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SENSITIVITY EQUATIONS FOR A THREE-STAGED POPULATION MODEL WITH AGE-SIZE-STRUCTURE

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Abstract. In this paper, we present an egg-juvenile-adult model, in which eggs and juveniles are structured by age, while adults by size. The model consists of three first-order partial differential equations with initial and boundary conditions. We derive sensitivity equations for the solutions with respect to the fecundity and mortality of adults.

Keywords: population model; sensitivity equations; age-size-structure; method of characteristics.

2010 AMS Subject Classification: 92D25, 49Q12.

1. Introduction

Body size is manifestly one of the most important physical attributes of an individual in a population. It is such a factor that determines an individual's energetic requirements and ability to exploit resources. It effects the nature of an individual's interaction with individuals intra- and

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inter-species and the habitat, including predation competition and cooperation. Since the classical Sinko-Streifer model [1] appeared in 1967, size-structured population models have been widely investigated. Most of these efforts have focused on well-posedness and stability analysis (e.g., see [2-11]), optimal control problems(e.g., see [12-16]),and numerical schemes(e.g., see [17-23]). However, there are only few results on the topic of sensitivity equations and related analysis for size-structured population models(e.g., [24-25]).

Sensitivity analysis has been a long-standing and distinguished tool in population ecology. It asks the question what is the linear response of some variable of interest to a change in some parameter. The derivation of sensitivity equations for population models (especially for matrix models) has drawn the attention of numerous researchers in the past few decades because the resulting sensitivity functions can be used in many areas, such as optimization and design[26-28], computation of standard errors [29-30]. Sensitivity functions can also be used in information theory, control theory, parameter estimation and inverse problems [29-30, 32-36]. However, little work has been done on the derivation of sensitivity equations for continuous structured population models.

To the best of our knowledge, the work of Banks, Ernstberger and Hu in [24] is the first literature on sensitivity equations and related analysis for size-structured population models, they considered the classical Sinko-Streifer size-structured population model and derived partial differential equations for the sensitivities of solutions with respect to initial conditions, growth rate, mortality and fecundity. Sample numerical results to illustrate use of these equations were also presented. In [25], Ackleh, Deng and Yang examined a model describing the dynamics of an amphibian population whose individuals were divided into juveniles and adults. They made sensitivity analysis for the solutions to the reproduction and mortality of adults.

Since there are many species whose life history consists of more than two stages (e.g. frogs and invertebrates), in this paper we propose an egg-juvenile-adult model. In the first two stages we consider age difference while size in the last one. The remainder of the paper is organized as follows. In Section 2, we present the model and state some assumptions. The existence result for directional derivatives with respect to parameters are established in Section 3. Section 4 derives sensitivity equations for the solutions with respect to reproduction and mortality. The final section contains some remarks.

2. The model description

In this paper, We propose the following three-staged population model with age-size-structure:

$$\frac{\partial n_e(x,t)}{\partial t}+\frac{\partial n_e(x,t)}{\partial x}+(\mu_e(x)+\gamma(x))n_e(x,t)=0\ ,\ 0<x<x_1,\ 0<t<T, \tag{2.1}$$

$$\frac{\partial n_j(x,t)}{\partial t}+\frac{\partial n_j(x,t)}{\partial x}+\mu_j(x)n_j(x,t)=0\ , \qquad 0<x<x_2,\ 0<t<T, \tag{2.2}$$

$$\frac{\partial n_a(s,t)}{\partial t}+\frac{\partial (g(s)n_a(s,t))}{\partial s}+\mu_a(N(t))n_a(s,t)=0\ ,\ s_1<s<s_2,\ 0<t<T, \tag{2.3}$$

$$n_e(0,t)=\int_{s_1}^{s_2}\beta(N(t))n_a(s,t)\mathrm{d}s\ , \qquad 0<t<T, \tag{2.4}$$

$$n_j(0,t)=\int_0^{x_1}\gamma(x)n_e(x,t)\mathrm{d}x\ , \qquad 0<t<T, \tag{2.5}$$

$$g(s_1)n_a(s_1,t)=n_j(x_2,t)\ , \qquad 0<t<T, \tag{2.6}$$

$$n_e(x,0)=n_{e0}(x)\ , \qquad 0\le x\le x_1, \tag{2.7}$$

$$n_j(x,0)=n_{j0}(x)\ , \qquad 0\le x\le x_2, \tag{2.8}$$

$$n_a(s,0)=n_{a0}(s)\ , \qquad s_1\le s\le s_2, \tag{2.9}$$

where $n_e(x,t)$, $n_j(x,t)$ and $n_a(s,t)$ denote the densities of eggs and juveniles of age x and adults of size s, respectively, at time t. The parameters μ_e, μ_j and μ_a are mortality for eggs, juveniles and adults, respectively. The function $\gamma(x)$ is the rate an egg of age x becomes juvenile. The functions β and g are the fertility and growth rates of adults, respectively. x_1 and x_2 denote the maximum age of eggs and juveniles, respectively. Equation (2.6) says that x_2 is the age at which juveniles mature into adults of minimum size s_1, and s_2 denotes the maximum size of adults. Thus, $N(t)=\int_{s_1}^{s_2}n_a(s,t)\mathrm{d}s$ denotes the total population of adults.

Throughout this paper the following assumptions hold:

(A1) : $\gamma,\ \mu_e\in L^\infty(0,x_1)$, μ_e is nonnegative on $(0,x_1)$;

(A2) : $\mu_j\in L^\infty(0,x_2)$, μ_j is nonnegative on $(0,x_2)$;

(A3) : μ_a is nonnegative, furthermore, μ_a and β are continuously differentiable with respect to N with $\frac{\partial \mu_a}{\partial N}\ge 0$ and $\frac{\partial \beta}{\partial N}\le 0$, respectively;

(A4) : $g \in C^1(s_1, s_2)$ and $g(s) > 0$ for $s < s_2$, $g(s_2) = 0$ for $t \in [0, T]$;

(A5) : $n_{e0} \in L^\infty(0, x_1)$, $n_{j0} \in L^\infty(0, x_2)$, $n_{a0} \in L^\infty(s_1, s_2)$;

(A6) : All of variables and parameters are nonnegative in their domains and are extended by zero outside their domains.

We first introduce the definition of the solution of problem (2.1)-(2.9) via the method of characteristics.

Definition 2.1 A triple of integrable nonnegative functions $(n_e(x,t), n_j(x,t), n_a(s,t))$ is said to be a solution of system (2.1)-(2.9) if it satisfies the following equations:

$$Dn_e(x,t) = -(\mu_e(x) + \gamma(x))n_e(x,t),$$

$$Dn_j(x,t) = -\mu_j(x)n_j(x,t),$$
$$Dn_a(s,t) = -[\mu_a(N(t)) + \frac{\partial g(s)}{\partial s}]n_a(s,t),$$

with

$$Dn_e(x,t) = \lim_{h \to 0} \frac{n_e(x+h, t+h) - n_e(x,t)}{h}$$
$$Dn_j(x,t) = \lim_{h \to 0} \frac{n_j(x+h, t+h) - n_j(x,t)}{h}$$
$$Dn_a(s,t) = \lim_{h \to 0} \frac{n_a(\Phi(t+h; s,t), t+h) - n_a(s,t)}{h}$$

where $\Phi(t; s_0, t_0)$ is the solution of the differential equation $s'(t) = g(s(t))$ with initial condition $s(t_0) = s_0$.

By (A4), the function Φ is strictly increasing, and therefore a unique inverse function $\Gamma(s; s_0, t_0)$ exists. Let $Z(s) = \Gamma(s; s_1, 0)$; then $(s, Z(s))$ represents the characteristic curve passing through $(s_1, 0)$, and this curve divides the (s,t)-plane into two parts.

Let $(n_e(x,t), n_j(x,t), n_a(s,t))$ be a solution of system (2.1)-(2.9). Using the method of characteristics, we obtain

$$n_e(x,t) = \begin{cases} n_{e0}(x-t)e^{-\int_{x-t}^{x}(\mu_e+\gamma)(\tau)\mathrm{d}\tau}, & t \le x, \\ \beta(N(t-x))N(t-x)e^{-\int_0^x(\mu_e+\gamma)(\tau)\mathrm{d}\tau}, & t > x, \end{cases} \tag{2.10}$$

$$n_j(x,t) = \begin{cases} n_{j0}(x-t)e^{-\int_{x-t}^{x}\mu_j(\tau)\mathrm{d}\tau}, & t \le x, \\ e^{-\int_0^x \mu_j(\tau)\mathrm{d}\tau}\int_0^{x_1}\gamma(\sigma)n_e(\sigma, t-x)\mathrm{d}\sigma, & t > x, \end{cases} \tag{2.11}$$

$$n_a(s,t) = \begin{cases} n_{a0}(\Phi(0;s,t))e^{-\int_0^t [\mu_a(N(\tau)) + \frac{\partial g(\Phi(\tau;s,t))}{\partial s}]\mathrm{d}\tau}, & t \le Z(s), \\ \dfrac{n_j(x_2,\Gamma(s_1;s,t))}{g(s_1)} e^{-\int_{\Gamma(s_1;s,t)}^t [\mu_a(N(\tau)) + \frac{\partial g(\Phi(\tau;s,t))}{\partial s}]\mathrm{d}\tau}, & t > Z(s). \end{cases} \tag{2.12}$$

Integration of (2.12) over (s_1, s_2) gives

$$N(t) = \int_0^t n_j(x_2,\tau)e^{-\int_\tau^t \mu_a(N(\sigma))\mathrm{d}\sigma}\mathrm{d}\tau + \int_{s_1}^{s_2} n_{a0}(s)e^{-\int_0^t \mu_a(N(\sigma))\mathrm{d}\sigma}\mathrm{d}s. \tag{2.13}$$

Taking (2.11) and (2.12) into account, we have

$$N(t) = \int_0^t n_{j0}(x_2-\tau)\delta(\tau)e^{-\int_\tau^t \mu_a(N(\sigma))\mathrm{d}\sigma}\mathrm{d}\tau + \int_{s_1}^{s_2} n_{a0}(s)e^{-\int_0^t \mu_a(N(\sigma))\mathrm{d}\sigma}\mathrm{d}s \quad \text{if } t \le x_2, \tag{2.14}$$

$$\begin{aligned} N(t) = &\int_0^{x_2} n_{j0}(x_2-\tau)\delta(\tau)e^{-\int_\tau^t \mu_a(N(\sigma))\mathrm{d}\sigma}\mathrm{d}\tau + \int_{s_1}^{s_2} n_{a0}(s)e^{-\int_0^t \mu_a(N(\sigma))\mathrm{d}\sigma}\mathrm{d}s \\ &+ \int_{x_2}^t \int_0^{x_1} \gamma(x)n_{e0}(x-\tau+x_2)e^{-\int_{x-\tau+x_2}^x (\mu_e+\gamma)(\sigma)\mathrm{d}\sigma}\mathrm{d}x \\ &\times e^{-\int_0^{x_2}\mu_j(\sigma)\mathrm{d}\sigma} e^{-\int_\tau^t \mu_a(N(s))\mathrm{d}s}\mathrm{d}\tau \qquad \text{if } x_2 < t \le x_2 + x, \end{aligned} \tag{2.15}$$

$$\begin{aligned} N(t) = &\int_0^{x_2} n_{j0}(x_2-\tau)\delta(\tau)e^{-\int_\tau^t \mu_a(N(\sigma))\mathrm{d}\sigma}\mathrm{d}\tau + \int_{s_1}^{s_2} n_{a0}(s)e^{-\int_0^t \mu_a(N(\sigma))\mathrm{d}\sigma}\mathrm{d}s \\ &+ \int_{x_2}^t \int_0^{x_1} \gamma(x)\beta(N(\tau-x_2-x))N(\tau-x_2-x)e^{-\int_0^x (\mu_e+\gamma)(\sigma)\mathrm{d}\sigma}\mathrm{d}x \\ &\times e^{-\int_0^{x_2}\mu_j(\sigma)\mathrm{d}\sigma} e^{-\int_\tau^t \mu_a(N(s))\mathrm{d}s}\mathrm{d}\tau \qquad \text{if } t > x_2 + x, \end{aligned} \tag{2.16}$$

where $\delta(\tau) = e^{-\int_{x_2-\tau}^{x_2}\mu_j(\sigma)\mathrm{d}\sigma}$.

3. Directional derivatives with respect to parameters

The main goal of this section is to prove the existence of the directional derivatives with respect to parameters, which will be needed in the derivation of the sensitivity equations. To do so, we introduce the directional derivative of a function f with respect to a parameter θ (see [24]):

Definition 3.1 Let Θ be a convex subset in some topological vector space, and $f : R_+ \times \Theta \to R$. Given θ and ϑ in Θ, we define the derivative $f_\theta(t;\theta,\vartheta-\theta)$ of a function f at θ in the direction $\vartheta - \theta$ to be

$$f_\theta(t;\theta,\vartheta-\theta) = \lim_{\varepsilon\to 0^+} \frac{f(t;\theta,\vartheta-\theta) - f(t;\theta)}{\varepsilon}, \tag{3.1}$$

provided this limit exists.

Theorem 3.2 For θ and ϑ in Θ, suppose that μ_a and β each have a bounded directional derivative $\mu_{a\theta}(N(t);\theta,\vartheta-\theta)$ and $\beta_\theta(N(t);\theta,\vartheta-\theta)$ on $[0,T]$, respectively, in the direction $\vartheta-\theta$. Furthermore, we assume that μ_{aN} and β_N are continuously dependent on θ. Then the directional derivative $N_\theta(t;\theta,\vartheta-\theta)$ of N with respect to θ in the direction $\vartheta-\theta$ exists and satisfies the following equation

$$\begin{aligned}M(t)=&-\int_0^t\int_\tau^t[\mu_{aN}(N(\sigma);\theta)M(\sigma)+\mu_{a\theta}(N(\sigma);\theta)]\mathrm{d}\sigma n_{j0}(x_2-\tau)\\&\times\delta(\tau)e^{-\int_\tau^t\mu_a(N(\sigma);\theta)\mathrm{d}\sigma}\mathrm{d}\tau-\int_{s_1}^{s_2}n_{a0}(s)e^{-\int_0^t\mu_a(N(\sigma);\theta)\mathrm{d}\sigma}\\&\times\int_0^t[\mu_{aN}(N(\sigma);\theta)M(\sigma)+\mu_{a\theta}(N(\sigma);\theta)]\mathrm{d}\sigma\mathrm{d}s\quad\text{if } t\le x_2,\end{aligned}\tag{3.2}$$

$$\begin{aligned}M(t)=&-\int_0^{x_2}\int_\tau^t[\mu_{aN}(N(\sigma);\theta)M(\sigma)+\mu_{a\theta}(N(\sigma);\theta)]\mathrm{d}\sigma n_{j0}(x_2-\tau)\\&\times\delta(\tau)e^{-\int_\tau^t\mu_a(N(\sigma);\theta)\mathrm{d}\sigma}\mathrm{d}\tau-\int_{s_1}^{s_2}n_{a0}(s)e^{-\int_0^t\mu_a(N(\sigma);\theta)\mathrm{d}\sigma}\\&\times\int_0^t[\mu_{aN}(N(\sigma);\theta)M(\sigma)+\mu_{a\theta}(N(\sigma);\theta)]\mathrm{d}\sigma\mathrm{d}s\\&-\int_{x_2}^t e^{-\int_0^{x_2}\mu_j(\sigma)\mathrm{d}\sigma}\int_0^{x_1}\gamma(x)n_{e0}(x-\tau+x_2)e^{-\int_{x-\tau+x_2}^{x}(\mu_e+\gamma)(\sigma)\mathrm{d}\sigma}\mathrm{d}x\\&\times e^{-\int_\tau^t\mu_a(N(s);\theta)\mathrm{d}s}\int_\tau^t[\mu_{aN}(N(\sigma);\theta)M(\sigma)+\mu_{a\theta}(N(\sigma);\theta)]\mathrm{d}\sigma\mathrm{d}\tau\\&\qquad\text{if } x_2<t\le x_2+x,\end{aligned}\tag{3.3}$$

(3.4)

$$\begin{aligned}M(t)=&-\int_0^{x_2}n_{j0}(x_2-\tau)\delta(\tau)e^{-\int_\tau^t\mu_a(N(\sigma);\theta)\mathrm{d}\sigma}\int_\tau^t[\mu_{aN}(N(\sigma);\theta)M(\sigma)+\mu_{a\theta}(N(\sigma);\theta)]\mathrm{d}\sigma\mathrm{d}\tau\\&-\int_{s_1}^{s_2}n_{a0}(s)e^{-\int_0^t\mu_a(N(\sigma);\theta)\mathrm{d}\sigma}\int_0^t[\mu_{aN}(N(\sigma);\theta)M(\sigma)+\mu_{a\theta}(N(\sigma);\theta)]\mathrm{d}\sigma\mathrm{d}s\\&+\int_{x_2}^t\int_0^{x_1}\gamma(x)\beta(N(\tau-x_2-x);\theta)M(\tau-x_2-x)e^{-\int_0^x(\mu_e+\gamma)(\sigma)\mathrm{d}\sigma}\mathrm{d}x\\&\quad\times e^{-\int_0^{x_2}\mu_j(\sigma)\mathrm{d}\sigma}e^{-\int_\tau^t\mu_a(N(s);\theta)\mathrm{d}s}\mathrm{d}\tau\\&+\int_{x_2}^t\int_0^{x_1}\gamma(x)[\beta_N(N(\tau-x_2-x);\theta)M(\tau-x_2-x)+\beta_\theta(N(\tau-x_2-x);\theta)]\\&\quad\times N(\tau-x_2-x)e^{-\int_0^x(\mu_e+\gamma)(\sigma)\mathrm{d}\sigma}\mathrm{d}xe^{-\int_0^{x_2}\mu_j(\sigma)\mathrm{d}\sigma}e^{-\int_\tau^t\mu_a(N(s);\theta)\mathrm{d}s}\mathrm{d}\tau\end{aligned}$$

$$-\int_{x_2}^{t}\int_0^{x_1}\gamma(x)\beta(N(\tau-x_2-x);\theta)N(\tau-x_2-x)e^{-\int_0^x(\mu_e+\gamma)(\sigma)\mathrm{d}\sigma}\mathrm{d}x$$
$$\times e^{-\int_0^{x_2}\mu_j(\sigma)\mathrm{d}\sigma}e^{-\int_\tau^t\mu_a(N(s);\theta)\mathrm{d}s}\int_\tau^t[\mu_{aN}(N(\sigma);\theta)M(\sigma)+\mu_{a\theta}(N(\sigma);\theta)]\mathrm{d}\sigma\mathrm{d}\tau$$
$$\text{if } t>x_2+x,$$

where $N(t)=N(t;\theta)$ and $M(t)=N_\theta(t;\theta,\vartheta-\theta)$.

Proof Note that there exists a positive constant R^* such that $N(t)$ given by (2.14)-(2.16) is bounded by R^* on $[0,\infty)$ (see Lemma 4.3 in [11]). Therefore, by assumptions (A2)-(A3), the vital rates μ_a, β and their derivatives are uniformly bounded. Thus, one can find that Eq. (3.2) is a linear equation of $M(t)$ and Eqs. (3.3)-(3.4) are linear equations with delay, which implies that there exists a unique solution $M(t)$ of Eqs. (3.2)-(3.4). The boundedness of $M(t)$ can be derived by Gronwall's inequality.

We then claim that $N(t;\theta)$ is continuously dependent on θ. For any $t\in[0,T]$ with $T\le x_2$, let $B(t;\theta,\vartheta-\theta)=N(t;\theta+\varepsilon(\vartheta-\theta))-N(t;\theta)$. From the assumptions (A1)-(A6) and relation (2.14), we have

$$\begin{aligned}
&|B(t;\theta,\vartheta-\theta)|\\
&\quad\le \bar{n}_{a0}(s_2-s_1)\textstyle\int_0^t|\mu_a(N(\sigma;\theta+\varepsilon(\vartheta-\theta));\theta+\varepsilon(\vartheta-\theta))-\mu_a(N(\sigma;\theta);\theta)|\mathrm{d}\sigma\\
&\qquad+\bar{n}_{j0}\textstyle\int_0^t\int_\tau^t|\mu_a(N(\sigma;\theta+\varepsilon(\vartheta-\theta));\theta+\varepsilon(\vartheta-\theta))-\mu_a(N(\sigma;\theta);\theta)|\mathrm{d}\sigma\mathrm{d}\tau\\
&\quad\le \bar{n}_{a0}(s_2-s_1)\textstyle\int_0^t|\mu_{aN}(\hat{N}(\sigma);\theta+\varepsilon(\vartheta-\theta))||B(\sigma;\theta,\vartheta-\theta)|\mathrm{d}\sigma\\
&\qquad+\bar{n}_{a0}(s_2-s_1)\textstyle\int_0^t|\mu_{a\theta}(N(\sigma;\theta);\hat{\theta})||\varepsilon(\vartheta-\theta)|\mathrm{d}\sigma\\
&\qquad+\bar{n}_{j0}\textstyle\int_0^t\int_\tau^t|\mu_{aN}(\tilde{N}(\sigma);\theta+\varepsilon(\vartheta-\theta))||B(\sigma;\theta,\vartheta-\theta)|\mathrm{d}\sigma\mathrm{d}\tau\\
&\qquad+\bar{n}_{j0}\textstyle\int_0^t\int_\tau^t|\mu_{a\theta}(N(\sigma;\theta);\tilde{\theta})||\varepsilon(\vartheta-\theta)|\mathrm{d}\sigma\mathrm{d}\tau,
\end{aligned}$$

where $\bar{n}_{a0}$,$\bar{n}_{j0}$ are the supremum of n_{a0} and n_{j0}, respectively. $\hat{N}(\sigma)$,$\tilde{N}(\sigma)$ are between $N(\sigma;\theta)$ and $N(\sigma;\theta+\varepsilon(\vartheta-\theta))$. $\hat{\theta}$, $\tilde{\theta}$ are between θ and $\theta+\varepsilon(\vartheta-\theta)$. Because $\mu_{a\theta}(N(t);\theta,\vartheta-\theta)$ is bounded on $[0,T]$, thus the second term and the fourth term on the right side of the above inequality converge to zero as $\varepsilon\to 0$. Hence, we obtain that $\lim\limits_{\varepsilon\to 0}|B(t;\theta,\vartheta-\theta)|=0$ via Gronwall's inequality. Making use of (2.15)-(2.16) and proceeding analogously, we can prove the claim for $t\in[0,T]$ whit $T>x_2$.

Now we show that $N_\theta(t;\theta,\vartheta-\theta)$ exists and satisfies equations (3.2)-(3.4). For any $t\in[0,T]$ with $T\le x_2$, let $D(t;\theta,\vartheta-\theta)=\frac{N(t;\theta+\varepsilon(\vartheta-\theta))-N(t;\theta)}{\varepsilon}-M(t)$. From (2.14) and (3.2), we find that there exists a positive constant C such that

$$
\begin{aligned}
\frac{1}{C}|D(t;\theta,\vartheta-\theta)| \le & \int_0^t\int_\tau^t|\mu_{aN}(\tilde{N}(\sigma);\theta+\varepsilon(\vartheta-\theta))||D(\sigma;\theta,\vartheta-\theta)|\mathrm{d}\sigma\mathrm{d}\tau \\
&+\int_0^t\int_\tau^t|\frac{\mu_a(N(\sigma;\theta);\theta+\varepsilon(\vartheta-\theta))-\mu_a(N(\sigma;\theta);\theta)|}{\varepsilon}-\mu_{a\theta}(N(\sigma;\theta);\theta)\mathrm{d}\sigma\mathrm{d}\tau \\
&+\int_0^t|e^{-\int_\tau^t\tilde{\mu}_a(\sigma)\mathrm{d}\sigma}\int_\tau^t\mu_{aN}(\tilde{N}(\sigma);\theta+\varepsilon(\vartheta-\theta))M(\sigma)\mathrm{d}\sigma \\
&\quad -e^{-\int_\tau^t\mu_a(N(\sigma;\theta);\theta)\mathrm{d}\sigma}\int_\tau^t\mu_{aN}(N(\sigma;\theta);\theta)M(\sigma)\mathrm{d}\sigma|\mathrm{d}\tau \\
&+\int_0^t|e^{-\int_\tau^t\tilde{\mu}_a(\sigma)\mathrm{d}\sigma}-e^{-\int_\tau^t\mu_a(N(\sigma;\theta);\theta)\mathrm{d}\sigma}||\int_\tau^t\mu_{a\theta}(N(\sigma;\theta);\theta)\mathrm{d}\sigma|\mathrm{d}\tau \\
&+\int_0^t|\mu_{aN}(\hat{N}(\sigma);\theta+\varepsilon(\vartheta-\theta))||D(\sigma;\theta,\vartheta-\theta)|\mathrm{d}\sigma \\
&+\int_0^t|\frac{\mu_a(N(\sigma;\theta);\theta+\varepsilon(\vartheta-\theta))-\mu_a(N(\sigma;\theta);\theta)|}{\varepsilon}-\mu_{a\theta}(N(\sigma;\theta);\theta)\mathrm{d}\sigma \\
&+|e^{-\int_\tau^t\hat{\mu}_a(\sigma)\mathrm{d}\sigma}\int_\tau^t\mu_{aN}(\hat{N}(\sigma);\theta+\varepsilon(\vartheta-\theta))M(\sigma)\mathrm{d}\sigma \\
&\quad -e^{-\int_\tau^t\mu_a(N(\sigma;\theta);\theta)\mathrm{d}\sigma}\int_\tau^t\mu_{aN}(N(\sigma;\theta);\theta)M(\sigma)\mathrm{d}\sigma| \\
&+|e^{-\int_\tau^t\hat{\mu}_a(\sigma)\mathrm{d}\sigma}-e^{-\int_\tau^t\mu_a(N(\sigma;\theta);\theta)\mathrm{d}\sigma}||\int_\tau^t\mu_{a\theta}(N(\sigma;\theta);\theta)\mathrm{d}\sigma|,
\end{aligned}
$$

where $\tilde{N}(\sigma)$, $\hat{N}(\sigma)$ are between $N(\sigma;\theta)$ and $N(\sigma;\theta+\varepsilon(\vartheta-\theta))$, and $\tilde{\mu}_a(\sigma)$, $\hat{\mu}_a(\sigma)$ are between $\mu_a(N(\sigma;\theta);\theta)$ and $\mu_a(N(\sigma;\theta+\varepsilon(\vartheta-\theta));\theta+\varepsilon(\vartheta-\theta))$. Because both N and $\mu_{a\theta}$ are continuously dependent on θ, the third term, the fourth term, the seventh term, and the eighth term on the right side of the above inequality converges to zero as $\varepsilon\to 0$. Moreover, $\mu_{a\theta}(N(t);\theta,\vartheta-\theta)$ is bounded on $[0,T]$ implies that the second term and the sixth term on the right side of the above inequality converges to zero as $\varepsilon\to 0$. Hence, we obtain that $\lim_{\varepsilon\to 0}|D(t;\theta,\vartheta-\theta)|=0$ by virtue of Gronwall's inequality. Making use of (2.15)-(2.16) and (3.3)-(3.4), we can obtain the same existence result for $t\in[0,T]$ whit $T>x_2$ in a similar manner, and thus the theorem follows. □

4. Sensitivity equations

In this section, we derive equations for the sensitivities of the solution (n_e,n_j,n_a) with respect to β and μ_a. To simplify the notation, we use h to denote a given direction in the corresponding parameter space. We first want to derive the sensitivity of (n_e,n_j,n_a) with respect to β. Let (m_e,m_j,m_a) be the unique solution (guaranteed by results in [11]) of the initial boundary value problem

$$
\begin{aligned}
&\frac{\partial m_e(x,t)}{\partial t}+\frac{\partial m_e(x,t)}{\partial x}+(\mu_e(x)+\gamma(x))m_e(x,t)=0\ ,\ 0<x<x_1,\ 0<t<T,\\
&\frac{\partial m_j(x,t)}{\partial t}+\frac{\partial m_j(x,t)}{\partial x}+\mu_j(x)m_j(x,t)=0\ , \qquad 0<x<x_2,\ 0<t<T,\\
&\frac{\partial m_a(s,t)}{\partial t}+\frac{\partial (g(s)m_a(s,t))}{\partial s}+\mu_a(N(t))m_a(s,t)=-\mu_{aN}(N(t))N_\beta(t)n_a(s,t)\\
&\qquad\qquad\qquad\qquad\qquad\qquad s_1<s<s_2,\ 0<t<T,\\
&m_e(0,t)=[\beta_N(N(t))N_\beta(t)+h(\beta)]N(t)+\beta(N(t))N_\beta(t), \quad 0<t<T,\\
&m_j(0,t)=\int_0^{x_1}\gamma(x)n_{e\beta}(x,t)\mathrm{d}x\ , \qquad 0<t<T,\\
&g(s_1)m_a(s_1,t)=m_j(x_2,t)\ , \qquad 0<t<T,\\
&m_e(x,0)=0, \qquad x\in[0,x_1],\\
&m_j(x,0)=0, \qquad x\in[0,x_2],\\
&m_a(s,0)=0, \qquad s\in[s_1,s_2].
\end{aligned}
\tag{4.1}
$$

Our aim here is to characterize the unique solution to (4.1) and to argue that $m_e=n_{e\beta}$, $m_j=n_{j\beta}$ and $m_a=n_{a\beta}$, which implies that system (4.1) can be used to solve for the sensitivity of (n_e,n_j,n_a) with respect to β.

By the solution representation formula (2.10)-(2.12) and the definition (3.1), we obtain that

$$
n_{e\beta}(x,t;\beta,h)=\begin{cases} 0\ , & t\le x,\\ \{[\beta_N(N(t-x;\beta,h);\beta,h)N_\beta(t-x;\beta,h)+h(\beta)]N(t-x;\beta,h) & \\ +\beta(N(t-x;\beta,h);\beta,h)N_\beta(t-x;\beta,h)\}e^{-\int_0^x(\mu_e+\gamma)(\sigma)\mathrm{d}\sigma}, & t>x,\end{cases}
\tag{4.2}
$$

$$
n_{j\beta}(x,t;\beta,h)=\begin{cases} 0\ , & t\le x,\\ e^{-\int_0^x\mu_j(\tau)\mathrm{d}\tau}\int_0^{x_1}\gamma(\sigma)n_{e\beta}(\sigma,t-x;\beta,h)\mathrm{d}\sigma, & t>x,\end{cases}
\tag{4.3}
$$

$$
n_{a\beta}(s,t;\beta,h)=\begin{cases} -n_a(s,t;\beta,h)\int_0^t\mu_{aN}(N(\tau;\beta,h);\beta,h)N_\beta(\tau;\beta,h)\mathrm{d}\tau\ , & t\le Z(s),\\ \dfrac{n_{j\beta}(x_2,\Gamma(s_1;s,t);\beta,h)}{g(s_1)}e^{-\int_{\Gamma(s_1;s,t)}^t[\mu_a(N(\tau;\beta,h);\beta,h)+\frac{\partial g(\Phi(\tau;s,t))}{\partial s}]\mathrm{d}\tau} & \\ -n_a(s,t;\beta,h)\int_{\Gamma(s_1;s,t)}^t\mu_{aN}(N(\tau;\beta,h);\beta,h)N_\beta(\tau;\beta,h)\mathrm{d}\tau, & t>Z(s).\end{cases}
\tag{4.4}
$$

Using the method of characteristics, we find that the implicit representation form for solution to (4.1) is given as follows:

$$m_e(x,t)=\begin{cases}0\,, & t\le x,\\ \{[\beta_N(N(t-x))N_\beta(t-x)+h(\beta)]N(t-x) & \\ +\beta(N(t-x))N_\beta(t-x)\}e^{-\int_0^x(\mu_e+\gamma)(\sigma)\mathrm{d}\sigma}, & t>x,\end{cases}\tag{4.5}$$

$$m_j(x,t)=\begin{cases}0\,, & t\le x,\\ e^{-\int_0^x\mu_j(\tau)\mathrm{d}\tau}\int_0^{x_1}\gamma(\sigma)n_{e\beta}(\sigma,t-x)\mathrm{d}\sigma, & t>x,\end{cases}\tag{4.6}$$

$$m_a(s,t)=\begin{cases}-\int_0^t e^{-\int_\tau^t[\mu_a(N(\sigma))+\frac{\partial g(\Phi(\sigma;s,t))}{\partial s}]\mathrm{d}\sigma}\mu_{aN}(N(\tau))N_\beta(\tau)n_a(\Phi(\tau;s,t),\tau)\mathrm{d}\tau\,, & t\le Z(s),\\ \dfrac{m_j(x_2,\Gamma(s_1;s,t))}{g(s_1)}e^{-\int_{\Gamma(s_1;s,t)}^t[\mu_a(N(\tau))+\frac{\partial g(\Phi(\tau;s,t))}{\partial s}]\mathrm{d}\tau}-\displaystyle\int_{\Gamma(s_1;s,t)}^t n_a(\Phi(\tau;s,t),\tau) & \\ \times\mu_{aN}(N(\tau))N_\beta(\tau)e^{-\int_\tau^t[\mu_a(N(\sigma))+\frac{\partial g(\Phi(\sigma;s,t))}{\partial s}]\mathrm{d}\sigma}\mathrm{d}\tau, & t>Z(s).\end{cases}\tag{4.7}$$

Comparing (4.5)-(4.6) with (4.2)-(4.3), we find that $m_e=n_{e\beta}$ and $m_j=n_{j\beta}$. In what follows we show that $m_a=n_{a\beta}$. From equation (4.7), we conclude that for $t\le Z(s)$

$$\begin{aligned}m_a(s,t)&=-\int_0^t e^{-\int_\tau^t[\mu_a(N(\sigma))+\frac{\partial g(\Phi(\sigma;s,t))}{\partial s}]\mathrm{d}\sigma}\mu_{aN}(N(\tau))N_\beta(\tau)n_a(\Phi(\tau;s,t),\tau)\mathrm{d}\tau\\&=-n_{a0}(\Phi(0;s,t))e^{-\int_0^t[\mu_a(N(\sigma))+\frac{\partial g(\Phi(\sigma;s,t))}{\partial s}]\mathrm{d}\sigma}\int_0^t\mu_{aN}(N(\tau))N_\beta(\tau)\mathrm{d}\tau\\&=-n_a(s,t)\int_0^t\mu_{aN}(N(\tau))N_\beta(\tau)\mathrm{d}\tau\end{aligned}\tag{4.8}$$

and for $t>Z(s)$

$$\begin{aligned}m_a(s,t)=&\frac{m_j(x_2,\Gamma(s_1;s,t))}{g(s_1)}e^{-\int_{\Gamma(s_1;s,t)}^t[\mu_a(N(\tau))+\frac{\partial g(\Phi(\tau;s,t))}{\partial s}]\mathrm{d}\tau}\\&-\int_{\Gamma(s_1;s,t)}^t n_a(\Phi(\tau;s,t),\tau)\mu_{aN}(N(\tau))N_\beta(\tau)e^{-\int_\tau^t[\mu_a(N(\sigma))+\frac{\partial g(\Phi(\sigma;s,t))}{\partial s}]\mathrm{d}\sigma}\mathrm{d}\tau\\=&\frac{m_j(x_2,\Gamma(s_1;s,t))}{g(s_1)}e^{-\int_{\Gamma(s_1;s,t)}^t[\mu_a(N(\tau))+\frac{\partial g(\Phi(\tau;s,t))}{\partial s}]\mathrm{d}\tau}-\frac{n_j(x_2,\Gamma(s_1;s,t))}{g(s_1)}\\&\times e^{-\int_{\Gamma(s_1;s,t)}^t[\mu_a(N(\sigma))+\frac{\partial g(\Phi(\sigma;s,t))}{\partial s}]\mathrm{d}\sigma}\int_{\Gamma(s_1;s,t)}^t\mu_{aN}(N(\tau))N_\beta(\tau)\mathrm{d}\tau\\=&\frac{n_{j\beta}(x_2,\Gamma(s_1;s,t))}{g(s_1)}e^{-\int_{\Gamma(s_1;s,t)}^t[\mu_a(N(\tau))+\frac{\partial g(\Phi(\tau;s,t))}{\partial s}]\mathrm{d}\tau}\\&-n_a(s,t)\int_{\Gamma(s_1;s,t)}^t\mu_{aN}(N(\tau))N_\beta(\tau)\mathrm{d}\tau\end{aligned}\tag{4.9}$$

Putting (4.8)-(4.9) and (4.4) together, it yields that for any $(s,t) \in [s_1,s_2] \times [0,T]$, the relation $m_a = n_{a\beta}$ holds ture. Thus, the system (4.1) can be used to solve for the sensitivity of (n_e,n_j,n_a) with respect to β.

Now, we consider the sensitivity of (n_e,n_j,n_a) with respect to μ_a. Let (l_e,l_j,l_a) be the unique solution (also guaranteed by results in [11]) to the equation

$$
\begin{aligned}
&\frac{\partial l_e(x,t)}{\partial t} + \frac{\partial l_e(x,t)}{\partial x} + (\mu_e(x)+\gamma(x))l_e(x,t) = 0\ , \ 0<x<x_1,\ 0<t<T,\\
&\frac{\partial l_j(x,t)}{\partial t} + \frac{\partial l_j(x,t)}{\partial x} + \mu_j(x)l_j(x,t) = 0\ , \qquad 0<x<x_2,\ 0<t<T,\\
&\frac{\partial l_a(s,t)}{\partial t} + \frac{\partial (g(s)l_a(s,t))}{\partial s} + \mu_a(N(t))l_a(s,t) =\\
&\qquad -[\mu_{aN}(N(t))N_{\mu_a}(t)+h(\mu_a)]n_a(s,t)\ , \quad s_1<s<s_2,\ 0<t<T,\\
&l_e(0,t) = [\beta_N(N(t))N(t)+\beta(N(t))]N_{\mu_a}(t), \qquad 0<t<T,\\
&l_j(0,t) = \int_0^{x_1} \gamma(x) n_{e\mu_a}(x,t)\mathrm{d}x\ , \qquad 0<t<T,\\
&g(s_1)l_a(s_1,t) = l_j(x_2,t)\ , \qquad 0<t<T,\\
&l_e(x,0)=0, \qquad x\in[0,x_1],\\
&l_j(x,0)=0, \qquad x\in[0,x_2],\\
&l_a(s,0)=0, \qquad s\in[s_1,s_2].
\end{aligned}
\tag{4.10}
$$

By the solution representation formula (2.10)-(2.12) and the definition (3.1), we have

$$
n_{e\mu_a}(x,t;\mu_a,h) = \begin{cases} 0\ , & t\le x,\\ \{\beta_N(N(t-x;\mu_a,h);\mu_a,h)N(t-x;\mu_a,h)+\beta(N(t-x;\mu_a,h);\mu_a,h)\} & \\ N_{\mu_a}(t-x;\mu_a,h)e^{-\int_0^x(\mu_e+\gamma)(\sigma)\mathrm{d}\sigma}, & t>x, \end{cases}
\tag{4.11}
$$

$$
n_{j\mu_a}(x,t;\mu_a,h) = \begin{cases} 0\ , & t\le x,\\ e^{-\int_0^x \mu_j(\tau)\mathrm{d}\tau}\int_0^{x_1}\gamma(\sigma)n_{e\mu_a}(\sigma,t-x;\mu_a,h)\mathrm{d}\sigma, & t>x, \end{cases}
\tag{4.12}
$$

$$n_{a\mu_a}(s,t;\mu_a,h)=\begin{cases} -\int_0^t[\mu_{aN}(N(\tau;\mu_a,h);\mu_a,h)N_{\mu_a}(\tau;\mu_a,h)+h(\mu_a)]\mathrm{d}\tau \\ \qquad \times n_a(s,t;\mu_a,h)\ , & t\le Z(s), \\ \Big\{\dfrac{n_{j_{\mu_a}}(x_2,\Gamma(s_1;s,t);\mu_a,h)}{n_j(x_2,\Gamma(s_1;s,t);\mu_a,h)}-\displaystyle\int_{\Gamma(s_1;s,t)}^t[\mu_{aN}(N(\tau;\mu_a,h);\mu_a,h) \\ \qquad \times N_{\mu_a}(\tau;\mu_a,h)+h(\mu_a)]\mathrm{d}\tau\Big\}n_a(s,t;\mu_a,h),\ t>Z(s). \end{cases} \tag{4.13}$$

Using the method of characteristics, we obtain that

$$l_e(x,t)=\begin{cases} 0\ , & t\le x, \\ \{\beta_N(N(t-x))N(t-x)+\beta(N(t))\}N_{\mu_a}(t-x)e^{-\int_0^x(\mu_e+\gamma)(\sigma)\mathrm{d}\sigma}, & t>x, \end{cases} \tag{4.14}$$

$$l_j(x,t)=\begin{cases} 0\ , & t\le x, \\ e^{-\int_0^x\mu_j(\tau)\mathrm{d}\tau}\int_0^{x_1}\gamma(\sigma)n_{e\mu_a}(\sigma,t-x)\mathrm{d}\sigma, & t>x, \end{cases} \tag{4.15}$$

Moreover, as in (4.8) we have that

$$\begin{aligned} l_a(s,t)&=-\int_0^t e^{-\int_\tau^t[\mu_a(N(\sigma))+\frac{\partial g(\Phi(\sigma;s,t))}{\partial s}]\mathrm{d}\sigma}[\mu_{aN}(N(\tau))N_{\mu_a}(\tau)+h(\mu_a)]n_a(\Phi(\tau;s,t),\tau)\mathrm{d}\tau \\ &=-n_{a0}(\Phi(0;s,t))e^{-\int_0^t[\mu_a(N(\sigma))+\frac{\partial g(\Phi(\sigma;s,t))}{\partial s}]\mathrm{d}\sigma}\int_0^t[\mu_{aN}(N(\tau))N_{\mu_a}(\tau)+h(\mu_a)]\mathrm{d}\tau \\ &=-n_a(s,t)\int_0^t[\mu_{aN}(N(\tau))N_{\mu_a}(\tau)+h(\mu_a)]\mathrm{d}\tau\ , \qquad \text{if } t\le Z(s) \end{aligned} \tag{4.16}$$

and as in (4.9) we have that

$$\begin{aligned} l_a(s,t)&=\frac{l_j(x_2,\Gamma(s_1;s,t))}{g(s_1)}e^{-\int_{\Gamma(s_1;s,t)}^t[\mu_a(N(\tau))+\frac{\partial g(\Phi(\tau;s,t))}{\partial s}]\mathrm{d}\tau} \\ &-\int_{\Gamma(s_1;s,t)}^t n_a(\Phi(\tau;s,t),\tau)[\mu_{aN}(N(\tau))N_{\mu_a}(\tau)+h(\mu_a)]e^{-\int_\tau^t[\mu_a(N(\sigma))+\frac{\partial g(\Phi(\sigma;s,t))}{\partial s}]\mathrm{d}\sigma}\mathrm{d}\tau \\ &=\frac{l_j(x_2,\Gamma(s_1;s,t))}{g(s_1)}e^{-\int_{\Gamma(s_1;s,t)}^t[\mu_a(N(\tau))+\frac{\partial g(\Phi(\tau;s,t))}{\partial s}]\mathrm{d}\tau}-\frac{n_j(x_2,\Gamma(s_1;s,t))}{g(s_1)} \\ &\times e^{-\int_{\Gamma(s_1;s,t)}^t[\mu_a(N(\sigma))+\frac{\partial g(\Phi(\sigma;s,t))}{\partial s}]\mathrm{d}\sigma}\int_{\Gamma(s_1;s,t)}^t[\mu_{aN}(N(\tau))N_{\mu_a}(\tau)+h(\mu_a)]\mathrm{d}\tau \\ &=\frac{n_{j_{\mu_a}}(x_2,\Gamma(s_1;s,t))}{g(s_1)}e^{-\int_{\Gamma(s_1;s,t)}^t[\mu_a(N(\tau))+\frac{\partial g(\Phi(\tau;s,t))}{\partial s}]\mathrm{d}\tau} \\ &\quad -n_a(s,t)\int_{\Gamma(s_1;s,t)}^t[\mu_{aN}(N(\tau))N_{\mu_a}(\tau)+h(\mu_a)]\mathrm{d}\tau \\ &=\Big\{\frac{n_{j_{\mu_a}}(x_2,\Gamma(s_1;s,t))}{n_j(x_2,\Gamma(s_1;s,t))}-\int_{\Gamma(s_1;s,t)}^t[\mu_{aN}(N(\tau))N_{\mu_a}(\tau)+h(\mu_a)]\mathrm{d}\tau\Big\}n_a(s,t) \\ &\qquad\qquad \text{if } t>Z(s) \end{aligned} \tag{4.17}$$

where we have used the relation $n_{j_{\mu_a}} = l_j$, which is come from comparing (4.12) and (4.15). Putting (4.10)-(4.17) together, we conclude that $n_{e\mu_a} = l_e$, $n_{j_{\mu_a}} = l_j$ and $n_{a\mu_a} = l_a$. That is the system (4.10) can be used to solve for the sensitivity of (n_e, n_j, n_a) with respect to μ_a.

5. Concluding remarks

Motivated by the fact that many species own a multi-staged, we address an age-size-structured model describing the dynamics of a population composed of eggs, juveniles and adults. In real ecological situations, the maturation age of different individuals, with different life histories, may be different, depending on forage, genetic heredity and so on. Hence we assume the maturation function is age-dependent rather than a fixed maturation age.

The key object in this paper is the establishment of the sensitivity equations with respect to the fecundity and mortality for adults. We believe that the results obtained will be helpful to the understanding of interactions of population evolution and vital parameters.

Conflict of Interests

The authors declare that there is no conflict of interests.

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