theta))\Phi(t)B(\tau;\theta+\varepsilon(\hat\theta-\theta))\varphi(\tau;\theta+\varepsilon(\hat\theta-\theta)) \\ &\qquad\qquad -\beta_P(P(t;\theta);\theta)\Phi(t)B(\tau;\theta)\varphi(\tau;\theta)|d\tau \\ &\qquad + \textstyle\int_0^t \left|\frac{\beta(P(t;\theta);\theta+\varepsilon(\hat\theta-\theta))-\beta(P(t;\theta);\theta)}{\varepsilon}B(\tau;\theta+\varepsilon(\hat\theta-\theta))\varphi(\tau;\theta+\varepsilon(\hat\theta-\theta))\right. \\ &\qquad\qquad -\beta_\theta(P(t;\theta);\theta)B(\tau;\theta)\varphi(\tau;\theta)|d\tau \\ &\qquad + \textstyle\int_0^t |\beta(P(t;\theta);\theta)D_2(\tau,\theta,\hat\theta,\varepsilon)\varphi(\tau;\theta+\varepsilon(\hat\theta-\theta))|d\tau \\ &\qquad + \textstyle\int_0^t |\beta(P(t;\theta);\theta)\Psi(\tau)||\varphi(\tau;\theta+\varepsilon(\hat\theta-\theta)) - \varphi(\tau;\theta)|d\tau \\ &\qquad + \textstyle\int_0^t |\beta(P(t;\theta);\theta)B(\tau;\theta)| \left|\frac{\varphi(\tau;\theta+\varepsilon(\hat\theta-\theta))-\varphi(\tau;\theta)}{\varepsilon} - \varphi_\theta(\tau;\theta)\right| d\tau \\ &\qquad + \textstyle\int_0^{\bar x} |u_0(\xi)\beta_P(P_4(t;\theta);\theta+\varepsilon(\hat\theta-\theta))D_1(t;\theta,\hat\theta,\varepsilon)\psi(\xi;\theta+\varepsilon(\hat\theta-\theta))|d\xi \\ &\qquad + \textstyle\int_0^{\bar x} |u_0(\xi)\Phi(t)||\beta_P(P_4(t;\theta);\theta+\varepsilon(\hat\theta-\theta))\psi(\xi;\theta+\varepsilon(\hat\theta-\theta)) \\ &\qquad\qquad -\beta_P(P(t;\theta);\theta)\psi(\xi;\theta)|d\xi \\ &\qquad + \textstyle\int_0^{\bar x} |u_0(\xi)| \left|\frac{\beta(P(t;\theta);\theta+\varepsilon(\hat\theta-\theta))-\beta(P(t;\theta);\theta)}{\varepsilon}\psi(\xi;\theta+\varepsilon(\hat\theta-\theta))\right. \\ &\qquad\qquad -\beta_\theta(P(t;\theta);\theta)\psi(\xi;\theta)|d\xi \\ &\qquad + \textstyle\int_0^{\bar x} |u_0(\xi)\beta(P(t;\theta);\theta)| \left|\frac{\psi(\xi;\theta+\varepsilon(\hat\theta-\theta))-\psi(\xi;\theta)}{\varepsilon} - \psi_\theta(\xi;\theta)\right| d\xi, \end{aligned} \tag{2.18}$$

where $P_3(t;\theta), P_4(t;\theta)$ are between $P(t;\theta)$ and $P(t;\theta+\varepsilon(\hat\theta-\theta))$. Because P, B, and β_P are continuously dependent on θ, the second term, the fifth term, and the eighth term on the right hand side of (2.18) approach zero as $\varepsilon\to 0$. Moreover, because β has a bounded directional derivative β_θ on $[0,T]$ in the direction $\hat\theta-\theta$, the third term and the ninth

term on the right hand side of (2.18) converge to zero as $\varepsilon \to 0$. Hence, substituting (2.17) into (2.18), we find that there exists a positive constant K_5 such that

$$\begin{aligned} D_2(t;\theta,\hat{\theta},\varepsilon) \le\ & K_5 \textstyle\int_0^t |D_2(\tau;\theta,\hat{\theta},\varepsilon)|d\tau \\ & + K_5 \textstyle\int_0^t \left| \frac{\phi(\tau;\theta+\varepsilon(\hat{\theta}-\theta))-\varphi(\tau;\theta)}{\varepsilon} - \varphi_\theta(\tau;\theta) \right| d\tau \\ & + K_5 \textstyle\int_0^{\bar{x}} \left| \frac{\psi(\xi;\theta+\varepsilon(\hat{\theta}-\theta))-\psi(\xi;\theta)}{\varepsilon} - \psi_\theta(\xi;\theta) \right| d\xi + E(\varepsilon), \end{aligned} \tag{2.19}$$

where $\lim_{\varepsilon\to 0^+} E(\varepsilon) = 0$. Furthermore, we have that

$$\begin{aligned} & \left| \tfrac{\varphi(\tau;\theta+\varepsilon(\hat{\theta}-\theta))-\varphi(\tau;\theta)}{\varepsilon} - \varphi_\theta(\tau;\theta) \right| \\ & \quad \le |\bar{\varphi}(\tau)| \textstyle\int_\tau^t |m_P(X(s;0,\tau), P_5(s;\theta);\theta+\varepsilon(\hat{\theta}-\theta))D_1(s;\theta,\hat{\theta},\varepsilon)|ds \\ & \qquad + \textstyle\int_\tau^t |\bar{\varphi}(\tau) m_P(X(s;0,\tau), P_5(s;\theta);\theta+\varepsilon(\hat{\theta}-\theta)) \\ & \qquad\quad - \varphi(\tau) m_P(X(s;0,\tau), P(s;\theta);\theta)||\Phi(s)|ds \\ & \qquad + \textstyle\int_\tau^t \left| \frac{m(X(s;0,\tau),P(s;\theta);\theta+\varepsilon(\hat{\theta}-\theta)) - m(X(s;0,\tau),P(s;\theta);\theta)}{\varepsilon} - m_\theta(s) \right| ds \end{aligned} \tag{2.20}$$

and

$$\begin{aligned} & \left| \tfrac{\psi(\xi;\theta+\varepsilon(\hat{\theta}-\theta))-\psi(\xi;\theta)}{\varepsilon} - \psi_\theta(\xi;\theta) \right| \\ & \quad \le |\bar{\psi}(\xi)| \textstyle\int_0^t |m_P(X(s;\xi,0), P_6(s;\theta);\theta+\varepsilon(\hat{\theta}-\theta))D_2(s;\theta,\hat{\theta},\varepsilon)|ds \\ & \qquad + \textstyle\int_0^t |\bar{\psi}(\xi) m_P(X(s;\xi,0), P_6(s;\theta);\theta+\varepsilon(\hat{\theta}-\theta)) \\ & \qquad\quad - \psi(\xi) m_P(X(s;\xi,0), P(s;\theta);\theta)||\Psi(s)|ds \\ & \qquad + \textstyle\int_0^t \left| \frac{m(X(s;\xi,0),P(s;\theta);\theta+\varepsilon(\hat{\theta}-\theta)) - m(X(s;\xi,0),P(s;\theta);\theta)}{\varepsilon} - m_\theta(s) \right| ds, \end{aligned} \tag{2.21}$$

where $\bar{\varphi}(\tau)$ is between $\varphi(\tau;\theta)$ and $\varphi(\tau;\theta+\varepsilon(\hat{\theta}-\theta))$, $\bar{\psi}(\xi)$ is between $\psi(\xi;\theta)$ and $\psi(\xi;\theta+\varepsilon(\hat{\theta}-\theta))$, and $P_5(s;\theta), P_6(s;\theta)$ are between $P(s;\theta)$ and $P(s;\theta+\varepsilon(\hat{\theta}-\theta))$. Because P and m_P are continuously dependent on θ, the second term on the right hand side of (2.20)-(2.21) approaches zero as $\varepsilon \to 0$. Moreover, because m has a bounded directional derivative m_θ on $[0,T]$ in the direction $\hat{\theta}-\theta$, the third term on the right hand side of (2.20)-(2.21) converges to zero as $\varepsilon \to 0$. Therefore, combining (2.17) and (2.19), taking account of (2.20)-(2.21), and using Gronwall's inequality, we obtain $\lim_{\varepsilon\to 0^+}(|D_1(t;\theta,\hat{\theta},\varepsilon)| + |D_2(t;\theta,\hat{\theta},\varepsilon)|) = 0$. □

3. Sensitivity equations. In this section, we derive sensitivity partial differential equations for the sensitivity of the solution u with respect to the reproduction rate β and the mortality rate m. For simplicity, we use $h(\theta)$ to denote a given direction in the respective parameter space. We first consider the sensitivity of u with respect to β. To this end, by Theorem 2.2, we can see that the directional derivatives of B and P with respect to β in the direction h exist. In addition, by (2.9) $B_\beta(t;\beta,h)$ takes the following form:

$$\begin{aligned} & B_\beta(t;\beta,h) \\ & \quad = \textstyle\int_0^t \beta_P(X(t;0,\tau),P(t;\beta,h))P_\beta(t;\beta,h)B(\tau;\beta,h) \\ & \qquad\quad \cdot \exp\left(-\textstyle\int_\tau^t m(X(s;0,\tau),P(s;\beta,h))ds\right) d\tau \\ & \qquad + \textstyle\int_0^t h(\beta)B(\tau;\beta,h)\exp\left(-\int_\tau^t m(X(s;0,\tau),P(s;\beta,h))ds\right) d\tau \\ & \qquad + \textstyle\int_0^t \beta(X(t;0,\tau),P(t;\beta,h))B_\beta(\tau;\beta,h)\exp\left(-\int_\tau^t m(X(s;0,\tau),P(s;\beta,h))ds\right) d\tau \end{aligned}$$

$$
\begin{aligned}
&- \int_0^t \beta(X(t;0,\tau),P(t;\beta,h))B(\tau;\beta,h)\exp\Big(-\int_\tau^t m(X(s;0,\tau),P(s;\beta,h))ds\Big)\\
&\qquad \cdot \int_\tau^t m_P(X(s;0,\tau),P(s;\beta,h))P_\beta(s;\beta,h)dsd\tau\\
&+ \int_0^{\bar{x}} \beta_P(X(t;\xi,0),P(t;\beta,h))P_\beta(t;\beta,h)u_0(\xi)\\
&\qquad \cdot \exp\Big(-\int_0^t m(X(s;\xi,0),P(s;\beta,h))ds\Big)d\xi\\
&+ \int_0^{\bar{x}} h(\beta)u_0(\xi)\exp\Big(-\int_0^t m(X(s;\xi,0),P(s;\beta,h))ds\Big)d\xi\\
&- \int_0^{\bar{x}} \beta(X(t;\xi,0),P(t;\beta,h))u_0(\xi)\exp\Big(-\int_0^t m(X(s;\xi,0),P(s;\beta,h))ds\Big)\\
&\qquad \cdot \int_0^t m_P(X(s;\xi,0),P(s;\beta,h))P_\beta(s;\beta,h)dsd\xi.
\end{aligned}
\tag{3.1}
$$

Let $u_\beta(x,t;\beta,h)$ be the directional derivative of u with respect to β in the direction h. Then by (2.2) and (2.6), we have that

$$
\begin{aligned}
&u_\beta(x,t;\beta,h)\\
&\quad = \tfrac{B_\beta(\Gamma(0;x,t);\beta,h)}{g(0)}\exp\Big(-\int_{\Gamma(0;x,t)}^t (g_x(X(s;x,t))+m(X(s;x,t),P(s;\beta,h)))ds\Big)\\
&\qquad -\tfrac{B(\Gamma(0;x,t);\beta,h)}{g(0)}\exp\Big(-\int_{\Gamma(0;x,t)}^t (g_x(X(s;x,t))+m(X(s;x,t),P(s;\beta,h)))ds\Big)\\
&\qquad\quad \cdot \int_{\Gamma(0;x,t)}^t m_P(X(s;x,t),P(s;\beta,h))P_\beta(s;\beta,h)ds, \qquad \text{if } x<z(t),
\end{aligned}
\tag{3.2}
$$

$$
\begin{aligned}
&u_\beta(x,t;\beta,h)\\
&\quad = -u_0(X(0;x,t))\exp\Big(-\int_0^t (g_x(X(s;x,t))+m(X(s;x,t),P(s;\beta,h)))ds\Big)\\
&\qquad \cdot \int_0^t m_P(X(s;x,t),P(s;\beta,h))P_\beta(s;\beta,h)ds, \qquad \text{if } x\geq z(t).
\end{aligned}
\tag{3.3}
$$

We then introduce the following initial-boundary value problem:

$$
\begin{aligned}
&v_t+(g(x)v)_x+m(x,P(t))v=-m_P(x,P(t))P_\beta(t)u, && (x,t)\in(0,\bar{x})\times(0,T),\\
&g(0)v(0,t)=\int_0^{\bar{x}}((\beta_P(x,P(t))P_\beta(t)+h(\beta))u(x,t)+\beta(x,P(t))v(x,t))dx, && t\in(0,T),\\
&v(x,0)=0, && x\in[0,\bar{x}].
\end{aligned}
\tag{3.4}
$$

Since the above equation is linear, it can be easily shown that there exists a unique solution of (3.4). Via the method of characteristics, we find that

$$
\begin{aligned}
v(x,t) &= \tfrac{D(\Gamma(0;x,t))}{g(0)}\exp\Big(-\int_{\Gamma(0;x,t)}^t (g_x(X(s;x,t))+m(X(s;x,t),P(s)))ds\Big)\\
&\qquad -\int_{\Gamma(0;x,t)}^t \exp\Big(-\int_s^t g_x(X(\eta;x,t))+m(X(\eta;x,t),P(\eta))d\eta\Big)\\
&\qquad\quad \cdot m_P(X(s;x,t),P(s))P_\beta(s)u(X(s;x,t),s)ds\\
&= \tfrac{D(\Gamma(0;x,t))}{g(0)}\exp\Big(-\int_{\Gamma(0;x,t)}^t (g_x(X(s;x,t))+m(X(s;x,t),P(s)))ds\Big)\\
&\qquad -\tfrac{B(\Gamma(0;x,t))}{g(0)}\exp\Big(-\int_{\Gamma(0;x,t)}^t (g_x(X(s;x,t))+m(X(s;x,t),P(s)))ds\Big)\\
&\qquad\quad \cdot \int_{\Gamma(0;x,t)}^t m_P(X(s;x,t),P(s))P_\beta(s)ds, \qquad \text{if } x<z(t),
\end{aligned}
\tag{3.5}
$$

where $D(t) = \int_0^{\bar{x}}((\beta_P(x,P(t))P_\beta(t) + h(\beta))u(x,t) + \beta(x,P(t))v(x,t))dx$. We also find that

$$\begin{aligned} v(x,t) &= -\int_0^t \exp\Big(-\int_s^t g_x(X(\eta;x,t)) + m(X(\eta;x,t),P(\eta))d\eta\Big) \\ &\qquad \cdot m_P(X(s;x,t),P(s))P_\beta(s)u(X(s;x,t),s)ds \\ &= -u_0(X(0;x,t))\exp\Big(-\int_0^t(g_x(X(s;x,t)) + m(X(s;x,t),P(s)))ds\Big) \\ &\qquad \cdot \int_0^t m_P(X(s;x,t),P(s))P_\beta(s)ds, \qquad \text{if } x \geq z(t). \end{aligned} \tag{3.6}$$

By means of the representation formulas (2.2) and (3.5)-(3.6), we can rewrite $D(t)$ as follows:

$$\begin{aligned} &D(t) \\ &= \int_0^{z(t)}(\beta_P(x,P(t))P_\beta(t) + h(\beta))\tfrac{B(\Gamma(0;x,t))}{g(0)} \\ &\quad \cdot \exp\Big(-\int_{\Gamma(0;x,t)}^t(g_x(X(s;x,t)) + m(X(s;x,t),P(s)))ds\Big)\,dx \\ &\quad + \int_0^{z(t)}\beta(x,P(t))\tfrac{D(\Gamma(0;x,t))}{g(0)}\exp\Big(-\int_{\Gamma(0;x,t)}^t(g_x(X(s;x,t)) + m(X(s;x,t),P(s)))ds\Big)dx \\ &\quad - \int_0^{z(t)}\beta(x,P(t))\tfrac{B(\Gamma(0;x,t))}{g(0)}\exp\Big(-\int_{\Gamma(0;x,t)}^t(g_x(X(s;x,t)) + m(X(s;x,t),P(s)))ds\Big) \\ &\qquad \cdot \int_{\Gamma(0;x,t)}^t m_P(X(s;x,t),P(s))P_\beta(s)dsdx \\ &\quad + \int_{z(t)}^{\bar{x}}(\beta_P(x,P(t))P_\beta(t) + h(\beta))u_0(X(0;x,t)) \\ &\qquad \cdot \exp\Big(-\int_0^t(g_x(X(s;x,t)) + m(X(s;x,t),P(s)))ds\Big)\,dx \\ &\quad - \int_{z(t)}^{\bar{x}}\beta(x,P(t))u_0(X(0;x,t))\exp\Big(-\int_0^t(g_x(X(s;x,t) + m(X(s;x,t),P(s)))ds\Big) \\ &\qquad \cdot \int_0^t m_P(X(s;x,t),P(s))P_\beta(s)dsdx. \end{aligned} \tag{3.7}$$

Using the same transformation as in (2.5) for $B(t)$, we then simplify $D(t)$ to obtain

$$\begin{aligned} D(t) = &\int_0^t \beta_P(X(t;0,\tau),P(t))P_\beta(t)B(\tau)\exp\Big(-\int_\tau^t m(X(s;0,\tau),P(s))ds\Big)\,d\tau \\ &+ \int_0^t h(\beta)B(\tau)\exp\Big(-\int_\tau^t m(X(s;0,\tau),P(s))ds\Big)\,d\tau \\ &+ \int_0^t \beta(X(t;0,\tau),P(t))D(\tau)\exp\Big(-\int_\tau^t m(X(s;0,\tau),P(s))ds\Big)\,d\tau \\ &- \int_0^t \beta(X(t;0,\tau),P(t))B(\tau)\exp\Big(-\int_\tau^t m(X(s;0,\tau),P(s))ds\Big) \\ &\qquad \cdot \int_\tau^t m_P(X(s;0,\tau),P(s))P_\beta(s)dsd\tau \\ &+ \int_0^{\bar{x}} \beta_P(X(t;\xi,0),P(t))P_\beta(t)u_0(\xi)\exp\Big(-\int_0^t m(X(s;\xi,0),P(s))ds\Big)\,d\xi \\ &+ \int_0^{\bar{x}} h(\beta)u_0(\xi)\exp\Big(-\int_0^t m(X(s;\xi,0),P(s))ds\Big)\,d\xi \\ &- \int_0^{\bar{x}} \beta(X(t;\xi,0),P(t))u_0(\xi)\exp\Big(-\int_0^t m(X(s;\xi,0),P(s))ds\Big) \\ &\qquad \cdot \int_0^t m_P(X(s;\xi,0),P(s))P_\beta(s)dsd\xi. \end{aligned} \tag{3.8}$$

Comparing (3.8) with (3.1) and by the uniqueness of $B_\beta(t;\beta,h)$, we can see that

$$D(t) = B_\beta(t;\beta,h).$$

Then by (3.2) and (3.5), we find that $u_\beta(x,t;\beta,h) = v(x,t)$ in the region $\{(x,t)|0 \leq x < z(t), t \geq 0\}$. Moreover, (3.3) and (3.6) indicate that $u_\beta(x,t;\beta,h) = v(x,t)$ in the region $\{(x,t)|z(t) \leq x \leq \bar{x}, t > 0\}$. Thus problem (3.4) can be used to solve for the sensitivity of u with respect to β.

Next we consider the sensitivity of u with respect to m. To this end, again by Theorem 2.2, we can see that the directional derivatives of B and P with respect to m in the direction h exist. In addition, by (2.9) $B_m(t;\beta,h)$ takes the following form:

$$\begin{aligned}
&B_m(t;\beta,h)\\
&\quad=\int_0^t \beta_P(X(t;0,\tau),P(t;\beta,h))P_m(t;\beta,h)B(\tau;\beta,h)\\
&\qquad\cdot\exp\Big(-\int_\tau^t m(X(s;0,\tau),P(s;\beta,h))ds\Big)\,d\tau\\
&\qquad+\int_0^t \beta(X(t;0,\tau),P(t;\beta,h))B_m(\tau;\beta,h)\exp\Big(-\int_\tau^t m(X(s;0,\tau),P(s;\beta,h))ds\Big)\,d\tau\\
&\qquad-\int_0^t \beta(X(t;0,\tau),P(t;\beta,h))B(\tau;\beta,h)\exp\Big(-\int_\tau^t m(X(s;0,\tau),P(s;\beta,h))ds\Big)\\
&\qquad\cdot\int_\tau^t(h(m)+m_P(X(s;0,\tau),P(s;\beta,h))P_m(s;\beta,h))dsd\tau\\
&\qquad+\int_0^{\bar{x}} \beta_P(X(t;\xi,0),P(t;\beta,h))P_m(t;\beta,h)u_0(\xi)\\
&\qquad\cdot\exp\Big(-\int_0^t m(X(s;\xi,0),P(s;\beta,h))ds\Big)\,d\xi\\
&\qquad-\int_0^{\bar{x}} \beta(X(t;\xi,0),P(t;\beta,h))u_0(\xi)\exp\Big(-\int_0^t m(X(s;\xi,0),P(s;\beta,h))ds\Big)\\
&\qquad\cdot\int_0^t(h(m)+m_P(X(s;\xi,0),P(s;\beta,h))P_m(s;\beta,h))dsd\xi.
\end{aligned}\tag{3.9}$$

Let $u_m(x,t;\beta,h)$ be the directional derivative of u with respect to m in the direction h. Then by (2.2) and (2.6), we have that

$$\begin{aligned}
&u_m(x,t;\beta,h)\\
&\quad=\tfrac{B_m(\Gamma(0;x,t);\beta,h)}{g(0)}\exp\Big(-\int_{\Gamma(0;x,t)}^t(g_x(X(s;x,t))+m(X(s;x,t),P(s;\beta,h)))ds\Big)\\
&\qquad-\tfrac{B(\Gamma(0;x,t);\beta,h)}{g(0)}\exp\Big(-\int_{\Gamma(0;x,t)}^t(g_x(X(s;x,t))+m(X(s;x,t),P(s;\beta,h)))ds\Big)\\
&\qquad\cdot\int_{\Gamma(0;x,t)}^t(h(m)+m_P(X(s;x,t),P(s;\beta,h))P_m(s;\beta,h))ds, \qquad \text{if } x<z(t),
\end{aligned}\tag{3.10}$$

$$\begin{aligned}
&u_m(x,t;\beta,h)\\
&\quad=-u_0(X(0;x,t))\exp\Big(-\int_0^t(g_x(X(s;x,t))+m(X(s;x,t),P(s;\beta,h)))ds\Big)\\
&\qquad\cdot\int_0^t(h(m)+m_P(X(s;x,t),P(s;\beta,h))P_m(s;\beta,h))ds, \qquad \text{if } x\geq z(t).
\end{aligned}\tag{3.11}$$

We now introduce the following initial-boundary value problem:

$$\begin{aligned}
&w_t+(g(x)w)_x+m(x,P(t))w=-(h(m)+m_P(x,P(t))P_\beta(t))u, && (x,t)\in(0,\bar{x})\times(0,T),\\
&g(0)w(0,t)=\int_0^{\bar{x}}(\beta_P(x,P(t))P_m(t)u(x,t)+\beta(x,P(t))w(x,t))dx, && t\in(0,T),\\
&w(x,0)=0, && x\in[0,\bar{x}].
\end{aligned}\tag{3.12}$$

Again we can see that there exists a unique solution w of (3.12). Using the method of characteristics, we have that

$$\begin{aligned} w(x,t) &= \tfrac{E(\Gamma(0;x,t))}{g(0)} \exp\Big(-\int_{\Gamma(0;x,t)}^{t} (g_x(X(s;x,t)) + m(X(s;x,t),P(s)))ds\Big) \\ &\quad - \int_{\Gamma(0;x,t)}^{t} \exp\Big(-\int_s^t g_x(X(\eta;x,t)) + m(X(\eta;x,t),P(\eta))d\eta\Big) \\ &\qquad \cdot (h(m) + m_P(X(s;x,t),P(s))P_m(s))u(X(s;x,t),s)ds \\ &= \tfrac{E(\Gamma(0;x,t))}{g(0)} \exp\Big(-\int_{\Gamma(0;x,t)}^{t} (g_x(X(s;x,t)) + m(X(s;x,t),P(s)))ds\Big) \\ &\quad - \tfrac{B(\Gamma(0;x,t))}{g(0)} \exp\Big(-\int_{\Gamma(0;x,t)}^{t} (g_x(X(s;x,t)) + m(X(s;x,t),P(s)))ds\Big) \\ &\qquad \cdot \int_{\Gamma(0;x,t)}^{t} (h(m) + m_P(X(s;x,t),P(s))P_m(s))ds, \qquad \text{if } x < z(t), \end{aligned} \tag{3.13}$$

where $E(t) = \int_0^{\bar{x}} (\beta_P(x,P(t))P_m(t)u(x,t) + \beta(x,P(t))w(x,t))dx$. We also have that

$$\begin{aligned} w(x,t) &= -\int_0^t \exp\Big(-\int_s^t g_x(X(\eta;x,t)) + m(X(\eta;x,t),P(\eta))d\eta\Big) \\ &\qquad \cdot (h(m) + m_P(X(s;x,t),P(s))P_m(s))u(X(s;x,t),s)ds \\ &= -u_0(X(0;x,t)) \exp\Big(-\int_0^t (g_x(X(s;x,t)) + m(X(s;x,t),P(s)))ds\Big) \\ &\qquad \cdot \int_0^t (h(m) + m_P(X(s;x,t),P(s))P_m(s))ds, \qquad \text{if } x \geq z(t). \end{aligned} \tag{3.14}$$

With the help of the representation formulas (2.2) and (3.13)-(3.14), we can rewrite $E(t)$ as follows:

$$\begin{aligned} &E(t) \\ &= \int_0^{z(t)} \beta_P(x,P(t))P_m(t)\tfrac{B(\Gamma(0;x,t))}{g(0)} \\ &\quad \cdot \exp\Big(-\int_{\Gamma(0;x,t)}^{t} (g_x(X(s;x,t)) + m(X(s;x,t),P(s)))ds\Big)\, dx \\ &\quad + \int_0^{z(t)} \beta(x,P(t))\tfrac{E(\Gamma(0;x,t))}{g(0)} \exp\Big(-\int_{\Gamma(0;x,t)}^{t} (g_x(X(s;x,t)) + m(X(s;x,t),P(s)))ds\Big)dx \\ &\quad - \int_0^{z(t)} \beta(x,P(t))\tfrac{B(\Gamma(0;x,t))}{g(0)} \exp\Big(-\int_{\Gamma(0;x,t)}^{t} (g_x(X(s;x,t)) + m(X(s;x,t),P(s)))ds\Big) \\ &\qquad \cdot \int_{\Gamma(0;x,t)}^{t} (h(m) + m_P(X(s;x,t),P(s))P_m(s))dsdx \\ &\quad + \int_{z(t)}^{\bar{x}} \beta_P(x,P(t))P_m(t)u_0(X(0;x,t)) \\ &\qquad \cdot \exp\Big(-\int_0^t (g_x(X(s;x,t)) + m(X(s;x,t),P(s)))ds\Big)\, dx \\ &\quad - \int_{z(t)}^{\bar{x}} \beta(x,P(t))u_0(X(0;x,t)) \exp\Big(-\int_0^t (g_x(X(s;x,t)) + m(X(s;x,t),P(s)))ds\Big) \\ &\qquad \cdot \int_0^t (h(m) + m_P(X(s;x,t),P(s))P_m(s))dsdx. \end{aligned} \tag{3.15}$$

Using the same transformation as in (2.5) for $B(t)$, we then simplify $E(t)$ to obtain

$$\begin{aligned}
E(t) = &\int_0^t \beta_P(X(t;0,\tau),P(t))P_m(t)B(\tau)\exp\Big(-\int_\tau^t m(X(s;0,\tau),P(s))ds\Big)\,d\tau \\
&+\int_0^t \beta(X(t;0,\tau),P(t))E(\tau)\exp\Big(-\int_\tau^t m(X(s;0,\tau),P(s))ds\Big)\,d\tau \\
&-\int_0^t \beta(X(t;0,\tau),P(t))B(\tau)\exp\Big(-\int_\tau^t m(X(s;0,\tau),P(s))ds\Big) \\
&\quad\cdot\int_\tau^t (h(m)+m_P(X(s;0,\tau),P(s))P_m(s))dsd\tau \\
&+\int_0^{\bar{x}} \beta_P(X(t;\xi,0),P(t))P_m(t)u_0(\xi)\exp\Big(-\int_0^t m(X(s;\xi,0),P(s))ds\Big)\,d\xi \\
&-\int_0^{\bar{x}} \beta(X(t;\xi,0),P(t))u_0(\xi)\exp\Big(-\int_0^t m(X(s;\xi,0),P(s))ds\Big) \\
&\quad\cdot\int_0^t (h(m)+m_P(X(s;\xi,0),P(s))P_m(s))dsd\xi.
\end{aligned} \tag{3.16}$$

Comparing (3.16) with (3.9) and by the uniqueness of $B_m(t;\beta,h)$, we can see that

$$E(t) = B_m(t;\beta,h).$$

Then by (3.10) and (3.13), we find that $u_m(x,t;\beta,h) = w(x,t)$ in the region $\{(x,t)|0 \le x < z(t), t \ge 0\}$. Moreover, (3.11) and (3.14) show that $u_m(x,t;\beta,h) = w(x,t)$ in the region $\{(x,t)|z(t) \le x \le \bar{x}, t > 0\}$. Hence problem (3.12) can be used to solve the sensitivity of u with respect to m.

REMARK 3.1. With the equivalence $u_\beta = v$ and $u_m = w$, one can see that $P_\beta(t)$ and $P_m(t)$ can be replaced with $\int_0^{\bar{x}} v(x,t)dx$ and $\int_0^{\bar{x}} w(x,t)dx$, respectively.

4. Numerical results. In this section, we present numerical results to illustrate the use of the sensitivity partial differential equations for the sensitivities of the solution with respect to the reproduction and mortality rates. For this purpose, we utilize the finite-difference scheme developed in [5]. We divide the intervals $[0,\bar{x}]$ and $[0,T]$ into n and l subintervals, respectively. The following notation will be used throughout the rest of the section: $\Delta x = \bar{x}/n$ and $\Delta t = T/l$ denote the size and time mesh lengths, respectively. The mesh points are given by $x_j = j\Delta x,\ j = 0,1,\ldots,n$, and $t_k = k\Delta t$, $k = 0,1,\ldots,l$. We denote by u_j^k and P^k the finite difference approximations of $u(x_j,t_k)$ and $P(t_k)$, respectively, and we let

$$g_j = g(x_j),\ C^k = C(t_k),\ \beta_j^k = \beta(x_j,P^k),\ m_j^k = m(x_j,P^k), \qquad 0 \le j \le n,\ 0 \le k \le l.$$

We then discretize the partial differential equation in (1.1) using the following implicit finite-difference approximation:

$$\begin{aligned}
&\tfrac{u_j^{k+1}-u_j^k}{\Delta t} + \tfrac{g_j u_j^{k+1} - g_{j-1}u_{j-1}^{k+1}}{\Delta x} + m_j^k u_j^{k+1} = 0, \qquad 1 \le j \le n, \quad 0 \le k \le l-1, \\
&g_0 u_0^{k+1} = C^k + \sum_{j=1}^n \beta_j^k u_j^k \Delta x, \qquad 0 \le k \le l-1, \\
&P^k = \sum_{j=1}^n u_j^k \Delta x, \qquad 0 \le k \le l-1,
\end{aligned} \tag{4.1}$$

with the initial condition

$$u_0^0 = u_0(0),\ u_j^0 = \frac{1}{\Delta x}\int_{(j-1)\Delta x}^{j\Delta x} u_0(x)dx, \quad j = 1,2,\ldots,n. \tag{4.2}$$

If we define

$$d_j^k = 1 + \frac{\Delta t}{\Delta x} g_j + \Delta t m_j^k, \quad j = 1, 2, \ldots, n, \tag{4.3}$$

then (4.1) can be equivalently written as the following system of linear equations for $\vec{u}^{k+1}$:

$$A^k \vec{u}^{k+1} = \vec{f}^k, \tag{4.4}$$

where $\vec{u}^{k+1} = [u_0^{k+1}, u_1^{k+1}, \ldots, u_n^{k+1}]^T$, $\vec{f}^k = [C^k + \sum_{j=1}^n \beta_j^k u_j^k \Delta x, u_1^k, \ldots, u_n^k]^T$, and A^k is the following lower triangular matrix:

$$\begin{pmatrix} g_0 & 0 & 0 & \cdots & 0 & 0 \\ -\frac{\Delta t}{\Delta x} g_0 & d_1^k & 0 & \cdots & 0 & 0 \\ 0 & -\frac{\Delta t}{\Delta x} g_1 & d_2^k & \cdots & 0 & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\ 0 & 0 & 0 & \cdots & -\frac{\Delta t}{\Delta x} g_{n-1} & d_n^k \end{pmatrix}.$$

Under the assumptions (A1)-(A5), it is shown in [5] that the system (4.4) has a unique solution satisfying $\vec{u}^{k+1} \geq \vec{0}$, $k = 0, 1, \ldots, l-1$, and this solution converges to the solution u of problem (1.1).

To make numerical simulations, we let $\bar{x} = 1$ and $T = 6$, and thus we let $n = 100$ and $l = 1800$, which are large enough to ensure convergence. The model parameters are chosen as

$$g(x) = 5(1-x), \ m(x, P) = \exp(4(x-0.4)^2)\frac{2P+1}{P+1}, \ \beta(x, P) = 6x(1-x)\frac{1}{P^2+1}, \tag{4.5}$$

and $C(t) = t$, $u_0(x) = 3\exp(-2(x-0.5)^2)$. Here g is the von Bertalanffy growth rate, and m and β are the under-compensatory mortality and reproduction rates, respectively.

We first consider the numerical computation of the sensitivity of u with respect to β. In view of the choice of β in (4.5), we let the direction $h = \frac{1}{P^2+1}$ when we take the directional derivative of u with respect to β. Noticing Remark 3.1, we discretize problem (3.4) to obtain the following system of linear equations:

$$\begin{aligned} &\tfrac{v_j^{k+1} - v_j^k}{\Delta t} + \tfrac{g_j v_j^{k+1} - g_{j-1} v_{j-1}^{k+1}}{\Delta x} + m_j^k v_j^{k+1} = -(m_P)_j^k (P_\beta)^k u_j^{k+1}, \quad 1 \leq j \leq n, \ 0 \leq k \leq l-1, \\ &g_0 v_0^{k+1} = \sum_{j=1}^n (((\beta_P)_j^k (P_\beta)^k + h^k) u_j^k + \beta_j^k v_j^k) \Delta x, \qquad 0 \leq k \leq l-1, \\ &(P_\beta)^k = \sum_{j=1}^n v_j^k \Delta x, \qquad 0 \leq k \leq l-1, \end{aligned} \tag{4.6}$$

with the initial condition $v_j^0 = 0, \quad j = 0, 1, \ldots, n$.

We then consider the numerical computation of the sensitivity of u with respect to m. By virtue of the choice of m in (4.5), we let the direction $h = 1$ when we take the directional derivative of u with respect to m. We discretize problem (3.12) to obtain the

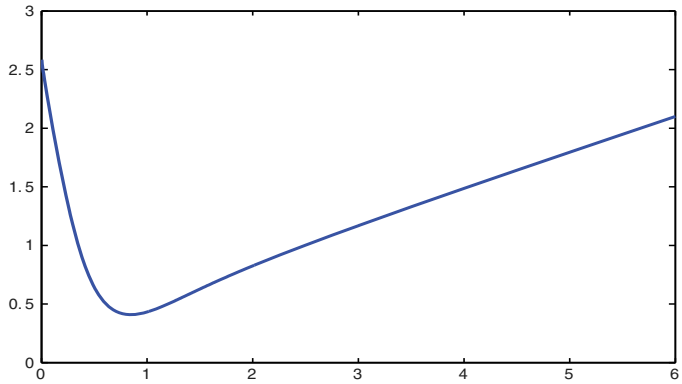

FIG. 1. Population P for $0 \le t \le 6$.

following system of linear equations:

$$\begin{aligned}
&\frac{w_j^{k+1}-w_j^k}{\Delta t} + \frac{g_j w_j^{k+1} - g_{j-1} w_{j-1}^{k+1}}{\Delta x} + m_j^k w_j^{k+1} = -(h^k + (m_P)_j^k (P_m)^k) u_j^{k+1}, \\
&\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad 1 \le j \le n,\ 0 \le k \le l-1, \\
&g_0 w_0^{k+1} = \sum_{j=1}^{n} ((\beta_P)_j^k (P_m)^k u_j^k + \beta_j^k w_j^k)\Delta x, \qquad\qquad 0 \le k \le l-1, \\
&(P_m)^k = \sum_{j=1}^{n} w_j^k \Delta x, \qquad\qquad\qquad\qquad\qquad\qquad\qquad 0 \le k \le l-1,
\end{aligned} \tag{4.7}$$

with the initial condition $w_j^0 = 0, j = 0, 1, \ldots, n$.

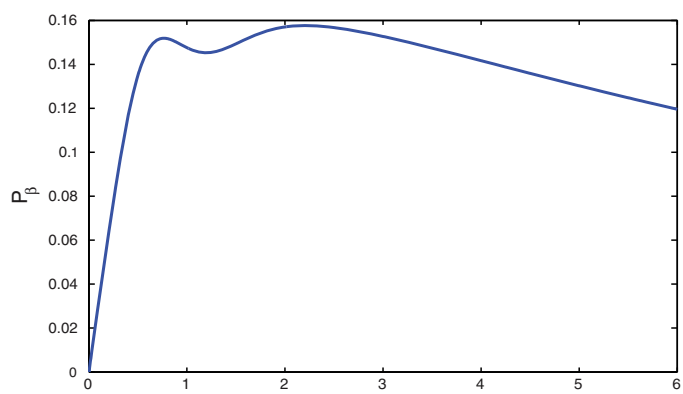

FIG. 2. Sensitivity of population P with respect to β for $0 \le t \le 6$.

In Figure 1, we plot the numerical solution for the total population P over the time interval $[0, 6]$. In Figure 2 and Figure 3, we plot the numerical solution for the sensitivity of the total population with respect to β and m, respectively. The numerical solution of the population density and its sensitivities with respect to β and m are plotted in Figure 4, Figure 5 and Figure 6, respectively. Clearly, the results indicate that for these

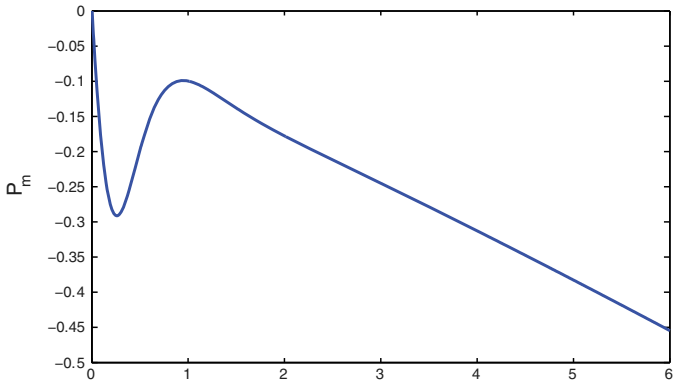

FIG. 3. Sensitivity of population P with respect to m for $0 \leq t \leq 6$.

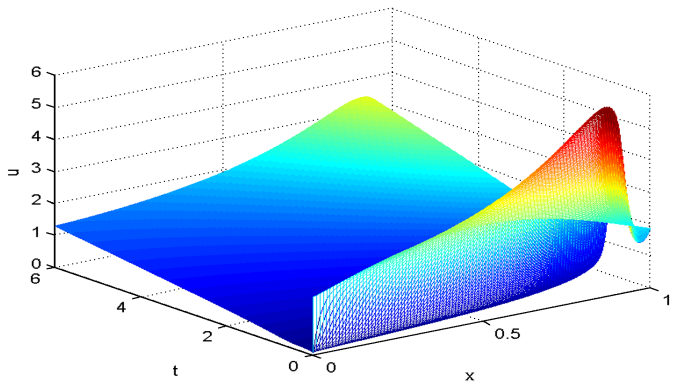

FIG. 4. Population density u.

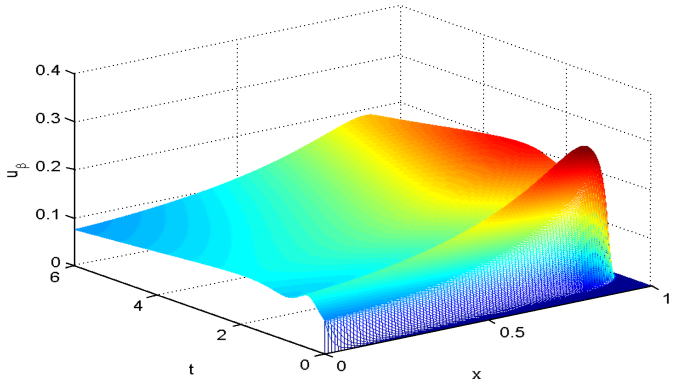

FIG. 5. Sensitivity of population density u with respect to β.

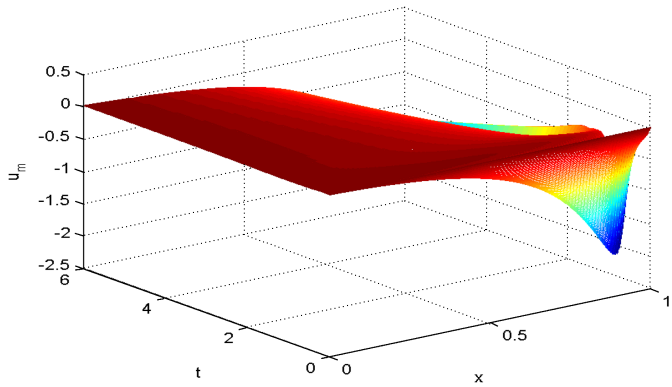

FIG. 6. Sensitivity of population density u with respect to m.

parameter values the total population is more sensitive to mortality than to reproduction. Furthermore, they show that in the time interval $[0, 1]$ the sensitivity to mortality and reproduction fluctuates the most, and so does the total population accordingly.

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