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ON THE WELL-POSEDNESS OF A NONLINEAR HIERARCHICAL SIZE-STRUCTURED POPULATION MODEL

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Abstract

We analyse a nonlinear hierarchical size-structured population model with time-dependent individual vital rates. The existence and uniqueness of nonnegative solutions to the model are shown via a comparison principle. Our investigation extends some results in the literature.

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1. Introduction

Physiologically structured population models have been extensively studied over the past four decades [4, 8, 9, 12–15], and most investigations have focused on age- or size-structured population models. Here, we briefly review a few of these models. The first linear continuous age-structured population models were established by Sharpe and Lotka [14] and McKendrick [12], while the first size-structured population model by Sinko and Streifer [15] appeared in 1967. Gurtin and MacCamy [8] extended the linear age-structured model to nonlinear situations. More details on physiologically structured models can be found in the literature [4, 9, 13].

On the other hand, hierarchies of individuals in biological populations can be commonly observed [11]. However, for hierarchically structured population models, considerably less work has been done due to their theoretical and numerical complexity. By hierarchical structuring, we mean the ranking of the individuals according to their age, body size or any other possible structuring variable affecting their vital rates. For a study of the importance of hierarchical rankings in biological

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populations (not necessarily based upon age), we may refer to Lomnicki's work [11]. To the best of our knowledge, the work of Gurney and Nisbet [7] is the first attempt to discuss the hierarchically structured population dynamics from a mathematical point of view. Cushing [6] considered a hierarchical age-structured population model, in which the vital rates of an individual depended on the number of older and (or) younger individuals than itself. Later, Calsina and Saldana [5] studied a hierarchically size-structured model, for which the existence, uniqueness and asymptotic behaviours of the solutions were obtained. Kraev [10] established the existence and uniqueness of solutions for height-structured hierarchical models. Ackleh and Deng [2] treated a nonlinear hierarchically age-structured model with time-dependent individual vital rates. They proved the existence and uniqueness of the solutions to the model. We refer to Ackleh [1, 3] for numerical integrations of hierarchical models.

In this paper, we investigate a nonlinear hierarchical size-structured population model with time-dependent individual vital rates. The rest of the paper is organized as follows. In Section 2 we present the model and state some assumptions. The existence and uniqueness of the solutions to this model are established by applying the upper–lower solution technique in Section 3. Some concluding remarks are presented in Section 4.

2. The hierarchical size-structured population model

We propose the following model to describe the dynamics of a hierarchical population with size structure:

$$\begin{cases} \dfrac{\partial p(s,t)}{\partial t} + \dfrac{\partial (g(s,t)p(s,t))}{\partial s} = -\mu(s,t,E(p)(s,t))p(s,t), \quad s_1 \le s \le s_2, \quad 0 \le t \le T, \\ g(s_1,t)p(s_1,t) = \displaystyle\int_{s_1}^{s_2} \beta(s,t,E(p)(s,t))p(s,t)\,ds, \quad 0 \le t \le T, \\ p(s,0) = p_0(s), \quad s_1 \le s \le s_2, \end{cases} \tag{2.1}$$

where $p(s,t)$ denotes the density of the individuals having size s at time t. The functions μ, β and g are respectively the mortality, fertility and growth rates of an individual. We define the nonlocal term

$$E(p)(s,t) = \alpha \int_{s_1}^{s} p(x,t)\,dx + \int_{s}^{s_2} p(x,t)\,dx, \quad 0 \le \alpha < 1. \tag{2.2}$$

The function $E(p)(s,t)$ depends on the density p in a global way, and it is usually referred to as the environment.

Throughout this paper, the following assumptions hold.

(A1) $g \in C^1((s_1,s_2)\times(0,T))$ and $g(s,t) > 0$ for $s < s_2$, $g(s_2,t) = 0$ for $t \in [0,T]$.
(A2) $\mu(\cdot,\cdot,E)$, $\beta(\cdot,\cdot,E) \in L^\infty((s_1,s_2)\times(0,T))$; furthermore, $\mu_E = \partial\mu/\partial E$ and $\beta_E = \partial\beta/\partial E$ exist with $0 \le \mu_E < \infty$ and $-\infty < \beta_E \le 0$, respectively.
(A3) $p_0(s) \in L^\infty(s_1,s_2)$.

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(A4) All variables and parameters are nonnegative in their domains, and are extended to zero outside their domains.

We introduce the definition of the solution to problem (2.1).

DEFINITION 2.1. A nonnegative function $p(s,t) \in L^\infty((s_1, s_2) \times (0, T))$ is said to be a solution of the system (2.1), if it satisfies the following condition: for every $t \in (0, T)$ and every nonnegative $\varphi \in C^1((s_1, s_2) \times (0, T))$,

$$\begin{aligned}\int_{s_1}^{s_2} p(s,t)\varphi(s,t)\,ds = &\int_{s_1}^{s_2} p(s,0)\varphi(s,0)\,ds \\ &+ \int_0^t \varphi(s_1,\tau)\int_{s_1}^{s_2} \beta(s,\tau,E(p)(s,\tau))p(s,\tau)\,ds\,d\tau \\ &+ \int_0^t\int_{s_1}^{s_2}\Big[\frac{\partial\varphi(s,\tau)}{\partial\tau} + g(s,\tau)\frac{\partial\varphi(s,\tau)}{\partial s}\Big]p(s,\tau)\,ds\,d\tau \\ &- \int_0^t\int_{s_1}^{s_2} \mu(s,\tau,E(p)(s,\tau))p(s,\tau)\varphi(s,\tau)\,ds\,d\tau. \end{aligned} \tag{2.3}$$

3. Existence and uniqueness of solutions to the model

We begin this section by establishing the following result on the uniqueness of solutions to the model.

THEOREM 3.1. *The system* (2.1) *admits at most one nonnegative solution.*

PROOF. Let $p_1(s,t)$ and $p_2(s,t)$ be nonnegative solutions of the system (2.1); denote $p = p_1 - p_2$. Using (2.3) and applying the mean value theorem for integrals, we have

$$\begin{aligned}\int_{s_1}^{s_2} p(s,t)\varphi(s,t)\,ds = &\int_0^t \varphi(s_1,\tau)\int_{s_1}^{s_2} \beta(s,\tau,E(p_1)(s,\tau))p(s,\tau)\,ds\,d\tau \\ &- \int_0^t \varphi(s_1,\tau)\int_{s_1}^{s_2} \beta_E(s,\tau,\xi_1(s,\tau))E(p)(s,\tau)p_2(s,\tau)\,ds\,d\tau \\ &+ \int_0^t\int_{s_1}^{s_2}\Big[\frac{\partial\varphi(s,\tau)}{\partial\tau} + g(s,\tau)\frac{\partial\varphi(s,\tau)}{\partial s}\Big]p(s,\tau)\,ds\,d\tau \\ &- \int_0^t\int_{s_1}^{s_2} \mu(s,\tau,E(p_1)(s,\tau))p(s,\tau)\varphi(s,\tau)\,ds\,d\tau \\ &+ \int_0^t\int_{s_1}^{s_2} \varphi(s,\tau)\mu_E(s,\tau,\xi_2(s,\tau))E(p)(s,\tau)p_2(s,\tau)\,ds\,d\tau, \end{aligned} \tag{3.1}$$

where $\xi_i(s,\tau)$ is between $E(p_1)(s,\tau)$ and $E(p_2)(s,\tau)$, $i = 1, 2$. Choose $\varphi \in C^1((s_1, s_2) \times (0, T))$ with

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$$\begin{aligned}
&\frac{\partial\varphi}{\partial\tau} + g\frac{\partial\varphi}{\partial s} = 0, \quad s_1 < s < s_2, \quad 0 < \tau < t,\\
&\varphi(s_2, \tau) = 0,\\
&\varphi(s, t) = \pi(s), \quad s_1 < s < s_2.
\end{aligned}$$

Here $\pi \in C_0^\infty(s_1, s_2)$, $0 \le \pi(s) \le 1$, which means that $0 \le \varphi(s, t) \le 1$. Substituting such a φ into equation (3.1) and using equation (2.2), we obtain

$$\int_{s_1}^{s_2} p(s,t)\pi(s)\,ds \le C_1 \int_0^t \int_{s_1}^{s_2} |p(s,\tau)|\,ds\,d\tau, \tag{3.2}$$

where $C_1 = \|\beta\|_\infty + \|\mu\|_\infty + (\|\beta_E\|_\infty + \|\mu_E\|_\infty)\sup_{[0,T]}\|p_2(\cdot, t)\|_1$.

Since inequality (3.2) holds for every function π, we can now choose a sequence $\{\pi_n\}$ on (s_1, s_2) converging almost everywhere (a.e.) to

$$\pi(s) = \begin{cases} 1 & \text{if } p(s,t) > 0,\\ 0 & \text{otherwise.}\end{cases}$$

Consequently, we find

$$\int_{s_1}^{s_2} |p(s,t)|\,ds \le C_1 \int_0^t \int_{s_1}^{s_2} |p(s,\tau)|\,ds\,d\tau,$$

which implies $\int_{s_1}^{s_2} |p(s,t)|\,ds = 0$ by Gronwall's inequality, that is, $p(s,t) \equiv 0$, which completes the proof. □

In what follows, we show the existence of the solutions to system (2.1). In the spirit of [2], we begin with the definition of upper and lower solutions to system (2.1).

Definition 3.1. A pair of functions $\overline{p}(s,t)$ and $\underline{p}(s,t)$ are called the upper solution and lower solution to (2.1), respectively, if all the following statements hold:

(i) $\overline{p}(s,t), \underline{p}(s,t) \in L^\infty((s_1, s_2) \times (0, T))$;
(ii) $\overline{p}(s, 0) \ge p_0(s) \ge \underline{p}(s, 0)$ a.e. in (s_1, s_2);
(iii) for every $t \in (0, T)$ and every nonnegative $\varphi \in C^1((s_1, s_2) \times (0, T))$,

$$\begin{aligned}
\int_{s_1}^{s_2} \overline{p}(s,t)\varphi(s,t)\,ds \ge{}& \int_{s_1}^{s_2} \overline{p}(s,0)\varphi(s,0)\,ds\\
&+ \int_0^t \varphi(s_1,\tau) \int_{s_1}^{s_2} \beta(s,\tau,E(\underline{p})(s,\tau))\overline{p}(s,\tau)\,ds\,d\tau\\
&+ \int_0^t \int_{s_1}^{s_2} \Big[\frac{\partial\varphi(s,\tau)}{\partial\tau} + g(s,\tau)\frac{\partial\varphi(s,\tau)}{\partial s}\Big]\overline{p}(s,\tau)\,ds\,d\tau\\
&- \int_0^t \int_{s_1}^{s_2} \mu(s,\tau,E(\underline{p})(s,\tau))\overline{p}(s,\tau)\varphi(s,\tau)\,ds\,d\tau
\end{aligned}$$

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and

$$\int_{s_1}^{s_2} \underline{p}(s,t)\varphi(s,t)\,ds \le \int_{s_1}^{s_2} \underline{p}(s,0)\varphi(s,0)\,ds$$
$$+ \int_0^t \varphi(s_1,\tau)\int_{s_1}^{s_2} \beta(s,\tau,E(\overline{p})(s,\tau))\underline{p}(s,\tau)\,ds\,d\tau$$
$$+ \int_0^t \int_{s_1}^{s_2} \Big[\frac{\partial\varphi(s,\tau)}{\partial\tau} + g(s,\tau)\frac{\partial\varphi(s,\tau)}{\partial s}\Big]\underline{p}(s,\tau)\,ds\,d\tau$$
$$- \int_0^t \int_{s_1}^{s_2} \mu(s,\tau,E(\overline{p})(s,\tau))\underline{p}(s,\tau)\varphi(s,\tau)\,ds\,d\tau.$$

We now establish the following comparison principle, which is needed later.

Theorem 3.2. *Let assumptions* (A1)–(A4) *hold. Let* $\overline{p}$ *and* $\underline{p}$ *be a nonnegative upper solution and a nonnegative lower solution to* (2.1)*, respectively. Then* $\overline{p} \ge \underline{p}$ *a.e. in* $(s_1,s_2)\times(0,T)$.

Proof. Let $\widehat{p} = \underline{p} - \overline{p}$. According to Definition 3.1(ii), $\widehat{p}$ satisfies $\widehat{p}(s,0) = \underline{p}(s,0) - \overline{p}(s,0) \le 0$, a.e. in (s_1,s_2), and

$$\int_{s_1}^{s_2} \widehat{p}(s,t)\varphi(s,t)\,ds \le \int_{s_1}^{s_2} \widehat{p}(s,0)\varphi(s,0)\,ds$$
$$+ \int_0^t \varphi(s_1,\tau)\int_{s_1}^{s_2} \beta(s,\tau,E(\overline{p})(s,\tau))\widehat{p}(s,\tau)\,ds\,d\tau$$
$$- \int_0^t \varphi(s_1,\tau)\int_{s_1}^{s_2} \beta_E(s,\tau,\xi_3(s,\tau))E(\widehat{p})(s,\tau)\overline{p}(s,\tau)\,ds\,d\tau$$
$$+ \int_0^t \int_{s_1}^{s_2} \Big[\frac{\partial\varphi(s,\tau)}{\partial\tau} + g(s,\tau)\frac{\partial\varphi(s,\tau)}{\partial s}\Big]\widehat{p}(s,\tau)\,ds\,d\tau$$
$$- \int_0^t \int_{s_1}^{s_2} \mu(s,\tau,E(\overline{p})(s,\tau))\widehat{p}(s,\tau)\varphi(s,\tau)\,ds\,d\tau$$
$$+ \int_0^t \int_{s_1}^{s_2} \varphi(s,\tau)\mu_E(s,\tau,\xi_4(s,\tau))E(\widehat{p})(s,\tau)\overline{p}(s,\tau)\,ds\,d\tau, \tag{3.3}$$

where $\xi_i(s,\tau)$ is between $E(\overline{p})(s,\tau)$ and $E(\underline{p})(s,\tau)$ for $i = 3,4$.

In order to establish that $\widehat{p}(s,t) \le 0$, it suffices to show that $\widehat{p}^{+}(s,t) = 0$, where $\widehat{p}^{+}(s,t) = \max\{\widehat{p}(s,t),0\}$. To this end, we let $\varphi(s,t) = e^{\lambda t}\psi(s,t)$, where $\psi(s,t) \in C^1((s_1,s_2)\times(0,T))$, and λ is chosen such that $\lambda - \mu(s,\tau,E(\overline{p})(s,\tau)) \ge 0$ on $(s_1,s_2)\times(0,T)$. From inequality (3.3), and the property of a solution to the problem,

$$\frac{\partial\psi}{\partial\tau} + g\frac{\partial\psi}{\partial s} = 0, \quad \psi(s_2,\tau) = 0, \quad \psi(s,t) = \pi(s) \quad \text{with } 0 \le \pi \le 1,$$

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it follows that

$$
\begin{aligned}
e^{\lambda t}\int_{s_1}^{s_2}\widehat{p}(s,t)\pi(s)\,ds \le{}& \int_0^t e^{\lambda\tau}\psi(s_1,\tau)\int_{s_1}^{s_2}\beta(s,\tau,E(\overline{p})(s,\tau))\widehat{p}(s,\tau)\,ds\,d\tau\\
&-\int_0^t e^{\lambda\tau}\psi(s_1,\tau)\int_{s_1}^{s_2}\beta_E(s,\tau,\xi_1(s,\tau))E(\widehat{p})(s,\tau)\overline{p}(s,\tau)\,ds\,d\tau\\
&+\int_0^t\int_{s_1}^{s_2} e^{\lambda\tau}[\lambda-\mu(s,\tau,E(\overline{p})(s,\tau))]\widehat{p}(s,\tau)\psi(s,\tau)\,ds\,d\tau\\
&+\int_0^t\int_{s_1}^{s_2} e^{\lambda\tau}\psi(s,\tau)\mu_E(s,\tau,\xi_2(s,\tau))E(\widehat{p})(s,\tau)\overline{p}(s,\tau)\,ds\,d\tau.
\end{aligned}
\tag{3.4}
$$

Hence, we have $\int_{s_1}^{s_2}\widehat{p}(s,t)\pi(s)\,ds \le C_2\int_0^t\int_{s_1}^{s_2}\widehat{p}^{+}(s,\tau)\,ds\,d\tau$, where

$$
C_2=\sup_{(s,t)\in[s_1,s_2]\times[0,T]}\{[\lambda-\mu(s,\tau,E(\overline{p})(s,\tau))]+\|\beta\|_\infty+(\|\beta_E\|_\infty+\|\mu_E\|_\infty)\|\overline{p}(\cdot,t)\|_1\}.
$$

Since inequality (3.4) holds for every π, the choice of a sequence $\{\pi_n\}$ on (s_1,s_2) converging a.e. to

$$
\pi(s)=\begin{cases}1 & \text{if } \widehat{p}(s,t)>0,\\ 0 & \text{otherwise,}\end{cases}
$$

yields $\int_{s_1}^{s_2}\widehat{p}^{+}(s,t)\,ds \le C_1\int_0^t\int_{s_1}^{s_2}\widehat{p}^{+}(s,\tau)\,ds\,d\tau$, which implies $\int_{s_1}^{s_2}\widehat{p}^{+}(s,t)\,ds=0$ by Gronwall's inequality. So $\widehat{p}(s,t)\le 0$, and the proof is complete. □

Next, we construct monotone sequences of upper and lower solutions to system (2.1). First, let $\underline{p}^0(s,t)=0$, and $\overline{p}^0(s,t)$ is obtained from the solution of the system

$$
\begin{cases}
\dfrac{\partial\overline{p}^0(s,t)}{\partial t}+\dfrac{\partial(g(s,t)\overline{p}^0(s,t))}{\partial s}=-\mu(s,t,E(0)(s,t))\overline{p}^0(s,t),\\
g(s_1,t)\overline{p}^0(s_1,t)=\displaystyle\int_{s_1}^{s_2}\beta(s,t,E(0)(s,t))\overline{p}^0(s,t)\,ds,\\
\overline{p}^0(s,0)=p_0(s).
\end{cases}
$$

It follows that $\underline{p}^0(s,t)$ and $\overline{p}^0(s,t)$ are a pair of lower and upper solutions of system (2.1).

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We then define two sequences $\{\underline{p}^k\}_1^\infty$ and $\{\overline{p}^k\}_1^\infty$ as follows : for $k = 1, 2, \ldots,$

$$\begin{cases} \dfrac{\partial \underline{p}^k(s,t)}{\partial t} + \dfrac{\partial (g(s,t)\underline{p}^k(s,t))}{\partial s} = -\mu(s,t,E(\overline{p}^{k-1})(s,t))\underline{p}^k(s,t), \\ g(s_1,t)\underline{p}^k(s_1,t) = \displaystyle\int_{s_1}^{s_2} \beta(s,t,E(\overline{p}^{k-1})(s,t))\underline{p}^k(s,t)\,ds, \\ \underline{p}^k(s,0) = p_0(s); \end{cases}$$

$$\begin{cases} \dfrac{\partial \overline{p}^k(s,t)}{\partial t} + \dfrac{\partial (g(s,t)\overline{p}^k(s,t))}{\partial s} = -\mu(s,t,E(\underline{p}^{k-1})(s,t))\overline{p}^k(s,t), \\ g(s_1,t)\overline{p}^k(s_1,t) = \displaystyle\int_{s_1}^{s_2} \beta(s,t,E(\underline{p}^{k-1})(s,t))\overline{p}^k(s,t)\,ds, \\ \overline{p}^k(s,0) = p_0(s). \end{cases}$$

By Definition 3.1, since $\underline{p}^0(s,t)$ and $\overline{p}^0(s,t)$ are a pair of lower and upper solutions, it follows that $\underline{p}^1(s,t)$ and $\overline{p}^1(s,t)$ are also a pair of lower and upper solutions. Then, by induction, for each $k = 0, 1, 2, \ldots,$ we claim that $\underline{p}^k(s,t)$ and $\overline{p}^k(s,t)$ are lower and upper solutions, respectively, and satisfy

$$\underline{p}^0 \le \underline{p}^1 \le \cdots \le \underline{p}^k \le \overline{p}^k \le \cdots \le \overline{p}^1 \le \overline{p}^0 \quad \text{in } [s_1,s_2]\times[0,T].$$

The monotonicity of the sequences $\{\underline{p}^k\}$ and $\{\overline{p}^k\}$ guarantees that there exist functions $\underline{p}$ and $\overline{p}$ such that $\underline{p}^k \to \underline{p}$ and $\overline{p}^k \to \overline{p}$ pointwise in $(s_1,s_2)\times(0,T)$.

We now present the following existence result for system (2.1).

THEOREM 3.3. *If assumptions* (A1)–(A4) *hold, then the two sequences* $\{\underline{p}^k\}_0^\infty$ *and* $\{\overline{p}^k\}_0^\infty$ *converge to a common limit, which is the solution to system* (2.1) *in* $L^\infty((s_1,s_2)\times(0,T))$.

PROOF. Since the sequences $\{\underline{p}^k\}_0^\infty$ and $\{\overline{p}^k\}_0^\infty$ are monotone and bounded by $\underline{p}^0(s,t)$ and $\overline{p}^0(s,t)$, they uniformly and monotonically converge to $\underline{p}(s,t)$ and $\overline{p}(s,t)$, respectively. We then show that $\underline{p}(s,t) = \overline{p}(s,t)$. To this end, let $\widehat{p} = \overline{p} - \underline{p}$. Since $\overline{p} \ge \underline{p}$, we get $\widehat{p}(s,t) \ge 0$ and $\widehat{p}(s,0) = 0$. By virtue of (3.3) and choosing $\varphi(s,t) \equiv 1$, we have

$$\begin{aligned} \int_{s_1}^{s_2} \widehat{p}(s,t)\,ds \le & \int_0^t \int_{s_1}^{s_2} \beta(s,\tau,E(\underline{p})(s,\tau))\widehat{p}(s,\tau)\,ds\,d\tau \\ & - \int_0^t \int_{s_1}^{s_2} \beta_E(s,\tau,\xi_5(s,\tau))E(\widehat{p})(s,\tau)\underline{p}(s,\tau)\,ds\,d\tau \\ & - \int_0^t \int_{s_1}^{s_2} \mu(s,\tau,E(\underline{p})(s,\tau))\widehat{p}(s,\tau)\,ds\,d\tau \\ & + \int_0^t \int_{s_1}^{s_2} \mu_E(s,\tau,\xi_6(s,\tau))E(\widehat{p})(s,\tau)\underline{p}(s,\tau)\,ds\,d\tau \\ \le & C_3 \int_0^t \int_{s_1}^{s_2} \widehat{p}(s,t)\,ds\,d\tau, \end{aligned}$$

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where $\xi_i(s,\tau)$ is between $E(\overline{p})(s,\tau)$ and $E(\underline{p})(s,\tau)$ for $i = 5, 6$, and

$$C_3 = \|\beta\|_\infty + (\|\beta_E\|_\infty + \|\mu_E\|_\infty) \sup_{[0,T]} \|\underline{p}(\cdot, t)\|_1.$$

Consequently, Gronwall's inequality gives $\widehat{p}(s,t) = 0$, that is, $\underline{p} = \overline{p}$. Denoting the common limit by $p(s,t)$, we see that $p(s,t)$ satisfies equation (2.3), which completes the proof. □

4. Concluding remarks

This paper addresses a nonlinear hierarchical size-structured population model with time-dependent individual vital rates. The existence and uniqueness of nonnegative solutions to the model are discussed. Our result can be used in modelling competition for light in a forest, whose distinctive feature is its hierarchical nature. This means that taller trees overshadow smaller ones, but not vice versa. To model this effect, the process rates at a point (s,t) should only depend on s and the height structure above s, hence in this situation we choose the parameter α to be zero.

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