

**ON THE ASYMPTOTIC BEHAVIOUR OF THE
NON-AUTONOMOUS GURTIN–MACCAMY EQUATION**

By

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1. Preliminaries

The Gurtin–MacCamy system, introduced in [5] and its generalizations, including vital rates depending on a finite number of weighted population size functions has been studied by many authors with different methods in different aspects [7], [1], [8], [9], [4]. It describes the dynamics of a single species population living in a closed territory, that is migration is excluded. The only way to leave the population is by death and the newborns of the individuals living in the population form the only after-growth. Thus, if these quantities are balanced the population can survive at a constant level. The measure of the balance is the so called inherent net reproduction number, the expected number of newborns for an individual in his lifetime.

The investigations of the stability of these constant level populations, i.e. stationary age-distributions, by linearization [3] lead to some results containing simple conditions for the net reproduction number [2].

In the present note we are going to investigate the asymptotic behaviour of solutions of the following (linear non-autonomous) model

$$(1.1) \quad \begin{aligned} p_t'(a, t) + p_a'(a, t) &= -\mu(a, t)p(a, t), \quad 0 \leq a < m < \infty, \quad t \geq 0 \\ p(0, t) &= \int_0^m \beta(a, t)p(a, t)da, \quad t > 0, \end{aligned}$$

with the initial condition $p(a, 0) =: p_0(a)$, which satisfies $p_0(0) = \int_0^m \beta(a, 0) \cdot p_0(a)da$. Here $p(a, t)$ denotes the density of members of age a at time $t \geq 0$.

This means that the quantity of members between age a and age $a + da$ is $p(a, t)da$ for small da . We assume finite life span denoted by m .

We believe that this linear but non-autonomous system is more useful modelling some population dynamical phenomena for example in the case of time periodic vital rate functions.

The dynamics of the system depends on the vital rates $\beta(a, t), \mu(a, t)$ for which we make the following general assumptions

$$(1.2) \quad \forall t \in [0, \infty), \forall a \in [0, m] \quad 0 \leq \beta(a, t) \leq k < \infty, \mu(a, t) \geq 0,$$

$$(1.3) \quad \forall t \in [0, \infty) \int_0^m \mu(a, t) da = \infty, \quad \forall t \in [0, \infty), a \in [0, m) \quad \mu(a, t) < \infty.$$

Later we are to make other conditions on the vital rates.

Integrating along the characteristics the model (1.1) can be reduced to a pair of integral equations that corresponds to the cases $t \geq a$ and $a > t$. Since we are investigating here the asymptotic behaviour we consider only the case $t > m \geq a$.

The ODE system of characteristics is

$$(1.4) \quad \frac{da}{d\tau} = \frac{dt}{d\tau} = 1, \quad \frac{dp}{d\tau} = -\mu(a, t)p(a, t).$$

From (1.4) we have the following formula for $p(a, t)$

$$(1.5) \quad p(a, t) = \varphi(t - a) e^{-\int_0^a \mu(s, t) ds},$$

where φ is an arbitrary C^1 function which has to satisfy the following equation

$$(1.6) \quad p(0, t) = \int_0^m \beta(x, t)p(x, t) dx = \varphi(t),$$

and from (1.6) we obtain

$$(1.7) \quad p(a, t) = e^{-\int_0^a \mu(s, t) ds} \int_0^m \beta(x, t - a)p(x, t - a) dx,$$

thus

$$(1.8) \quad p(a, t) = p(0, t - a)\pi(a, t), \quad \text{with } \pi(a, t) = e^{-\int_0^a \mu(s, t) ds}.$$

Here $\pi(a, t)$ denotes the probability for an individual to survive the age a at time t .

Finally recall the net reproduction function

$$(1.9) \quad R(t) = \int_0^m \beta(a, t) e^{-\int_0^a \mu(s, t) ds} da = \int_0^m \beta(a, t) \pi(a, t) da,$$

which is the expected number of newborns of an individual at time t .

2. Extinction

In [6] Iannelli et al. studied the global boundedness of solutions of a generalized Gurtin–MacCamy system, where the vital rates depend on a weighted size of the population $S(t) = \int_0^m \gamma(a) p(a, t) da$. Under some natural condition

they proved boundedness for the total population quantity $P(t) = \int_0^m p(a, t) da$.

They investigated two cases, first if the fertility function $\beta(a, S(t))$ is bounded by a non-increasing function $\phi(S)$ for which $\lim_{S \rightarrow \infty} \phi(S) = 0$ holds.

Then they proved boundedness under conditions mainly for the mortality, namely $\beta(a, S) \leq C\gamma(a)$, $\mu(a, S) \geq \mu_0(a) + \omega(S)$, where γ is the weight function, C a positive constant and ω is a non-decreasing function of the weighted population size S , $\lim_{S \rightarrow \infty} \omega(S) = \infty$.

In this section we are going to apply some of the idea of their proof for the non-autonomous system. That is first we show that under similar conditions for the fertility function the population goes to extinction. Then we consider the connection between the mortality and the fertility functions and establish a result in which a condition for the net reproduction number function $R(t)$ is given.

Consider the following assumptions on the fertility function $\beta(a, t)$

$$(2.1) \quad \beta(a, t) \leq \phi(t), \quad \forall t \geq 0, \quad \exists T \geq m : \phi(T) \leq \frac{1}{2m},$$

where $\phi(t)$ is a positive non-increasing function of $t \in [0, \infty)$.

THEOREM 1. *Let the conditions (2.1) be satisfied. For each non-negative initial age distribution $p(\cdot, 0) \in L^1$ we have $\int_0^m p(a, t) da = P(t) \rightarrow 0$ if $t \rightarrow \infty$.*

PROOF. From (1.7) we have

$$p(a, t) = p(0, t - a)\pi(a, t),$$

where $\pi(a, t) \leq 1$ for all $a \in [0, m]$, $t \in [m, \infty)$.

For the density of newborns at time t we have

$$(2.2) \quad p(0, t) = \int_0^m \beta(a, t)p(a, t)da \leq \phi(t)P(t).$$

That is we have

$$(2.3) \quad \int_0^m p(a, t)da = P(t) \leq \int_0^m p(0, t - a)da \leq \int_0^m \phi(t - a)P(t - a)da.$$

Now let $I_n := [(n - 1)m, nm]$, ($n = 2, 3, \dots$) and $P_n = \max_{t \in I_n} P(t)$.

Then for $t \in I_{n+1}$ and $a \in [0, m]$ we have $(t - a) \in I_n \cup I_{n+1}$ thus, from (2.3) we obtain

$$P_{n+1} \leq \max\{P_n, P_{n+1}\} * m * \phi((n - 1)m).$$

Let n_* be sufficiently great to have $(n_* - 1)m \geq T$. Then we have

$$(2.4) \quad P_{n_*+1} \leq \frac{\max\{P_{n_*}, P_{n_*+1}\}}{2}.$$

Then it follows that for $n \geq n_*$ we have $P_{n+1} \leq \frac{P_n}{2}$.

That is we have

$$\int_0^m p(a, t)da = P(t) \rightarrow 0, \text{ if } t \rightarrow \infty. \quad \blacksquare$$

As we have mentioned the net reproduction rate $R(t)$ is a key parameter to decide stability of stationary solutions of the autonomous model.

Now suppose that there exists a non-negative $\phi(\cdot)$ function and some constant $\epsilon > 0$ such that

$$(2.5) \quad \beta(a, t) \leq \phi(t), \quad \phi(t - a) \leq (1 + \epsilon)\beta(a, t), \quad a \in [0, m], t > m.$$

Moreover suppose

$$(2.6) \quad \exists T \geq 0 \text{ s.t. } R(T) \leq \frac{1}{1 + \delta} \text{ for } \delta > \epsilon,$$

and $R(t)$ is non-increasing.

THEOREM 2. *With the conditions (2.5)–(2.6) for each non-negative initial age distribution $p(a, 0) \in L^1$, $\int_0^m p(a, t) da = P(t) \rightarrow 0$ if $t \rightarrow \infty$.*

PROOF. We have again

$$p(a, t) = p(0, t - a)\pi(a, t), \quad t \in [m, \infty)$$

and in the same way as in the proof of Th.1 we obtain

$$P(t) \leq \int_0^m \phi(t - a)P(t - a)\pi(a, t) da$$

From the conditions in (2.5) we obtain

$$(2.7) \quad P(t) \leq \int_0^m (1 + \epsilon)\beta(a, t)\pi(a, t)P(t - a) da,$$

and with the same $I_n := [(n - 1)m, nm]$, ($n = 2, 3, \dots$) and $P_n := \max_{t \in I_n} P(t)$, if $t \in I_{n+1}$, $a \in [0, m]$, $(t - a) \in I_n \cup I_{n+1}$ thus we obtain

$$(2.8) \quad P_{n+1} \leq \max\{P_n, P_{n+1}\}(1 + \epsilon) \int_0^m \beta(a, t)\pi(a, t) da,$$

and because $\int_0^m \beta(a, t)\pi(a, t) da = R(t) \leq \frac{1}{1+\delta}$ for $t \geq T$, for sufficiently large n_* we have for $n \geq n_*$

$$(2.9) \quad P_{n+1} \leq \frac{1 + \epsilon}{1 + \delta} \max\{P_n, P_{n+1}\},$$

from where follows that $P_{n+1} \leq P_n \frac{1+\epsilon}{1+\delta} < P_n$, for $n \geq n_*$.

That is $P(t) \rightarrow 0$ if $t \rightarrow \infty$. ■

REMARKS. The conditions in Th.2 for the fertility function is quite technical and the condition for $R(t)$ is the essential one. Roughly speaking it means that if there exists some finite $T \geq 0$ such that $R(t)$ is bounded by some $\frac{1}{1+\delta} \leq 1$ for $t \geq T$ then the population goes to extinction. In other words if the expected number of newborns at time t is less than 1 for $t \geq T$ then the total population quantity tends to zero, of course.

3. Sharper upper bound

In the previous section we determined conditions for the vital rates which guarantees the extinction of the population. One may expect that if there exists some finite T such that for $t \geq T$ the inherent net reproduction number $R(t)$ is lower than 1 in other words the number of per capita offspring is below 1 then the total population quantity decreases and the population goes to extinction.

In this section we are going to formulate some sharper “upper bound” for the total population quantity, which is also in close relation with the net reproduction rate R as we will see.

Integrating both sides of the equation in (1.1) from 0 to m we have

$$\begin{aligned} \dot{P}(t) &= - \int_0^m \mu(a, t) p(a, t) da - \int_0^m p'_a(a, t) da = p(0, t) - \int_0^m \mu(a, t) p(a, t) da = \\ (3.1) \quad &= \int_0^m \beta(a, t) p(a, t) da - \int_0^m \mu(a, t) p(a, t) da. \end{aligned}$$

The solution of the ODE (3.1) obtained easily

$$(3.3) \quad P(t) = \int_0^t \int_0^m (p(a, s) \beta(a, s) - p(a, s) \mu(a, s)) da ds + P(0),$$

and we have

$$(3.4) \quad \lim_{t \rightarrow \infty} P(t) = \int_0^\infty \int_0^m (p(a, s) \beta(a, s) - p(a, s) \mu(a, s)) da ds + P(0).$$

Thus the question is when does the function

$$(3.5) \quad F(s) = \int_0^m (p(a, s) \beta(a, s) - p(a, s) \mu(a, s)) da$$

belong to $L^1_{[0, \infty)}$.

From (1.4) we have $p(a, s) = p(0, s - a) \pi(a, s)$ for $s \geq a$, that is we have

$$(3.6) \quad F(s) = \int_0^m p(0, s - a) (\beta(a, s) \pi(a, s) - \mu(a, s) \pi(a, s)) da$$

for $s \geq m$, and clearly $\int_0^m F(s) ds < \infty$ holds.

If the density of newborns $p(0, t)$ is finite for every t then there exists a function $C(s)$ which is also bounded, such that $p(0, s - a) < C(s)p(0, s)$ for every $a \in [0, m]$.

That is we have

$$(3.7) \quad F(s) \leq p(0, s)C(s) \left| \int_0^m \beta(a, s)\pi(a, s)da - \int_0^m \mu(a, s)\pi(a, s)da \right|.$$

Now observe that $\int_0^m \beta(a, s)\pi(a, s)da = R(s)$ by definition and $\int_0^m \mu(a, s) \cdot \pi(a, s)da = 1$ because $\mu(a, s)\pi(a, s)da$ is the probability for an individual to survive the age a and then die in $[a, a + da]$.

That is we have

$$(3.8) \quad \lim_{t \rightarrow \infty} P(t) \leq \int_0^{\infty} p(0, s)C(s)|R(s) - 1|ds + P(0).$$

Note that if the net reproduction number $R(s) < M$ is bounded by some $M < \infty$ for every s , then the density of newborns $p(0, s)$ and the function $C(s)$ is bounded for every s , too. So if for example $(R(s) - 1) \leq \frac{1}{s^{1+\alpha}}$ for some $\alpha > 0$, then the improper integral in (2.7) is convergent.

EXAMPLE. Consider the following special vital rate functions with maximal life span $m = 100$

$$\beta(a, t) = b(a)f(t) = \frac{a^4}{C}(100 - a)^2 1.11^{-a} \left(1 + \frac{1}{t^2 + 1}\right), \quad \mu(a) = \frac{1}{100 - a},$$

with $C = \int_0^{100} a^4(100 - a)^2 1.11^{-a} \pi(a)da \sim 0,4045064485 * 10^{10}$.

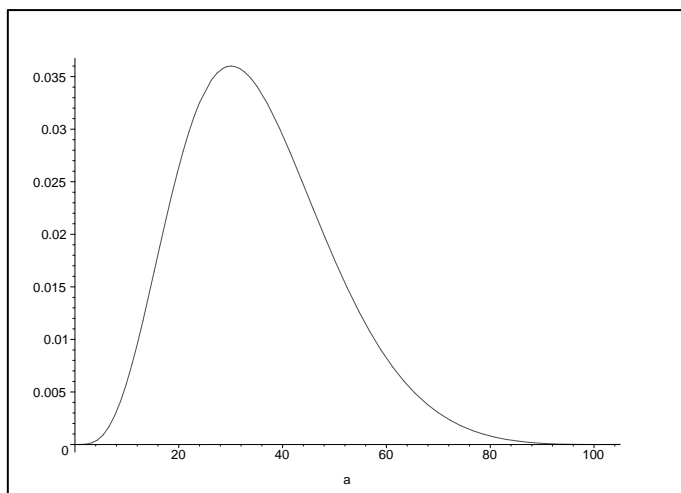


FIG. 1. $b(a) = \frac{a^4}{C} (100 - a)^2 1.11^{-a}$

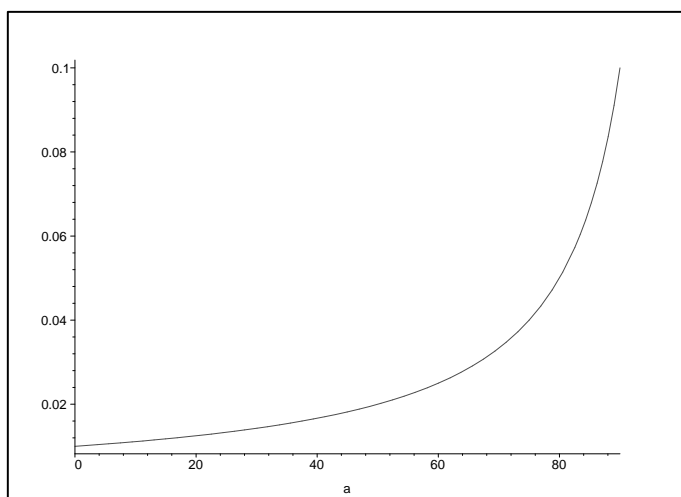
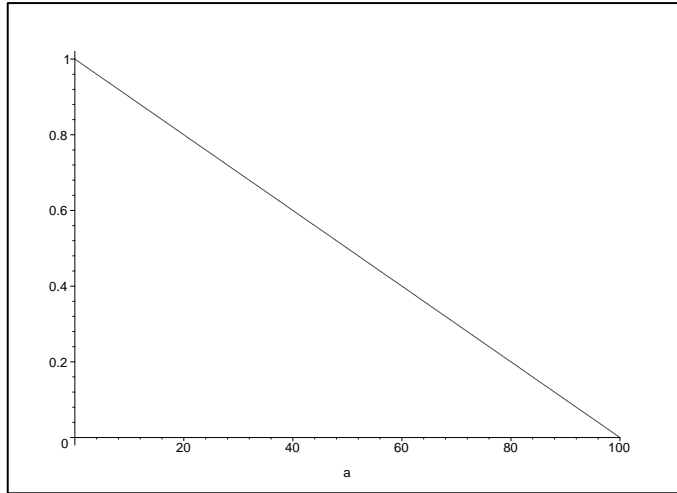


FIG. 2. $\mu(a) = \frac{1}{100 - a}$

It is easy to show that these functions satisfy the conditions (1.2)–(1.3).

With $\pi(a) = 1 - \frac{a}{100}$

FIG. 3. $\pi(a) = 1 - \frac{a}{100}$

we arrive at

$$R(t) = \int_0^{100} \frac{a^4}{C} (100 - a)^2 1.11^{-a} \left(1 + \frac{1}{t^2 + 1}\right) \left(1 - \frac{a}{100}\right) da = 1 + \frac{1}{1 + t^2}$$

Thus $R(t) \geq 1$ for $t \geq 0$ and $R(t) \rightarrow 1$ in a sufficient order.

From (3.8)

$$(3.9) \quad \lim_{t \rightarrow \infty} P(t) \leq \int_0^{\infty} \frac{p(0, s)C(s)}{1 + s^2} ds + P(0),$$

that is for any given initial age distribution $p_0(a)$ which satisfies the compatibility condition

$$p_0(0) = \int_0^{100} 2p_0(a) \frac{a^4}{C} (100 - a)^2 1.11^{-a} da$$

the solution $p(a, t) \rightarrow p_*(a)$ if $t \rightarrow \infty$ with some non-trivial age distribution $p_*(a)$ in the following L^1 norm:

$$(3.10) \quad \|p(\cdot, t)\| := \int_0^m |p(a, t)| da.$$

REMARKS. The example above is a very special one but shows the essential role of the net reproduction function $R(t)$. Thus the general problem namely the formulation of necessary or sufficient conditions for the convergence to a non-trivial age distribution seems to be still open. As the probably much more interesting case of time periodic vital rates on which we are working.

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References

- [1] J. M. CUSHING: *An Introduction to Structured Population Dynamics*, SIAM, Philadelphia, PA, 1998.
- [2] J. Z. FARKAS: Stability conditions for the non-linear McKendrick equations, to appear in *Applied Mathematics and Computations*.
- [3] M. FARKAS: On the stability of stationary age distributions, *Applied Mathematics and Computation* **131**(1) (2002), 107–123.
- [4] M. FARKAS: *Dynamical Models in Biology*, San Diego, Academic Press, 2001.
- [5] M. E. GURTIN and R. C. MACCAMY: Non-linear age-dependent populations dynamics, *Arch. Rat. Mech. Anal.* **54** (1974), 281–300.
- [6] M. IANNELLI, M.-Y. KIM, E.-J. PARK and A. PUGLIESE: Global boundedness of the solutions to a Gurtin–MacCamy system, *NoDEA* **9** (2002), 197–216.
- [7] M. IANNELLI: *Mathematical Theory of Age-Structured Population Dynamics*, Applied Mathematics Monographs, Comitato Nazionale per le Scienze Matematiche, (C.N.R.), Vol. **7**, Giardini, Pisa, 1995.
- [8] J. A. J. METZ and O. DIEKMANN: *The Dynamics of Physiologically Structured Populations*, Lecture Notes in Biomath. **68**, Springer-Verlag, Berlin, 1986.
- [9] G. WEBB: *Theory of Nonlinear Age-Dependent Population Dynamics*, Marcel Dekker, New York, 1985.

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