LOCAL STABILITY OF A QUASI-LINEAR AGE-SIZE STRUCTURED POPULATION DYNAMICS MODEL[1]

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In memory of C.O.A. Sowunmi (1934-2007)

ABSTRACT. The local stability of a quasi-linear age-size structured population model studied in Tchuenche (2007) is analysed. If a certain threshold parameter known as the basic reproductive rate is less than unity, then the trivial steady state is locally asymptotically stable. Also, it is shown that if the only real root of the equation $\mathcal{R}(m') = 1$ is negative, then, the non trivial steady state is locally exponentially asymptotically stable.

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1. INTRODUCTION

Any realistic model of population dynamics must take into consideration factors such as age, weight, size, which influence the dynamics of changes in the total population. By keeping track of the size of the total population, one must account for its composition as a function of mathematically tractable parameters. Age, size, physiological factors, density dependence, gestation period, and the mating pattern are some of the key factors to be included in a realistic mathematical model (Sowunmi, 2004) of population biology. However, the need for mathematical convenience and tractability imposes constraints on the number of factors that a simple model can accommodate. We have considered mating pattern and physiological factors (which are among the least favoured parameters) elsewhere (cf. Tchuenche 2003, 2007). The dynamics of a population system is a sequence of stages that can be divided into groups or substages according to their age, size, gender, functions and so on (Hritonenko, 2006). Herein, age and size will be accounted for.

Age-structured models have been extensively studied, but such models appropriately describe populations in which the vital rates (birth and death) are age-dependent. There are many models in which age alone is not sufficient (Sloboolkin, 1953). For instance, it is the weighted gain in most insects that triggers the various moult (Chapmann, 1969). Thus, there is need to demonstrate the compromise between the conflicting demands of mathematical tractability and biological realism.

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Models mathematically describe our conception of nature, and their primary requirement in ecology, biology and other fields is that they should be realistic (Streifer, 1974). Nature is exceedingly complex and rich in phenomena and perhaps one of the most important attribute of individuals in a population is their chronological age (Brewer, 1989) and so, the inclusion of age-structure is the first logical step to increase the realism and degree of complexity of population models. Nevertheless, at least two bio-demographic factors should be included in any model which aims at describing the dynamics of individuals in the population, since the former in many species have vital rates which depend not only on their age, but also on their size, as well as other attributes.

For the sake of simplicity, we shall assume in the sequel that age and body size or weight are important characteristics that govern the expressed physiology, ecology and behaviour of individuals. The model described herein is 1-sex, where only females are counted; that is, the model is female dominant (Sowunmi, 1976). In such a case, males are present only for reproductive purposes. This makes sense in the human setting and some higher species for the following reasons:- Females know well who their offsprings are - and more importantly, they have a physically and biologically well-specified beginning and end to their reproductive period. For instance, female reproductive period spans a closed interval of age $[a_{2j}, a_{2r}]$, where pregnancy cannot occur earlier than age a_{2j}, and cannot continue beyond age a_{2r}, $(a_{2j} > 0)$ (Sowunmi, 1993).

Our motivation comes from the fact that some authors have considered the population size as an additional variable, but do not include the body weight of neonates and consequently, we shall take into consideration here the body weight of individuals (mother and child). Therefore, this study aims at investigating the stability of the quasi-linear version of an age-size structured model in which the renewal equation includes the average body weight of new born individuals. We note that the basic reproductive number which determnines the average number of birth from a mother throughout her period of fertility will depend on the average body weight of her offsprings.

2. THE MODEL

We define an integro-differentiable age-size density function $u(a, m, t)$, where a represents the chronological age, or physiological age (Brewer, 1989), while m represents the mass or body weight which without any ambiguity, we shall refer to as size, and t is the time.

In general, the units of a and m should appropriately be chosen for the species being modelled. These critical variables describe the attributes which distinguish individuals in a population. $a \in [0, A]$, A is the life span, $t \in \mathbb{R}^+$, $m \in (m_1, m_2)$ where $m_1 > 0$ is the minimum size and m_2 the maximum value of m. For the purpose of mathematical tractability, we shall take $m \in (m_1, +\infty)$. The density function $u(t, a, m) \in L^1(Q)$ where $Q := [0, T] \times [0, A] \times (m_1, m_2)$ is continuous and monotone in its domain, and contains a great deal of information about the population. If we assume that there are no very small or very large individuals, nor any very old individuals, then $u = 0$ near $m = 0$ and $u \to 0$ as m or a approaches

maximum biologically attainable values for the species under consideration (Castillo-Chavez, 1987). A brief comment on previous works provides the context of this paper.

The model equation used below was probably first derived by Sinko (1967). Nisbet and Gurney (1983) modified this model equations to study an insect population with dynamically varying instar duration and the complex inertplay in the population with long time delay. Indeed, they specify assumptions which result in the instantaneous subpopulations of various instars obeying delay-defferential equations with time delays (representing instar duration) which are themselves dynamic variables, changing in response to the availability of food. The density function u defined above satisfies the following non-linear first order partial differential equation for which the initial and boundary conditions will be specified for the quasi-linear case below.

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} + \frac{\partial (Gu)}{\partial m} = -\mu u \tag{1}$$

where G and μ are the growth and death rates, respectively. A detail discussion of these functions can be found in Streifer (1974).
The parameter G may be written as $G(t, a, m)$, which implicitly depends on the state of the environment, while in $\mu(t, a, m, u)$, the dependence on u enables us to include crowding effects, interference and cannibalistic phenomena (Streifer, 1974). A model with these parameters is as complex as those prevalent in physics, although the belief is commonly expressed that physical models are elegant and general, which is true only to some extend! This is quite interesting, because models are descriptive approximations of real life phenomena, and knowing the degree of complexity of models which will eventually be employed to study complicated ecological systems will clear the desk of most researchers in this area. This is indeed a difficult task! For the sake of simplicity and without loss of generality, we assume that $\mu(t, a, m, u)$ is time independent and overcrowding effects and/or cannibalism is not taken into consideration here. For a recent model including cannibalism, see El-Doma (2007b).

As females give birth, they experience abrupt decrease in mass. We shall assume that environmental response of individuals in the population is implicitly incorporated in the vital rates. This assumption can be improved upon at the expense of some additional complexity, but the simplification, however, is for mathematical convenience and tractability. Thus, the discussion that follows is limited to the most basic considerations and ideas.

The pointers to potential simplifications are found in the analysis of a few idealized cases, which help elucidate the mathematical structures inherent in age structured problems. If the vital rates are autonomous systems, then the survival probability (denoted by π) would be explicitly independent of time. Thus, from the aforementioned, we consider the quasi-linear form of equation (1) in which $G(t, a, m)$ does not explicitly depend on size m, so that our original model equation (1) containing non-locally dependent

coefficients together with the initial and boundary conditions now reads:

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} + G(a,t)\frac{\partial u}{\partial m} = -\mu(a,m)u$$

$$u(0,a,m) = u_0(a,m) \tag{2}$$

$$B(t,m') := u(t,0,m') = \int_0^\infty \int_{m_1}^\infty \beta(a,m',m)u(t,a,m)dmda$$

where m' is the average body weight of newborn from parents of mass m. $u(t,a,m)$ is the population density with respect to the chronological age $a \in [0,\infty)$ at time t with mass/size m. Model system (2) will be studied under the following general conditions: $\int_0^\infty \mu(a,m)da = +\infty$, $\int_0^\infty \pi(0,a,m)da < +\infty$, where $\pi(0,a,m) = exp\{-\int_0^a \mu(\alpha,m)d\alpha\}$.
Since the model system (2) under consideration is quasi-linear, by assuming further that $G(t,a) = G(a)$ because time and age have the same unit, then, the explicit solution of (2) using the method of characteristics exists and it is given by:

$$u(t,a,m) = \begin{cases} \pi(0,a,\bar{m})B(t-a,\bar{m});\ a < t, \\ \\ \pi(a-t,a,\bar{m})u_0(a-t,\bar{m}+\Gamma(a-t));\ t \leq a, \end{cases} \tag{3}$$

where $\pi(0,a,\bar{m}) = exp\{-M(0,a,\bar{m})\}$, $\pi(a-t,a,\bar{m}) = exp\{-M(a,a-t,\bar{m})\}$, $\bar{m} = m - \Gamma(a)$, $M(0,a,\bar{m}) = \int_0^a \mu(\xi,\bar{m})d\xi$, and $\Gamma(a) = \int_0^a G(\alpha)d\alpha$. More details on the above solution can be found in Sinko and Streifer, 1967; Tchuenche (2007). We also note that under certain conditions, this solution is unique (see Theorem 2 in Tchuenche, 2007).
When $a < t$, the mother body weight decrease due to birth $(m - \Gamma(a))$. Since G is the size growth rate, $\Gamma(a)$ could simply be regarded as m' on the average. Also, immediately after birth, the mother body weight increases steadily via the parameter $\Gamma(a-t)$ (when $t \leq a$). Thus, equation (3) above describes the female population density and gives us the pattern of weight dynamics soon after birth.

3. EQUILIBRIUM SOLUTIONS

Most natural processes are generally nonlinear. One of their most important characteristics is their equilibrium, which is one of the basic ultimate goals of stability in nature, as well as in mathematical modelling. In this respect, we ask: Are there steady states solutions? If yes, are they stable or unstable? and what drives the dynamics of these processes to equilibrium? The time independent solutions of equation (1) above is obtain when

$$u(a,m,t) \equiv \varphi(a,m), \tag{4}$$

where

$$\frac{\partial \varphi}{\partial a} + G(a)\frac{\partial \varphi}{\partial m} + \mu(a,m)\varphi = 0$$

$$\varphi(0,m') = \int_0^\infty \int_{m_1}^\infty \beta(a,m',m)\varphi(a,m)dmda. \tag{5}$$

By the method of characteristics, equation (2b) is equivalent to:

$$\begin{cases} u(a,m) = u(0,m)e^{\int_0^a -\mu(\alpha,m)d\alpha} \\ \\ m(a) = m(0) + \int_0^a G(\alpha)d\alpha. \end{cases} \tag{6}$$

Equation (6) can simply be referred to as an *equilibrium-size-age-dependent* distribution.
The trivial equilibrium solution $u(a,m,t) = 0$ is less interesting and shall not be considered in this study. It is important to note that systems (2) and (4) above are well-posed and the necessary condition for the existence of non-trivial equilibrium was derived (see Lemma 3 in Tchuenche, 2007). This non-trivial steady state was also shown to be exponentially bounded (Theorem 4, Tchuenche, 2007).
The above formalism presupposes knowledge of the entire history of the recruitment rate β, and death rate μ, which although very valuable in strategic modelling, it is not directly applicable to models of specific population. Let $\xi(a,m,t)$ be a little perturbation of the steady state solution φ, then, we define

$$u = \varphi(a,m) + \xi(a,m,t)$$

Thus, ξ will satisfy the following system of equations

$$\frac{\partial \xi}{\partial t} + \frac{\partial \xi}{\partial a} + G(a,t)\frac{\partial \xi}{\partial m} = \mu(a,m)\xi$$

$$B(m',t) := \xi(0,m',t) = \int_0^\infty \int_{m_1}^\infty \beta(a,m',m)\xi(a,m,t)dmda \tag{7}$$

$$\xi(a,m,0) = \xi_0(a,m)$$

The first integral solution of the above system is given by (see Tchuenche 2003, 2007).

$$\xi(a,m,t) = \xi(0,m',t-a)H(t-a)\pi(0,a,m') + \xi_0(a-t,m)H(a-t)\pi(a-t,a,m'), \tag{8}$$

where $\xi(0,m',t-a)$ can also be denoted as $B(m't)$. The solution for $a > t$ depends on ξ_0 but not on $B(m',t)$, and that of $t > a$ depends on $B(m',t)$. This shows that the population density is a positive functions which is defined only for values of $t, a > 0$. Values taken by the function in the range $t < 0$ are irrelevant and meaningless (Watson, 1980), and no one cares about what happens to population density functions when t is negative (Rosen, 1993).

4. STABILITY OF STEADY STATES

The concept of stability has different definitions depending on whether the discussion is primarily linear time-invariant systems or non-linear systems. Linear time-invariant systems are modelled as differential equations with constant coefficients. A determination of stability for these types of systems can be found through the use of Laplace transform techniques. If the poles of the system lie in the left-hand plane, then the time domain solution will fall to zero as time approaches infinity. If, on the other hand, the poles lie in the right hand plane, then the time domain solution will increase without bound as time approaches infinity. Stability, in the linear sense, is thought of in terms of the exact solution to the defining differential equation. Stability of steady states is an important physical concept. Indeed, an equilibrium state of a physical system is said to be stable when small departures from equilibrium remain so with the lapse of time, and unstable when arbitrarily small initial deviations from equilibrium can ultimately become quite large (Birkhoff and Rota, 1978).

Theorem 1: The perturbation term $\xi(a, m, t)$ of the steady state solution of model system (2) tends to zero asymptotically as $t \to \infty$ if $p_1(< 0)$ is the only real root of the equation $\hat{L}(p, m') = 1$.

Proof: Following the approach of Gurtin and McCamy (1974) with appropriate modifications, we proceed as follows:
Substituting (8) into $(7)_2$, and interchanging the order of integration yields

$$\begin{aligned} B(m', t) &= \int_{m_1}^{\infty} \int_0^t \beta(a, m', m)\xi(0, m', t-a)\pi(0, a, m')dadm \\ &\quad + \int_{m_1}^{\infty} \int_0^t \beta(a, m', m)\xi_0(a-t, m)\pi(a-t, a, m')dadm \end{aligned} \tag{9}$$

Now, re-write (9) in a compact form, in order to obtain an integral equation. That is,

$$B(m', t) = \int_{m_1}^{\infty} \int_0^t K(a, m', m)B(m', t-a)dadm + N(m', t) \tag{10}$$

where

$$K(a, m', m) = \beta(a, m', m)\pi(0, a, m')$$

$$N(m', t) = \int_{m_1}^{\infty} \int_0^t \beta(a, m', m)\xi_0(a-t, m)\pi(a-t, a, m')dadm$$

Equation (10) can simply be written as

$$B(m', t) = \int_0^t L(a, m')B(m', t-a)da + N(m', t) \tag{11}$$

$$L(a, m') = \int_{m_1}^{\infty} K(a, m', m)dm$$

A little transformation of equation (11) gives

$$B(m',t) = \int_0^t L(t-a,m')B(m',a)da + N(m',t) \tag{12}$$

which is a non-homogeneous Volterra integral equation (Petrovskii, 1957; Kanwal, 1971).
Here, we note that L is continuous for $0 < t < T$, $0 < m' < M$
N is continuous in both its variables.
Since equation (12) is an integral equation of convolution type (Wilson, 1992, Kanwal, 1971), we can take its Laplace transform with respect to the time variable t, with p as the transform variable (Watson, 1981).

Let $\hat{}$ represents the operation of Laplace transform, then

$$\hat{B}(m',p) = \hat{L}(p,m')\hat{B}(m',p) + \hat{N}(m',p). \tag{13}$$

Solving for $\hat{B}$ in (13), we obtain

$$\hat{B}(m',p) = \frac{\hat{N}(m',p)}{1-\hat{L}(p,m')}, \tag{14}$$

where $1-\hat{L}(p,m') \neq 0$.
$\hat{L}(0,m)$ is known as the basic reproductive number of newborn with weight m' often denoted by $\mathcal{R}(m')$. We now show that $1-\hat{L}(p,m')$ has exactly one root $p = p_1$, say.

The function $\hat{L}(p,m')$ has the following characteristics:
* $\hat{L}(p,m') \to \infty$ as $p \to -\infty$,
* $\hat{L}(p,m') \to 0$ as $p \to +\infty$,

and finally,
$\hat{L}(p,m')$ decreases monotonically with respect to p. That is,

$$\frac{d\hat{L}(p,m')}{dp} = -\int_0^\infty e^{-pt}L(t,m')dt < 0, \tag{15}$$

so that for $p = p_1$, $\hat{L}(p_1,m') = 1$ which is the only real root.

In order to find the inverse transform of equation (9), we proceed as follows: From equation (10), let

$$F(m',p) = \frac{1-\hat{L}(p,m')}{\hat{N}(m',p)} = \frac{1}{B(m',p)}, \tag{16}$$

then, recalling the complex inversion formula for the recovery of $B(m',p)$, we have:

$$B(m',p) = \frac{1}{2\pi i}\int_{u_0-i\infty}^{u_0+i\infty} \frac{e^{pt}}{F(m',p)}dp \tag{17}$$

where $p < u_0 < 0$, and $\hat{F}(m', p) = \dfrac{1}{\hat{B}(m', p)}$.
For more details on the above approach, see Sowunmi (2000). In order to estimate the integral in (10), let $p := u_0 + i\eta$, then it can be shown after some little algebraic manipulations that

$$\left| \int_{u_0 - i\infty}^{u_0 + i\infty} \frac{e^{pt}}{F(m', p)} dp \right| \leq K e^{u_0 t}, \tag{18}$$

where K depends on u_0 and m'.
Thus,

$$B(m', t) \leq c \cdot e^{p_1 t}, \qquad u_0 < p_1 < 0. \tag{19}$$

Making use of equation (19), we have that

$$\lim_{t \to \infty} \xi(a, m, t) = c \cdot e^{p_1 (t-a)} \pi(0, a, m').$$

Thus, if $p_1 < 0$, then, $\xi(a, m, t) \to 0$ as $t \to \infty$.
Hence,

$$u(a, m, t) = \varphi(a, m) + \xi(a, m, t) \to \varphi(a, m) \ \text{ as } \ t \to \infty.$$

This terminates the proof. □

Using Theorem 2 of van den Driessche and Watmough (2000), the following result is established:

Lemma 1: The trivial steady state solution of model system (2) is locally asymptotically stable if $\mathcal{R}(m') < 1$ and unstable if $\mathcal{R}(m') > 1$.

Proof: We follow the approcah in El-Doma (2007a). At the trivial equilibrium, the birth rate is assumed to be a decreasing function. Consequently, by substituting $\beta(a, m', m) = \beta(a, m) e^{-\lambda a}$ where λ is a complex number, we obtain $L(a, m') = \int_{m_1}^{\infty} e^{-\lambda a} \beta(a, m) \pi(0, a, m') da$. Therefore, $|L(a, m')| \leq \int_{m_1}^{\infty} e^{-a Re \lambda} \beta(a, m) \pi(0, a, m') da \leq \mathcal{R}(m') < 1$. Therefore, the trivial steady state is locally asymptotically stable if $\mathcal{R}(m') < 1$.
To prove the second part of the Lemma, when $\mathcal{R}(m') > 1$, we define a function $g(\lambda)$ by $g(\lambda) = \int_{m_1}^{\infty} e^{-\lambda a} \beta(a, m) \pi(0, a, m') da$ and suppose that λ is real. Then, it can be seen that $g(\lambda)$ is a decreasing function of $\lambda > 0$, $g(\lambda) \to 0$ as $\lambda \to +\infty$ and $g(0) = \mathcal{R}(m')$. Accordingly, if $\mathcal{R}(m') > 1$, then, there exists $\lambda^* > 0$ such that $g(\lambda^*) = 1$, and hence, the trivial steady state is unstable. □

We note that $\mathcal{R}(m') > 1$ implies $1 - \hat{L}(p, m')$ is negative, which is not biologically relevant, consequently, we take its modulus so that $|1 - \hat{L}(p, m')| > 0$. The following results which we state without proofs are directly derived from

Theorem 1 above.

Lemma 2: All nontrivial solutions of $\hat{L}(p, m') = 1 = \mathcal{R}(m')$ are nontrivial steady states of model system (2).

Lemma 3: A nontrivial steady state is unstable if $\dfrac{\hat{L}(p, m')}{dp} \approx \dfrac{\mathcal{R}(m')}{dp} > 0$.

The proof is immediate from equation 15.

5. CONCLUSION

The local stability of an age-size structured population dynamics model is analyzed. Such a model was previously considered by Tchuenche (2007) for the dynamics of Sickle-Cell patients. Therefore, the formalism is not the same, as the renewal function is not genotype-oriented herein. Also, the model is assumed to be well-posed and the existence and uniqueness of solutions are assumed to hold as in Tchuenche (2007). Nevertheless, there are basic differences in the two studies: The present study, which incorporates an age-dependent growth rate shows that:

(a) The trivial equilibrium is locally asymptotically stable if a certain threshold parameter, $\mathcal{R}(m')$, say, known as the basic reproductive rate is less than unity.

(b) If the only real root of the equation $\mathcal{R}(m') = 1$ is negative, then, the nontrivial steady state is locally exponentially asymptotically stable.

The analysis in this paper can be extended in various ways. For instance, once could attempt the global stability analysis of the current model. Also, explicitly incorporting overcrowding effects or cannibalism can provide and improve on the results of this study.

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