ASYMPTOTIC ANALYSIS OF A SIZE-STRUCTURED CANNIBALISM MODEL WITH INFINITE DIMENSIONAL ENVIRONMENTAL FEEDBACK

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Abstract. In this work we consider a size-structured cannibalism model with the model ingredients (fertility, growth, and mortality rate) depending on size (ranging over an infinite domain) and on a general function of the standing population (environmental feedback). Our focus is on the asymptotic behavior of the system, in particular on the effect of cannibalism on the long-term dynamics. To this end, we formally linearize the system about steady state and establish conditions in terms of the model ingredients which yield uniform exponential stability of the governing linear semigroup. We also show how the point spectrum of the linearized semigroup generator can be characterized in the special case of a separable attack rate and establish a general instability result. Further spectral analysis allows us to give conditions for asynchronous exponential growth of the linear semigroup.

1. Introduction. Cannibalism is a phenomenon observed among many species, e.g. certain fish populations. Sophisticated population models are capable of elucidating a potentially stabilizing effect of cannibalism, underscoring that certain populations may benefit from cannibalism when resources are limited. Consequently, the effects of cannibalism on the long-term dynamics of populations have attracted considerable interest and have been analyzed for various structured population models (see [5, 14] for further references).

Structured population models are typically formulated as partial differential equations for population densities. Diekmann et al. have developed a general mathematical framework to study analytical questions for structured populations (see [7, 8, 9]), including those pertaining to linear/nonlinear stability of population equilibria. In this context it was recently proven for large classes of structured population models, formulated as integral (or delay) equations, that the nonlinear stability/instability of a population equilibrium is completely determined by...
its linear stability/instability, a result commonly referred to as the “Principle of Linearized Stability”.

In a series of recent papers we have successfully applied linear semigroup and spectral methods to formulate biologically interpretable conditions for the linear stability/instability of equilibria of various structured population models, see [11, 12] and the references therein. In these problems we assumed that any effect of intraspecific competition between individuals of different sizes on individual behavior is primarily due to a change in population size and that every individual in the population can influence the vital rates of other individuals (“scramble competition”).

When the competition among individuals is based upon some hierarchy in the population, often related to the size of individuals, environmental feedback is incorporated in the model through infinite dimensional interaction variables (“contest competition”). This situation in its simplest form is of relevance for a forest consisting of tree individuals in which the height of a tree determines its rank in the population. Taller individuals have higher efficiency when competing for resources such as light, while individuals of lower rank do not influence the vital rates of individuals of higher rank.

Of interest in this work is the linear stability analysis of population equilibria of a continuous quasilinear size-structured model, recently discussed in [7]. In particular, it was proven there that the Principle of Linearized Stability holds true for this model. The density evolution of individuals of size $s$ is assumed to be governed by the partial differential equation

$$n_t(s,t) + (\gamma(s, E(s,t)) n(s,t))_s + (\mu(s, E(s,t)) + M(s,t)) n(s,t) = 0, \quad (1)$$

defined for $s \in (0, \infty)$ and $t > 0$. The density of zero (or minimal) size individuals is given by the nonlocal boundary condition

$$\gamma(0, E(0,t)) n(0,t) = \int_0^\infty \beta(s) n(s,t) \, ds, \quad t > 0. \quad (2)$$

The initial condition reads

$$n(s,0) = n_0(s), \quad s \in [0, \infty). \quad (3)$$

Here $\beta$, $\mu$ and $\gamma$ denote the fertility, mortality and growth rate of individuals, respectively. All vital rates are size-dependent. Moreover, it is assumed that the mortality and growth rates of individuals depend on the function

$$E(s,t) = \int_0^\infty c(y) \alpha(y, s) n(y,t) \, dy. \quad (4)$$

Here $\alpha$ denotes the size-specific attack rate, while $c$ denotes the energetic value of the attacked prey. Hence the function $E$ models the assumption that the extra energy available due to cannibalism is channeled into the growth of individuals and affects their starvation-driven mortality. The extra size-specific mortality rate due to cannibalism is given by

$$M(s,t) = \int_0^\infty \alpha(s, y) n(y,t) \, dy. \quad (5)$$

(Note the switch of variables in $\alpha$ in contrast to (4).) We remark that the cannibalism model discussed here incorporates the environmental feedback variable used in the hierarchical size-structured model in [13].

We impose the following regularity conditions on the model ingredients:

- $\mu = \mu(s, E) \in C_b([0, \infty); C^1_b([0, \infty)), \quad \mu \geq 0$
\begin{itemize}
\item $\gamma = \gamma(s, E) \in C^1_b([0, \infty); C^1_b([0, \infty)))$, $\gamma \geq \gamma_0 > 0$ for some constant $\gamma_0$
\item $\beta = \beta(s) \in C_b([0, \infty))$, $\beta \geq 0$
\item $c = c(s) \in C_b([0, \infty))$, $c \geq 0$
\item $\alpha = \alpha(y, s) \in C_b([0, \infty); C^1_b([0, \infty)))$, $\alpha \geq 0$.
\end{itemize}

The subscript $b$ indicates that functions (and derivatives in case of $C^1$) are bounded.

For clarity in later developments we will write $D_2\alpha$ for the derivative of $\alpha$ with respect to its second argument. The regularity assumptions above are tailored toward the linear analysis of this work. They might, however, not suffice to guarantee the existence and uniqueness of solutions of Eqs. (1)–(5), even in the steady-state case. Well-posedness of structured partial differential equation models with infinite dimensional environmental feedback variables is in general an open question. It has recently been shown in [1] that population models with infinite dimensional interaction variables may exhibit a more complicated dynamical behavior than the simple size-structured model of scramble competition.

The study of hierarchical models in the literature (see e.g. [3] and the references therein) is largely based on a decoupling of the total population quantity from the governing equations and a transformation of the nonlocal partial differential equation (1) into a local one. This technique allows to prove well-posedness and to study the asymptotic behavior of solutions by means of ODE methods. For Eqs. (1)–(5) this approach fails, however, since the mortality and growth rates depend on both size $s$ and on the environment $E(s, t)$. Therefore it seems unavoidable to study the original partial differential equation (1) with the nonlocal integral boundary condition (2) directly. Moreover, studying the linear stability of stationary solutions for models with infinite dimensional interaction variables by spectral analysis (as done previously for simpler cases in [11, 12, 20]) has proven difficult since eigenvalues are not given by an explicitly available characteristic equation (see [13]). Therefore we devised a different approach in [13] to establish a linear stability condition for a particular model with infinite dimensional interaction variables.

Clearly, system (1)-(5) admits the trivial solution $n \equiv 0$. In general, system (1)-(5) yields for a stationary solution $n_*$

$$n_*(s) = \frac{n_*(0) \gamma(0, E_*(0))}{\gamma(s, E_*(s))} \exp \left\{ - \int_0^s \frac{\mu(y, E_*(y)) + M_*(y)}{\gamma(y, E_*(y))} dy \right\},$$

where

$$E_*(s) = \int_0^\infty c(y) \alpha(y, s) n_*(y) dy, \quad M_*(s) = \int_0^\infty \alpha(s, y) n_*(y) dy.$$

Here and later on, starred quantities are stationary counterparts of the time-dependent functions in Eqs. (1)–(5). For obvious reasons, we shall exclusively consider positive stationary solutions of the form (6) or the trivial solution $n_* \equiv 0$ in the following. Moreover, to be consistent with later developments, we shall assume throughout that stationary solutions $n_*$ have the regularity $W^{1,1}(0, \infty)$.

For fixed model ingredients $\beta$, $\mu$, $\gamma$, $\alpha$, $c$, a positive stationary solution $n_*$ with $E_*$ and $M_*$ as before satisfies the equation

$$\int_0^\infty \frac{\beta(s)}{\gamma(s, E_*(s))} \exp \left\{ - \int_0^s \frac{\mu(y, E_*(y)) + M_*(y)}{\gamma(y, E_*(y))} dy \right\} ds = 1.$$
Therefore, for solutions \( n = n(s, t) \) of the governing equations, it is natural to define the functional

\[
R(n) = \int_0^\infty \frac{\beta(s)}{\gamma(s, E(s, \cdot))} \exp \left\{ - \int_0^s \frac{\mu(y, E(y, \cdot)) + M(y, \cdot)}{\gamma(y, E(y, \cdot))} dy \right\} ds,
\]

where \( n \), of course, determines the quantities \( E \) and \( M \) via (4), (5). \( R \) may be regarded as the net reproduction rate of the standing population. Note that Eq. (8) requires \( R(n_*) = 1 \) for any positive stationary solution \( n_* \).

In [9] a general framework was developed to establish the existence of steady states for general physiologically structured population models, however with finite dimensional interaction variables. For models with infinite dimensional interaction variables one can usually not formulate elegant necessary and sufficient conditions for the existence of steady state solutions. In this situation, one can construct positive stationary solutions by perturbation of solutions with \( \alpha \equiv \text{const} \). In the latter case, the interaction variables \( E \) and \( M \) are constant, hence the results in [9] apply. For an alternative approach we refer the reader to [2]. Throughout the rest of the paper we will tacitly assume that stationary solutions of the required regularity are available.

2. Stability via dissipativity. Given a stationary solution \( n_* \), we formally linearize the governing equations by introducing the infinitesimal perturbation \( u = u(s, t) \) and making the ansatz \( n = u + n_* \). After inserting this expression in the governing equations and omitting all nonlinear terms, we obtain the linearized problem

\[
\begin{align*}
u_t(s, t) + \gamma^*(s) u(s, t) + \gamma_E(s, E_*(s)) n_*(s) F(s, t) + \mu(s, E_*(s)) u(s, t) \\
+ \mu_E(s, E_*(s)) n_*(s) F(s, t) + M_*(s) u(s, t) + n_*(s) N(s, t) = 0,
\end{align*}
\]

where we have set \( F(s, t) = \int_0^\infty c(y) \alpha(y, s) u(y, t) dy, \quad N(s, t) = \int_0^\infty \alpha(s, y) u(y, t) dy, \)

and

\[
\gamma^*(s) = \gamma(s, E_*(s)), \quad s \in [0, \infty).
\]

We denote the Lebesgue space \( L^1(0, \infty) \) with its usual norm \( \| \cdot \| \) by \( \mathcal{X} \) and introduce the bounded linear functional \( \Lambda \) on \( \mathcal{X} \) by

\[
\Lambda(u) = \int_0^\infty \left( \frac{\beta(s)}{\gamma^*(s)} - \frac{\gamma_E(0, E_*(0)) n_*(0)}{\gamma^*(0)} c(s) \alpha(s, 0) \right) u(s) ds.
\]

Next we define the operators

\[
\begin{align*}
\mathcal{A}u &= -\gamma^*(\cdot) u_s, \quad \text{Dom}(\mathcal{A}) = \{ u \in W^{1,1}(0, \infty) \mid u(0) = \Lambda(u) \}, \\
\mathcal{B}u &= -(\mu(\cdot, E_*(\cdot)) + \gamma_*(\cdot) + M_*(\cdot)) u = -\rho^*(\cdot) u \quad \text{on } \mathcal{X}, \\
\mathcal{C}u &= -\int_0^\infty u(y) [c(y) \alpha(y, s) ((\gamma_E(\cdot, E_*(\cdot)) n_*(\cdot))_s + \mu_E(\cdot, E_*(\cdot)) n_*(\cdot)) \\
+ c(y) D_\alpha(y, s) \gamma_E(\cdot, E_*(\cdot)) n_*(\cdot) + \alpha(\cdot, y) n_*(\cdot)] dy \quad \text{on } \mathcal{X}.
\end{align*}
\]

Our regularity assumptions on the model ingredients and the stationary solution guarantee that these operators are well-defined, that the operators \( \mathcal{B} \) and \( \mathcal{C} \) are bounded on \( \mathcal{X} \), and that the operator \( \mathcal{A} \) is closed and densely defined on \( \mathcal{X} \). Thus,
the linearized system (10), (11) assumes the form of an initial value problem for an ordinary differential equation on $X$

$$\frac{d}{dt} u = (A + B + C) u,$$

with the initial condition

$$u(0) = u_0.$$  \hfill (19)

Our objective in the following is to apply the Lumer-Phillips Theorem from linear semigroup theory (see [18]). To obtain stability by virtue of this result, we will extend our approach in [13], which was previously devised for elongational flows in [16].

**Theorem 2.1.** The operator $A + B + C$ is the infinitesimal generator of a quasi-contraction semigroup $T = \{T(t)\}_{t \geq 0}$ of bounded linear operators on $X$. The semigroup is uniformly exponentially stable if

$$\mu(s, E_*(s)) + M_*(s) > |\beta(s) - \gamma_E(0, E_*(0)) n_*(0) c(s) \alpha(s, 0)|$$

$$+ \int_0^\infty |c(s) \alpha(s, y) [(\gamma_E(y, E_*(y)) n_*(y))_y + \mu_E(y, E_*(y)) n_*(y)] + c(s) D_2 \alpha(s, y) \gamma_E(y, E_*(y)) n_*(y) + \alpha(y, s) n_*(y)| dy, \quad s \geq 0.$$  \hfill (20)

**Proof.** Assume that, for given $h \in X$ and fixed $\kappa \in \mathbb{R}$, $u \in \text{Dom}(A)$ is such that, for some $\lambda > 0$,

$$u - \lambda (A + B + C + \kappa I) u = h.$$  \hfill (21)

Then we have

$$\|u\| = \int_0^\infty u(s) \text{sgn} u(s) ds$$

$$= \int_0^\infty h(s) \text{sgn} u(s) ds - \lambda \int_0^\infty (\gamma^*(s) u(s))_s \text{sgn} u(s) ds$$

$$+ \lambda \int_0^\infty (\kappa - \mu(s, E_*(s)) - M_*(s)) u(s) \text{sgn} u(s) ds$$

$$- \lambda \int_0^\infty \int_0^\infty u(y) |c(y) \alpha(y, s) ((\gamma_E(s, E_*(s)) n_*(s))_s + \mu_E(s, E_*(s)) n_*(s)) + c(y) D_2 \alpha(y, s) \gamma_E(s, E_*(s)) n_*(s) + \alpha(s, y) n_*(s)| dy \text{sgn} u(s) ds.$$  \hfill (22)

First by changing the order of integration, we obtain

$$- \lambda \int_0^\infty \int_0^\infty u(y) |c(y) \alpha(y, s) ((\gamma_E(s, E_*(s)) n_*(s))_s + \mu_E(s, E_*(s)) n_*(s)) + c(y) D_2 \alpha(y, s) \gamma_E(s, E_*(s)) n_*(s) + \alpha(s, y) n_*(s)| dy \text{sgn} u(s) ds$$

$$\leq \lambda \int_0^\infty |u(s)| \int_0^\infty |c(s) \alpha(s, y) ((\gamma_E(y, E_*(y)) n_*(y))_y + \mu_E(y, E_*(y)) n_*(y)) + c(s) D_2 \alpha(s, y) \gamma_E(y, E_*(y)) n_*(y) + \alpha(y, s) n_*(y)| dy ds.$$  \hfill (23)

Then we note that the set of points in the interval $(0, \infty)$ where $u$ is nonzero is the countable union of disjoint open intervals $(a_i, b_i)$ with $a_i \in [0, \infty)$ and $b_i \in (0, \infty]$ such that on each of these intervals either $u > 0$ or $u < 0$ holds true with $u(a_i) = 0$.  

Combining inequalities (23)-(25) we get the estimate

\[ \|u\| = \sum_i \int_{a_i}^{b_i} u(s) \text{sgn} u(s) \, ds \leq \|h\| + \lambda \gamma^+(0) |u(0)| \]

\[ + \lambda \int_0^\infty |u(s)| \left( \kappa - \mu(s, E_*(s))) - M_*(s) + \int_0^\infty |c(s) \alpha(s, y) \times [\gamma_E(y, E_*(y)) n_*(y)] + \gamma_E(y, E_*(y)) n_*(y) + \alpha(y, s) n_*(y) \right) \, dy \, ds. \]

Next we note that

\[ |u(0)| = |\Lambda(u)| \leq \int_0^\infty \left| \frac{\beta(s)}{\gamma^+(0)} - \frac{\gamma_E(0, E_*(0) n_*(0))}{\gamma^+(0)} c(s) \alpha(s, 0) \right| |u(s)| \, ds. \]

Now choose \( \kappa \in \mathbb{R} \) such that, for \( s \in [0, \infty) \),

\[ \kappa \leq \mu(s, E_*(s)) + M_*(s) - |\beta(s) - \gamma_E(0, E_*(0)) n_*(0)| \]

\[ + \int_0^\infty \left| c(s) \alpha(s, y) \left[ \gamma_E(y, E_*(y)) n_*(y) \right] + \mu_E(y, E_*(y)) n_*(y) \right| \, dy. \]

For such \( \kappa \), we have the desired inequality

\[ \|u\| \leq \|h\| \quad \text{for} \ \lambda > 0, \]

thus establishing dissipativity. We observe that the operator \( \mathcal{A} + \mathcal{B} + \mathcal{C} + \kappa \mathcal{I} \) is densely defined and that the equation

\[ (\lambda I - \mathcal{A}) u = f \]
for \( f \in \mathcal{X} \) and \( \lambda > 0 \) sufficiently large has a unique solution \( u \in \text{Dom} \mathcal{A} \), given by

\[
\begin{aligned}
u(s) &= \exp \left\{ - \int_0^s \frac{\lambda}{\gamma^*(y)} \, dy \right\} \\
&\quad \times \left( \Lambda(u) + \int_0^s \exp \left\{ \int_0^r \frac{\lambda}{\gamma^*(y)} \, dy \right\} \frac{f(r)}{\gamma^*(r)} \, dr \right) \\
\end{aligned}
\]

with

\[
\Lambda(u) = \left( 1 - \Lambda \left( \exp \left\{ - \int_0^s \frac{\lambda}{\gamma^*(y)} \, dy \right\} \right) \right)^{-1} \\
\Lambda \left( \int_0^s \frac{\lambda}{\gamma^*(y)} \, dy - \int_0^s \frac{\lambda}{\gamma^*(y)} \, dy \right) \frac{f(r)}{\gamma^*(r)} \, dr \right). 
\]

The fact that \( u \in \text{Dom} \mathcal{A} \) is well defined by \((31), (32)\) follows immediately from the regularity of the functions involved and their growth behavior. Since \( B + C + \kappa I \) is bounded, the Lumer-Phillips Theorem gives that the operator \( \mathcal{A} + B + C + \kappa I \) generates a quasi-contraction semigroup. Specifically, the semigroup \( T = \{T(t)\}_{t \geq 0} \), generated by the operator \( \mathcal{A} + B + C \), satisfies

\[
\|T(t)\| \leq e^{-\kappa t}, \quad t \geq 0.
\]

Finally, if condition \((20)\) holds, we can choose \( \kappa > 0 \). Hence the semigroup \( T = \{T(t)\}_{t \geq 0} \) is uniformly exponentially stable.

**Corollary 1.** A stationary solution \( n^* \) of Eqs. \((1)–(5)\) is linearly asymptotically stable if condition \((20)\) holds true.

**Remark 1.** For the stability of the trivial equilibrium \( n^* \equiv 0 \), the criterion \((20)\) reduces to

\[
\mu(s, 0) > \beta(s), \quad s \in [0, \infty).
\]

Since

\[
R(0) = \int_0^\infty \frac{\beta(s)}{\gamma(s, 0)} \exp \left\{ - \int_0^s \frac{\mu(y, 0) + 0}{\gamma(y, 0)} \, dy \right\} \, ds \\
< \int_0^\infty \frac{\mu(s, 0)}{\gamma(s, 0)} \exp \left\{ - \int_0^s \frac{\mu(y, 0)}{\gamma(y, 0)} \, dy \right\} \, ds = 1
\]

with \( \bar{\mu}(s, 0) = \mu(s, 0)/\gamma(s, 0) \), \((34)\) implies \( R(0) < 1 \). This is the well-known stability criterion of the trivial steady state in scramble competition. In the case of the hierarchical model discussed in [13] our stability condition for the trivial steady state implied \( R(0) < 1 \) as well.

**3. Instability via eigenvalues.** In this section we will characterize part of the point spectrum of the linear semigroup generator when the attack rate \( \alpha \) assumes a special form. This result allows us to establish an instability result, thus complementing our stability result in the previous section.

Throughout this section we make the assumption that the attack rate is separable, i.e.

\[
\alpha(x_1, x_2) = \alpha_1(x_1) \alpha_2(x_2), \quad (x_1, x_2) \in [0, \infty) \times [0, \infty).
\]

We can interpret \( \alpha_2(x_2) \) as a measure for the likelihood that individuals of size \( x_2 \) attack, while \( \alpha_1(x_1) \) represents the likelihood of being attacked at size \( x_1 \). Note that condition \((36)\) assumes no correlation between these two events. Even though this assumption might appear as unsatisfactory from a biological point of view, it makes, however, analytical progress possible and henceforth has the potential to
shed light on the case of a general attack rate. The main difficulty in case of general attack rates is that the operator \( \mathcal{C} \) need not be a finite rank operator. However, our characterization of the point spectrum of the linearized operator \( \mathcal{A} + \mathcal{B} + \mathcal{C} \) in the following developments relies essentially on this fact.

We also make the biologically plausible assumption that there is a constant \( \mu_0 > 0 \) such that
\[
\mu(s, E_*(s)) + M_*(s) \geq \mu_0 \quad \text{for all} \quad s \in [0, \infty).
\] (37)

Clearly, this assumption is automatically guaranteed if we suppose that \( \mu \geq \mu_0 \).

The particular choice of the attack rate \( (\pi, \alpha) \) by
\[
\pi(s, \lambda) = \exp \{ -\int_0^s \rho^*(y) + \lambda \} \frac{g_1(r)}{\gamma^r(r) \pi(r, \lambda)} \, dr
\]
where we have made use of the notation
\[
\gamma^r(s) = \exp \left\{ -\int_0^s \frac{\rho^*(y) + \lambda}{\gamma^r(y)} \, dy \right\} = \frac{\gamma^*(0)}{\gamma^*(s)} \exp \left\{ -\int_0^s \frac{\mu(y, E_*(y)) + M_*(y) + \lambda}{\gamma^*(y)} \, dy \right\}.
\] (44)

Note that condition (42) ensures that \( u, \) given by Eq. (43), is in \( W^{1,1}(0, \infty) \). We multiply equation (43) by \( c(s) \alpha_1(s) \) and \( \alpha_2(s) \), respectively, and integrate from zero to infinity to obtain
\[
\begin{align*}
u(0) a_1(\lambda) + \bar{u}_1 (1 + a_2(\lambda)) + \bar{u}_2 a_3(\lambda) &= 0, \\
u(0) a_4(\lambda) + \bar{u}_1 a_5(\lambda) + \bar{u}_2 (1 + a_6(\lambda)) &= 0,
\end{align*}
\] (45, 46)
where
\[
\begin{align*}
  a_1(\lambda) &= -\int_0^\infty c(s) \alpha_1(s) \pi(s, \lambda) \, ds, \\
  a_2(\lambda) &= \int_0^\infty c(s) \alpha_1(s) \pi(s, \lambda) \int_0^s \frac{g_1(r)}{\gamma^*(r) \pi(r, \lambda)} \, dr \, ds, \\
  a_3(\lambda) &= \int_0^\infty c(s) \alpha_1(s) \pi(s, \lambda) \int_0^s \frac{g_2(r)}{\gamma^*(r) \pi(r, \lambda)} \, dr \, ds, \\
  a_4(\lambda) &= -\int_0^\infty \alpha_2(s) \pi(s, \lambda) \, ds, \\
  a_5(\lambda) &= \int_0^\infty \alpha_2(s) \pi(s, \lambda) \int_0^s \frac{g_1(r)}{\gamma^*(r) \pi(r, \lambda)} \, dr \, ds, \\
  a_6(\lambda) &= \int_0^\infty \alpha_2(s) \pi(s, \lambda) \int_0^s \frac{g_2(r)}{\gamma^*(r) \pi(r, \lambda)} \, dr \, ds.
\end{align*}
\]

Next we insert the solution (43) into the boundary condition (41) to obtain
\[
u(0) (1 + a_7(\lambda)) + \bar{u}_1 (a_8(\lambda) + g_3) + \bar{u}_2 a_9(\lambda) = 0, \tag{47}
\]
where
\[
\begin{align*}
  a_7(\lambda) &= -\int_0^\infty \frac{\beta(s)}{\gamma^*(0)} \pi(s, \lambda) \, ds, \\
  a_8(\lambda) &= \int_0^\infty \frac{\beta(s)}{\gamma^*(0)} \pi(s, \lambda) \int_0^s \frac{g_1(r)}{\gamma^*(r) \pi(r, \lambda)} \, dr \, ds, \\
  a_9(\lambda) &= \int_0^\infty \frac{\beta(s)}{\gamma^*(0)} \pi(s, \lambda) \int_0^s \frac{g_2(r)}{\gamma^*(r) \pi(r, \lambda)} \, dr \, ds.
\end{align*}
\]

Now we can give a characterization of part of the point spectrum of the operator \(A + B + C\).

**Theorem 3.1.** For any \(\lambda \in \{\zeta \in \mathbb{C} | \text{Re } \zeta > -\mu_0\}\), we have \(\lambda \in \sigma_p(A + B + C)\) if and only if \(\lambda\) satisfies the equation
\[
K(\lambda) = \text{det} \begin{pmatrix}
  a_1(\lambda) & 1 + a_2(\lambda) & a_3(\lambda) \\
  a_4(\lambda) & a_5(\lambda) & 1 + a_6(\lambda) \\
  1 + a_7(\lambda) & g_3 + a_8(\lambda) & a_9(\lambda)
\end{pmatrix} = 0. \tag{48}
\]

**Proof.** If \(\lambda \in \sigma_p(A + B + C)\), then Eqs. (40), (41) admit a nontrivial solution \(u\). Hence for this \(\lambda\) there exists a nonzero solution vector \((u(0), \bar{u}_1, \bar{u}_2)\) such that Eqs. (45)-(47) hold true. Thus \(K(\lambda) = 0\). Conversely, if \(K(\lambda) = 0\) for some \(\lambda\) and \((u(0), \bar{u}_1, \bar{u}_2)\) is a nonzero solution of Eqs. (45)-(47), then \(u\), given by Eq. (43), is a nonzero solution of Eqs. (40)-(41) at least if \(u(0) \neq 0\). If, however, \(u(0) = 0\), the only possible scenario for \(u\) to vanish when defined by Eq. (43) would be the condition that
\[
\bar{u}_1 g_1 = -\bar{u}_2 g_2 \tag{49}
\]
hold true. Then Eqs. (45),(46) would immediately give \(\bar{u}_1 = 0 = \bar{u}_2\) in contradiction to our assumption on \((u(0), \bar{u}_1, \bar{u}_2)\). \(\square\)

Since
\[
\lim_{\lambda \to +\infty} K(\lambda) = \text{det} \begin{pmatrix}
  0 & 1 & 0 \\
  0 & 0 & 1 \\
  1 & g_3 & 0
\end{pmatrix} = 1, \tag{50}
\]
the limit being taken in $\mathbb{R}$, we can formulate the following simple instability criterion, which follows immediately from the Intermediate Value Theorem.

**Theorem 3.2.** A stationary solution $n_*$ of Eqs. (1)-(5) is linearly unstable if $K(0) < 0$.

Note that for $n_* \equiv 0$

$$K(0) = 1 - R(0).$$

Hence the stationary solution $n_* \equiv 0$ is linearly unstable if $R(0) > 1$. In the remainder of this section we will concentrate on positive stationary solutions.

Let us assume that the rate of an individual of size $s$ to attack another individual is proportional to the product of the probability for an individual of size $s$ to be attacked and its energetic value. Mathematically, this condition is modeled by the relation

$$c(s)\alpha_1(s) = p\alpha_2(s), \quad s \in [0, \infty), \quad p \in \mathbb{R}^+. \quad (52)$$

The constant $p$ denotes here the proportionality factor. This condition is biologically relevant since environmental pressure conceivably makes individuals of higher energetic value, which are usually larger in size, not only more prone to be attacked, but also more aggressive. In addition we will assume that the attack rate of minimal size individuals (newborns) equals zero, i.e. $\alpha_2(0) = 0$. With

$$\pi(s) = \pi(s, 0) \quad (53)$$

we obtain

$$K(0) = \int_0^\infty \alpha_2(s) \pi(s) ds \int_0^\infty \frac{\beta(s)}{\gamma^*(0)} \pi(s) \int_s^\infty \frac{p g_1(r) + g_2(r)}{\gamma^*(r) \pi(r)} dr ds. \quad (54)$$

Note that $\beta \not\equiv 0$ by Eq. (8). Hence the instability criterion of Theorem 3.2 is satisfied if, for $s \geq 0$,

$$p^{-1} \alpha_1(s) + \alpha_2'(s) \gamma_E(s, E_*(s)) + \alpha_2(s) \left( \frac{d}{ds} \gamma_E(s, E_*(s)) \right) - \gamma_E(s, E_*(s)) \left( \frac{\gamma_*(s) + \mu(s, E_*(s)) + M_*(s)}{\gamma^*(s)} \right) + \mu_E(s, E_*(s)) < 0, \quad (55)$$

where we have used the relation

$$n'_*(s) = -n_*(s) \left( \frac{\gamma_*(s) + \mu(s, E_*(s)) + M_*(s)}{\gamma^*(s)} \right).$$

This instability condition automatically excludes the case $\alpha_2 \equiv 0$.

**Remark 2.** In the age-structured case where $\gamma \equiv 1$ and where we may use $a$ for age in lieu of size $s$ we find for the preceding example

$$M(a, t) = E(a, t) p^{-1} \frac{\alpha_1(a)}{\alpha_2(a)} \quad (56)$$

assuming that $\alpha_2$ does not vanish. Hence the net reproduction function $R(n)$ – as in the case of scramble competition – can be considered a function of the environment $E$, i.e.

$$R(n) = \tilde{R}(E) = \int_0^\infty \beta(a) \exp \left\{ - \int_a^\infty \mu(y, E(y, \cdot)) + E(y, \cdot) p^{-1} \frac{\alpha_1(y)}{\alpha_2(y)} dy \right\} da. \quad (57)$$

When interpreting $\tilde{R}$ as a nonlinear operator between sets of bounded continuous functions and ignoring all issues pertaining to regularity, we may formally deduce
the Fréchet derivative of $\tilde{R}$ at a stationary state $E_*$. The result of this formal calculation is

$$\tilde{R}_E(E_*) = -\int_0^\infty \beta(a) \exp \left\{ -\int_0^a \mu(y, E_*(y)) + E_*(y) \, p^{-1} \frac{\alpha_1(y)}{\alpha_2(y)} \, dy \right\}$$

$$\times \left( \int_0^a \mu_E(y, E_*(y)) + p^{-1} \frac{\alpha_1(y)}{\alpha_2(y)} \, dy \right) \, da.$$

(58)

Since in the scenario considered the instability condition (55) reduces to

$$p^{-1} \alpha_1(a) + \alpha_2(a) \mu_E(a, E_*(a)) < 0, \quad a \in [0, \infty),$$

(59)

Eq. (58) implies

$$\tilde{R}_E(E_*) > 0.$$

(60)

Hence in this special case of model ingredients condition (55) allows a formal, but intuitively clear biological interpretation, similar to the scramble competition case in [12]: if the net reproduction rate $\tilde{R}$ is increasing at a stationary environment $E_*$, then the equilibrium is unstable.

4. **Further spectral analysis.** Throughout this section we consider a positive stationary solution $n_*$ and assume that condition (37) holds true.

**Theorem 4.1.**

$$\sigma(A + B) \cap \{ z \in \mathbb{C} \mid \text{Re } z > -\mu_0 \} = P \cup \{ 0 \},$$

(61)

where the set $P \cup \{ 0 \}$ consists of simple, isolated eigenvalues $\lambda$ of $A + B$ such that

$$-\mu_0 < \text{Re } \lambda < 0 \quad \text{for } \lambda \in P.$$

(62)

**Proof.** Suppose first that $\lambda \in \mathbb{C}$ with $\text{Re } \lambda > -\mu_0$ is such that

$$\Lambda \left( \exp \left\{ -\int_0^s \frac{\rho^*(r) + \lambda}{\gamma^*(r)} \, dr \right\} \right) \neq 1.$$

(63)

Then the equation

$$(\lambda I - (A + B)) \, u = f$$

(64)

with $f \in L^1(0, \infty)$ has the unique solution

$$u(s) = u(0) \exp \left\{ -\int_0^s \frac{\rho^*(r) + \lambda}{\gamma^*(r)} \, dr \right\}$$

$$+ \int_0^s \exp \left\{ -\int_y^s \frac{\rho^*(r) + \lambda}{\gamma^*(r)} \, dr \right\} \, f(y) \, \frac{\gamma^*(y)}{\gamma^*(y)} \, dy,$$

(65)

where

$$u(0) = \frac{\Lambda \left( \int_0^s \exp \left\{ -\int_y^s \frac{\rho^*(r) + \lambda}{\gamma^*(r)} \, dr \right\} \, f(y) \, \frac{\gamma^*(y)}{\gamma^*(y)} \, dy \right)}{1 - \Lambda \left( \exp \left\{ -\int_0^s \frac{\rho^*(r) + \lambda}{\gamma^*(r)} \, dr \right\} \right)}.$$

(66)

Note that our condition on $\lambda$ ensures that $\Lambda$ can be applied to deduce (66). Moreover, it readily follows that $u$ belongs to $W^{1,1}(0, \infty)$. Hence we conclude that $\lambda \in \rho(A + B)$. Now suppose that $\lambda \in \mathbb{C}$ with $\text{Re } \lambda > -\mu_0$ is such that

$$\Lambda \left( \exp \left\{ -\int_0^s \frac{\rho^*(r) + \lambda}{\gamma^*(r)} \, dr \right\} \right) = 1.$$

(67)
In light of Eq. (8), \( \lambda = 0 \) solves (67). In fact, \( \lambda = 0 \) is the only solution with \( \text{Re} \lambda \geq 0 \). Let

\[
L(\lambda) = \Lambda \left( \exp \left\{ - \int_0^\infty \frac{\rho^*(r) + \lambda}{\gamma^*(r)} \, dr \right\} \right) - 1
\]

(68)

for \( \text{Re} \lambda > -\mu_0 \). Then \( L \) is analytic for \( \text{Re} \lambda > -\mu_0 \) and

\[
L'(0) = -\int_0^\infty \frac{\beta(s)}{\gamma^*(0)} \exp \left\{ - \int_0^s \frac{\rho^*(r)}{\gamma^*(r)} \, dr \right\} \int_0^s \frac{1}{\gamma^*(r)} \, dr \, ds < 0.
\]

Hence 0 is a pole of the resolvent operator of \( A + B \). Any other zero of \( L \) gives rise to a pole of the resolvent operator of \( A + B \) since \( L \) is analytic and nonconstant in the simply connected set \( \text{Re} \lambda > -\mu_0 \). Finally, the representation of the resolvent operator, given through the solution \( u \) in (65), (66), shows that the spectral projection associated with each pole of the resolvent operator is a rank one operator. \qed

When the operator \( C \) is compact as in the special class of attack rates given in (38), we immediately obtain the following result.

**Corollary 2.** Suppose that the operator \( C \) is compact. Then \( \sigma(A + B + C) \cap \{ z \in \mathbb{C} | \text{Re} z > -\mu_0 \} \) consists of isolated eigenvalues of \( A + B + C \) of finite multiplicity.

5. **Asynchronous exponential growth.** The purpose of this section is to gain deeper insight into asymptotic properties of solutions of the linearized system (10)-(11). In particular, we are interested in solutions of the linearized problem which grow exponentially in time such that the proportion of individuals within any size range compared to the total population approaches a limiting value as time tends to infinity, independently of the size distribution of the initial population. This phenomenon is called asynchronous exponential growth and is known to be present, e.g., in the age-structured case. Mathematical definitions will be given below. The property of asynchronous exponential growth is important insofar as solutions can be regarded as asymptotically factorizable (with respect to time and size). Populations of this kind are often called ergodic (see [17]). We refer to [4, 10, 15, 19, 23] for this and related notions.

In the framework of linear semigroup theory a strongly continuous semigroup \( S = \{ S(t) \}_{t \geq 0} \) on a Banach space \( \mathcal{Y} \) with generator \( \mathcal{A}_S \) and growth bound

\[
s(\mathcal{A}_S) = \sup \{ \text{Re} \lambda | \lambda \in \sigma(\mathcal{A}_S) \}
\]

(70)
is said to exhibit balanced exponential growth (BEG for short) if there exists a bounded linear projection \( \Pi \) on \( \mathcal{Y} \) such that

\[
\lim_{t \to -\infty} \| e^{-s(\mathcal{A}_S) \, t} S(t) - \Pi \| = 0.
\]

(71)
The semigroup \( S = \{ S(t) \}_{t \geq 0} \) is said to exhibit asynchronous exponential growth (AEG for short) if it exhibits BEG with a rank one projection \( \Pi \). For positive semigroups there exist well-known characterizations of BEG and AEG, see [4, 10]. Our analytical approach will be guided toward these results.

**Theorem 5.1.** Suppose that, for every \( y \geq 0 \) and a.e. \( s \geq 0 \),

\[
c(y) \alpha(y, s) \left( (\gamma_E(s, \mathcal{E}_s) n_*(s)) + \mu_E(s, \mathcal{E}_s) n_*(s) \right) + c(y) D_2 \alpha(y, s) \gamma_E(s, \mathcal{E}_s) n_*(s) + \alpha(s, y) n_*(s) \leq 0,
\]

(72)

\[
\beta(s) - \gamma_E(0, \mathcal{E}_s) n_*(0) c(s) \alpha(s, 0) \geq 0.
\]

(73)

Then the semigroup \( \{ T(t) \}_{t \geq 0} \), generated by the operator \( A + B + C \), is positive.
Proof. Condition (72) implies that the operator $C$ is positive, hence we can restrict ourselves to the operator $A + B$. Condition (73) ensures that the functional $\Lambda$ is nonnegative. Consequently, the solution $(65), (66)$ of the resolvent equation (64) is well-defined and nonnegative if $\lambda > 0$ is sufficiently large. □

Corollary 3. Suppose that condition (73) holds true. Then the semigroup, generated by $A + B$, is positive.

Let us recall a useful characterization of irreducibility on $L^1(\Omega, m)$ (see [10]): A strongly continuous, positive semigroup $S = \{S(t)\}_{t \geq 0}$ on the Banach lattice $Y = L^1(\Omega, m)$ with generator $A_S$ is irreducible if, for $f \in Y$ with $f > 0$, $(\lambda I - A_S)^{-1} f(s) > 0$ for $m$-almost all $s \in \Omega$ and some $\lambda > s(A_S)$ sufficiently large.

Theorem 5.2. Suppose that the positivity conditions (72), (73) hold true. Then the semigroup $T = \{T(t)\}_{t \geq 0}$, generated by $A + B + C$, is irreducible.

Proof. Since $C$ is positive and since, for $\lambda > 0$ sufficiently large, the resolvent operator of $A + B$ is positive as a consequence of Corollary 3, we deduce from

$$(\lambda I - (A + B + C))^{-1} = \sum_{n=0}^{\infty} \left(\left((\lambda I - (A + B))^{-1} C\right)^n (\lambda I - (A + B))^{-1}\right) (74)$$

that it suffices to prove the irreducibility of the semigroup generated by $A + B$. This result, however, follows immediately from the representation of solutions of the resolvent equation (64), given by (65), (66). □

Before we formulate the main result of this section, let us review the notions of essential norm, growth bound, and essential growth bound, and some of their properties. Our discussion follows closely [10]. Suppose that $A_S$ is the infinitesimal generator of the strongly continuous semigroup $S = \{S(t)\}_{t \geq 0}$ on a Banach space $Y$. Then the growth bound of the semigroup is defined by

$$\omega_0(A_S) = \lim_{t \to \infty} \frac{\ln \|S(t)\|_t}{t}. \quad (75)$$

For a bounded linear operator $T$ on $Y$, the essential norm is given by

$$\|T\|_{\text{ess}} = \text{dist} (T, K(Y)), \quad (76)$$

where $K(Y)$ denotes the set of compact linear operators on $Y$. Of course, the essential norm is generally not a norm on the set of bounded linear operators on $Y$. It is, however, a norm on the Calkin algebra of $Y$, see [10] and the references therein. Finally, the essential growth bound of the semigroup $S = \{S(t)\}_{t \geq 0}$ on $Y$ with generator $A_S$ is defined by

$$\omega_{\text{ess}}(A_S) = \lim_{t \to \infty} \frac{\ln \|S(t)\|_{\text{ess}}}{t}. \quad (77)$$

It is readily seen that, for $K \in K(Y)$,

$$\omega_{\text{ess}}(A_S) = \omega_{\text{ess}}(A_S + K). \quad (78)$$

The significance of the essential growth bound lies in the central fact that

$$\omega_0(A_S) = \max \{\omega_{\text{ess}}(A_S), s(A_S)\}. \quad (79)$$
Theorem 5.3. Given a positive stationary solution \( n_* \), suppose that conditions (37), (72), and (73) hold true and that the operator \( C \) is compact. If
\[
\sigma(A + B + C) \cap \{z \in \mathbb{C} \mid \text{Re} z > 0\} \neq \emptyset,
\]
then the linear semigroup \( T = \{T(t)\}_{t \geq 0} \), generated by \( A + B + C \), exhibits AEG.

Proof. First we note that \( A + B \) has nonempty spectrum and generates a positive semigroup by Theorem 4.1 and Corollary 3. Hence Derndinger’s Theorem (see \([6, 10]\)) proves that
\[
\omega_0(A + B) = s(A + B) = 0,
\]
where the last equality follows from Theorem 4.1. Similarly, we obtain from Theorem 5.1 and Derndinger’s Theorem that
\[
\omega_0(A + B + C) = s(A + B + C) > 0.
\]
Here the last inequality is given by assumption (80). Consequently, in light of Eqs. (77), (78), we have
\[
\omega_{\text{ess}}(A + B + C) = \omega_{\text{ess}}(A + B) \leq \omega_0(A + B) = 0 < \omega_0(A + B + C).
\]
Hence by Theorem 5.1 and Theorem 5.2, the semigroup \( T = \{T(t)\}_{t \geq 0} \) is positive and irreducible with essential growth bound strictly smaller than its growth bound. The claim follows now immediately from Theorems 9.10 and 9.11 in \([4]\).

6. Conclusion. In this work we have studied the asymptotic behavior of solutions of a linearized size-structured cannibalism model, recently introduced in \([7]\). The vital rates in this model depend on a structuring variable (size), which takes values in an unbounded set, and on an infinite dimensional interaction variable (environment), describing the environmental feedback on individuals. Population models of this type are notoriously difficult to analyze. The reason for this difficulty is that the essential spectrum of the linearized operator is typically not empty, and even the point spectrum cannot be characterized in general via zeros of a characteristic function. The latter obstacle has already been observed in \([13]\) for a similar quasilinear hierarchically size-structured model. Therefore, analytical results, in particular with respect to the qualitative behavior of solutions, are rather rare in the literature, at least to our knowledge. We would like to point out that the emphasis in the present work was to demonstrate how analytical techniques can be developed and used to treat qualitative questions of physiologically structured population models, where the structuring variable is unbounded and competition is incorporated through infinite dimensional interaction variables.

Here, using two different strategies, we have formulated linear stability and instability criteria for equilibrium solutions of the model. We derived a general instability criterion in the case of a separable attack rate and extended our dissipativity approach, employed in \([13]\) for a model with finite size span, to the case of infinite size span. We also carried out a more refined spectral analysis of the linearized operator which allowed us to gain deeper insights into the asymptotic behavior of solutions of the linearized system. In particular, we investigated the question whether solutions of the linearized problem exhibit asynchronous exponential growth and gave sufficient conditions for an affirmative answer. There are only few results of this type for models with unbounded structuring variable, see \([19, 20, 21, 22]\). In passing, we also note that our spectral analysis gives rise to an extension of our stability results in \([12]\) for a model with finite size span to one with infinite size span.
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