The population size has far-reaching effects on the fitness of a population that in turn influences the population extinction or persistence. Understanding the density- and age-dependent factors will facilitate more accurate predictions about the population dynamics and its asymptotic behavior. In this paper, we develop a rigorous mathematical analysis of the study of positive and negative effects of the increased population density in the classical nonlinear age-structured population model. One of the main results expresses the global stability of the system in terms of the newborn function only. We establish the existence of a threshold population size implying the population extinction, which is well known in the population dynamics as the Allee effect. Bibliography: 18 titles. Illustrations: 1 figure.

Dedicated to N. N. Uraltseva on the occasion of her 85th birthday

1 Introduction

In biological populations, the density–dependent regulation represents a change in individual fitness caused by changes in the population size or density. The negative density–dependence, often explained by intraspecific competition and overcrowding effect, is characterized by a decline in fitness with an increase in the population size or density. In sharp contrast with this is the positive density–dependence, or the Allee effect, characterized by an increase in fitness with an increase in the population size. Various mechanisms have been considered as a source of the Allee effect (cf. [1]–[3]), pointing out that an increase in fitness can come through an increase in the birth rate, a decrease in the death rate, or both.

Mathematical models of age–structured populations usually use the density–dependent vital
rate without any special regard to the type of feedback that produces the density–dependence (cf., for example, [4]–[9]). On the other hand, some authors investigate consequences of the Allee effect in age–structured populations (cf., for example, [10, 11]) or intraspecific competition [12].

The importance of this paper is twofold. First, we expand the mathematical theory of age–structured population dynamics by including density–dependent regulation. Second, the Allee effect can give a positive contribution to the population survival. In the era of massive extinction of species, it is important to study conditions under which a population can survive.

In this paper, we study consequences of different types of density–dependence on permanence of age–structured populations. It is known that the general problem is described by the Gurtin–MacCamy delay equations and the stability of steady states is governed by nonlinear characteristic equations that are not easy to analyze analytically (cf., however, a recent book [13], where the stability of equilibria and local asymptotic behavior of solutions are studied for a model with several significant variables, the so–called sizes). Typical sizes are the total population and the number of juveniles or adults at time \( t \).

Using the framework proposed in [13], we improve the assumptions made in [12] and [14] that intraspecific competition occurs only among individuals of the same age by using a more realistic age, the density–dependent mortality \( \mu(a, P(t)) \), and the fertility \( \beta(a, Q(t)) \), where

\[
P(t) = \int_0^\infty p(a)n(a,t)\,da, \quad Q(t) = \int_0^\infty q(a)n(a,t)\,da
\]

are weighted populations. Here, \( n(a,t) \) denotes the number of individuals of age \( a \) at time \( t \) and \( p(a), q(a) \) are certain weight functions. For example, the choice \( p(a) \equiv 1 \) if \( A_1 \leq a \leq A_2 \) or \( p(a) \equiv 0 \) otherwise yields the population size at time \( t \) in the age interval \([A_1, A_2]\).

One of our main assumptions is that the mortality rate tends to infinity with the population size. This assumption has a biological explanation: intraspecific competition is increasing in any large population due to limited resources in the habitat. An important consequence of this assumption, stated in Section 3, is the existence of an upper bound for a population. Moreover, this result improves a similar result in [15], which becomes possible by allowing two different weight functions for the mortality and fertility rates and by the relaxing condition of Lipschitz continuity for the weight functions.

In Section 4, the stability analysis is performed on the trivial equilibrium \((\rho, P, Q) = (0, 0, 0)\). The stability of the trivial equilibrium depends on the net reproductive rate

\[
R_0 = \int_0^\infty \beta(a, 0) e^{-\int_0^a \mu(v, 0)\,dv} \, da.
\]

Our main result expresses the global stability of the system in terms of the newborn function only. More specifically, in Section 5, we investigate the global stability of the system in terms of newborns only. We restrain the mortality rate to be increasing with \( P \) and thus we do not incorporate the Allee effect on the mortality. Under this assumption, we derive conditions based on the net reproduction rate \( R_0 \) for extinction and persistence. The population will go extinct if \( R_0 \leq 1 \) and will be persistent in the case \( R_0 > 1 \).

In Section 6, we remove the restriction on the mortality function made in Section 5. This corresponds to such an intraspecific mechanism as the Allee effect. More precisely, if \( R_0 < 1 \),
we conclude whether the population is extinct or persistent. We note that if the number of newborns is ever small enough, then this implies extinction. This effectively means that the trivial equilibrium is locally stable.

2 The Model Setup

A density–dependent regulation acts on a population by changing its birth and death rates. Gurtin and MacCamy [8] and Chipot [5] assumed that the strength of a density–dependent regulation always depends on the total population, while Kozlov et al. [12] took the opposite approach by assuming that competition occurs only within each age-class. Here, we follow the model from [13, Chapter 5] with some restrictions. In order to encompass various mechanisms through which a density–dependent regulation can manifest, we introduce the weighted age-class functions

\[ P(t) = \int_0^\infty p(a)n(a,t)\,da, \quad (2.1) \]

\[ Q(t) = \int_0^\infty q(a)n(a,t)\,da, \quad (2.2) \]

where \( n(a,t) \) is the number of individuals of age \( a \) at time \( t \), whereas \( p(a) \) and \( q(a) \) are nonnegative weight functions. Then the balance equation can be written as

\[ \frac{\partial n(a,t)}{\partial t} + \frac{\partial n(a,t)}{\partial a} = -\mu(a,P(t))n(a,t), \quad a, t > 0, \quad (2.3) \]

where the function \( \mu(a,P(t)) \) is the death rate depending on the weighted age-class function \( P(t) \). The boundary condition is given by

\[ n(0,t) = \int_0^\infty \beta(a,Q(t))n(a,t)\,da, \quad t > 0, \quad (2.4) \]

where the birth rate \( \beta(a,Q(t)) \) incorporates the effect of the age-class density through the weighted age-class function \( Q(t) \). The initial condition is given by

\[ n(a,0) = g(a), \quad a > 0. \quad (2.5) \]

The initial–boundary value problem (2.3)–(2.5), together with the weighted age-class-functions (2.1) and (2.2), constitutes a density–dependent population growth model. For purposes of our analysis and in line with the theory in [13, Chapter 5] we assume that the parameters satisfy the following conditions.

\( (H_1) \) The function \( \mu(a,x) \) has the form

\[ \mu(a,x) = \mu_0(a) + \mathcal{M}(a,x), \quad (2.6) \]

where for some \( a_\dagger > 0 \)

\[ \mu_0 \in L^1_{loc}([0,a_\dagger)), \quad \mu_0(a) \geq 0 \quad \text{a.e. in } [0,a_\dagger], \quad \int_0^{a_\dagger} \mu_0(\sigma)d\sigma = +\infty, \quad (2.7) \]
and $\mathcal{M}(\cdot, x)$ is a continuous operator that for each $x \in \mathbb{R}_+ = \{x \in \mathbb{R} : x \geq 0\}$ gives a function in $L^1(0, a_\dagger)$, i.e., $\mathcal{M}(\cdot, x) \in C(\mathbb{R}_+, L^1(0, a_\dagger))$. Moreover,

$$\mathcal{M}(a, x) \geq 0 \quad \text{a.e. in } [0, a_\dagger] \times \mathbb{R}_+, \tag{2.8}$$

Moreover,

$$\mathcal{M}(a, 0) = 0 \quad \text{a.e. in } [0, a_\dagger]. \tag{2.9}$$

$$(H_2)$$ The function $\beta$ is such that

$$\beta(\cdot, x) \in C(\mathbb{R}_+, L^\infty(0, a_\dagger)), \tag{2.9}$$

$$0 \leq \beta(a, x) \leq \beta_+ \quad \text{a.e. in } [0, a_\dagger] \times \mathbb{R}_+. \tag{2.10}$$

Moreover, $\beta(a, x)$ and $\mu(a, x)$ are Lipschitz continuous with respect to the second variable on bounded sets, uniformly on $a \in [0, a_\dagger]$, i.e., for all $M > 0$ there exists a constant $H(M) > 0$ such that for $x, \overline{x} \in [0, M]$

$$|\mu(a, x) - \mu(a, \overline{x})| \leq H(M)|x - \overline{x}|, \tag{2.11}$$

$$|\beta(a, x) - \beta(a, \overline{x})| \leq H(M)|x - \overline{x}|. \tag{2.12}$$

$$(H_3)$$ The weight functions are nonnegative and belong to $L^\infty(0, a_\dagger)$:

$$p, q \in L^\infty(0, a_\dagger), \quad 0 \leq p(a) \leq ||p||_{\infty}, \quad 0 \leq q(a) \leq q_+ \quad \text{a.e. in } [0, a_\dagger]. \tag{2.13}$$

$$(H_4)$$ The initial distribution $f$ satisfies

$$f \in L^1(0, a_\dagger), \quad g(a) \geq 0 \quad \text{a.e. in } [0, a_\dagger]. \tag{2.14}$$

These assumptions can be found in [13]. To study the behavior of a population for large $t$, some additional properties of the birth rate $\beta$ and the weight function $p$ are required. Namely, we assume that there exist constants $a_2 > b_2 > b_1 > a_1 > 0$ and $\delta > 0$ such that

$$\beta(a, x) = 0, \quad a \notin (a_1, a_2), \tag{2.15}$$

$$\beta(a, x) > \delta, a \in (b_1, b_2), \tag{2.16}$$

and there exist $p_2 > p_1 > 0$ such that

$$p(a) > \delta \quad \forall a \in [p_1, p_2]. \tag{2.17}$$

We begin our analysis by deriving an integral formulation of the model (2.3)–(2.5). Our results are based on the reduction of the initial-boundary value problem to a system of nonlinear integral equations for the number of newborns, denoted by

$$\rho(t) = n(0, t), \quad t > 0, \tag{2.18}$$

and for the functions $P(t)$ and $Q(t)$.

As stated in [13, Section 5.1], making the change of variables $a = x$ and $t = x + y$ and integrating along the characteristic lines $y = C$, where $C$ is a constant, we can write the balance equation (2.3) in the form

$$n(a, t) = \begin{cases} 
\rho(t - a)e^{\int_0^t \mu(v, P(v+t-a))dv}, & a < t, \\
\rho(t - a)e^{\int_{t-a}^a \mu(v, P(v+t-a))dv}, & a \geq t.
\end{cases} \tag{2.19}$$
From (2.4), (2.16), and (2.17) we obtain the system of integral equations

\[
\begin{align*}
\rho(t) &= \int_0^t \beta(a, Q(t)) \rho(t - a) e^{-\int_0^{a-t} \mu(v, P(v + t - a)) dv} da \\
&\quad + \int_t^\infty \beta(a, Q(t)) f(a - t) e^{-\int_a^{a-t} \mu(v, P(v + t - a)) dv} da, \\

P(t) &= \int_0^t p(a) \rho(t - a) e^{-\int_0^{a-t} \mu(v, P(v + t - a)) dv} da + \int_t^\infty p(a) f(a - t) e^{-\int_a^{a-t} \mu(v, P(v + t - a)) dv} da, \\

Q(t) &= \int_0^t q(a) \rho(t - a) e^{-\int_0^{a-t} \mu(v, P(v + t - a)) dv} da + \int_t^\infty q(a) f(a - t) e^{-\int_a^{a-t} \mu(v, P(v + t - a)) dv} da.
\end{align*}
\]  

(2.18) 

Then we have the existence and uniqueness of a solution to the problem (2.18)-(2.20). More precisely, the following assertion holds.

**Theorem 2.1.** Let Assumptions \((H_1)-(H_4)\) hold. Then there exist unique nonnegative functions \(\rho, P, Q \in C(\mathbb{R}_+)\) satisfying the problem (2.18)-(2.20).

This result is well known and comes back to the analysis of age-structured population models in [8] and [5]. The proof (even for a more general model involving arbitrarily many weight functions) can be found, for example, in [13, Section 5.1].

### 3 Boundedness of Solutions

The negative density-dependence is observed in biological populations as intraspecific competition or overcrowding effects and is investigated both practically and theoretically. Mathematical representation of the negative density-dependence begins with the Verhulst model for an unstructured population (cf., for example, [16]), and the consequences of this type regulation are the bounded growth and stabilization of the population around its carrying capacity. Effects of the negative density-dependence on the age-structured population are studied in [12]. Under the assumption that only members of the same age-class compete, the existence of a bounded solution has been proved. In what follows, we prove the existence of a bounded solution considering a more general mortality function which includes competition between different age classes. For this purpose we consider the problem (2.3)-(2.5), where the nonnegativity condition on \(\mathcal{M}\) in Assumption \((H_1)\) is removed and, instead, the following conditions hold.

\(\mathcal{A}_1\) There exists a function \(\psi \in C(\mathbb{R}_+)\) such that \(\mathcal{M}(a, x) \geq \psi(x) \geq -\sup a \mu_0(a)\) for all \(a\) and \(x\), where \(\psi(\cdot)\) is nondecreasing and \(\lim_{x \to \infty} \psi(x) = \infty\).

\(\mathcal{A}_2\) There exists a constant \(c > 0\) such that \(\beta(a) \leq cp(a)\) for all \(a\).

Assumption \(\mathcal{A}_1\) corresponds to the fact that for large populations the mortality rate increases with the population size; moreover, it generalizes the mortality rate used in [12]. Note
that for small populations this correlation does not need to hold. This allows us to include mortality functions that satisfy $\mu(a, P)$ is decreasing for $P \in (0, \delta)$ and increasing for $P > \delta$. Such mortality functions can be related to the Allee effect to describe situations, where for small population sizes an increase in the population size increases fitness by reducing mortality. Assumption $(A_1)$ implies the unboundedness of the density-dependent mortality rate, which corresponds to our expectations since intraspecific competition increases with the population size.

Assumption $(A_2)$ does not restrict the birth rate $\beta$ or the weight function $p$ since $\beta$ is already bounded and $p$ is nonnegative according to Assumptions $(H_2)$ and $(H_3)$. However, it does provide a relation between the individual contribution to fecundity and mortality: individuals in every fertile age group are competing for resources and are contributing to the mortality rate of individuals of their age or older.

We will show that Assumptions $(A_1)$ and $(A_2)$ are sufficient for the boundedness of $P(t)$, $Q(t)$, $\rho(t)$ for all $t$. This improves the result of [15], where the weight function $p(a)$ is assumed to be Lipschitz continuous.

The following assertion is proved in Appendix A below.

**Lemma 3.1.** Let $\rho$ be a nonnegative continuous function on $[0, \infty)$, and let $\psi(x)$ satisfy $(A_1)$. We define $\psi^{-1}(x)$ by $\max\{y \geq 0 : \psi(y) = x\}$. Let $\gamma = 1 - \psi(0)$. If there exist constants $c > 0$ and $M > 1 + \psi(\rho(0)/c)$ such that

$$\rho(t) \leq M \max_{x \leq t} \frac{\rho(x)}{\psi(\frac{\rho(x)}{c}) + \gamma} \quad \forall \ t, \quad (3.1)$$

then

$$\rho(t) \leq M \max_{k \leq c\psi^{-1}(M-\gamma)} \frac{k}{\psi(\frac{k}{c}) + \gamma} < \infty. \quad (3.2)$$

We state and prove the main result of this section.

**Theorem 3.1.** If the functions $\beta$, $\mu$, $f$, $p$, $q$ satisfy Assumptions $(H_2)$–$(H_4)$, $(A_1)$, and $(A_2)$, then the functions $\rho$, $P$, $Q$ are bounded.

**Proof.** Making the change of variables $x = t - a$ and $v_{\text{new}} = v_{\text{old}} + x$ in the first integrals of (2.18) and (2.19) and assuming that $t \geq a_\dagger$, we find

$$\rho(t) = \int_0^t \beta(t - x, Q(t))\rho(x)e^{-\int_x^t \mu(v-x, P(v))dv} \, dx, \quad (3.3)$$

$$P(t) = \int_0^t p(t - x)\rho(x)e^{-\int_x^t \mu(v-x, P(v))dv} \, dx, \quad (3.4)$$

$$Q(t) = \int_0^t q(t - x)\rho(x)e^{-\int_x^t \mu(v-x, P(v))dv} \, dx. \quad (3.5)$$

This, together with Assumption $(A_2)$, implies

$$P(t) = \int_0^t p(t - x)\rho(x)e^{-\int_x^t \mu(v-x, P(v))dv} \, dx$$
\[ \geq \frac{1}{\epsilon} \int_0^t \beta(t-x, Q(t)) \rho(x) e^{-\int_x^t \mu(v-x, P(v)) dv} \, dx \geq \frac{1}{\epsilon} \rho(t). \quad (3.6) \]

Using \((A_1), (A_2), \text{and (3.6)}\), from \((3.3)\) we derive the following estimate for \(\rho\):

\[ \rho(t) \leq \int_{t-a_t}^t \beta_{\max} \rho(x) e^{-\int_x^t \psi(\rho(v)/c) dv} \, dx \leq \int_{t-a_t}^t \beta_{\max} \rho(x) e^{-\int_x^t \psi(\rho(v)/c) dv} \, dx. \]

Multiplying the nominator and denominator by \(\psi(\rho(x)/c) + \gamma > 0\), we get

\[ p(t) \leq \int_{t-a_t}^t \beta_{\max} \frac{\rho(x)}{\psi(\rho(x)/c)} \left( \psi\left( \frac{\rho(x)}{c} \right) + \gamma \right) e^{-\int_x^t \psi(\rho(v)/c) dv} \, dx \]

\[ \leq \beta_{\max} \max_{x \leq t} \frac{\rho(x)}{\psi(\rho(x)/c)} \left( \int_{t-a_t}^t \psi\left( \frac{\rho(x)}{c} \right) e^{-\int_x^t \psi(\rho(v)/c) dv} \, dx + \int_{t-a_t}^t e^{-\int_x^t \psi(\rho(v)/c) dv} \, dx \right) \]

\[ \leq \beta_{\max} \max_{x \leq t} \frac{\rho(x)}{\psi(\rho(x)/c)} + \gamma \left[ e^{-\int_{t-a_t}^t \psi(\rho(v)/c) dv} \right]_{t-a_t}^t \]

\[ \leq \beta_{\max} (\gamma + a_t) \max_{x \leq t} \frac{\rho(x)}{\psi(\rho(x)/c)} + \gamma. \]

Lemma 3.1 infers that \(\rho\) is bounded by

\[ M \max_{k \leq (e^{c\psi^{-1}(M-\gamma)} - 1)} \frac{k}{\psi(\frac{k}{c}) + \gamma}, \quad (3.7) \]

where \(M = \max(\beta_{\max}(\gamma + a_t), \gamma + \psi(\rho(0)/c))\). Finally, to prove the boundedness of \(P\) and \(Q\), it suffices to use the boundedness of \(\rho\) and \((2.19)\). \(\square\)

### 4 Local Stability of Trivial Equilibrium

To investigate the local stability of the trivial equilibrium \((\rho, P, Q) = (0, 0, 0)\), we linearize the problem \((2.1)-(2.3)\). Let \((\rho, P, Q) = (z, \mathcal{P}, \mathcal{Q})\) be a solution to the problem \((2.1)-(2.3)\). Assume that \((z(a, t), \mathcal{P}(t), \mathcal{Q}(t))\) is close to zero. For linearization we assume, in addition to the above assumptions on \(\beta\) and \(\mu\), that \(\beta(a, x)\) and \(\mu(a, x)\) have continuous partial derivatives with respect to the second variable, uniformly in \(a \in [0, a_\dagger]\). Linearizing around zero, we get

\[ \frac{\partial z(a, t)}{\partial t} + \frac{\partial z(a, t)}{\partial a} = -\mu(a, 0) z(a, t), \quad (4.1) \]

\[ z(0, t) = \int_0^\infty \beta(a, 0) z(a, t) \, da. \quad (4.2) \]
If \( z \) is known, then \( \mathcal{P} \) and \( \mathcal{Q} \) can be calculated from formulas (2.1)–(2.2).

In the age-structured population models, the net reproduction rate defined by

\[
R_0 = \int_0^\infty \beta(a,0)e^{-\int_0^\infty \mu(v,0)dv} - \int_0^\infty \lambda da \tag{4.3}
\]

measures the number of offspring of an individual during its lifetime [17, 12]. It is often used as an indicator of the large time population behavior, and a dichotomy between the population survival for \( R_0 > 1 \) and extinction for \( R_0 \leq 1 \) is proved in [17, 12]. The stability of the trivial equilibrium \((\rho, P, Q) = (0, 0, 0)\) of the linear problem (4.1)–(4.2) can be assessed by using \( R_0 \), and we have the following result.

**Proposition 4.1.** The solution to the problem (4.1)–(4.2) converges to zero if \( R_0 < 1 \) and increases to infinity if \( R_0 > 1 \). If \( R_0 = 1 \), then the solution is bounded and persistent.

**Proof.** Let \( \lambda \) be such that

\[
\int_0^\infty \beta(a,0)e^{-\int_0^\infty \mu(v,0)dv - \lambda a} \, da = 1 \tag{4.4}
\]

We note that the left-hand side of (4.4) is a strictly decreasing continuous function with respect to \( \lambda \), with the values ranging from \( \infty \) to 0. Thus, \( \lambda \) is well defined. By [17, Theorems 3.2 and 3.3], for \( \sigma = \lambda \) and \( z(0, t) \neq 0 \) there exist constants \( C_1, C_2 > 0 \) such that

\[
C_1 e^{\lambda t} \leq z(0, t) \leq C_2 e^{\lambda t}. \tag{4.5}
\]

We have \( \lambda < 0 \) if \( R_0 < 1 \) and \( \lambda > 0 \) if \( R_0 > 1 \), which, together with (4.5), implies the required assertion.

**Remark 4.1.** By the linearized stability principle [18], the asymptotic stability and instability of the linearized problem (4.1)-(4.2) imply the asymptotic stability and instability of the nonlinear problem (2.1)-(2.5) respectively. This means that for the problem (2.1)-(2.5) the trivial equilibrium is locally stable if \( R_0 < 1 \) and locally unstable if \( R_0 > 1 \).

We refer the reader to [18] for more details, but for guidance note that (2.3)–(2.5) defines a family of operators \( T(t) : L^1(0, a_1) \to C(\mathbb{R}) \) which has an initial distribution \( f(a) \) and gives a solution to the problem (2.3)–(2.5) evaluated at \( t \), i.e., \( n(\cdot, t) \). This family turns out to be a semigroup, and the Fréchet derivative of \( T(t) \) is the corresponding operator derived from the linear problem (4.1)–(4.2).

In the next section, we improve our recent results about local stability by deriving conditions for persistence of the solution and for global extinction.

## 5 Global Stability Analysis

The net reproduction rate \( R_0 \) defined by (4.3) can be used to determine the large time behavior of the solution to the problem (2.3)-(2.5). Theorem 5.1 claims that the functions \( \rho, Q, P \) are separated from zero if the net reproduction rate is greater than one; otherwise, \( \rho, Q, P \) converge to zero.
Theorem 5.1. Assume that

\[ \psi(P) > 0 \quad \forall \ P > 0, \]  
\[ \beta(a, 0) > \beta(a, Q) \quad \forall \ Q > 0. \]  

Then the following assertions hold.

(a) If \( R_0 \leq 1 \), then \( \rho(t) \to 0 \), \( P(t) \to 0 \), \( Q(t) \to 0 \) as \( t \to \infty \).

(b) If \( R_0 > 1 \), then there exist positive constants \( 0 < a_k < b_k \), \( k = 1, 2, 3 \), independent of \( f \) such that \( a_1 \leq \rho(t) \leq b_1 \), \( a_2 \leq P(t) \leq b_2 \), and \( a_3 \leq Q(t) \leq b_3 \) for large \( t \).

To prove Theorem 5.1, we need the following lemma which will be proved in Appendix B.

Lemma 5.1. Let \( \rho = \rho(t) \) be a nonnegative function defined for \( t > 0 \) and satisfying

\[ c_1 \int_{t-b_1}^{t-a_1} \rho(\tau) \, d\tau \leq \rho(t) \leq c_2 \int_{t-a_2}^{t-b_2} \rho(\tau) \, d\tau, \quad t > a_2, \]  

where \( 0 < a_1 < b_1 < a_2 < b_2 \) and \( c_1 \) and \( c_2 \) are positive constants. Let

\[ \int_{t_1-\beta_1}^{t_1-\beta_2} \rho(\tau) \, d\tau \leq c_3 \Lambda \quad \text{for certain} \ t_1 \]  

with some constants \( \beta_1 \) and \( \beta_2 \). Then for each \( \hat{t} \) there exist constants \( t_1 \) and \( c^* \) independent of \( \Lambda, \rho, t \) such that for \( t_1 \geq t_1 \)

\[ \max_{t_1 - \hat{t} \leq \tau \leq t_1} \rho(\tau) \leq c^* \Lambda. \]  

We note that Equation (2.18), together with the boundedness of \( \beta \), implies that the number of newborns satisfies the upper estimate in (5.3). Since \( P \) is bounded and \( \beta \) is bounded from below on \( (b_1, b_2) \), the left-hand side of (5.3) is true as well. Lemma 5.1 now tells us that for large \( t \), if the integral over \( \rho \) is small, i.e., \( \Lambda \) is small, then \( \rho \) is also small in the interval over which \( \rho \) was integrated.

Proof of Theorem 5.1. (a) Suppose that \( R_0 < 1 \), \( \varepsilon > 0 \), \( \rho^* = \limsup_{t \to \infty} \rho(t) \). From (3.3) it follows that

\[ \rho(t) \leq \int_0^\infty \beta(a, Q(t))(\rho^* + \varepsilon)e^{-\int_0^a \mu(v,P(t)) \, dv} \, da \leq \int_0^\infty \beta(a, 0)(\rho^* + \varepsilon)e^{-\int_0^a \mu(v,0) \, dv} \, da = (\rho^* + \varepsilon)R_0 \]  

for large \( t \). Moreover, there exists a sequence \( \{t_k\} \), \( k = 1, 2, ... \), such that \( t_k \to \infty \) and \( \rho(t_k) \geq \rho^* - \varepsilon \). Hence

\[ \rho^* - \varepsilon \leq (\rho^* + \varepsilon)R_0, \ \ \rho^* \leq \varepsilon \frac{1 + R_0}{1 - R_0}, \]
which implies $\rho^* = 0$. This, together with Equations (2.19) and (2.20), leads us to the conclusion that $P(t) \to 0$ and $Q(t) \to 0$ as $t \to \infty$.

Let us consider the case $R_0 = 1$. Using Assumption $(A_1)$ and Equation (3.3), we get

$$\rho(t) \leq \int_0^t \beta(a,0) e^{-\int_0^a \mu(v,P(v+t-a))\,dv} \rho(t-a) \, da + \int_t^\infty \beta(a,0) f(a-t) e^{-\int_{a-t}^0 \mu(v,P(v+t-a))\,dv} \, da, \quad (5.6)$$

and for $t > a^*$ we have

$$\rho(t) = \int_0^t \beta(a,0) e^{-\int_0^a \mu(v,P(v+t-a))\,dv} \rho(t-a) \, da. \quad (5.7)$$

Similarly, from Assumption $(A_1)$ and Equation (3.4) we get

$$P(t) \leq \int_0^t p(a)e^{-\int_0^a \mu_0(v)\,dv} \rho(t-a) \, da + \int_t^\infty p(a) f(a-t) e^{-\int_{a-t}^0 \mu_0(v)\,dv} \, da. \quad (5.8)$$

Making the change of variables $x = t - a$, $y = v + t - a$ in the first terms and $x = a - t$, $y = v + t - a$ in the second terms of the right-hand sides of (5.6) and (5.8) respectively, we find

$$\rho(t) \leq \int_0^t \beta(t-x,0) \rho(x) e^{-\int_0^{t-x} \mu_0(y-x)\,dy} \, dx + \int_0^\infty \beta(t+x,0) f(x) e^{-\int_0^x \mu_0(y+x)\,dy} \, dx,$$

$$P(t) \leq \int_0^t p(t-x) \rho(x) e^{-\int_0^{t-x} \mu_0(y-x)\,dy} \, dx + \int_0^\infty p(t+x) f(x) e^{-\int_0^x \mu_0(y+x)\,dy} \, dx,$$

which can be written as

$$\rho(t) \leq \int_0^t \beta(t-x,0) e^{-\int_0^{t-x} \mu_0(y)\,dy} \rho(x) e^{-\int_0^x \psi(y)\,dy} \, dx + \int_0^\infty \beta(t+x,0) e^{-\int_0^x \mu_0(y)\,dy} \, dx,$$

and

$$P(t) \leq \int_0^t p(t-x) e^{-\int_0^{t-x} \mu_0(y)\,dy} \rho(x) e^{-\int_0^x \psi(y)\,dy} \, dx + \int_0^\infty p(t+x) e^{-\int_0^x \mu_0(y)\,dy} \, dx.$$
Multiplying both equations by \( e^t \int \psi(P(y)) dy \) and introducing the notation

\[
\alpha_1(t) = \rho(t) e^t \int_0^t \psi(P(y)) dy, \quad \alpha_2(t) = P(t) e^t \int_0^t \psi(P(y)) dy,
\]

\[
M(a) = \beta(a,0) e^{-\int_0^a \mu(v) dv}, \quad S(a) = p(a) e^{-\int_0^a \mu_0(v) dv}, \quad F(a) = f(a) e^0 \int_0^a \mu_0(v) dv,
\]

we get

\[
\alpha_1(t) \leq \int_0^t M(t-x) \alpha_1(x) \, dx + \int_0^\infty M(t+x) F(x) \, dx,
\]

\[
\alpha_2(t) \leq \int_0^t S(t-x) \alpha_1(x) \, dx + \int_0^\infty S(t+x) F(x) \, dx.
\]

We note that \( \alpha_1(t) \) is the number of newborns for a density-independent variant of the original problem (2.3)–(2.5) with \( R_0 = 1 \) and initial age distribution \( F(a) \). Since \( R_0 = 1 \), from Theorem 3.2 in [17] with \( \sigma = 0 \) it follows that \( \alpha_1(t) \leq C \) and from (5.12) it follows that \( \alpha_2(t) \) is also bounded. From (5.9) we get

\[
\rho(t) e^t \int_0^t \psi(P(y)) dy \leq C, \quad P(t) e^t \int_0^t \psi(P(y)) dy \leq C.
\]

To prove the convergence of \( \rho, P, Q \), we distinguish two cases.

If \( \rho(t) \to 0 \), then \( P(t) \to 0 \) and \( Q(t) \to 0 \) as \( t \to \infty \), and the claim holds. Otherwise,

\[
\int_0^\infty \psi(P(y)) dy \leq C.
\]

In this case, by the assumption (5.1), there exists a sequence \( t_k \to \infty \) as \( k \to \infty \) such that \( \varepsilon_k = P(t_k) \to 0 \) as \( k \to \infty \). We can, in addition, require that \( |t_k - t_{k-1}| < 1 \). Equation (2.19) and Assumption \( (H_3) \) imply the existence of a constant \( c \) such that for all \( k \)

\[
\int_{t_{k-2}}^{t_{k-1}} \rho(\tau) \, d\tau \leq c\varepsilon_k, \quad \text{supp}(p) = [p_1,p_2].
\]

By Lemma 5.1 with comments, for large enough \( k \) we have \( \max_{t_{k-1} \leq \tau \leq t_k} \rho(\tau) \leq c^* \varepsilon_k \). By the requirement \( |t_k - t_{k-1}| < 1 \), we can now conclude that \( \rho(t) \to 0 \). From (2.19) and (2.20) we also see that \( P(t) \to 0 \) and \( Q(t) \to 0 \).

Finally, we consider the case \( R_0 > 1 \) and show that \( \rho(t) \geq \delta_1 > 0 \) for large \( t \). For this purpose we assume that there exists a sequence \( t_k \to \infty \) as \( k \to \infty \) such that \( \varepsilon_k = P(t_k) \to 0 \). Without loss of generality we can assume that \( \rho(t_k) = \inf_{t_{k-2} \leq t \leq t_k} \rho(t) \). Since

\[
\int_{t_{k-2}}^{t_{k-1}} \rho(\tau) \, d\tau \leq c_1 \rho(t_k),
\]

\[
\int_{t_{k-2}}^{t_{k-1}} \rho(\tau) \, d\tau \leq c_1 \rho(t_k) \quad (2.20)
\]
from Lemma 5.1 it follows that

\[
\max_{t_k - t \leq \tau \leq t_k} \rho(\tau) \leq c_3 \rho(t_k) = c_3 \varepsilon_k,
\]

which implies

\[
\max_{t_k - t \leq \tau \leq t_k} P(\tau) \leq c \varepsilon_k.
\]

Using (3.3), for \( t = t_k \) we get

\[
\rho(t_k) \geq \rho(t_k) \int_0^{t_k} \beta(a,0)e^{-\int_0^a (\mu(v,P) - \mu(v,0)) dv} da \geq \rho(t_k) R_0 (1 + o(\varepsilon_k)),
\]

which is impossible because \( R_0 > 1 \). We can now conclude that \( a_1 < \rho(t) < b_1 \).

Suppose now that there exists a sequence \( t_k \to \infty \) as \( k \to \infty \) such that \( P(t_k) \to 0 \) or \( Q(t_k) \to 0 \) as \( k \to \infty \). Then from (3.4) and (3.5) it follows that

\[
\varepsilon_k \geq c \int_{t_k - p_1}^{t_k - p_2} \rho(\tau) d\tau.
\]

By Lemma 5.1,

\[
\liminf_{t \to \infty} \rho(t) = 0,
\]

which is impossible according to the previous part of the proof. \( \square \)

Note that, in the case where the maximum of \( \beta(a, \cdot) \) and minimum of \( \mu(a, \cdot) \) are not attained at zero, we can still come to similar conclusions by using the same technique and redefining \( R_0 \). For example, assume that there exist functions \( \mu_\cdot \) and \( \beta_\cdot \) such that

\[
\mu(a,p) \geq \mu_\cdot (a), \quad \beta(a,Q) \leq \beta_\cdot (a)
\]

for all \( a \). Let

\[
R_0^+ = \int_0^\infty \beta(a,Q)e^{-\int_0^a \mu_\cdot (v) dv} da.
\]

Then \( R_0^+ < 1 \) implies \( \rho(t) \to 0, P(t) \to 0, Q(t) \to 0 \).

6 Permanence by Positive Density-Dependence

Let us assume that the influence of the Allee effect manifests through changes in the death rate. This means that, in a small population, every increase in an age-class decreases the death rate. In other words, for every \( a \) the death rate \( \mu(a,P) \) is a decreasing function of \( P \) for \( P \in (0, \delta) \).

We prove that, if \( R_0 = 1 \), then survival is possible due to the Allee effect.

**Theorem 6.1.** If \( \mu(a,P) - \mu(a,0) < 0 \) for \( P \in (0, \delta) \) and \( R_0 = 1 \), then

\[
\liminf_{t \to \infty} \rho(t) > 0, \quad \liminf_{t \to \infty} P(t) > 0.
\]
Proof. Let
\[ M(a) = \beta(a, Q(t)) e^{-\int_0^a \mu(v) dv}. \] (6.1)

Using (3.3), (6.1) and the assumption of the theorem, for \( P < \delta \) and sufficiently large \( t \) we obtain
\[ \rho(t) = \int_0^t M(a) \rho(t - a) e^{-\int_0^a \mu(v) dv} da \geq \int_0^t M(a) \rho(t - a) da. \]

To prove the claim, we suppose that \( \liminf_{t \to \infty} \rho(t) = 0 \). Then there exists a sequence \( \{t_k\} \) such that \( \rho(t_k) \to 0 \) as \( k \to \infty \). Without loss of generality we can assume that \( \rho(t_k) = \inf_{t_k - a_2 < t < t_k} \rho(t) \). To show that \( \rho(t) \) is small on \([t_k - 1, t_k]\), we note that
\[ \epsilon_k = \rho(t_k) = \int_0^t \beta(a, Q(t)) \rho(t_k - a) e^{-\int_0^a \mu(v, P(v + t - a)) dv} da, \int_{t_k - a_2}^{t_k - a_1} \rho(\tau) d\tau \leq c \epsilon_k. \]

Then, by Lemma 5.1,
\[ \max_{t_k - t \leq \tau \leq t_k} \rho(\tau) \leq c^* \epsilon_k, \]
which implies
\[ P(t) = \int_0^t p(a) \rho(t - a) e^{-\int_0^a \mu(v, P(v + t - a)) dv} da \leq \delta \]
on \( t_k - \hat{t} + M \leq \tau \leq t_k \). This also implies
\[ \rho(t_k) > \int_0^\infty M(a) \rho(t_k) da = \rho(t_k), \]
which is impossible. \( \square \)

Our goal is to prove conditions for extinction and permanence in the case of the Allee effect. Under the assumption that the weighted age-class function is constant \( P(t) = \mathcal{P} \) and \( Q(t) = \mathcal{Q} \) is constant over the individual lifetime, the weighted net reproduction rate \( R(\mathcal{P}, \mathcal{Q}) \) is defined by the formula
\[ R(\mathcal{P}, \mathcal{Q}) = \int_0^\infty \beta(a, \mathcal{Q}) e^{-\int_0^a \mu(v) dv} da. \] (6.2)

We note that \( R(0, 0) = R_0 \), as defined in (4.3).

**Lemma 6.1.** Assume that \( R(\mathcal{P}, \mathcal{Q}) < 1 \) for \( \mathcal{P} < P^* \), \( \mathcal{Q} < Q^* \). Let \( \rho^* > 0 \) be such that
\[ \rho^* < \frac{P^*}{\int_0^\infty p(a) da}, \quad \rho^* < \frac{Q^*}{\int_0^\infty q(a) da}. \] (6.3)

If \( \rho(t) < \rho^* \) on some interval \( t^* - a_t < t < t^* \), then \( \rho, Q, P \to 0 \).
Remark 6.1. Lemma 6.1 tells us that, to conclude extinction, in some cases it suffices to look at the number of newborns during a time period of the maximal lifetime.

Remark 6.2. In [13], it is concluded that $R_0 < 1$ implies the asymptotic stability of the trivial equilibrium in the sense that there exists $\delta$ such that, if $||f(a)||_1 < \delta$, then

$$\lim_{t \to \infty} ||\mu(t)||_1 = 0.$$ 

Lemma 6.1 is a similar result, but differs in the way that we look at the number of newborns to conclude the pointwise convergence of $\rho$, $P$, $Q$.

As we will see, the restriction on $\rho^*$ is chosen to guarantee that, if $\rho(t - v) < \rho^*$ on $0 < v < a^+$, then $P(t) < P^*$ and $Q(t) < Q^*$, which implies that for all times each individual would live a life with the net reproductive rate less than one. This in turn would imply extinction.

Proof of Lemma 6.1. Let $\rho_+$ be the theoretical maximum of $\rho$ as in (3.7), and let $||p||_\infty = \sup p$. Let

$$\varepsilon_P = \frac{P^* - \int_0^\infty p(a)\rho^* da}{2||p||_\infty \rho_+} > 0, \quad \varepsilon_Q = \frac{Q^* - \int_0^\infty q(a)\rho^* da}{2||p||_\infty \rho_+} > 0,$$

$$\delta_P = \left(1 - \frac{\rho^* \int_0^\infty p(a) da}{2P^*}\right), \quad \delta_Q = \left(1 - \frac{\rho^* \int_0^\infty q(a) da}{2Q^*}\right).$$

Furthermore, let $\varepsilon = \min(\varepsilon_P, \varepsilon_Q)$. For $t^* < t < t^* + \varepsilon$ we have

$$P(t) = \int_0^t p(a)\rho(t - a)e^{-\int_0^a \mu(v,P(v+t-a))dv} da + \int_t^\infty p(a)f(a-t)e^{-\int_a^{a-t} \mu(v,P(v+t-a))dv} da$$

$$= \int_0^\varepsilon p(a)\rho(t - a)e^{-\int_0^a \mu(v,P(v+t-a))dv} da + \int_0^t p(a)\rho(t - a)e^{-\int_0^{a-t} \mu(v,P(v+t-a))dv} da$$

$$< \varepsilon_P ||p||_\infty \rho_+ + \int_0^\infty p(a)\rho^* da = \delta_P P^*$$

(6.4)

In the same way, for $t^* < t < t^* + \varepsilon$ we have

$$Q(t) < \delta_Q Q^*.$$ 

(6.5)

Let

$$R_1 = \max_{\rho \in \delta_P P^*, \mathcal{Q} \in \delta_Q Q^*} R(\mathcal{Q}, \mathcal{P}).$$

(6.6)

Now, we estimate the number of newborns $\rho$ on the interval $t^* \leq t < t^* + \varepsilon$,

$$\rho(t) = \int_0^t \beta(a, Q(t))\rho(t - a)e^{-\int_0^a \mu(v,P(v+t-a))dv} da$$

$$+ \int_t^\infty \beta(a, Q(t))f(a-t)e^{-\int_a^{a-t} \mu(v,P(v+t-a))dv} da$$
\[
\leq \rho^* \int_t^\infty \beta(a, Q(t)) e^{-\int_0^a \mu(v, P(v+a)) \, dv} \, da + \rho^* \int_0^\infty \beta(a, Q(t)) e^{-\int_0^a \mu(v, P(v-a)) \, dv} \, da
\]

\[
+ \rho^* \int_t^\infty \beta(a, Q(t)) e^{-\int_0^{a-t} \mu(v, P(v+a)) \, dv} \, da \leq \rho^* R_1 + \varepsilon \rho_+.
\] (6.7)

If
\[
\varepsilon \leq \frac{\rho^*(1 - R_1)}{2\rho_+},
\]
from the above inequality it follows that
\[
\rho \leq \frac{1 + R_1}{2} \rho^* < \rho^* \text{ on } t^* < t < t^* + \varepsilon.
\]

So, let
\[
\gamma = \min(\varepsilon, \frac{\rho^*(1 - R_1)}{2\rho_+}).
\] (6.8)

Then
\[
\rho(t) < \frac{1 + R_1}{2} \rho^* \text{ on } t^* < t < t^* + \gamma.
\]

Iterating finitely many times, we get
\[
\rho(t) < \frac{1 + R_1}{2} \rho^* \text{ on } t^* < t < t^* + a_1.
\]

We can use this result yet again to conclude that
\[
\rho(t) < \left(\frac{1 + R_1}{2}\right)^2 \rho^* \text{ on } t^* + a_1 < t < t^* + 2a_1,
\]
\[
\rho(t) < \left(\frac{1 + R_1}{2}\right)^3 \rho^* \text{ on } t^* + a_1 < t < t^* + 3a_1
\]
and so on. This implies that \(\rho\) converges to zero. From (2.19) and (2.20) we see that \(Q\) and \(P\) also converge to zero. \(\square\)

The following theorem shows that a population that is not converging to zero is necessarily persistent.

**Theorem 6.2.** If \(R_0 < 1\), then either \(\rho, Q, P \to 0\) or there exist \(\varepsilon_{\rho}, \varepsilon_P, \varepsilon_Q > 0\) such that \(\rho > \varepsilon_{\rho}, P > \varepsilon_P, Q > \varepsilon_Q\), i.e., the population is persistent.

**Proof.** If \(\varepsilon_{\rho}\) exists, then from Assumptions \((H_2)\) and \((H_3)\) it follows that \(\varepsilon_P\) and \(\varepsilon_Q\) necessarily exist. Conversely, if \(\varepsilon_{\rho}\) does not exist, then there exists a sequence \(t_k > a_1\) such that \(t_k \to \infty\) and \(\rho(t_k) \to 0\) as \(k \to \infty\). Let \(\varepsilon > 0\) be arbitrary. There exists \(K\) such that \(\rho(t_k) < \varepsilon\) if \(k > K\). For these \(k\) we have
\[
\int_0^{t_k} \beta(a, Q(t_k)) \rho(t_k - a) e^{-\int_0^a \mu(v, P(v+a)) \, dv} \, da < \varepsilon.
\]
This, together with Theorem 3.1 and Assumption \((H_2)\), implies that there exists \(C > 0\) such that
\[
\int_{t-b_1}^{t-b_2} \rho(t-a)da < C\varepsilon.
\]
By Lemma 5.1, there exist constants \(t_1\) and \(c^*\) independent of \(\varepsilon\) such that for \(t_k > t_1\)
\[
\max_{t_{k-1} \leq \tau \leq t_k} \rho(\tau) \leq c^*\varepsilon.
\]
If we take \(\varepsilon\) such that
\[
c^*\varepsilon < \min\left(\frac{P^*}{\int_0^\infty p(a)da}, \frac{Q^*}{\int_0^\infty q(a)da}\right),
\]
then Lemma 6.1 guarantees that \(\rho \to 0\), and we reach a contradiction. \(\square\)

7 Equilibrium Points of (2.18)—(2.20) and Stability Analysis

Here, we derive the equilibrium points to our model, i.e., solutions that are constant in time, and then continue with the stability analysis for these equilibrium points. A similar analysis of equilibria and their stability has been done in [13, Section 5.3 and Chapter 6] for a more general model including arbitrarily many weighted sizes. We derive explicit criteria by means of the characteristic equation (7.8) and then relate the obtained threshold parameter to an analogue of the net reproductive rate \(R_0\).

Let \((\rho^*, P^*, Q^*)\) be a constant solution. From Equations (2.18), (2.19), (2.20) we get
\[
\rho^* = \int_0^\infty \beta(a, Q^*) \rho^* e^{-\int_0^a \mu(v, P^*) dv} da,
\]
\[
P^* = \int_0^\infty p(a) \rho^* e^{-\int_0^a \mu(v, P^*) dv} da,
\]
\[
Q^* = \int_0^\infty p(a) \rho^* e^{-\int_0^a \mu(v, P^*) dv} da.
\]
If \(\rho^* = 0\), then \((\rho^*, P^*, Q^*) = (0, 0, 0)\). Otherwise, we have
\[
\rho^* = \frac{P^*}{\int_0^\infty p(a) e^{-\int_0^a \mu(v, P^*) dv} da}, \quad Q^* = P^* \Gamma(P^*),
\]
where
\[
\Gamma(P^*) := \frac{\int_0^\infty q(a) e^{-\int_0^a \mu(v, P^*) dv} da}{\int_0^\infty p(a) e^{-\int_0^a \mu(v, P^*) dv} da}
\]
and

\[ 1 = \int_0^\infty \beta(a, P^* \Gamma(P^*)) e^{-\int_0^a \mu(v, P^*) dv} da. \quad (7.1) \]

So, we first solve the last equation (7.1) with respect to \( P^* \) and then compute \( Q^* \) and \( \rho^* \) from the other two equations. If \( R_0 > 1 \), then a solution necessarily exists since the right-hand side of (7.1) goes continuously from \( R_0 \) to zero as \( P^* \) goes to infinity.

Let \( \rho^*(a) \) be an equilibrium point. We set \( n(a,t) = \rho^*(a) + z(a,t) \), where \( z \) is a small perturbation. To analyze, we need to assume that \( \mu \) and \( \beta \) are differentiable with respect to the second variable. We denote by \( \mu_P \) and \( \beta_Q \) the derivatives of \( \mu \) and \( \beta \) with respect to the second variable respectively. Linearizing Equation (2.3), we get

\[
\frac{\partial z(a,t)}{\partial t} + \frac{\partial \rho^*(a)}{\partial a} + \frac{\partial z(a,t)}{\partial a} = -\mu(a, P(t))(\rho^*(a) + z(a,t))
\]

\[
= -(\mu(a, P^*) + \mathcal{P}(t)\mu_P(a, P^*)) (\rho^*(a) + z(a,t))
\]

\[
= -\mu(a, P^*)\rho^*(a) - \mathcal{P}(t)\mu_P(a, P^*)\rho^*(a) - \mu(a, P^*) z(a,t).
\]

From Equation (2.4) it follows that

\[
\rho^*(0) + z(0, t) = \int_0^a \beta(a, Q(t))(\rho^*(a) + z(a,t)) da
\]

\[
= \int_0^a (\beta(a, Q^*) + \mathcal{Q}(t)\beta_Q(a, Q^*)) (\rho^*(a) + z(a,t)) da,
\]

\[
= \int_0^a \beta(a, Q^*)\rho^*(a) + \beta(a, Q^*) z(a,t) + \mathcal{Q}(t)\beta_Q(a, Q^*)\rho^*(a) da,
\]

and from (2.1) and (2.2) we get

\[
P(t) = \int_0^\infty p(a)(\rho^*(a) + z(a,t)) da = P^* + \mathcal{P}(t), \quad \mathcal{P}(t) = \int_0^\infty p(a)z(a,t) da,
\]

\[
Q(t) = \int_0^\infty q(a)(\rho^*(a) + z(a,t)) da = P^* + \mathcal{Q}(t), \quad \mathcal{Q}(t) = \int_0^\infty q(a)z(a,t) da.
\]

Using the fact that \( \rho^*(a) \) is an equilibrium point, we get

\[
\frac{\partial z(a,t)}{\partial t} + \frac{\partial \rho^*(a)}{\partial a} = -\mathcal{P}(t)\mu_P(a, P^*)\rho^*(a) - \mu(a, P^*) z(a,t),
\]

\[
z(0, t) = \int_0^\infty (\mathcal{Q}(t)\beta_Q(a, Q^*)\rho^*(a) + \beta(a, Q^*) z(a,t)) da,
\]

\[
\mathcal{P}(t) = \int_0^\infty p(a)z(a,t) da, \quad \mathcal{Q}(t) = \int_0^\infty q(a)z(a,t) da.
\]
We look for solutions of the form
\[ z(a, t) = g(a)e^{\lambda t}, \quad z(0, t) = C_1 e^{\lambda t}, \quad \mathcal{P}(t) = C_2 e^{\lambda t}, \quad \mathcal{Q}(t) = C_3 e^{\lambda t}. \]
Substituting these data, we get
\[
g(a)\lambda + \frac{dg(a)}{da} = -C_2 \mu P(a, P^*) \rho^*(a) - \mu(a, P^*) g(a),
\]
(7.2)
\[
C_1 = \int_0^\infty C_3 \beta Q(a, Q^*) \rho^*(a) + \beta(a, Q^*) g(a) \, da,
\]
(7.3)
\[
C_2 = \int_0^\infty p(a) g(a) \, da,
\]
(7.4)
\[
C_3 = \int_0^\infty q(a) g(a) \, da.
\]
(7.5)
Equation (7.2) can be solved with respect to \( g(a) \) by the integrating factor method, with the solution
\[
g(a) = \frac{C_1 - \int_0^a C_2 \mu P(\sigma, P^*) \rho^*(\sigma) e^{\int_0^\sigma \mu(\tau, P^*) d\tau} d\sigma}{e^{a \lambda + \int_0^a \mu(\sigma, P^*) d\sigma}}.
\]
(7.6)
Inserting (7.6) into the system of equations (7.3)–(7.5), we get
\[
C_1 = \int_0^\infty \left( C_3 \beta Q(a, Q^*) \rho^*(a) + \beta(a, Q^*) \frac{C_1 - \int_0^a C_2 \mu P(\sigma, P^*) \rho^*(\sigma) e^{\int_0^\sigma \mu(\tau, P^*) d\tau} d\sigma}{e^{a \lambda + \int_0^a \mu(\sigma, P^*) d\sigma}} \right) \, da,
\]
\[
C_2 = \int_0^\infty \frac{C_1 - \int_0^a C_2 \mu P(\sigma, P^*) \rho^*(\sigma) e^{\int_0^\sigma \mu(\tau, P^*) d\tau} d\sigma}{e^{a \lambda + \int_0^a \mu(\sigma, P^*) d\sigma}} p(a) \, da,
\]
\[
C_3 = \int_0^\infty \frac{C_1 - \int_0^a C_2 \mu P(\sigma, P^*) \rho^*(\sigma) e^{\int_0^\sigma \mu(\tau, P^*) d\tau} d\sigma}{e^{a \lambda + \int_0^a \mu(\sigma, P^*) d\sigma}} q(a) \, da.
\]
To simplify calculations, we introduce the notation
\[
A_1 = \int_0^\infty \beta Q(a, Q^*) \rho^*(a) \, da,
\]
\[ A_2(\lambda) = - \int_0^\infty \beta(a, Q^*) \int_0^a \mu P(\sigma, P^*) e^{\int_0^\sigma \mu(\tau, P^*) d\tau} d\sigma da, \]

\[ A_3(\lambda) = \int_0^\infty \beta(a, Q^*) e^{-a\lambda - \int_0^\sigma \mu(\tau, P^*) d\tau} da, \]

\[ A_4(\lambda) = - \int_0^\infty p(a) \int_0^a \mu P(\sigma, P^*) e^{\int_0^\sigma \mu(\tau, P^*) d\tau} d\sigma da, \]

\[ A_5(\lambda) = \int_0^\infty p(a) e^{-a\lambda - \int_0^\sigma \mu(\tau, P^*) d\tau} da, \]

\[ A_6(\lambda) = - \int_0^\infty q(a) \int_0^a \mu P(\sigma, P^*) e^{\int_0^\sigma \mu(\tau, P^*) d\tau} d\sigma da, \]

\[ A_7(\lambda) = \int_0^\infty q(a) e^{-a\lambda - \int_0^\sigma \mu(\tau, P^*) d\tau} da. \]

Then the system of equations can be written as

\[
\begin{pmatrix}
A_3(\lambda) - 1 & A_2(\lambda) & A_1 \\
A_5(\lambda) & A_4(\lambda) - 1 & 0 \\
A_7(\lambda) & A_6(\lambda) & -1
\end{pmatrix}
\begin{pmatrix}
C_1 \\
C_2 \\
C_3
\end{pmatrix}
= 0.
\]

(7.7)

The system (7.7) has small nonzero solutions \( C_1, C_2, C_3 \) if and only if

\[
\det \begin{pmatrix}
A_3(\lambda) - 1 & A_2(\lambda) & A_1 \\
A_5(\lambda) & A_4(\lambda) - 1 & 0 \\
A_7(\lambda) & A_6(\lambda) & -1
\end{pmatrix} = 0.
\]

(7.8)

For the trivial equilibrium we get

\[ A_3(\lambda) = \int_0^\infty \beta(a, 0) e^{-a\lambda - \int_0^\sigma \mu(\tau, 0) d\tau} da = 1. \]

(7.9)

If we set \( \text{Re}(\lambda) = \gamma \) and \( \text{Im}(\lambda) = \varphi \), then (7.9) takes the form

\[
\int_0^\infty \beta(a, 0) e^{-a\gamma - \int_0^\sigma \mu(\tau, 0) d\tau} e^{-ia\varphi} da = \text{Re} A_3(\gamma, \varphi) + i \text{Im} A_3(\gamma, \varphi) = 1
\]

(7.10)

where

\[
\text{Re} A_3(\gamma, \varphi) = \int_0^\infty \beta(a, 0) e^{-a\gamma - \int_0^\sigma \mu(\tau, 0) d\tau} \cos(a\varphi) da,
\]

\[
\text{Im} A_3(\gamma, \varphi) = -\int_0^\infty \beta(a, 0) e^{-a\gamma - \int_0^\sigma \mu(\tau, 0) d\tau} \sin(a\varphi) da.
\]
We observe that $\text{Re} \ A_3(\cdot,0) : \mathbb{R} \to (0, \infty)$ is strictly decreasing and "onto," so that, under the made assumptions, the equation

$$\text{Re} \ A_3(\gamma,0) = 1$$

has a unique solution $\gamma^*$. Furthermore, $\text{Re} \ A_3(\gamma^*,\cdot)$ attains its unique maximum if $\varphi = 0$. Then for all solutions with $\varphi \neq 0$ to Equation (7.10) we have $\gamma < \gamma^*$. Let

$$R_0 = \text{Re} \ A_3(0,0) = \int_0^\infty \beta(a,0)e^{-\int_0^a \mu(\tau,0)d\tau} \, da$$

If $R_0 < 1$, then $\gamma^* < 0$ which implies $\gamma < 0$ for all solutions, and we can conclude that the trivial equilibrium point is stable. If $R_0 > 1$, then $\gamma^* > 0$, and the trivial equilibrium point is unstable.

### Appendix. Proof of Lemma 3.1

If the right-hand side of (3.2) is greater of or equal to the right-hand side of (3.1), then (3.2) follows from (3.1). Let $\gamma = 1 - \psi(0)$. Assume that there exists $T \geq 0$ such that

$$\max_{x \leq T} \frac{\rho(x)}{\psi(\frac{\rho(x)}{c}) + \gamma} > \max_{0 < k \leq cv^{-1}(M-\gamma)} \frac{k}{\psi(\frac{k}{c}) + \gamma}.$$ 

Due to the condition on $M$, we have $T > 0$. There exists $0 < t_1 \leq T$ such that

$$\frac{\rho(t_1)}{\psi(\frac{\rho(t_1)}{c}) + \gamma} = \max_{x \leq T} \frac{\rho(x)}{\psi(\frac{\rho(x)}{c}) + \gamma} = \max_{x \leq t_1} \frac{\rho(x)}{\psi(\frac{\rho(x)}{c}) + \gamma},$$

and, since

$$\frac{\rho(t_1)}{\psi(\frac{\rho(t_1)}{c}) + \gamma} > \max_{0 < k \leq cv^{-1}(M-\gamma)} \frac{k}{\psi(\frac{k}{c}) + \gamma},$$

we have $\rho(t_1) > cv^{-1}(M - \gamma)$. By the definition of $\psi^{-1}$, this means that

$$\psi\left(\frac{\rho(t_1)}{c}\right) > \psi\left(\frac{cv^{-1}(M - \gamma)}{c}\right) = M - \gamma.$$ 

Now, from (3.1) we get

$$\rho(t_1) \leq M \max_{x \leq t_1} \frac{\rho(x)}{\psi(\frac{\rho(x)}{c}) + \gamma} = M \frac{\rho(t_1)}{\psi(\frac{\rho(t_1)}{c}) + \gamma} < \rho(t_1)$$

and we reach a contradiction. This proves the lemma.

### Appendix. Proof of Lemma 5.1

We will repeatedly use the following identity: for constants $\beta_1 < \beta_2$ and $b_1 < b_2$ we have

$$\int_{t-\beta_2}^{t-\beta_1} \int_{\tau-b_2}^{\tau-b_1} \rho(s) \, ds \, d\tau = \int_{t-\beta_2-b_2}^{t-\beta_1-b_1} \int_{\min(t-\beta_1,s+b_2)}^{\min(t-\beta_2,s+b_1)} \rho(\tau) \, d\tau \, ds.$$ 

(B.1)
Figure below shows this fact.

Using the left-hand side of (5.3) to estimate (5.4) from below, we get

\[
c_3 \Lambda \geq \int_{t^* - \beta_1}^{t^* - \beta_2} \rho(\tau) d\tau \geq \int_{t^* - \beta_1}^{t^* - \beta_2} \int_{\tau - \beta_1}^{\tau - \beta_2} \rho(\tau) d\tau ds. \tag{B.2}
\]

Let \( b'_1, b'_2 \) be constants such that \( b_1 < b'_1 < b'_2 < b_2 \). By (B.1), we get

\[
c_3 \Lambda \geq c_1 \int_{t^* - \beta_1 - b_1}^{t^* - \beta_2 - b_2} \min(t^* - \beta_1, s + b_2) \int_{t^* - \beta_2 - b_2}^{\max(t^* - \beta_2, s + b_1)} \rho(\tau) d\tau ds \geq c_1 \int_{t^* - \beta_1 - b'_1}^{t^* - \beta_2 - b'_2} \min(t^* - \beta_1, s + b_2) \int_{t^* - \beta_2 - b'_2}^{\max(t^* - \beta_2, s + b_1)} \rho(\tau) d\tau ds. \tag{B.3}
\]

Since

\[
\min(t^* - \beta_1, s + b_2) \int_{t^* - \beta_2 - b_2}^{\max(t^* - \beta_2, s + b_1)} \rho(\tau) d\tau > \gamma > 0
\]

is bounded from below on the interval \( s \in [t - \beta_2 - b'_2, t - \beta_1 - b'_1] \) (cf. Figure), we get

\[
\gamma c_1 \int_{t^* - \beta_2 - b'_2}^{t^* - \beta_1 - b'_1} \rho(s) ds \leq c'_k \Lambda. \tag{B.4}
\]

Iterating \( k \) times, we get

\[
\int_{t^* - \beta_1 - kb'_1}^{t^* - \beta_2 - kb'_2} \rho(s) ds \leq c' \Lambda \tag{B.5}
\]

for some \( c' > 0 \) depending on \( b_1, b_2, b'_1, b'_2, m, \beta_1, \beta_2, k \). Using the right-hand side of (5.3), from the previous inequality we derive

\[
\rho(T) \leq c_2 \int_{T - a_1}^{T - a_2} \rho(\tau) d\tau \leq c_2 \int_{T - a_2}^{T - a_1} \int_{t^* - \beta_1 - kb'_1}^{t^* - \beta_2 - kb'_2} \rho(\tau) d\tau ds \leq c_2 c' \Lambda,
\]

where \( d_1 = t^* - \beta_2 - kb'_2 + a_2 \leq T \leq t^* - \beta_1 - kb'_1 + a_1 = d_2 \). Here, \( d_1 \) and \( d_2 \) are required to be larger than \( a_2 \), which gives us the value of \( t_1 \):

\[
t_1 = \beta_2 + kb'_2. \tag{B.6}
\]

We assume that \( k \) is chosen large enough to satisfy \( d_2 - d_1 > a_2 - a_1 \). Then for \( T \in [d_2, d_2 + a_1] \) we have

\[
\rho(T) \leq c \int_{T - a_1}^{T - a_2} \rho(\tau) d\tau \leq c \int_{T - a_2}^{T - a_1} \int_{T - a_2}^{T - a_1} c' \Lambda d\tau \leq cc'(a_2 - a_1) \Lambda
\]

according to (B.5). Hence there exists a constant \( c_1 \) such that \( \rho(T) \leq c_1 \Lambda, d_1 \leq T \leq d_2 + a_2 \). Continuing this procedure, we get a constant \( \tilde{c} \) such that \( \rho(T) \leq \tilde{c}_1 \Lambda, d_1 \leq T \leq d_2 + \tilde{a}_2 \). Choosing
$k$ large enough to satisfy $d_1 \leq t^* - \hat{t}$ and then choosing $l$ large enough to satisfy $d_2 + la_2 \geq t^*$, we arrive at (5.5).

**Figure.** The parallelogram is the area over which $\rho$ is integrated in the middle of formula (B.3). The grey area is the domain over which $\rho$ is integrated on the right-hand side of (B.3).

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