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Remarks on the Stability of Some Size-Structured Population Models IV: The General Case of Juveniles and Adults

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Abstract

The stability of some size-structured population dynamics models is investigated when the population is divided into adults and juveniles. We determine the steady states and study their stability. We also give examples that illustrate the stability results. The results in this paper generalize previous results, for example, see Calsina, et al. (2003), El-Doma (2006), Farkas, et al. (2008), and El-Doma (2008 a).

1. Introduction

IN this paper, we study a size-structured population dynamics model that divides the population at any time t into adults, we denote by $A(t)$, and juveniles, we denote by $J(t)$. Adults are individuals with size larger than the maturation size $T \geq 0$. Juveniles are individuals with size smaller than the maturation size T. The model takes the following form:

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$$\frac{\partial p(a,t)}{\partial t} + \frac{\partial}{\partial a}(V(a, J(t), A(t))p(a,t)) + \mu(a, J(t), A(t))p(a,t) = 0,$$
$$a \in [0, l), l \leq +\infty, \ t > 0,$$
$$V(0, J(t), A(t))p(0,t) = \int_T^l \beta(a, J(t), A(t))p(a,t)da, \ t \geq 0,$$
$$p(a, 0) = p_0(a), \ a \in [0, l), \tag{1}$$
$$J(t) = \int_0^T p(a,t)da, \ t \geq 0,$$
$$A(t) = \int_T^l p(a,t)da, \ t \geq 0,$$

where, $p(a,t)$, is the density of the population with respect to size $a \in [0, l)$ at time $t \geq 0$, where, $0 < l \leq +\infty$, is the maximum size an individual in the population can attain; $P(t) = \int_0^l p(a,t)da = J(t) + A(t)$, is the total population size at time t; $\beta(a, J(t), A(t)), \mu(a, J(t), A(t))$, are, respectively, the birth rate i.e. the average number of offspring, per unit time, produced by an individual of size a when the population size is $P(t)$, and the mortality rate i.e. the death rate at size a, per unit population, when the population size is $P(t)$; $0 < V(a, J(t), A(t))$, is the individual growth rate at the population size $P(t)$.

We study problem (1) under the following general assumptions:

$0 \leq p_0(a) \in L^1([0, l)) \cap L_\infty[0, l), \mathbb{R}^+ = [0, \infty);$

$V(a, J, A), \beta(a, J, A), \mu(a, J, A) \in C([0, l) \times \mathbb{R}^{+2})$, and are nonnegative functions; \qquad (2)

$V_P(a, J, A), V_{Pa}(a, J, A), \beta_P(a, J, A), \mu_P(a, J, A)$ exist $\forall a \geq 0, J \geq 0, A \geq 0;$

$V_P(., J, A), V_{Pa}(., J, A), \beta(., J, A), \beta_P(., J, A), \mu(., J, A), \mu_P(., J, A) \in C([0, l) : L_\infty(\mathbb{R}^{+2})).$

Models of size-structured populations were first derived in Sinko et al. (1967), where the population density and the vital rates depend on age, size and time. Due to its complication, this type of model has been ignored by mathematicians, for example, see Metz, et al. (1986). Problem (1) generalizes those given in Calsina, et al. (2003), El-Doma (2006), where the vital rates are taken to depend on the population size only, and El-Doma (2008 a), where juveniles are not considered.

Size-structured population models are studied by many authors, for example, Mimura, et al. (1988), studied a size-structured population model where the vital rates depend on a weighted population size $r(t)$ i.e., $r(t) = \int_0^l \omega(a)p(a,t)da, \omega \geq 0$, as well as the size, and the growth rate V is of separable form that is a special case of that in problem (1); they proved the global existence and uniqueness of non-negative solutions, and obtained some stability results when the death rate μ depends on the weighted population size $r(t)$ only. Calsina, et al. (1995), studied a size-structured population model with the additional assumption that there is an inflow of newborns (of zero-size) from an external source, like seeds in plants when carried by wind, or eggs from fish when carried by water, and proved the existence and uniqueness of solution; and the existence of

a global attractor when the inflow of newborns is a constant. A similar size-structured population model is also considered in Farkas, et al. (2007), El-Doma (2008 a), and El-Doma (2008 b), and stability results are obtained. In Cushing (1985), the existence of stable positive steady states for a size-structured population model is studied using bifurcation theory methods, and in Cushing (1987), these results are generalized to systems of interacting populations. In Cushing (1990), a competition model for several size-structured species exploiting a single resource is derived. It is shown that, under suitable conditions, the asymptotic dynamics can be reduced to a system of ordinary differential equations via which global stability results are obtained. In Cushing (1992), a size-structured population model for cannibalism is studied, and, under suitable conditions, global stability results are obtained. In Cushing (1996), a size-structured hierarchical model for intra-specific competition is studied, and under suitable conditions, a single scalar differential equation for the dynamics of a weighted population size is derived via which global stability results are obtained. In Farkas, et al. (2008), problem (1) is studied using semigroups theory method with the objective to obtain conditions for the stability of the steady states. However, only two special cases are considered, namely, the case when $\mu(a, J, A) = \mu(a), V(a, J, A) = V(a)$ and the case when $\beta(a, J, A) = \beta(a, A), \mu(a, J, A) = \mu(a, A), V(a, J, A) = V(a, A)$. In addition, they also considered the case when there is a constant inflow of newborns from an external source, in this case they looked into the steady states of the system, provided some examples, and relegated further analysis to future work.

Further generalization of size-structured population dynamics models involved the additional assumption of subdividing the population into subgroups based on growth rates, these growth rates can be finite in number leading to a finite number of subgroups, for example, see Ackleh, et al. (2005) or infinitely many different growth rates, for example, see Huyer (1994). These studies proved existence and uniqueness results; and provided numerical results as in Huyer (1994), and numerical and statistical results as in Ackleh, et al. (2005).

Our motivation for the present study is to extend the work in size-structured population dynamics models where juveniles are not considered, for example, see El-Doma (2008 a), to the general case of problem (1) in order to compare results and determine the effects of adults on juveniles and vice versa.

In this paper, we study problem (1) and determine its steady states and examine their stability. We prove that the trivial steady state is always a steady state and that there are as many nontrivial steady states, $P_\infty = J_\infty + A_\infty$, as the nonnegative solutions of two equations, namely, $R(J_\infty, A_\infty) = 1, J_\infty + A_\infty > 0$, see Section 2 for the definition of $R(J, A)$, and, either equation (8) or equation (9). We also show that these steady states remain unchanged if each of the vital rates i.e., the birth rate, the death rate, and the growth rate is multiplied by any positive continuous function $f(J, A)$. Furthermore, we give sufficient conditions for their existence and uniqueness.

Then we study the stability of the trivial steady state and show that if $R(0, 0) < 1$, then the trivial steady state is locally asymptotically stable and if $R(0, 0) > 1$, then the trivial steady state is unstable. We also determine sufficient conditions for the local asymptotic stability of a nontrivial steady state, $P_\infty = J_\infty + A_\infty$, for the general model, and then we give several corollaries to this result, and we also give a condition for the instability of a nontrivial steady state. We also prove

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that these (in)stability results remain unchanged if each of the vital rates is multiplied by any positive function $f(J, A) \in C^1(\mathbb{R}^{+2})$. Finally, we also give examples that illustrate our theorems.

In a series of two subsequent papers, further stability results will be given for three special cases, the first case is when, $V(a, J, A) = V(a), \mu(a, J, A) = \mu(A)$, the second case is when, $V(a, J, A) = V(a), \mu(a, J, A) = \mu(J)$, and the third case is when, $V(a, J, A) = V(a), \mu(a, J, A) = \mu(a)$.

The organization of this paper as follows: in Section 2 we determine the steady states; in Section 3 we study the stability of the steady states and give examples that illustrate some of our theorems; in Section 4 we conclude our results.

2.   The Steady States

In this section, we determine the steady states of problem (1). A steady state of problem (1) satisfies the following:

$$
\frac{d}{da}[V(a, J_\infty, A_\infty)p_\infty(a)] + \mu(a, J_\infty, A_\infty)p_\infty(a) = 0, \;\; a \in [0, l),
$$

$$
V(0, J_\infty, A_\infty)p_\infty(0) = \int_T^l \beta(a, J_\infty, A_\infty)p_\infty(a)da, \tag{3}
$$

$$
J_\infty = \int_0^T p_\infty(a)da,
$$

$$
A_\infty = \int_T^l p_\infty(a)da.
$$

From (3), by solving the differential equation, we obtain that

$$
p_\infty(a) = p_\infty(0)V(0, J_\infty, A_\infty)\frac{\pi(a, J_\infty, A_\infty)}{V(a, J_\infty, A_\infty)}, \tag{4}
$$

where $\pi(a, J_\infty, A_\infty)$ is defined as

$$
\pi(a, J_\infty, A_\infty) = e^{-\int_0^a \frac{\mu(\tau, J_\infty, A_\infty)}{V(\tau, J_\infty, A_\infty)}d\tau}.
$$

We note that we similarly define $\pi(a), \pi(a, J_\infty), \pi(a, A_\infty)$ by the same formula, for example, $\pi(a) = e^{-\int_0^a \frac{\mu(\tau)}{V(\tau)}d\tau}$, and $\pi(a, J_\infty) = e^{-\int_0^a \frac{\mu(\tau, J_\infty)}{V(\tau, J_\infty)}d\tau}$.

Also, from (3) and (4), we obtain that $p_\infty(0)$ satisfies the following:

$$
p_\infty(0) = p_\infty(0)\int_T^l \frac{\beta(a, J_\infty, A_\infty)}{V(a, J_\infty, A_\infty)}\pi(a, J_\infty, A_\infty)da. \tag{5}
$$

Accordingly, from (5), we conclude that either $p_\infty(0) = 0$ or the pair J_∞, A_∞ satisfy the following:

$$
1 = \int_T^l \frac{\beta(a, J_\infty, A_\infty)}{V(a, J_\infty, A_\infty)}\pi(a, J_\infty, A_\infty)da. \tag{6}
$$

In order to facilitate our writing, we define a threshold parameter $R(J, A)$ by

$$R(J, A) = \int_T^l \frac{\beta(a, J, A)}{V(a, J, A)} \pi(a, J, A) da, \tag{7}$$

which is interpreted as the number of children expected to be born to an individual, in a life time, when the population size is $P = J + A$.

We note that from equation (4),

$$p_\infty(0) = \frac{[J_\infty + A_\infty]}{V(0, J_\infty, A_\infty) \int_0^l \frac{\pi(a, J_\infty, A_\infty)}{V(a, J_\infty, A_\infty)} da},$$

and accordingly, either $p_\infty(a) \equiv 0$ or $p_\infty(a)$ is completely determined by a solution of the pair $J_\infty \geq 0, A_\infty \geq 0$ of the following pair of equations which must also satisfy equation (6):

$$J_\infty = \frac{[J_\infty + A_\infty]}{\int_0^l \frac{\pi(a, J_\infty, A_\infty)}{V(a, J_\infty, A_\infty)} da} \int_0^T \frac{\pi(a, J_\infty, A_\infty)}{V(a, J_\infty, A_\infty)} da, \tag{8}$$

$$A_\infty = \frac{[J_\infty + A_\infty]}{\int_0^l \frac{\pi(a, J_\infty, A_\infty)}{V(a, J_\infty, A_\infty)} da} \int_T^l \frac{\pi(a, J_\infty, A_\infty)}{V(a, J_\infty, A_\infty)} da. \tag{9}$$

In the following theorem, we describe the steady states of problem (1).

Theorem 2.1

1) Problem (1) has the trivial steady state, $P_\infty = J_\infty + A_\infty = 0$.
2) All pairs, (J_∞, A_∞), satisfying $J_\infty \geq 0, A_\infty \geq 0, (J_\infty, A_\infty) \neq (0, 0), R(J_\infty, A_\infty) = 1$, and, equation (8) or equation (9), are nontrivial steady states of problem (1).

Proof. We note that 1) is easy to prove. To prove 2), suppose that we have a nontrivial steady state, then it is easy to see that it satisfies the conditions of the theorem. On the other hand, suppose that the pair, (J_∞, A_∞), satisfies, $R(J_\infty, A_\infty) = 1$, and, equation (8). Then let $P_\infty = J_\infty + A_\infty$, and determine $p_\infty(a)$ by setting $P_\infty = \int_0^l p_\infty(a) da$ and using equation (4) to obtain that $p_\infty(a) = \frac{P_\infty}{\int_0^l \frac{\pi(a, J_\infty, A_\infty)}{V(a, J_\infty, A_\infty)} da} \frac{\pi(a, J_\infty, A_\infty)}{V(a, J_\infty, A_\infty)}$. Since by equation (8) $J_\infty = \int_0^T p_\infty(a) da$; then from $P_\infty = J_\infty + A_\infty$, we obtain that $A_\infty = \int_T^l p_\infty(a) da$, and hence A_∞ satisfies equation (9). Accordingly, $p_\infty(a)$ satisfies system (3).

Similarly we can prove the result using equation (9) instead of equation (8). This completes the proof of the theorem.

We note that in Farkas, et al. (2008), a similar theorem to Theorem 2.1 is given, but they do not use equations (8)-(9), instead they combine these two equations into one equation for the ratio of J_∞ and A_∞ together with the equation, $R(J_\infty, A_\infty) = 1$, as well as an extra condition that $0 < T < l$. However, in this case, we are not able to verify that J_∞ and A_∞ satisfy the boundary

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conditions in system 2.1, namely, $J_\infty = \int_0^T p_\infty(a)da$, and, $A_\infty = \int_T^l p_\infty(a)da$. So, in contrast to the result in Farkas, et al. (2008), Theorem 2.1 seems to be correct and concise.

In the next result, we determine conditions for the existence and uniqueness of a nontrivial steady state when, $R(J, A)$, given by equation (7), takes the special form, $R(J, A) = F(P)$, i.e., we assume that $\beta(a, J, A) = \beta(a, P), \mu(a, J, A) = \mu(a, P), V(a, J, A) = V(a, P)$. In this case, P_∞, is the only unknown and is given as the positive solutions of the equation, $F(P_\infty) = R(J_\infty, A_\infty) = 1$.

Theorem 2.2 A nontrivial steady state for the special case when, $\beta(a, J, A) = \beta(a, P), \mu(a, J, A) = \mu(a, P), V(a, J, A) = V(a, P)$, exists and is unique in each of the following cases:

1) $F'(x) < 0 \forall x \geq 0, F(0) > 1$, and, $\exists x^* > 0$ such that $F(x^*) < 1$, where $F(P) = R(J, A)$,
2) $F'(x) > 0 \forall x \geq 0, F(0) < 1$, and, $\exists x^* > 0$ such that $F(x^*) > 1$.

Proof. The proof of the theorem follows immediately from the monotonicity of $F(x)$ and the conditions on $F(0)$. Therefore, we omit the details of the proof. This completes the proof of the theorem.

We note that a similar result to 2 in Theorem 2.2 is given in Diekmann, et al. (2008). Also see Calsina, et al. (2003), for an equivalent result.

We also note that in the general case, we assume that $R_A(J_\infty, A_\infty) \neq 0$, or $R_J(J_\infty, A_\infty) \neq 0$. Then we can use the Implicit Function Theorem for the equation, $R(J_\infty, A_\infty) = 1$, and in this case A_∞ is determined uniquely as a function of J_∞ or vice versa. Then according to Theorem 2.1 all nontrivial steady states are the fixed points of a function of a single variable given by the right-hand side of equation (8) in case $R_A(J_\infty, A_\infty) \neq 0$, or equation (9) in case $R_J(J_\infty, A_\infty) \neq 0$. We also have the well-known formula $\frac{dA}{dJ} = -\frac{R_J}{R_A}$ in the former case, and a similar formula in the latter case.

In the following result, we obtain a result about the steady states of problem (3) that tell us that we can multiply all the vital rates by any positive continuous function of the pair, (J, A), without affecting the steady state.

Theorem 2.3 Suppose that, $\beta = \beta(a, J, A)f(J, A), \mu = \mu(a, J, A)f(J, A), V = V(a, J, A) \times f(J, A)$, where, f, is a positive continuous function. Then the steady states of problem (3) are the same as when, $\beta = \beta(a, J, A), \mu = \mu(a, J, A), V = V(a, J, A)$.

Proof. The proof is straightforward by using Theorem 2.1. Therefore, we omit the details. This completes the proof of the theorem.

We note that the result in Theorem 2.3 seems to be very interesting since it proves that there is a family of vital rates, in fact an infinite one that corresponds to a single steady state.

In the next result, we use Theorems 2.2-2.3 to extend the result given in Theorem 2.2.

Corollary 2.4 A nontrivial steady state for the special case, $\beta = \beta(a, P)f(J, A), \mu = \mu(a, P)f(J, A), V = V(a, P)f(J, A)$, where, f is a positive continuous function, exists and unique in each of

the cases given in Theorem 2.2.

Proof. The result follows directly from Theorems 2.2–2.3. This completes the proof of the corollary.

3.   Stability of the Steady States

In this section, we study the stability of the steady states for problem (1) as given by Theorem 2.1.

To study the stability of a steady state $p_\infty(a)$, which is a solution of (3) and is given by equation (4), we linearize problem (1) at $p_\infty(a)$ in order to obtain a characteristic equation, which in turn will determine conditions for the stability. To that end, we consider a perturbation $\omega(a,t)$ defined by $\omega(a,t) = p(a,t) - p_\infty(a)$, where $p(a,t)$ is a solution of problem (??). Accordingly, we obtain that $\omega(a,t)$ satisfies the following:

$$
\frac{\partial \omega(a,t)}{\partial t} + \frac{\partial}{\partial a}\Big[V(a, J_\infty, A_\infty)\omega(a,t) + p_\infty(a)\Big(V_J(a, J_\infty, A_\infty)\int_0^T \omega(b,t)db
$$
$$
+ V_A(a, J_\infty, A_\infty)\int_T^l \omega(b,t)db\Big)\Big] + \mu(a, J_\infty, A_\infty)\omega(a,t)
$$
$$
+ p_\infty(a)\Big[\mu_J(a, J_\infty, A_\infty)\int_0^T \omega(b,t)db + \mu_A(a, J_\infty, A_\infty)\int_T^l \omega(b,t)db\Big] = 0,
$$
$$
a \in [0,l), \ t > 0, \tag{10}
$$
$$
\omega(0,t)V(0, J_\infty, A_\infty) = \int_T^l \beta(a, J_\infty, A_\infty)\omega(a,t)da + D_J(J_\infty, A_\infty)\int_0^T w(a,t)da
$$
$$
+ D_A(J_\infty, A_\infty)\int_T^l \omega(a,t)da, \ t \geq 0,
$$
$$
D_J(J_\infty, A_\infty) = \int_T^l p_\infty(a)\beta_J(a, J_\infty, A_\infty)da - p_\infty(0)V_J(0, J_\infty, A_\infty),
$$
$$
D_A(J_\infty, A_\infty) = \int_T^l p_\infty(a)\beta_A(a, J_\infty, A_\infty)da - p_\infty(0)V_A(0, J_\infty, A_\infty).
$$

By substituting $\omega(a,t) = \phi(a)e^{\xi t}$ in (10), where ξ is a complex number, and straightforward calculations, we obtain the following characteristic equation:

$$
1 =
$$
$$
\frac{\Big[(1 + G_A(T,l,\xi))(1 + G_J(0,T,\xi)) - G_J(T,l,\xi)G_A(0,T,\xi)\Big]}{V(0, J_\infty, A_\infty)}\int_T^l e^{-\int_0^a E(\tau)d\tau}\beta(a, J_\infty, A_\infty)da
$$
$$
- G_J(0,T,\xi) - G_A(T,l,\xi) - G_J(0,T,\xi)G_A(T,l,\xi) + G_A(0,T,\xi)G_J(T,l,\xi) \tag{11}
$$
$$
+ \frac{\Big[(1 + G_A(T,l,\xi))\int_0^T e^{-\int_0^a E(\tau)d\tau}da - G_A(0,T,\xi)\int_T^l e^{-\int_0^a E(\tau)d\tau}da\Big]}{V(0, J_\infty, A_\infty)}\Big[D_J - G_{J\beta}(\xi)\Big]
$$

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$$+\frac{\left[(1+G_J(0,T,\xi))\int_T^l e^{-\int_0^a E(\tau)d\tau}da - G_J(T,l,\xi)\int_0^T e^{-\int_0^a E(\tau)d\tau}da\right]}{V(0,J_\infty,A_\infty)}\left[D_A - G_{A\beta}(\xi)\right],$$

where $G_J(0,T,\xi), G_J(T,l,\xi), G_{J\beta}(\xi), D_J, E(a)$ are, respectively, given by

$$G_J(0,T,\xi) = \int_0^T \int_0^a e^{-\int_\sigma^a E(\tau)d\tau}g_J(\sigma,J_\infty,A_\infty)d\sigma da, \tag{12}$$

$$G_J(T,l,\xi) = \int_T^l \int_0^a e^{-\int_\sigma^a E(\tau)d\tau}g_J(\sigma,J_\infty,A_\infty)d\sigma da, \tag{13}$$

$$G_{J\beta}(T,l,\xi) = \int_T^l \int_0^a e^{-\int_\sigma^a E(\tau)d\tau}\beta((a,J_\infty,A_\infty)g_J(\sigma,J_\infty,A_\infty)d\sigma da, \tag{14}$$

$$D_J = \int_T^l \beta_J(a,J_\infty,A_\infty)p_\infty(a)da - p_\infty(0)V_J(0,J_\infty,A_\infty), \tag{15}$$

$$E(\sigma) = \frac{\xi + V_\sigma(\sigma,J_\infty,A_\infty) + \mu(\sigma,J_\infty,A_\infty)}{V(\sigma,J_\infty,A_\infty)}, \tag{16}$$

where $g(\sigma)$ is given by

$$g_J(\sigma) = \frac{\frac{\partial}{\partial\sigma}\left(V_J(\sigma,J_\infty,A_\infty)p_\infty(\sigma)\right) + p_\infty(\sigma)\mu_J(\sigma,J_\infty,A_\infty)}{V(\sigma,J_\infty,A_\infty)}. \tag{17}$$

We note that $G_A(0,T,\xi), G_A(T,l,\xi), G_{A\beta}(\xi), D_A, g_A(\sigma,J_\infty,A_\infty)$, are defined similarly.

In the following theorem, we describe the stability of the trivial steady state, $p_\infty(a) \equiv 0$.

Theorem 3.1 The trivial steady state, $p_\infty(a) \equiv 0$, is locally asymptotically stable if $R(0,0) < 1$, and is unstable if $R(0,0) > 1$.

Proof. We note that for the trivial steady state, $p_\infty(a) \equiv 0$, $P_\infty = 0$, and therefore, from the characteristic equation (11), we obtain the following characteristic equation:

$$1 = \int_T^l e^{-\xi\int_0^a \frac{d\tau}{V(\tau,0,0)}}\frac{\beta(a,0,0)}{V(a,0,0)}\pi(a,0,0)da. \tag{18}$$

To prove the local asymptotic stability of the trivial steady state, we note that if $R(0,0) < 1$, then equation (18) can not be satisfied for any ξ with, $Re\xi \geq 0$, since

$$\left|\int_T^l e^{-\xi\int_0^a \frac{d\tau}{V(\tau,0,0)}}\frac{\beta(a,0)}{V(a,0,0)}\pi(a,0,0)da\right| \leq \int_T^l e^{-Re\xi\int_0^a \frac{d\tau}{V(\tau,0,0)}}\frac{\beta(a,0)}{V(a,0,0)}\pi(a,0,0)da$$
$$\leq R(0,0) < 1.$$

Accordingly, the trivial steady state is locally asymptotically stable if $R(0,0) < 1$.

To prove the instability of the trivial steady state when, $R(0,0) > 1$, we note that if we define a function $h(\xi)$ by

$$h(\xi) = \int_T^l e^{-\xi\int_0^a \frac{d\tau}{V(\tau,0,0)}}\frac{\beta(a,0,0)}{V(a,0,0)}\pi(a,0,0)da,$$

and suppose that ξ is real, then we can easily see that $h(\xi)$ is a decreasing function if $\xi > 0$, $h(\xi) \longrightarrow 0$ as $\xi \longrightarrow +\infty$, and $h(0) = R(0,0)$. Therefore, if $R(0,0) > 1$, then there exists $\xi^* > 0$ such that $h(\xi^*) = 1$, and hence the trivial steady state is unstable. This completes the proof of the theorem.

Theorem 3.1 is ecologically intuitive since $R(0,0)$ represents the number of children expected to be born to an individual, in a life time, when the population size is zero. So, it is clear that if $R(0,0) < 1$, then the population will not grow and the trivial steady state is locally asymptotically stable. Whereas if $R(0,0) > 1$, then the population will eventually grow and accordingly, instability occurs.

In the next theorem, we give a condition for the instability of a nontrivial steady state.

Theorem 3.2 A nontrivial steady state is unstable if

$$\Xi = \Big[(1 + G_A(T,l,0))J_\infty - G_A(0,T,0)A_\infty\Big]R_J(J_\infty, A_\infty) +$$
$$+ \Big[(1 + G_J(0,T,0))A_\infty - G_J(T,l,0)J_\infty\Big]R_A(J_\infty, A_\infty) > 0. \qquad (19)$$

Proof. If we suppose that ξ is real and denote the right-hand side of the characteristic equation (11) by $H(\xi)$, and also suppose that the inequality in (19) is satisfied, we obtain that $H(0) = 1 + \Big[(1 + G_A(T,l,0))J_\infty - G_A(0,T,0)A_\infty\Big]R_J(J_\infty, A_\infty) +$ $\Big[(1+G_J(0,T,0))A_\infty - G_J(T,l,0)J_\infty\Big]R_A(J_\infty, A_\infty) = 1 + \Xi > 1$, and $H(\xi) \longrightarrow 0$ as $\xi \longrightarrow +\infty$. Accordingly, $\exists \xi^* > 0$ such that $H(\xi^*) = 1$, and hence a nontrivial steady state is unstable. This completes the proof of the theorem.

We note that Theorem 3.2 is a generalization of Theorem 3.2 in El-Doma (2008 a), for the special case when $T \equiv 0$, and if we set $T = 0$, i.e., $J_\infty = 0$, then from (19), we obtain that $\Xi = A_\infty R_A(0, A_\infty)$, and therefore, we retain the result given by Theorem 3.2 in El-Doma (2008 a).

We also note that, Ξ, can be viewed as the directional derivative of, $R(J, A)$, at (J_∞, A_∞) in the direction of the vector

$$\Big((1 + G_A(T,l,0))J - G_A(0,T,0)A, (1 + G_J(0,T,0))A - G_J(T,l,0)J\Big).$$

We also note that in Farkas, et al. (2008), the special case $\mu(a, J, A) = \mu(a), V(a, J, A) = V(a)$ is considered, and in this case, it is easy to see that $g_J = g_A = 0$, and accordingly, $G_J = G_A = 0$, therefore, using Theorem 3.2, we obtain the following condition for the instability of a nontrivial steady state:

$$\Xi = J_\infty R_J(J_\infty, A_\infty) + A_\infty R_A(J_\infty, A_\infty) > 0.$$

We also note that this result is in agreement with the result given in Farkas, et al. (2008).

In the next theorem, we prove that, $\xi = 0$, is a root of the characteristic equation (11) iff $\Xi = 0$, where, Ξ, is given by (19).

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Theorem 3.3 $\xi = 0$, is a root of the characteristic equation (11) iff $\Xi = 0$.

Proof. We note that if $\xi = 0$, then using equation (6), the characteristic equation (11) becomes,

$$\Big[(1 + G_A(T, l, 0))J_\infty - G_A(0, T, 0)A_\infty\Big]R_J(J_\infty, A_\infty) +$$
$$\Big[(1 + G_J(0, T, 0))A_\infty - G_J(T, l, 0)J_\infty\Big]R_A(J_\infty, A_\infty) = \Xi = 0.$$

This completes the proof of the theorem.

We note that according to Theorem 3.2 a nontrivial steady state is unstable i.e., $\xi > 0$, is a root of the characteristic equation (11) if $\Xi > 0$. Also, by Theorem 3.3 if $\Xi = 0$, then, $\xi = 0$, is a root of the characteristic equation (11). Therefore, a nontrivial steady state can only be hyperbolic and locally asymptotically stable when, $\Xi < 0$.

To obtain further stability results, we note that by suitable changes of the variables of the integrations, we can rewrite the characteristic equation (11) in the form given in equation $\mathbf{A_1}$ of **Appendix A**.

In the next theorem, we give a sufficient condition for the local asymptotic stability of a nontrivial steady state. We note that this result is for the general problem (1), and in the sequel we give other conditions which are for special cases of problem (1).

Theorem 3.4 Suppose that condition, $\mathbf{B_1}$, of **Appendix B** holds. Then a nontrivial steady state is locally asymptotically stable.

Proof. We note that the proof follows directly from the characteristic equation $\mathbf{A_1}$ of **Appendix A** and Theorem (13) in El-Doma (2008 a). Therefore, the details are omitted. This completes the proof of the theorem.

We note that condition $\mathbf{B_1}$ of **Appendix B** is for the general model and is apparently unwieldy, but its importance stems from the fact it encompasses all other special cases, and accordingly, it can be used to obtain conditions for the local asymptotic stability of a nontrivial steady state for any special case, for example, see Farkas, et al. (2008).

The following corollaries also follow directly from Theorem 3.4, and therefore, the details of the proofs are omitted.

Corollary 3.5 Suppose that, $\mu(a, J, A) = \mu(a), V(a, J, A) = V(a)$. Then a nontrivial steady state is locally asymptotically stable if the following holds:

$$\int_T^l \frac{\pi(a)}{V(a)}\Big|\Big[\beta(a, J_\infty, A_\infty) + \int_T^l \beta_A(a, J_\infty, A_\infty)p_\infty(a)da\Big]\Big|da +$$
$$\Big|\int_T^l \beta_J(a, J_\infty, A_\infty)p_\infty(a)da\Big|\int_0^T \frac{\pi(a)}{V(a)}da < 1. \tag{20}$$

We note that $\int_T^l \beta_J(a, J_\infty, A_\infty)p_\infty(a)da$ represents the total change in the birth rate, at the steady state, due to a change in juveniles only. If we assume that

$\int_T^l \beta_J(a, J_\infty, A_\infty)p_\infty(a)da = 0$, then we retain the result of Theorem 3.4 in El-Doma (2008 a).

We also note that in Farkas, et al. (2008), the special case considered in Corollary 3.5 is also considered, however, due to their different method which uses semigroups theory, a different set of conditions is imposed in order to obtain the stability of a nontrivial steady state. In Example 2 below we will show that if the conditions of their theorem for the local asymptotic stability of a nontrivial steady state are assumed, then Corollary 3.5 also gives the same result.

Anticipating our future needs, we define $F(a, \sigma)$ by

$$F(a, \sigma) = \frac{V(\sigma, J_\infty, A_\infty)}{V(a, J_\infty, A_\infty)} e^{-\int_\sigma^a \frac{\mu(\tau, J_\infty, A_\infty)}{V(\tau, J_\infty, A_\infty)}d\tau}. \tag{21}$$

Corollary 3.6 Suppose that, $\mu(a, J, A) = \mu(a, J), V(a, J, A) = V(a, J)$. Then a nontrivial steady state is locally asymptotically stable if the following holds:

$$\int_T^l \frac{\pi(a, J_\infty)}{V(a, J_\infty)} \left| \left[\beta(a, J_\infty, A_\infty) + \int_T^l \beta_A(c, J_\infty, A_\infty)p_\infty(c)dc \right] \right| da + |D_J| \int_0^T \frac{\pi(a, J_\infty)}{V(a, J_\infty)} da$$

$$+ \int_0^T \int_0^a F(a, \sigma)|g_J(\sigma, J_\infty, A_\infty)|d\sigma da$$

$$+ \int_0^T \int_T^l \int_0^a \frac{\pi(b, J_\infty)}{V(b, J_\infty)} F(a, \sigma) \left| g_J(\sigma, J_\infty, A_\infty)\left(\beta(a, J_\infty, A_\infty) + \int_T^l \beta_A(c, J_\infty, A_\infty)p_\infty(c)dc \right) \right| d\sigma dadb$$

$$+ \int_T^l \int_0^T \int_0^a \frac{\pi(b, J_\infty)}{V(b, J_\infty)} F(a, \sigma) \left| g_J(\sigma, J_\infty, A_\infty)\left(\beta(b, J_\infty, A_\infty) + \int_T^l \beta_A(c, J_\infty, A_\infty)p_\infty(c)dc \right) \right| d\sigma dadb$$

$$< 1.$$

We note that the conditions of Corollary 3.6 represents a situation where juveniles control the population in terms of the death rate as well as the growth rate. If we further assume that they also control the population in terms of the birth rate i.e., we assume that $\beta = \beta(a, J)$, then we obtain the following condition for the stability of a nontrivial steady state:

$$\int_T^l \frac{\pi(a, J_\infty)}{V(a, J_\infty)} \beta(a, J_\infty)da + |D_J| \int_0^T \frac{\pi(a, J_\infty)}{V(a, J_\infty)} da + \int_0^T \int_0^a F(a, \sigma)|g_J(\sigma, J_\infty, A_\infty)|d\sigma da$$

$$+ \int_0^T \int_T^l \int_0^a \frac{\pi(b, J_\infty)}{V(b, J_\infty)} F(a, \sigma) \left| g_J(\sigma, J_\infty, A_\infty) \right| \beta(a, J_\infty)d\sigma dadb$$

$$+ \int_T^l \int_0^T \int_0^a \frac{\pi(b, J_\infty)}{V(b, J_\infty)} F(a, \sigma) \left| g_J(\sigma, J_\infty, A_\infty) \right| \beta(b, J_\infty)d\sigma dadb < 1.$$

We note the above condition is impossible because of equation (6).

Corollary 3.7 Suppose that, $\mu(a, J, A) = \mu(a, A), V(a, J, A) = V(a, A)$. Then a nontrivial steady

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state is locally asymptotically stable if the following holds:

$$
\int_T^l \frac{\pi(a, A_\infty)}{V(a, A_\infty)} \Big| \Big[\beta(a, J_\infty, A_\infty) + D_A \Big] \Big| da + \Big| \int_T^l \beta_J(a, J_\infty, A_\infty) p_\infty(a) da \Big| \int_0^T \frac{\pi(a, A_\infty)}{V(a, A_\infty)} da
$$

$$
+ \int_T^l \int_0^a F(a, \sigma) \Big| g_A(\sigma, J_\infty, A_\infty) \Big| d\sigma da
$$

$$
+ \int_T^l \int_T^l \int_0^a \frac{\pi(b, A_\infty)}{V(b, A_\infty)} F(a, \sigma) \Big| g_A(\sigma, J_\infty, A_\infty) \Big[\beta(b, J_\infty, A_\infty) - \beta(a, J_\infty, A_\infty) \Big] \Big| d\sigma da db
$$

$$
+ \Big| \int_T^l \beta_J(a, J_\infty, A_\infty) p_\infty(a) da \Big| \int_0^T \int_T^l \int_0^a \frac{\pi(b, A_\infty)}{V(b, A_\infty)} F(a, \sigma) \Big| g_A(\sigma, J_\infty, A_\infty) \Big| d\sigma da db +
$$

$$
\Big| \int_T^l \beta_J(a, J_\infty, A_\infty) p_\infty(a) da \Big| \int_T^l \int_0^T \int_0^a \frac{\pi(b, A_\infty)}{V(b, A_\infty)} F(a, \sigma) \Big| g_A(\sigma, J_\infty, A_\infty) \Big| d\sigma da db < 1.
$$

We note that the conditions of Corollary 3.7 represents a situation where adults control the population in terms of the death rate as well as the growth rate.

We also note that Farkas, et al. (2008), considered the case when $\mu(a, J, A) = \mu(a, A), V(a, J, A) = V(a, A), \beta(a, J, A) = \beta(a, A)$. We note that these conditions represents a situation where adults control the population. Under such conditions Corollary 3.7 gives the following condition for the local asymptotic stability of a nontrivial steady state:

$$
\int_T^l \frac{\pi(a, A_\infty)}{V(a, A_\infty)} \Big| \Big[\beta(a, A_\infty) + D_A \Big] \Big| da + \int_T^l \int_0^a F(a, \sigma) \Big| g_A(\sigma, A_\infty) \Big| d\sigma da
$$

$$
+ \int_T^l \int_T^l \int_0^a \frac{\pi(b, A_\infty)}{V(b, A_\infty)} F(a, \sigma) \Big| g_A(\sigma, A_\infty) \Big[\beta(b, A_\infty) - \beta(a, A_\infty) \Big] \Big| d\sigma da db < 1.
$$

We note that this result corresponds exactly to Theorem 3.4 in El-Doma (2008 a), where juveniles are not considered.

As we noted before, the method in Farkas, et al. (2008) is different accordingly, they obtained a different set of conditions for the local asymptotic stability of a nontrivial steady state in this case.

We also, note that under such conditions Theorem 3.2 gives the following condition for the instability of a nontrivial steady state:

$$
R_A(J_\infty, A_\infty) > 0.
$$

This result corresponds exactly to Theorem 3.2 in El-Doma (2008 a), where juveniles are not considered. However this result is not obtained in Farkas, et al. (2008), instead they obtained two different conditions under which a nontrivial steady state is unstable.

Corollary 3.8 Suppose that, $\mu(a, J, A) = \mu(J, A), V(a, J, A) = V(J, A), \beta(a, J, A) = \beta(J, A)$.

Then a nontrivial steady state is locally asymptotically stable if the following holds:

$$\int_T^l \frac{\pi(a, J_\infty, A_\infty)}{V(J_\infty, A_\infty)} \left| \left[\beta(J_\infty, A_\infty) + D_A \right] \right| da + |D_J| \int_0^T \frac{\pi(a, J_\infty, A_\infty)}{V(J_\infty, A_\infty)} da$$

$$+ \int_0^T \int_0^a F(a, \sigma) \left| g_J(\sigma, J_\infty, A_\infty) \right| d\sigma da + \int_T^l \int_0^a F(a, \sigma) \left| g_A(\sigma, J_\infty, A_\infty) \right| d\sigma da$$

$$+ \int_0^T \int_T^l \int_0^a \frac{\pi(b, J_\infty, A_\infty)}{V(J_\infty, A_\infty)} F(a, \sigma) \left| \left[D_J g_A(\sigma, J_\infty, A_\infty) - g_J(\sigma, J_\infty, A_\infty)\left(\beta(J_\infty, A_\infty) + D_A \right) \right] \right| d\sigma da db$$

$$+ \int_T^l \int_0^T \int_0^a \frac{\pi(b, J_\infty, A_\infty)}{V(J_\infty, A_\infty)} F(a, \sigma) \left| \left[g_J(\sigma, J_\infty, A_\infty)\left(\beta(J_\infty, A_\infty) + D_A \right) - D_J g_A(\sigma, J_\infty, A_\infty) \right] \right| d\sigma da db$$

$$< 1.$$

We note that the conditions of Corollary 3.8 represents a situation where both adults and juveniles affect the vital rates and therefore the population, hence the condition for the local asymptotic stability of a nontrivial steady state is complicated.

We also note that we have listed only few corollaries, of course, we can have many more for any possible situation that we choose and this is the advantage of the general formulation in the present work.

In the following result, we prove that the characteristic equation (11) remains unchanged if each of the vital rates is multiplied by any positive function, $f(J, A) \in C^1(\mathbb{R}^{+2})$.

Theorem 3.9 Suppose that, $\beta = \beta(a, J, A)f(J, A), \mu = \mu(a, J, A)f(J, A), V = V(a, J, A) \times f(J, A)$, where, $f(J, A) \in C^1(\mathbb{R}^{+2})$, is a positive function. Then the characteristic equation (11) for problem (1), in this case, is the same as when, $\beta = \beta(a, J, A), \mu = \mu(a, J, A), V = V(a, J, A)$, i.e., it satisfies (11) too.

Proof. By Theorem 2.3, the steady states are the same. So, we linearize problem (1) at $p_\infty(a)$, as before, but this time we use the new vital rates, $\beta = \beta(a, J, A)f(J, A), \mu = \mu(a, J, A)f(J, A), V = V(a, J, A)f(J, A)$. Then we obtain (10) again after simple manipulations and using (3). This completes the proof of the theorem.

In the next result, we generalize the (in)stability results obtained so far to the general case when the vital rates, respectively, assume $\beta = \beta(a, J, A)f(J, A), \mu = \mu(a, J, A)f(J, A), V = V(a, J, A)f(J, A)$.

Corollary 3.10 Suppose that, $\beta = \beta(a, J, A)f(J, A), \mu = \mu(a, J, A)f(J, A), V = V(a, J, A) \times f(J, A)$, where, $f(J, A) \in C^1(\mathbb{R}^{+2})$, is a positive function. Then the (in)stability results for problem (1), in this case, are the same as when, $\beta = \beta(a, J, A); \mu = \mu(a, J, A); V = V(a, J, A)$.

Proof. We note that the (in)stability results given in Theorem 3.1 follow in this case because by Theorem 3.9 we obtain the same characteristic equation (11), accordingly, we obtain the characteristic equation (18). We also note that the instability result given in Theorem 3.2 follows in this case because by Theorem 3.9 we use the same characteristic equation (11). A similar reasoning as above holds for Theorem 3.3. We also note that Theorem 3.4 and all its corollaries

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are obtained from the characteristic equation (11), and therefore, the results follow in this case too. This completes the proof of the corollary.

We also note that we can produce further stability results for three special cases, namely, the case when

$$l = +\infty, V(a, J, A) = V(a), \mu(a, J, A) = \mu(A), \int_0^\infty \frac{d\tau}{V(\tau)} = +\infty,$$

the case when

$$l = +\infty, V(a, J, A) = V(a), \mu(a, J, A) = \mu(J), \int_0^\infty \frac{d\tau}{V(\tau)} = +\infty,$$

and the case when

$$l = +\infty, V(a, J, A) = V(a), \mu(a, J, A) = \mu(a), \int_0^\infty \frac{\mu(\tau)}{V(\tau)} d\tau = +\infty.$$

The analysis of these special cases will be the subject of a series of two subsequent papers.

Example 1: In this example, we consider an example originally considered in Cushing, et al. (1991), and later in Farkas, et al. (2008). Their interest is to determine the juvenile competitive effects on adult's fertility. They assumed that $\beta(a, J, A) = \beta(a, W), W = \alpha J + A, \alpha > 0; W_\infty = \alpha J_\infty + A_\infty, \mu(a, J, A) = \mu(a)$, and $V(a, J, A) = 1$, where the constant, α, measures the depressive effects of juveniles on adult's fertility.

We note that, in this case, from Corollary 3.5, we obtain the following condition for a nontrivial steady state to be locally asymptotically stable:
$$\int_T^l \pi(a) \Big| \beta(a, W_\infty) + \int_T^l \beta_W(c, W_\infty) p_\infty(c) dc \Big| da + \alpha \Big| \int_T^l \beta_W(c, W_\infty) p_\infty(c) dc \Big| \int_0^T \pi(a) da < 1.$$
Also, Theorem 3.2 gives the following condition for a nontrivial steady state to be unstable:

$$[\alpha J_\infty + A_\infty] \int_T^l \beta_W(a, W_\infty) p_\infty(a) da > 0.$$

Accordingly, from Theorem 3.2, for a nontrivial steady state to be locally asymptotically stable we must have $\int_T^l \beta_W(a, W_\infty) p_\infty(a) da < 0$, and therefore, Farkas, et al. (2008), concluded that their method fails to establish conditions for a nontrivial steady state to be locally asymptotically stable. Also if we assume that $\beta(a, J_\infty, A_\infty) + \int_T^l \beta_A(a, J_\infty, A_\infty) p_\infty(a) da \geq 0$, together with the just mentioned condition, we obtain the following condition for a nontrivial steady state to be locally asymptotically stable:

$$\int_T^l \pi(a) da - \alpha \int_0^T \pi(a) da > 0.$$

Hence, due to monotonicity, there exists a unique $T^* > 0$ satisfying

$$\int_{T^*}^l \pi(a) da = \alpha \int_0^{T^*} \pi(a) da,$$

such that for any $T \in [0, T^*)$ a nontrivial steady state is locally asymptotically stable. From the above inequality we note that if α, is large i.e., when adult's fertility is adversely affected by competition from juveniles, then it is a destabilizing effect that can induce instability. This is in agreement with Cushing, et al. (1991), and the references therein. We also note that if T is sufficiently small then that will decrease the competitive effects of juveniles on adult's fertility. We also note that, $\frac{\partial}{\partial \alpha} p_\infty(a) < 0$, that means the density of the population $p_\infty(a)$ given by equation (4) is decreased by the depression coefficient, α, this result is proved in Cushing, et al. (1991), which also proved that, $\frac{\partial}{\partial \alpha} \left(\frac{p_\infty(a)}{P_\infty} \right) = 0$, which means that the proportion of the density to the total population remains constant independent of the depression coefficient, α.

Example 2: Corollary 3.5 states that if $\mu(a, J, A) = \mu(a)$, and, $V(a, J, A) = V(a)$. Then a nontrivial steady state is locally asymptotically stable if (20) holds.

Also, Theorem 3.2 gives that a nontrivial steady state is unstable if

$$J_\infty \int_T^l \beta_J(a, J_\infty, A_\infty) p_\infty(a) da + A_\infty \int_T^l \beta_A(a, J_\infty, A_\infty) p_\infty(a) da > 0.$$

Also, by Theorem 3.1, a trivial steady state is locally asymptotically stable if $\int_T^l \frac{\beta(a, 0, 0)}{V(a, 00)} \pi(a) da < 1$, and unstable if $\int_T^l \frac{\beta(a, 0, 0)}{V(a, 0, 0)} \pi(a) da > 1$.

We also note that in Farkas, et al. (2008), the following conditions for a nontrivial steady state to be locally asymptotically stable are given:

1) $J_\infty \int_T^l \beta_J(a, J_\infty, A_\infty) p_\infty(a) da + A_\infty \int_T^l \beta_A(a, J_\infty, A_\infty) p_\infty(a) da < 0,$

2) $\beta(a, J_\infty, A_\infty) + \int_T^l \beta_A(a, J_\infty, A_\infty) p_\infty(a) da \geq 0,$

3) $\int_T^l \beta_J(a, J_\infty, A_\infty) p_\infty(a) da \geq 0.$

Now, if we assume 1-3, then from the left-hand side of inequality (20), we obtain

$$\int_T^l \frac{\pi(a)}{V(a)} \left| \left[\beta(a, J_\infty, A_\infty) + \int_T^l \beta_A(a', J_\infty, A_\infty) p_\infty(a') da' \right] \right| da +$$

$$\left| \int_T^l \beta_J(a', J_\infty, A_\infty) p_\infty(a') da' \right| \int_0^T \frac{\pi(a)}{V(a)} da$$

$$= 1 + \frac{1}{p_\infty(0) V(0)} \left[J_\infty \int_T^l \beta_J(a, J_\infty, A_\infty) p_\infty(a) da + A_\infty \int_T^l \beta_A(a, J_\infty, A_\infty) p_\infty(a) da \right] < 1.$$

However, the result in Farkas, et al. (2008), fails in some cases, for example, when $\int_T^l \beta_J(a, J_\infty, A_\infty) p_\infty(a) da < 0, \int_T^l \beta_A(a, J_\infty, A_\infty) p_\infty(a) da < 0, T = 0$, and condition 2. holds, whereas our result in Corollary 3.5 gives that a nontrivial steady state is locally asymptotically stable. In fact, if we do not assume that, $T = 0$, then the condition for the local asymptotic

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stability of a nontrivial steady state is given by

$$\delta \int_T^l \frac{\pi(a)}{V(a)} da - \gamma \int_0^T \frac{\pi(a)}{V(a)} da < 0,$$

where δ, γ are defined as

$$\delta = \int_T^l \beta_A(a, J_\infty, A_\infty) p_\infty(a) da, \qquad (22)$$

$$\gamma = \int_T^l \beta_J(a, J_\infty, A_\infty) p_\infty(a) da. \qquad (23)$$

We note that δ can be interpreted as the total change in the birth rate, at the steady state, due to a change in adults only. Also, note that γ is interpreted similarly.

Example 3: In this example, we consider the case when $\beta(a, J, A) = \dfrac{c}{J + A}, c > 0$ is a constant; $\mu(a, J, A) = \mu(a), V(a, J, A) = V(a)$.

In this case using equation (6), we obtain that $P_\infty = c \int_T^l \dfrac{\pi(a)}{V(a)} da$ as the unique solution. We also note that from equations (8)-(9), we obtain

$$J_\infty = \frac{c \int_T^l \frac{\pi(a)}{V(a)} da}{\int_0^l \frac{\pi(a)}{V(a)} da} \int_0^T \frac{\pi(a)}{V(a)} da, \quad A_\infty = \frac{c \left[\int_T^l \frac{\pi(a)}{V(a)} da \right]^2}{\int_0^l \frac{\pi(a)}{V(a)} da}. \qquad (24)$$

In order to determine the stability of this steady state, we apply Corollary (14) to obtain the following condition for local asymptotic stability:

$$\frac{J_\infty}{A_\infty} < 1.$$

Example 4: In this example, we consider the case when $\beta(a, J, A) = \dfrac{c}{JA}, c > 0$ is a constant; $\mu(a, J, A) = \mu(a), V(a, J, A) = V(a)$.

In this case using equation (6), we obtain the following equation for a hyperbola:

$$J_\infty A_\infty = c \int_T^l \frac{\pi(a)}{V(a)} da. \qquad (25)$$

Now, by solving simultaneously equation (25) and equation (8), we obtain a unique steady state given by

$$J_\infty = \sqrt{c} \sqrt{\int_0^T \frac{\pi(a)}{V(a)} da}, \quad A_\infty = \frac{\sqrt{c} \int_T^l \frac{\pi(a)}{V(a)} da}{\sqrt{\int_0^T \frac{\pi(a)}{V(a)} da}}.$$

In order to determine the stability of this steady state, we note that in this case, from Theorem 3.3, we obtain that, $\xi = 0$, is not a root of the characteristic equation (11). And from the characteristic

equation $\mathbf{A_1}$ of **Appendix A**, we obtain the following characteristic equation:

$$1 = -\frac{A_\infty}{J_\infty} \frac{\int_0^T e^{-\xi \int_0^a \frac{d\tau}{V(\tau)}} \frac{\pi(a)}{V(a)} da}{\int_T^l \frac{\pi(a)}{V(a)} da}. \tag{26}$$

Now, let $\xi = x + iy$, and suppose that $x \geq 0$. Then the real part of the characteristic equation (26) becomes

$$1 = -\frac{A_\infty}{J_\infty} \frac{\int_0^T e^{-x \int_0^a \frac{d\tau}{V(\tau)}} \frac{\pi(a)}{V(a)} \cos y \int_0^a \frac{d\tau}{V(\tau)} da}{\int_T^l \frac{\pi(a)}{V(a)} da}. \tag{27}$$

From the right-hand side of equation (27), we obtain that, except when $x = y = 0$, we have

$$\left| \frac{A_\infty}{J_\infty} \frac{\int_0^T e^{-x \int_0^a \frac{d\tau}{V(\tau)}} \frac{\pi(a)}{V(a)} \cos y \int_0^a \frac{d\tau}{V(\tau)} da}{\int_T^l \frac{\pi(a)}{V(a)} da} \right| < \frac{A_\infty}{J_\infty} \frac{\int_0^T \frac{\pi(a)}{V(a)} da}{\int_T^l \frac{\pi(a)}{V(a)} da} = 1.$$

Accordingly, the nontrivial steady state is locally asymptotically stable.

Regarding Example 1 - Example 4, we note that we can use Theorem 2.3 and Corollary 3.10 to show that these steady states as well as their stability results remain unchanged if each of the vital rates is multiplied by any positive function $f(J, A) \in C^1(\mathbb{R}^{+2})$.

4. Conclusion

In this paper, we studied a size-structured population dynamics model where the maximum size is either finite or infinite and the population is divided into adults and juveniles. The vital rates i.e., the birth rate, the death rate, and the growth rate, depend on size, adults, and juveniles, therefore, the model takes into account the limited resources as well as the intra-specific competition between adults and juveniles.

We determined the steady states of the model and examined their stability. We proved that the trivial steady state is always a steady state and that there are as many nontrivial steady states as the nonnegative solutions of two equations (8) or (9), and, $R(J_\infty, A_\infty) = 1$, where, $R(J, A)$, is given by equation (7), and, $J_\infty + A_\infty > 0$. We also showed that these steady states remain unchanged if each of the vital rates is multiplied by any positive continuous function $f(J, A)$. Furthermore, we gave some sufficient conditions for their existence and uniqueness.

Then we studied the stability of the trivial steady state and showed that if $R(0, 0) < 1$, then the trivial steady state is locally asymptotically stable and if $R(0, 0) > 1$, then the trivial steady state is unstable.

In addition, we studied the stability of a nontrivial steady state and we proved a theorem that provided a sufficient condition for the local asymptotic stability of a nontrivial steady state of the general model, we note that this theorem generalizes the stability results given in Farkas, et al. (2008), in that they studied only two special cases whereas here we give the complete

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characteristic equation, and derive a general stability result. We also stated several corollaries to that theorem for some special cases, and these were just a few from that can be stated. We also gave a condition for a nontrivial steady state to be unstable, and this condition can be viewed as the positiveness of the directional derivative of $R(J, A)$ at (J_∞, A_∞). We also proved that these (in)stability results remain unchanged if each of the vital rates is multiplied by any positive function $f(J, A) \in C^1(\mathbb{R}^{+2})$. Finally, we illustrated our stability results by examples.

We note that in this paper as well as in our previous papers El-Doma (2008 a) and El-Doma (2008 b), we assumed the principle of linearized stability for size-structured models, which has received considerable attention in recent years. This principle consists of two parts, namely, stability part and instability part, for example, see Diekmann, et al. (2007 b). The stability part says that a nontrivial steady state is locally asymptotically stable if all the roots of the corresponding characteristic equation, which results from the linearization of the model equations at a steady state, lie to the left of the imaginary axis. The instability part says that a nontrivial steady state is unstable if the corresponding characteristic equation has at least one root that lie to the right of the imaginary axis. For example, Tucker, et al. (1988), proved the stability part for a general size-structured model that incorporated several structuring variables i.e., several growth rates. De Roos, et al. (1990), concluded that their numerical results are in agreement with the stability results obtained via linearization for a size-structured model of Daphnia. Calsina, et al. (1995), proved the existence of a global attractor for a size-structured model that is similar to the model considered in this paper with the additional assumption that there is an inflow of newborns from an external source, but without assuming that the population is divided into adults and juveniles. Diekmann, et al. (2007 a), conjectured the principle and outlined preliminary steps for a proof. Diekmann, et al. (2007 b), proved the principle for cases when the maximum attainable size for an individual is finite and the death rate assumes the affine form i.e., $\mu_0(a) + \mu_1(P(t))$. Diekmann, et al. (Preprint a), relaxed the condition on the maximum attainable size for an individual in the population and the condition on the death rate is improved so that the death rate can take the form, $\mu(a, P(t))$. Further examples that illustrated the previous results are given in Diekmann, et al. (2008).

In a series of subsequent two papers, we study three special cases, namely, the first case is when, $V(a, J, A) = V(a), \mu(a, J, A) = \mu(A)$, the second case is when, $V(a, J, A) = V(a), \mu(a, J, A) = \mu(J)$, and the third case is when, $V(a, J, A) = V(a), \mu(a, J, A) = \mu(a)$. We note that the first special case linked our study of the stability of our size-structured population dynamics model to the study of the classical Gurtin-MacCamy's age-structured population dynamics model given in Gurtin, et al. (1974), specifically, the studies for the stability given in Gurney, et al. (1980), and Weinstock, et al. (1987), in fact, the characteristic equation for this special case, when juveniles are not considered i.e. when, $T = 0$, has the same qualitative properties as the characteristic equation of the Gurtin-MacCamy's age-structured population dynamics model, this fact is proved in El-Doma (2008 a). Also similarly, the third special case linked our study to studies related to cannibalism, for example, see Iannelli (1995), Bekkal-Brikci, et al. (2007), and El-Doma (2007).

Appendices

A. The Characteristic Equation

$$
\begin{aligned}
1 = {} & \frac{1}{V(0, J_\infty, A_\infty)} \int_T^l e^{-\int_0^a E(\tau)d\tau} \Big[\beta(a, J_\infty, A_\infty) + D_A \Big] da + \frac{D_J}{V(0, J_\infty, A_\infty)} \int_0^T e^{-\int_0^a E(\tau)d\tau} da \\
& - \int_0^T \int_0^a e^{-\int_\sigma^a E(\tau)d\tau} g_J(\sigma, J_\infty, A_\infty) d\sigma da - \int_T^l \int_0^a e^{-\int_\sigma^a E(\tau)d\tau} g_A(\sigma, J_\infty, A_\infty) d\sigma da \\
& + \int_T^l \int_T^l \int_0^a e^{-\int_0^b E(\tau)d\tau} e^{-\int_\sigma^a E(\tau)d\tau} g_A(\sigma, J_\infty, A_\infty) \left[\frac{\beta(b, J_\infty, A_\infty) - \beta(a, J_\infty, A_\infty)}{V(0, J_\infty, A_\infty)} \right] d\sigma da db \\
& + \int_0^T \int_T^l \int_0^a e^{-\int_0^b E(\tau)d\tau} e^{-\int_\sigma^a E(\tau)d\tau} \left[\frac{D_J g_A(\sigma, J_\infty, A_\infty) - g_J(\sigma, J_\infty, A_\infty)\Big(\beta(a, J_\infty, A_\infty) + D_A \Big)}{V(0, J_\infty, A_\infty)} \right] d\sigma da db \\
& + \int_T^l \int_0^T \int_0^a e^{-\int_0^b E(\tau)d\tau} e^{-\int_\sigma^a E(\tau)d\tau} \left[\frac{g_J(\sigma, J_\infty, A_\infty)\Big(\beta(b, J_\infty, A_\infty) + D_A \Big) - D_J g_A(\sigma, J_\infty, A_\infty)}{V(0, J_\infty, A_\infty)} \right] d\sigma da db \\
& - \int_0^T \int_0^b \int_T^l \int_0^a e^{-\int_\sigma^a E(\tau)d\tau} e^{-\int_e^b E(\tau)d\tau} B(\sigma, e) d\sigma da de db \\
& + \int_0^T \int_T^l \int_0^b \int_T^l \int_0^a e^{-\int_0^c E(\tau)d\tau} e^{-\int_\sigma^a E(\tau)d\tau} e^{-\int_e^b E(\tau)d\tau} \frac{B(\sigma, e)\beta(a, J_\infty, A_\infty)}{V(0, J_\infty, A_\infty)} d\sigma da de db dc \\
& + \int_T^l \int_0^T \int_0^b \int_T^l \int_0^a e^{-\int_0^c E(\tau)d\tau} e^{-\int_\sigma^a E(\tau)d\tau} e^{-\int_e^b E(\tau)d\tau} B(\sigma, e) \frac{\Big[\beta(c, J_\infty, A_\infty) - \beta(a, J_\infty, A_\infty)\Big]}{V(0, J_\infty, A_\infty)} d\sigma da de db dc,
\end{aligned}
$$

$$\mathbf{A_1}$$

where $B(\sigma, e)$ is given by

$$
B(\sigma, e) = g_A(\sigma, J_\infty, A_\infty) g_J(e, J_\infty, A_\infty) - g_J(\sigma, J_\infty, A_\infty) g_A(e, J_\infty, A_\infty).
$$

B. A Sufficient Condition for Local Asymptotic Stability

$$
\begin{aligned}
& \int_T^l \frac{\pi(a, J_\infty, A_\infty)}{V(a, J_\infty, A_\infty)} \Big| \Big[\beta(a, J_\infty, A_\infty) + D_A \Big] \Big| da + |D_J| \int_0^T \frac{\pi(a, J_\infty, A_\infty)}{V(a, J_\infty, A_\infty)} da \\
& + \int_0^T \int_0^a F(a, \sigma) |g_J(\sigma, J_\infty, A_\infty)| d\sigma da + \int_T^l \int_0^a F(a, \sigma) |g_A(\sigma, J_\infty, A_\infty)| d\sigma da \qquad (28) \\
& + \int_T^l \int_T^l \int_0^a \frac{\pi(b, J_\infty, A_\infty)}{V(b, J_\infty, A_\infty)} F(a, \sigma) \Big| g_A(\sigma, J_\infty, A_\infty) \Big[\beta(b, J_\infty, A_\infty) - \beta(a, J_\infty, A_\infty) \Big] \Big| d\sigma da db \\
& + \int_0^T \int_T^l \int_0^a \frac{\pi(b, J_\infty, A_\infty)}{V(b, J_\infty, A_\infty)} F(a, \sigma) \Big| \Big[D_J g_A(\sigma, J_\infty, A_\infty) - g_J(\sigma, J_\infty, A_\infty)\Big(\beta(a, J_\infty, A_\infty) + D_A \Big) \Big] \Big| d\sigma da db \\
& + \int_T^l \int_0^T \int_0^a \frac{\pi(b, J_\infty, A_\infty)}{V(b, J_\infty, A_\infty)} F(a, \sigma) \Big| \Big[g_J(\sigma, J_\infty, A_\infty)\Big(\beta(b, J_\infty, A_\infty) + D_A \Big) - D_J g_A(\sigma, J_\infty, A_\infty) \Big] \Big| d\sigma da db
\end{aligned}
$$

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$$+ \int_0^T \int_0^b \int_T^l \int_0^a F(a,\sigma)F(b,e)|B(\sigma,e)|d\sigma\,da\,de\,db$$

$$+ \int_0^T \int_T^l \int_0^b \int_T^l \int_0^a \frac{\pi(c,J_\infty,A_\infty)}{V(c,J_\infty,A_\infty)}F(a,\sigma)F(b,e)\beta(a,J_\infty,A_\infty)|B(\sigma,e)|d\sigma\,da\,de\,db\,dc$$

$$+ \int_T^l \int_0^T \int_0^b \int_T^l \int_0^a \frac{\pi(c,J_\infty,A_\infty)}{V(c,J_\infty,A_\infty)}F(a,\sigma)F(b,e)\Big|B(\sigma,e)\Big[\beta(c,J_\infty,A_\infty)-\beta(a,J_\infty,A_\infty)\Big]\Big|d\sigma\,da\,de\,db\,dc$$

$$< 1, \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad \mathbf{B_1}$$

where $F(a,\sigma)$ is given by

$$F(a,\sigma) = \frac{V(\sigma,J_\infty,A_\infty)}{V(a,J_\infty,A_\infty)}e^{-\int_\sigma^a \frac{\mu(\tau,J_\infty,A_\infty)}{V(\tau,J_\infty,A_\infty)}d\tau}.$$

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