Mathematical Biosciences
and Engineering

https://www.aimspress.com/journal/mbe

MBE, 22(6): 1263–1279.
DOI: 10.3934/mbe.2025047
Received: 11 December 2024
Revised: 12 February 2025
Accepted: 19 March 2025
Published: 21 April 2025

Research article

A Darwinian version of the Leslie logistic model for age-structured populations

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Abstract: The known global dynamics of the classic Leslie logistic model for the dynamics of an age-structured population are extended to a Darwinian dynamic version of the model for a single phenotypic trait (that is subject to natural selection). This is done under the assumption that the speed of evolution does not exceed an upper bound and that the maximum intraspecific competition intensity experienced by an individual occurs when its inherited trait equals that of the population mean trait. An example is given that applies the results to a model in which age-specific birth rates are subject to natural selection and that illustrates conditions under which evolution favors an iteroparous-type or a semelparous-type of life history strategy.

Keywords: Leslie matrix; logistic growth; age-structured population dynamics; Darwinian dynamics

1. Introduction

In a classic paper [1] in 1945, Leslie introduced the now widely used method of matrix analysis in studying the discrete time dynamics of age-structured populations [2, 3]. In a later paper [4] Leslie considered nonlinear matrix models in order to extend the notion of logistic growth to age-structured populations. These models provide a means by which to model and study life history strategies in that they account for age-specific birth and survival rates and any biological (physiological, behavioral, etc.) or environmental mechanisms that might affect them. They provide the means to study such basic features as the age of first reproduction (maturation period), the allocation of resources to reproduction versus growth and survival, and so on, and of their effects on population survival and its long-term dynamics. A fundamental principle in biology is that these features, as modeled by the coefficients in a Leslie matrix, are not necessarily fixed in time but can be subject to evolutionary change by natural selection. One methodology for incorporating evolution by natural selection into a dynamic model is that of Darwinian dynamics (evolutionary game theory); see [5–8] and the many references contained therein. After summarizing the global dynamics of the Leslie logistic model in Section 2, we derive and study a Darwinian dynamic version of the model in Section 3, one that involves a single phenotypic trait on which age class-specific fertility and survival rates depend and which is subject to natural selection. Under a restraint on the trait dependence of the competition coefficient (implying that maximal intraspecific competition intensity is experienced when an individual's inherited trait equals the population mean trait) and on the speed of evolution, we obtain in that section an extension of the global dynamic properties of the Leslie logistic model to its Darwinian version. A short example in Section 4 illustrates a use of these results in studying the life history strategy favored by natural selection (in this case, the allocation of reproduction effort by age class).

2. Preliminaries

Let $\mathbb{R}$ denote the set of real numbers, $\mathbb{R}_+$ the set of positive real numbers, and $\overline{\mathbb{R}}_+$ the set of nonnegative real numbers. Let $\mathbb{R}^n := \mathbb{R} \times \mathbb{R} \times \cdots \times \mathbb{R}$ denote the n-dimensional Euclidean space of vectors $\mathbf{x} = (x_i)_{i=1}^n$, where $x_i \in \mathbb{R}$. The positive cone $\mathbb{R}_+^n := \mathbb{R}_+ \times \mathbb{R}_+ \times \cdots \times \mathbb{R}_+$ is the set of positive n-vectors $\mathbf{x} = (x_i)$, $x_i \in \mathbb{R}_+$. The closure $\overline{\mathbb{R}}_+^n := \overline{\mathbb{R}}_+ \times \overline{\mathbb{R}}_+ \times \cdots \times \overline{\mathbb{R}}_+$ of $\mathbb{R}_+^n$ is the set of nonnegative n-vectors. We denote the set of nonnegative integers by $\mathbb{Z}_+ = \{0, 1, 2, \cdots\}$.

The famous Leslie model for an age-structured population is described by the $n \times n$ matrix equation

$$\mathbf{x}(t+1) = \mathbf{L}\mathbf{x}(t), \quad t \in \mathbb{Z}_+, \tag{2.1}$$

with $\mathbf{L} = \mathbf{F} + \mathbf{T}$ where

$$\mathbf{F} = \begin{pmatrix} b_1 & b_2 & \cdots & b_{n-2} & b_{n-1} & b_n \\ 0 & 0 & \cdots & 0 & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 & 0 \end{pmatrix}, \quad \mathbf{T} = \begin{pmatrix} 0 & 0 & \cdots & 0 & 0 & 0 \\ s_1 & 0 & \cdots & 0 & 0 & 0 \\ 0 & s_2 & \cdots & 0 & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots & \vdots \\ 0 & 0 & \cdots & s_{n-2} & 0 & 0 \\ 0 & 0 & \cdots & 0 & s_{n-1} & s_n \end{pmatrix}$$

and where $\mathbf{x}(t) = (x_i(t)) \in \overline{\mathbb{R}}_+^n$ is the demographic n-vector of age class-specific population numbers (or densities) [1]. The time unit and the age classes have the same length (e.g., a year, a decade, etc.). The parameter s_i denotes the fraction of the age class $i-1$ that survives a time unit and which therefore shows up in age class i at the next census. We can also think of s_i as the probability that an individual of age $i-1$ will survive a time unit and thereby transition to the age class i. All newborns are assumed to lie in class $i = 1$ and coefficient b_i (the i-class fertility) is the number of newborns produced by an individual of age i per unit time. The population projection matrix

$$\mathbf{L} = \mathbf{F} + \mathbf{T} = \begin{pmatrix} b_1 & b_2 & \cdots & b_{n-2} & b_{n-1} & b_n \\ s_1 & 0 & \cdots & 0 & 0 & 0 \\ 0 & s_2 & \cdots & 0 & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots & \vdots \\ 0 & 0 & \cdots & s_{n-2} & 0 & 0 \\ 0 & 0 & \cdots & 0 & s_{n-1} & s_n \end{pmatrix} \tag{2.2}$$

is called an extended Leslie matrix (and simply a Leslie matrix if $s_n = 0$, i.e., no individual lives past the n^{th} age class). If we assume

A1: $b_n > 0, 0 \leq s_n < 1$ and $b_i \in \bar{\mathbb{R}}_+, 0 < s_i \leq 1$ for all $i = 1, 2, \cdots, n-1$,

then **L** is a nonnegative and irreducible matrix. By the Perron-Frobenius Theorem **L** has a dominant, positive eigenvalue $r > 0$ which is simple and is associated with unique, positive left and right eigenvectors $\mathbf{w}^T, \mathbf{v} \in \mathbb{R}^n_+$ satisfying $||\mathbf{w}|| = ||\mathbf{v}|| = 1$ where $||\mathbf{v}|| := \Sigma^n_{i=1} |v_i|$. (A superscript T denotes the transpose of a vector.) Note that $||\mathbf{x}|| = \Sigma^n_{i=1} x_i$ is the total size of the population.

We assume moreover that r is strictly dominant, i.e., that

A2: **L** is primitive.

Some useful criteria for the primitivity of **L** are contained in the following Lemma. (See, for example [9].)

Lemma 2.1. *Assume A1. Then the Leslie matrix* **L** *is primitive if one of the following hold:*
(a) $b_1 > 0$ *or* $s_n > 0$ *(***L** *has a positive diagonal element);*
(b) $b_1 = s_n = 0$ *and the greatest common divisor of the set of indices for which* $b_i > 0$ *equals* 1*;*
(c) two consecutive classes are fertile.

The Fundamental Theorem of Demography (or the Strong Ergodic Theorem) [10] tells us, for all nonzero initial conditions $\mathbf{x}(0) \in \bar{\mathbb{R}}^n_+ \backslash \{\mathbf{0}\}$, that

$$\lim_{t\to\infty} \frac{\mathbf{x}(t)}{r^t} = c_1 \mathbf{v} \quad \text{where} \quad c_1 = \mathbf{w}^T \mathbf{x}(0) > 0$$

and

$$\lim_{t\to\infty} \frac{\mathbf{x}(t)}{||\mathbf{x}(t)||} = \mathbf{v}$$

from which we obtain the following theorem.

Theorem 1. Assume A1 and A2. For all initial conditions $\mathbf{x}(0) \in \bar{\mathbb{R}}^n_+ \backslash \{\mathbf{0}\}$ the solutions of the linear Leslie matrix model (2.1) with (2.2) have a stable age distribution, namely,

$$\lim_{t\to\infty} \frac{\mathbf{x}(t)}{||\mathbf{x}(t)||} = \mathbf{v}$$

and

$$r < 1 \text{ implies } \lim_{t\to+\infty} ||\mathbf{x}(t)|| = 0$$

$$r > 1 \text{ implies } \lim_{t\to+\infty} ||\mathbf{x}(t)|| = +\infty.$$

At $r = 1$ there exists an unbounded continuum of positive equilibria, namely, positive constant multiples of $\mathbf{v}$. Thus, as r increases through 1, the extinction equilibrium destabilizes and a vertical bifurcation of positive equilibria occurs. By "vertical" we mean that the spectrum of r values associated with the positive equilibria is a point spectrum consisting of the single value $r = 1$. See Figure 1.

In [4] Leslie modified the linear matrix model (2.1) to include density effects and incorporate logistic-type population growth. He did this under the assumption that the survival probability of every age class is affected the same way by population density and hence every parameter in **L** is multiplied by a common density factor. To describe logistic growth, Leslie chose the density factor $1/\left(1+c\left\|\mathbf{x}\right\|\right)$, $c>0$, and considered the nonlinear matrix equation

$$\mathbf{x}\left(t+1\right)=\frac{1}{1+c\left\|\mathbf{x}\left(t\right)\right\|}\mathbf{L}\mathbf{x}\left(t\right). \tag{2.3}$$

The coefficient c measures the intensity of the population density effects on vital fertility and survival rates. The following Lemma is proved in [11].

Lemma 2.2. *Assume A1 and A2. For all initial conditions* $\mathbf{x}\left(0\right)\in\mathbb{R}_{+}^{n}\setminus\{\mathbf{0}\}$ *the solutions of the Leslie logistic matrix model (2.3) have a stable age distribution, namely*

$$\lim_{t\to\infty}\frac{\mathbf{x}\left(t\right)}{\left\|\mathbf{x}\left(t\right)\right\|}=\mathbf{v}.$$

Moreover, the total population size

$$p\left(t\right):=\left\|\mathbf{x}(t)\right\|$$

satisfies the difference equation

$$p\left(t+1\right)=\left\|\mathbf{L}\frac{\mathbf{x}\left(t\right)}{p\left(t\right)}\right\|\frac{1}{1+cp\left(t\right)}p\left(t\right) \tag{2.4}$$

for $t\in\mathbb{Z}_{+}$.

Note that Eq (2.4) is an asymptotically autonomous, scalar difference equation for $p\left(t\right)$ whose limit equation is the autonomous difference equation (the often called discrete logistic or Beverton-Holt equation)

$$q\left(t+1\right)=r\frac{1}{1+cq\left(t\right)}q\left(t\right).$$

It is well known about this equation that $r<1$ implies that the equilibrium $q^{*}=0$ is globally asymptotically stable on R_{+}^{1} and that $r>1$ implies it is unstable while the positive equilibrium $q^{*}=\left(r-1\right)/c$ is globally asymptotically stable on $\mathbb{R}_{+}\setminus\{0\}$.

One can use theorems relating the asymptotic dynamics of a nonautonomous difference equation to that of its limit equation, together with Lemma 2.2, to determine the asymptotic dynamics of the total population size $p\left(t\right)=\left\|\mathbf{x}(t)\right\|$ of the Leslie logistic matrix model. This is done in [11] with the following result.

Lemma 2.3. *Assume A1 and A2. For all initial conditions* $\mathbf{x}\left(0\right)\in\bar{\mathbb{R}}_{+}^{n}\setminus\{\mathbf{0}\}$ *the solutions of the Leslie logistic matrix model (2.3) satisfy*

$$\lim_{t\to+\infty}\left\|\mathbf{x}(t)\right\|=0 \text{ if } r<1$$

$$\lim_{t\to+\infty}\left\|\mathbf{x}(t)\right\|=\frac{r-1}{c} \text{ and } \lim_{t\to+\infty}\mathbf{x}(t)=\frac{r-1}{c}\mathbf{v} \text{ if } r>1.$$

Lemma 2.3 gives conditions under which the extinction and survival equilibria are attracting. Our next theorem deals with their global stability. Global asymptotic stability requires, in addition to being attracting, that an equilibrium be locally asymptotically stable. To inquire into the local stability of these equilibria, we utilize the linearization principle, which requires a calculation of the Jacobian associated with the Leslie logistic equation. In general, the Jacobian of a nonlinear matrix model

$$\mathbf{x}_{t+1} = \mathbf{A}(\mathbf{x}_t)\,\mathbf{x}_t$$

evaluated at an equilibrium $\mathbf{x}^* = \mathbf{A}(\mathbf{x}^*)\,\mathbf{x}^*$ is

$$\mathbf{J}(\mathbf{x}^*) = \mathbf{A}(\mathbf{x}^*) + \begin{pmatrix} \frac{\partial \mathbf{A}(\mathbf{x}^*)}{\partial x_1}\mathbf{x}^* & \frac{\partial \mathbf{A}(\mathbf{x}^*)}{\partial x_2}\mathbf{x}^* & \cdots & \frac{\partial \mathbf{A}(\mathbf{x}^*)}{\partial x_{n-1}}\mathbf{x}^* & \frac{\partial \mathbf{A}(\mathbf{x}^*)}{\partial x_n}\mathbf{x}^* \end{pmatrix}. \tag{2.5}$$

See [2] (p. 520).

Theorem 2. Assume A1 and A2.

(a) For $r < 1$ the (extinction) equilibrium $\mathbf{x}^* = \mathbf{0}$ of the Leslie logistic matrix model (2.3) is globally asymptotically stable on $\bar{\mathbb{R}}^n_+ \setminus \{\mathbf{0}\}$.

(b) For $r > 1$ the equilibrium $\mathbf{x}^* = \mathbf{0}$ is unstable and the (positive or survival) equilibrium $\mathbf{x}^* = \frac{r-1}{c}\mathbf{v}$ of the Leslie logistic matrix model (2.3) is globally asymptotically stable on $\bar{\mathbb{R}}^n_+ \setminus \{\mathbf{0}\}$.

Proof. (a) As pointed out above, in view of Lemma 2.3 we only need establish that the extinction equilibrium is locally asymptotically stable when $r < 1$. From (2.5) with

$$\mathbf{A}(\mathbf{x}) = \frac{1}{1 + c\,\|\mathbf{x}\|}\mathbf{L} \tag{2.6}$$

and $\mathbf{x}^* = \mathbf{0}$ we find that $\mathbf{J}(\mathbf{0}) = \mathbf{L}$. Since r is the dominant eigenvalue of $\mathbf{L}$ we find from the linearization principle that $\mathbf{x}^* = \mathbf{0}$ is locally asymptotically stable if $r < 1$ and unstable if $r > 1$. (b) In view of Lemma 2.3 we only need establish that the survival equilibrium $\mathbf{x}^* = \frac{r-1}{c}\mathbf{v}$ is locally asymptotically stable when $r > 1$. From (2.6) we find, for this equilibrium, that

$$\frac{\partial \mathbf{A}(\mathbf{x}^*)}{\partial x_j} = -c\left(\frac{1}{1 + c\,\|\mathbf{x}^*\|}\right)^2 \mathbf{L} = -c\frac{1}{r^2}\mathbf{L}$$

for all $j = 1, 2, ..., n$. Thus (since $\mathbf{L}\mathbf{x}^* = \frac{r-1}{c}\mathbf{L}\mathbf{v} = \frac{r-1}{c}r\mathbf{v}$), we see from formula (2.5) that

$$\begin{aligned}\mathbf{J}(\mathbf{x}^*) &= \frac{1}{1 + c\,\|\mathbf{x}^*\|}\mathbf{L} + \begin{pmatrix} -c\frac{1}{r^2}\mathbf{L}\mathbf{x}^* & -c\frac{1}{r^2}\mathbf{L}\mathbf{x}^* & \cdots & -c\frac{1}{r^2}\mathbf{L}\mathbf{x}^* & -c\frac{1}{r^2}\mathbf{L}\mathbf{x}^* \end{pmatrix} \\ &= \frac{1}{r}\mathbf{L} - \frac{1}{r}(r-1)\begin{pmatrix} \mathbf{v} & \mathbf{v} & \cdots & \mathbf{v} & \mathbf{v} \end{pmatrix}.\end{aligned}$$

Note that the spectral radius of $\frac{1}{r}\mathbf{L}$ equals 1. Since $\mathbf{v}$ is a positive vector, this formula for the Jacobian $\mathbf{J}(\mathbf{x}^*)$ subtracts the positive number $\frac{1}{r}(r-1) > 0$ from every entry in $\frac{1}{r}\mathbf{L}$ which implies the spectral radius of the resulting matrix decreases from that of $\frac{1}{r}\mathbf{L}$ and is therefore less than 1. By the linearization principle $\mathbf{x}^*$ is locally asymptotically stable. □

As r increases through 1 and the extinction equilibrium destabilizes, Theorem 2 describes the bifurcation of an unbounded continuum of positive equilibria that occurs from the extinction equilibrium at $r = 1$. This is similar to the linear Leslie model, but has the crucial difference that the spectrum of r values from the bifurcating continuum is no longer the single point $r = 1$ (a vertical bifurcation); it is instead the half line $r > 1$. See Figure 1.

The inherent reproduction number (the density-free number of newborns produced by a newborn over its life time) is

$$\begin{aligned} R_0 &:= b_1 + s_1 b_2 + s_1 s_2 b_3 + \cdots + (s_1 s_2 \cdots s_{n-1}) \frac{1}{1-s_n} b_n \\ &= \sum\nolimits_{j=1}^{n-1} \pi_j b_j + \pi_n \frac{1}{1-s_n} b_n \end{aligned}$$

where

$$\pi_1 := 1, \quad \pi_j := \prod\nolimits_{i=1}^{j-1} s_i, \quad j = 2, 3, ..., n$$

are the probabilities that a newborn lives to reach age class j (to reach age $j-1$). The alternatives of $r < 1$ and $r > 1$ in Theorem 2 that determine the (global) asymptotic dynamics are equivalent to $R_0 < 1$ and $R_0 > 1$, respectively [12, 13]. Thus, R_0 can replace r in Figure 1.

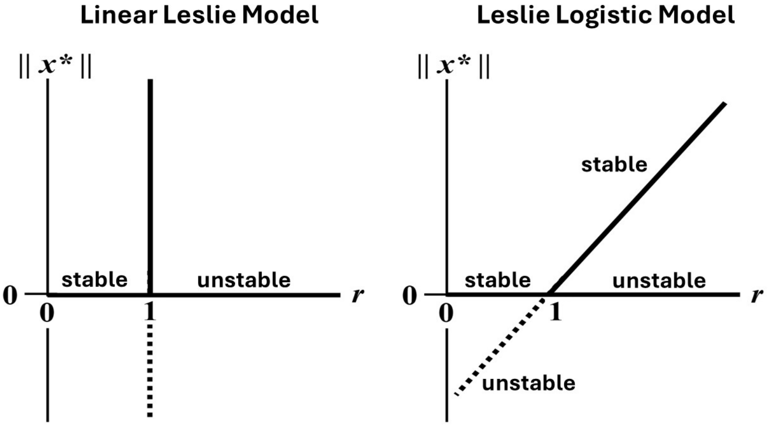

Figure 1. The bifurcation diagrams for the linear Leslie matrix model (2.1) and the Leslie logistic model (2.3) show plots of the total population size of all equilibria as functions of the dominant eigenvalue $r > 0$. The extinction equilibrium $\mathbf{x}^* = \mathbf{0}$ loses stability as r increases through 1 where a continuum of nonzero equilibria bifurcate. For the linear Leslie model the bifurcation is vertical and nonzero equilibria exists at and only at $r = 1$. For the Leslie logistic model the bifurcation is not vertical and nonzero equilibria exist for all $r > 0$. Only the positive equilibria (for $r > 1$) are biologically relevant and they are shown as a solid line (the dashed line corresponds to non-positive equilibria). In all cases, stability means globally asymptotic stability on $\bar{\mathbb{R}}_+^n \setminus \{\mathbf{0}\}$.

3. A Darwinian version of the Leslie logistic model

The coefficients appearing in the linear Leslie model (2.1) and the nonlinear Leslie logistic model (2.3) are assumed constant through time, i.e., the models define autonomous dynamical systems. The values of the coefficients describe the life history of organisms in the population (birth and survival rates, time of first and last reproduction, etc.). There are many reasons, however, why any one or all of these coefficients might not remain constant over time. They could change from one set of values to another (e.g., due to environmental climate change), periodically oscillate (due to daily, monthly, seasonal, or yearly environmental oscillations), or fluctuate randomly (due to any number of environmental or demographic stochastic fluctuations). These would lead, respectively, to Leslie models that are asymptotically autonomous, periodically forced, or stochastic, respectively. Our interest here is not in these causes of changes in coefficient values, but instead to changes due to the fundamental biological principle of evolution by natural selection. We will incorporate natural selection into the Leslie logistic model by making use of Darwinian dynamics (evolutionary game theory) methodology [5, 8].

We assume that (at least some) coefficients in the Leslie logistic model (2.3) depend on phenotypic trait v (physiological, behavioral, metabolic, etc.) that is subject to natural selection. The methodology of Darwinian dynamics assumes that v is symmetrically distributed at all times with variance θ and population mean trait u. Since the coefficients appearing in the Leslie matrix $\mathbf{L}$ are per-capita, age-specific birth and survival rates, we view them as dependent on the trait v inherited by an individual. Thus, we write $b_i = b_i(v)$, $s_i = s_i(v)$, and $\mathbf{L} = \mathbf{L}(v)$. The dominant eigenvalue $r = r(v)$ of the Leslie matrix is then a function of v. The remaining coefficient c in the Leslie logistic equation (2.3) measures the effect that total population size has on an individual's survival rate through competitive (or cooperative) effects with other individuals in the population. We therefore assume that this coefficient depends not only on the individual's inherited trait v but also on the traits of the most typical trait in the population, namely u. Thus, we write $c = c(v, u)$. The entries in the resulting coefficient matrix

$$\frac{1}{1 + c(v, u)\, \|\mathbf{x}\|} \mathbf{L}(v) \tag{3.1}$$

are the vital parameters of an individual with trait v when in a population of size $\|\mathbf{x}\|$ that has a mean trait u. Note that the dominant eigenvalue of this matrix is a function of $\mathbf{x}$, v, and u and we denote it by $r(\mathbf{x}, v, u)$. Since $r(v)$ is the dominant eigenvalue of the Leslie matrix $\mathbf{L}(v)$ it follows that

$$r(\mathbf{x}, v, u) = \frac{1}{1 + c(v, u)\, \|\mathbf{x}\|} r(v) \tag{3.2}$$

is the dominant eigenvalue of the matrix (3.1).

The method of Darwinian dynamics tracks the demographic population vector $\mathbf{x}(t)$ and the population mean trait $u(t)$ using the equations

$$\mathbf{x}(t+1) = \frac{1}{1 + c(v, u(t))\, \|\mathbf{x}(t)\|} \mathbf{L}(v)\Big|_{v=u(t)} \mathbf{x}(t) \tag{3.3}$$

$$u(t+1) = u(t) + \theta \left. \frac{\partial \ln r(\mathbf{x}, v, u(t))}{\partial v} \right|_{v=u(t)} . \tag{3.4}$$

See [5, 8, 14] for derivations. In this model $\ln r(\mathbf{x}, v, u)$ is called fitness and its derivative appearing in the mean trait equation (3.4) is called the fitness gradient. Equation (3.4) states that the change in the population mean trait $u(t)$ is proportional to the fitness gradient and is often called Lande's equation (or Fisher's equation or the canonical equation of evolution). The constant $\theta \geq 0$ is called the *speed of evolution*. If $\theta = 0$ then evolution does not occur, in which case given $u(t) \equiv u(0)$ the population equation (3.3) reduces to the Leslie logistic equation in Section 2. Our main mathematical goal here is to investigate the extent to which the global dynamics described in Theorem 2 for the non-evolutionary Leslie logistic equation hold for this Darwinian Leslie logistic model. Let Ω be an open set in $\mathbb{R}^n$ that contains $\bar{\mathbb{R}}^n_+$ and Υ be an open set in $\mathbb{R}$.

H1: Assume $\mathbf{L}(v)$ is primitive for $v \in \Upsilon$ and its entries satisfy $b_i(\cdot) \in C^2\left(\Upsilon \to \bar{\mathbb{R}}_+\right)$ and $s_i(\cdot) \in C^2(\Upsilon \to [0,1))$. Assume $c(\cdot,\cdot) \in C^1\left(\Upsilon \times \Upsilon \to \bar{\mathbb{R}}_+\right)$.

With regard to the effect of population density on an individual's vital rates, we assume that if an individual inherits the population mean trait $v = u$ then the density effect on that individual's vital rates is given by a coefficient $c_0(u) > 0$. If, on the other hand, the individual inherits a trait $v \neq u$, then we assume the density effect on its vital rates is reduced. This assumption is inspired by Darwin's well-known observation that maximal competition occurs between similar individuals and species. We capture this assumption by assuming that the fractional decrease in the density effect depends on how different an individual's inherited trait v is from the population mean trait u, i.e., it depends on the difference $v - u$. If we denote this decrease by $c_1(v-u)$, where the fraction $c_1(z) > 0$ has a maximum of 1 at $z = 0$ and hence $c'(0) = 0$, then the density factor in the Leslie logistic model is $c(v,u) = c_0(u)c_1(v-u)$. Note that $\partial_v c(v,u)|_{v=u} \equiv 0$ for all u, which is a consequence of our assumption that in a population with mean trait u, the maximal density effect occurs on those individuals who inherit trait $v = u$. In this paper we assume

H2: $\left.\frac{\partial c(v,u)}{\partial v}\right|_{v=0} \equiv 0$ for $u \in \Upsilon$.

As a specific illustration of H2, consider normal distribution type factors: $c_0(u) = \psi_1 \exp\left(-\psi_2 u^2\right)$ and $c_1(z) = \exp\left(-\psi_4 z^2\right)$ with $\psi_1 > 0$ and $\psi_2 \geq 0$, $\psi_4 \geq 0$. Here the maximal density effect is set to occur at population mean trait $u = 0$. The resulting density coefficient

$$c(v,u) = \psi_1 \exp\left(-\psi_2 u^2\right) \exp\left(-\psi_4 (v-u)^2\right)$$

satisfies H2. Such exponential model components are commonly used in [8]. The special case $\psi_2 = 0$ has frequently been used in Darwinian model studies [6, 14–20].

We point out that assumptions on the density coefficient $c(v,u)$ different from H2 can arise from other ecological assumptions. For example, consider a hierarchical-type scenario where a larger trait always infers a smaller density effect due, say, to less intraspecific competition (which might arise due to a physiological characteristic such as larger body size, taller height, quicker mobility, larger claws or body armor, etc.). Then $c(v,u)$ would be a decreasing function of v, which describes a situation when, in a population with fixed mean trait u, the individuals with larger traits v always experience less intense intraspecific competition. Furthermore in this scenario, for those individuals with any specific trait v the competitive effect increases as the population mean trait increases (i.e., a typical competitor's trait increases), which makes $c(v,u)$ an increasing function of u. In such a scenario $c(v,u)$ would not satisfy H2. A specific illustration is $c(v,u) = c_0(u)c_1(v)$ where $c_0(u)$ and $c_1(v)$ are increasing and decreasing functions of u and v, respectively. For example, exponential functions $c_0(u) = \psi_1 \exp(\psi_2 u)$ and $\psi_3 c_1(-\psi_4 v)$ with $\psi_i > 0$ could be used for these purposes. The special case $c(v,u) = \psi_1\psi_3 \exp(-\psi(v-u))$ is obtained when $\psi_2 = \psi_4 = \psi$ and has frequently been used in Darwinian model studies [6, 14–20].

In this paper we study the Darwinian Leslie logistic under the assumption H2. One consequence of H2 is that it affords us, as we will see, a great deal of mathematical tractability due to the fact that the mean trait dynamics uncouple from the demographic population dynamics. Using formula (3.2) we have

$$\ln r(\mathbf{x}, v, u) = -\ln(1 + c(v,u)\|\mathbf{x}\|) + \ln r(v)$$

and

$$\frac{\partial \ln r(\mathbf{x}, v, u)}{\partial v} = -\frac{1}{1 + c(v, u)\|\mathbf{x}\|} \frac{\partial c(v, u)}{\partial v} \|\mathbf{x}\| + \frac{r'(v)}{r(v)}$$

where we use the notation

$$r'(v) := \frac{dr(v)}{dv}, \quad r''(v) := \frac{d^2 r(v)}{dv^2}, \quad \text{etc.}$$

Under assumption H2, the model equations (3.3) and (3.4) become

$$\mathbf{x}(t+1) = \frac{1}{1 + c(v, u(t))\|\mathbf{x}(t)\|} \mathbf{L}(v)\Big|_{v=u(t)} \mathbf{x}(t) \tag{3.5}$$

$$u(t+1) = u(t) + \theta \frac{r'(u(t))}{r(u(t))}\,. \tag{3.6}$$

Note that the mean trait equation (3.6) is uncoupled from the population equation (3.5). If $\theta > 0$, then the difference equation (3.6) has an equilibrium (fixed point) u^* if and only if u^* is a critical point of $r(v)$, i.e., if and only if $r'(u^*) = 0$.

H3: Assume $r(v)$ has at least one critical point $u^* \in \Upsilon$.

For each solution $u(t)$ of the trait equation (3.6) we can view the population equation (3.5) as a nonautonomous matrix equation. In particular, if a solution $u(t)$ of Eq (3.6) approaches an equilibrium u^*, then Eq (3.5) is asymptotically autonomous with limit equation

$$\mathbf{y}(t+1) = \frac{1}{1 + c(u^*, u^*)\|\mathbf{y}(t)\|} \mathbf{L}(u^*)\mathbf{y}(t)\,.$$

This limit equation is a Leslie logistic equation of the form (2.3) to which Theorems 1 and 2 apply. These theorems and an application of Theorem 3.2 in [19] (that connects the dynamics of an asymptotically autonomous equation to that of its limit equation) yield the following results.

Lemma 3.1. *Assume H1, H2, and H3 hold. Suppose u^* is (locally asymptotically) stable and that $\mathbb{B} \subset \Upsilon$ is its basin of attraction.*

(a) If $r(u^*) < 1$ then for any initial condition $\begin{pmatrix} \mathbf{x}(0) \\ u(0) \end{pmatrix} \in \bar{\mathbb{R}}_+ \times \mathbb{B}$ the solution of the Darwinian Leslie logistic model (3.5)-(3.6) satisfies

$$\lim_{t\to\infty} \begin{pmatrix} \mathbf{x}(t) \\ u(t) \end{pmatrix} = \begin{pmatrix} \mathbf{0} \\ u^* \end{pmatrix}.$$

(b) If $r(u^*) > 1$ then for any initial condition $\begin{pmatrix} \mathbf{x}(0) \\ u(0) \end{pmatrix} \in (\bar{\mathbb{R}}_+ \setminus \{\mathbf{0}\}) \times \mathbb{B}$ the solution of the Darwinian Leslie logistic (3.5)-(3.6) satisfies

$$\lim_{t\to\infty} \begin{pmatrix} \mathbf{x}(t) \\ u(t) \end{pmatrix} = \begin{pmatrix} \mathbf{x}^* \\ u^* \end{pmatrix}$$

where

$$\mathbf{x}^* = \frac{r(u^*) - 1}{c(u^*, u^*)} \mathbf{v}(u^*) \in \bar{\mathbb{R}}_+$$

and $\mathbf{v}(u^*)$ is the positive eigenvector of $\mathbf{L}(u^*)$ satisfying $\|\mathbf{v}(u^*)\| = 1$.

By definition a critical trait u^* is an equilibrium of the trait equation (3.6). By the Linearization Principle, u^* is a locally asymptotically stable equilibrium of the scalar difference equation (3.6) if

$$-1 < 1 + \theta \frac{r''(u^*)}{r(u^*)} < 1. \tag{3.7}$$

Given that θ and $r(u^*)$ are positive, the right inequality holds if and only if $r''(u^*) < 0$. Thus, the local asymptotic stability for u^* is obtained by the Linearization Principle if and only if the following assumptions hold.

H4: Assume $u^* \in \Upsilon$ is a critical trait for which $r''(u^*) < 0$ and assume $0 < \theta < -2\frac{r(u^*)}{r''(u^*)}$.

The following theorem is our main result concerning the Darwinian Leslie logistic model (3.5) and (3.6).

Theorem 3. Assume H1, H2, H3, and H4 hold and let $B \subset \Upsilon$ denote the basin of attraction of u^*.

(a) If $r(u^*) < 1$ then the extinction equilibrium

$$\begin{pmatrix} \mathbf{x}^* \\ u^* \end{pmatrix} = \begin{pmatrix} \mathbf{0} \\ u^* \end{pmatrix} \tag{3.8}$$

is globally asymptotically stable on $\bar{\mathbb{R}}_+^n \times \mathbb{B}$.

(b) If $r(u^*) > 1$ then the positive equilibrium

$$\begin{pmatrix} \mathbf{x}^* \\ u^* \end{pmatrix} = \begin{pmatrix} \frac{r(u^*)-1}{c(u^*,u^*)}\mathbf{v}(u^*) \\ u^* \end{pmatrix} \tag{3.9}$$

is globally asymptotically stable on $\bar{\mathbb{R}}_+^n \backslash \{\mathbf{0}\} \times \mathbb{B}$.

Proof. Global asymptotic stability requires global attractivity and local asymptotic stability. Globally attractivity in both cases (a) and (b) is guaranteed by Lemma 3.1. To address local asymptotic stability, by means of the Linearization Principle, we consider the Jacobian associated with the Darwinian Leslie logistic model (3.5) and (3.6), which when evaluated at an equilibrium $\begin{pmatrix} \mathbf{x}^* \\ u^* \end{pmatrix}$ has the form

$$\begin{pmatrix} \mathbf{J}(\mathbf{x}^*, u^*) & * \\ \mathbf{0}_{1\times n} & 1 + \theta\frac{r''(u^*)}{r(u^*)} \end{pmatrix} \tag{3.10}$$

where $\mathbf{J}(\mathbf{x}^*, u^*)$ is the Jacobian of the Leslie logistic equation (3.5), $\mathbf{0}_{1\times n}$ is the n-dimensional row vector of zeros, and the asterisk denotes a column of unneeded entries. The $n+1$ eigenvalues λ_i, $i = 1, 2, ..., n+1$, of this Jacobian are the n eigenvalues of $\mathbf{J}(\mathbf{x}^*, u^*)$ and

$$\lambda_{n+1} = 1 + \theta\frac{r''(u^*)}{r(u^*)}. \tag{3.11}$$

(a) Since $r(u^*)$ is the dominant eigenvalue of $\mathbf{J}(\mathbf{0}, u^*)$, the inequality $r(u^*) < 1$ together with (3.7) imply all eigenvalues of the Jacobian (3.10) satisfy $|\lambda_i| < 1$. The Linearization Principle implies the extinction equilibrium (3.8) is locally asymptotically stability. (b) As shown in the proof of Theorem 2(b), the n eigenvalues of $\mathbf{J}(\mathbf{x}^*, u^*)$ satisfy $|\lambda_i| < 1$ at the positive equilibrium (3.9). This, together with (3.7), implies that all eigenvalues of the Jacobian (3.10) evaluated at this equilibrium satisfy $|\lambda_i| < 1$. The local asymptotic stability of the equilibrium (3.9) follows from the Linearization Principle. □

Remark 1. In the Darwinian Leslie logistic model (3.5) and (3.6) some or all of the entries in the Leslie matrix $\mathbf{L}(v)$ can depend on v and hence so does the inherent reproduction number

$$R_0(v) = \sum\nolimits_{j=1}^{n-1} \pi_j(v)\, b_j(v) + \pi_n(v)\, \frac{1}{1 - s_n(v)} b_n(v).$$

Using the well-known relationship between r and R_0 associated with general matrix models for structured population dynamics [12, 13], we can replace the inequalities $r(u^*) < 1$ and $r(u^*) > 1$ in parts (a) and (b) of Theorem 3 by the inequalities $R_0(u^*) < 1$ and $R_0(u^*) > 1$. respectively.

Remark 2. Theorem 3 describes a bifurcation that occurs at $r(u^*) = 1$ in the sense that the dynamics are significantly different for $r(u^*) < 1$ from what they are for $r(u^*) > 1$; specifically the population goes extinct for $r(u^*) < 1$ and survives if $r(u^*) > 1$. Schematically we have a bifurcation diagram similar to that of the non-evolutionary Leslie logistic as shown in the right-hand diagram in Figure 1. This bifurcation occurs at a critical trait u_c^* where $r(u_c^*) = 1$, which can be found, using Theorem 1 in [21], from the equations $R_0(u_c^*) = 1$ and $R_0'(u_c^*) = 0$ in place of $r(u_c^*) = 1$ and $r'(u_c^*) = 0$.

As seen in the proof of Theorem 3, both the extinction equilibrium and the positive equilibrium are unstable (by the Linearization Principle) if $r''(u^*) > 0$. Since u^*, by definition, satisfies $r'(u^*) = 0$, this means both equilibria are unstable if $v = u^*$ is located at a local minimum of $r(v)$. It is easy to see that this is equivalent to being located a at local minimum of the fitness function

$$\ln r(\mathbf{x}^*, v, u^*) = -\ln\left(1 + c(v, u^*)\, \|\mathbf{x}^*\|\right) + \ln r(v). \tag{3.12}$$

A graph of this function of v is called the fitness (or adaptive) landscape. Note that in Theorem 3(b) the stable positive equilibrium is located at a local maximum of this fitness landscape. If it is located at a global maximum on the adaptive landscape then (and only then), according to the ESS Maximum Principle [8], u^* is what is called an evolutionarily stable strategy (or trait), which means it is invasion-proof to the entry of low-level mutant strategies.

The global stability results in Theorem 3 also require that the speed of evolution θ not exceed the threshold level in H2. The proof of Theorem 3 shows that if this threshold is exceeded, i.e., the speed of evolution is too fast, then both the extinction equilibrium and the positive equilibrium are unstable. The destabilization of the positive equilibrium as θ increases through this threshold is caused by the real eigenvalue (3.11) decreasing through -1. This suggests, according to general bifurcation theory results, that a period doubling bifurcation will likely occur. We do not investigate either this bifurcation nor the occurrence of further bifurcations (periodic oscillations and even chaos) as θ is increased, but restrict ourselves only to stable equilibrium analysis in this paper.

4. An example application

A basic problem in the life history strategy of individuals in a population concerns the timing of reproduction [22]. Is it optimal to reproduce early or to postpone reproduction to a later age? Obviously the answer depends on many trade-offs involved between such factors as the age-specific birth rates, offspring viability, age-specific survival rates, and so on. Evolution by natural selection can play a determining role in the answer. Here, as an example of the modeling methodology and results in

Section 3, we consider a low-dimensional model, specifically an $n = 2$ dimensional Leslie model with matrix

$$\mathbf{L} = \begin{pmatrix} b_1 & b_2 \\ s & 0 \end{pmatrix}$$

that considers simply the trade-offs between the birth rates of the two age classes. (We relabeled the survival probability s_{12} as s, for notational simplification.) We assume that the per-capita birth rates $b_i = b_i(v)$ depend upon a phenotypic trait $v \geq 0$ subject to natural selection. Specifically, for this example, we assume the birth rates as distributed as functions of the trait v by Poisson-type distributions, specifically, we replace b_1 and b_2 in $\mathbf{L}$ by

$$b_1 v e^{1-v} \quad \text{and} \quad b_2 \frac{v}{\beta} e^{1-\frac{v}{\beta}},$$

respectively, to obtain the matrix

$$\mathbf{L}(v) = \begin{pmatrix} b_1 v e^{1-v} & b_2 \frac{v}{\beta} e^{1-\frac{v}{\beta}} \\ s & 0 \end{pmatrix} \tag{4.1}$$

in the Darwinian logistic model in Section 3. These specifications imply that the maximal birth rate of the first age class (younger) individuals is b_1 and that it occurs when an individual inherits trait $v = 1$. This implies that the maximal birth rate of the second age class (older) individuals is b_2 and that it occurs when an individual inherits trait $v = \beta$. We are interested in the case when $\beta \neq 1$, so we assume $\beta > 1$. The biological question in which we are interested is: what population mean trait will evolution favor? Specifically, we ask under what conditions (if any) will evolution favor a mean trait near 1 so as to maximize early reproduction or favor a mean trait near β so as to maximize later reproduction?

Clearly $b_1(v)$ and $b_2(v)$ satisfy H1 and H2 with $\Upsilon = \bar{\mathbb{R}}_+$ and we assume $c(v, u)$ satisfies H1 and H2. The application of the equilibrium stability results in Section 3 require, of course, the existence of equilibria, i.e., the existence of critical traits of the dominant eigenvalue

$$r(v) = \frac{1}{2} b_1 v e^{1-v} + \frac{1}{2}\sqrt{\left(b_1 v e^{1-v}\right)^2 + 4s\frac{1}{\beta} b_2 v e^{1-\frac{v}{\beta}}}$$

of $\mathbf{L}(v)$. Rather than study this problem in general here, we will choose some specific parameter values that will serve to illustrate the application of the results in Section 3 and the kinds of conclusions that can be reached. Let the maximal older individual birth rate occur at trait $\beta = 10$ and assume the younger age class have survival probability $s = 0.9$. It is natural to assume that the relative sizes of the maximal birth rates b_1 and b_2 will play a significant role in the ultimate population dynamics.

As a start, we assume the maximal birth rate of older individuals is significantly larger than that of the younger individuals, specifically three times as larger, so we let $b_1 = 1$ and $b_2 = 3$. Numerical calculations (by means of a computer algebra program) give the results in Table 1, which show that there exist three critical points and three associated positive equilibria of this Darwinian model. The critical traits $u^* \approx 1.650$ and $u^* \approx 9.929$ maximize (nearly) the birth rates of the younger and older individuals, respectively. The values of $r'(u^*)$ and $r''(u^*)$ given in Table 1 imply, by Theorems 3 and 2, that both of the positive equilibria associated with these trait components

$$E_1 : \begin{pmatrix} x_1 \\ x_2 \\ u^* \end{pmatrix} \approx \begin{pmatrix} 33.49 \\ 19.68 \\ 1.650 \end{pmatrix}$$

$$E_3 : \begin{pmatrix} x_1 \\ x_2 \\ u^* \end{pmatrix} \approx \begin{pmatrix} 41.60 \\ 22.78 \\ 9.929 \end{pmatrix}$$

are stable for speeds of evolution θ less than the threshold $-2r(u^*)/r''(u^*)$ shown in Table 1. These theorems and Table 1 also show that the positive equilibrium

$$E_2 : \begin{pmatrix} x_1 \\ x_2 \\ u^* \end{pmatrix} \approx \begin{pmatrix} 30.91 \\ 18.61 \\ 3.219 \end{pmatrix}$$

with trait component $u^* \approx 3.219$ is unstable. Figure 2 shows plots of sample solutions that illustrate these results.

The ESS Maximum Principle and the plots of the adaptive landscapes at the stable equilibria, also shown in Figure 2, indicate that the trait component associated with E_1 is not an ESS while that associated with E_3 is an ESS. We conclude, in this particular example, that evolution favors the population mean trait $u^* \approx 9.929$, i.e., later reproduction. In fact, note in Table 1 that at this equilibrium reproduction at the younger age is virtually absent (the birth rate at equilibrium is 1.316×10^{-3}). Thus, although which equilibrium is reached depends on the initial conditions, in this example evolution favors an ESS semelparous life history strategy [23].

A second numerical example in which the older maximal birth rate is lowered to $b_2 = 2$ (but still remains higher that the younger maximal birth rate $b_1 = 1$), shows a similar result but with the significant difference that the trait component $u^* \approx 1.397$ near the younger maximal birth rate trait is now the ESS. See Table 2 and Figure 3. The three positive equilibria are, in this case,

$$E_1 : \begin{pmatrix} x_1 \\ x_2 \\ u^* \end{pmatrix} \approx \begin{pmatrix} 22.49 \\ 14.75 \\ 1.397 \end{pmatrix}$$

$$E_3 : \begin{pmatrix} x_1 \\ x_2 \\ u^* \end{pmatrix} \approx \begin{pmatrix} 20.49 \\ 13.74 \\ 9.911 \end{pmatrix}$$

$$E_2 : \begin{pmatrix} x_1 \\ x_2 \\ u^* \end{pmatrix} \approx \begin{pmatrix} 14.47 \\ 18.61 \\ 10.43 \end{pmatrix}.$$

Although which equilibrium is reached depends on initial conditions, in this example evolution favors an ESS iteroparous life history strategy.

More Darwinian model studies of semelparity and interoparity can be found in [24] and [25].

Table 1. Shown are the critical traits and other diagnostic quantities for the $n = 2$ dimensional Darwinian logistic model (3.5)-(3.6) with matrix (4.1) and parameter values $b_1 = 1$, $b_2 = 3$, $s = 0.9$, and $\beta = 10$.

Equilibrium	u^*	$r(u^*)$	$r''(u^*)$	$-\frac{2r(u^*)}{r''(u^*)}$	$b_1(u^*)$	$b_2(u^*)$
E_1: stable (non-ESS)	1.650	1.532	−0.1792	17.10	0.8615	1.141
E_2: unstable	3.219	1.495	0.04124	*	*	*
E_3: stable (ESS)	9.929	1.644	−0.007808	421.0	0.001316	3.000

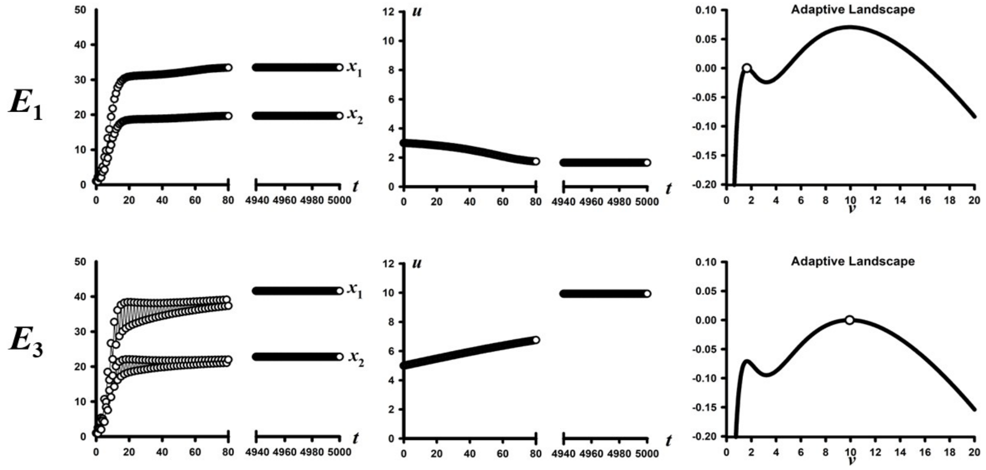

Figure 2. Shown are time series plots of two sample solutions of the Darwinian Leslie logistic model (3.5)-(3.6) with matrix (4.1), parameter values $b_1 = 1$, $b_2 = 3$, $s = 0.9$, $\beta = 10$, and constant competition coefficient $c(v,u) \equiv c_0 = 0.01$. The top row of plots shows the solution with initial conditions $\begin{pmatrix} x_1(0) \\ x_2(0) \\ u(0) \end{pmatrix} = \begin{pmatrix} 1 \\ 1 \\ 3 \end{pmatrix}$ equilibrating (after some transitions) to E_1. The bottom row shows the solution with initial conditions $\begin{pmatrix} x_1(0) \\ x_2(0) \\ u(0) \end{pmatrix} = \begin{pmatrix} 1 \\ 1 \\ 5 \end{pmatrix}$ equilibrating to E_3. The right-most plots are those of the adaptive landscapes at these equilibria with open circles indicating the location of the equilibria trait components.

Table 2. Shown are the critical traits and other diagnostic quantities for the $n = 2$ dimensional Darwinian logistic model (3.5) and (3.6) with matrix (4.1) and parameter values $b_1 = 1$, $b_2 = 2$, $s = 0.9$, and $\beta = 10$.

Equilibrium	u^*	$r(u^*)$	$r''(u^*)$	$-\frac{2r(u^*)}{r''(u^*)}$	$b_1(u^*)$	$b_2(u^*)$
E_1: stable (ESS)	1.397	1.372	−0.3524	7.790	0.9394	0.001337
E_2: unstable	3.864	1.249	0.03474	*	*	*
E_3: stable (non-ESS)	9.911	1.342	−0.006295	426.5	0.001316	2.000

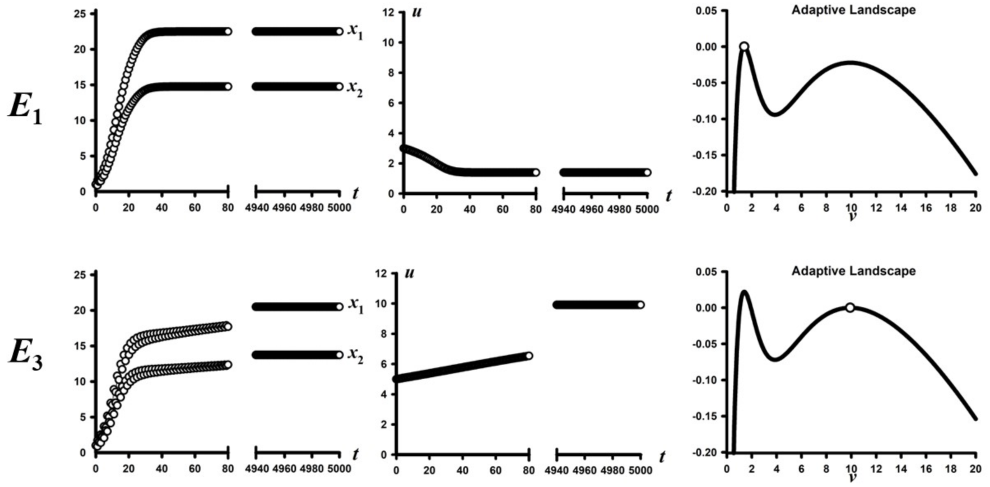

Figure 3. Shown are time series plots of two sample solutions of the Darwinian Leslie logistic model (3.5)-(3.6) with matrix (4.1) and the same parameter values and initial conditions as in Figure 2 except that b_2 has been decreased from 3 to 2.

5. Conclusions

We have investigated a Darwinian dynamic version of the classic Leslie logistic model for the evolutionary dynamics of an age-structured population. The global dynamics known for the non-evolutionary Leslie logistic, as given in Section 2, are extended in Section 3 to the Darwinian version under the assumption H2 on the properties of the trait-dependent competition coefficient $c(v, u)$ and assumption H4 on the geometry of the fitness landscape (3.12) at the equilibrium trait component (that it is located at a local maximum) and on the speed of evolution (that it does not exceed the threshold given in H4). Under these conditions, our results provide the means by which one can study the life history strategies favored by natural selection under various assumed trade-offs, as illustrated by the example in Section 4. Interesting and challenging open problems remain when H4 is not met because the speed of evolution exceeds the threshold, which we showed leads to equilibrium destabilization. This likely results in nonequilibrium dynamics (periodic and aperiodic oscillations and possibly chaotic dynamics). Numerical simulations also suggest that it is possible for sufficiently large evolutionary speeds θ to yield nonequilibrium extinction (evolutionary suicide). Another interesting problem is to establish the results of Theorem 3 for a Darwinian model with more than one evolving trait [8, 26].

Use of AI tools declaration

The authors declare they have not used Artificial Intelligence (AI) tools in the creation of this article.

Conflict of interest

The authors declare there is no conflict of interest.

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