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Asynchronous Exponential Growth of Semigroups of Nonlinear Operators

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The property of asynchronous exponential growth is analyzed for the abstract nonlinear differential equation $z'(t) = Az(t) + F(z(t))$, $t \geqslant 0$, $z(0) = x \in X$, where A is the infinitesimal generator of a semigroup of linear operators in the Banach space X and F is a nonlinear operator in X. Asynchronous exponential growth means that the nonlinear semigroup $S(t)$, $t \geqslant 0$ associated with this problem has the property that there exists $\lambda > 0$ and a nonlinear operator Q in X such that the range of Q lies in a one-dimensional subspace of X and $\lim_{t \to \infty} e^{-\lambda t} S(t)x = Qx$ for all $x \in X$. It is proved that if the linear semigroup generated by A has asynchronous exponential growth and F satisfies $\|F(x)\| \leqslant f(\|x\|)\, \|x\|$, where $f: \mathbb{R}_+ \to \mathbb{R}_+$ and $\int^\infty (f(r)/r)\, dr < \infty$, then the nonlinear semigroup $S(t)$, $t \geqslant 0$ has asynchronous exponential growth. The method of proof is a linearization about infinity. Examples from structured population dynamics are given to illustrate the results. © 1992 Academic Press, Inc.

INTRODUCTION

The concept of asynchronous exponential growth arises from linear models of cell population dynamics. It is well known to cell biologists that a population of dividing cells that is initially synchronized with respect to position in the cell cycle loses synchrony after a few generations [29]. This asynchronization of the population results from an inherent variability of cells with respect to their age or size at time of division. Asynchronization

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means a loss of initial information, but not a loss due to convergence to equilibrium. Instead the population continues to grow exponentially and as it does population structure reorganizes so that proportions of the population with respect to structure converge to constant values independent of initial data. This kind of behavior is called asynchronous exponential growth by cell biologists. It is observed in growing cell populations unconstrained by resource limitations. The mathematical models that describe these phenomena fall within the subject of linear structured population dynamics and have been extensively developed by many researchers [1–3, 11, 14, 15, 17, 19, 21, 26, 28, 31, 33, 34].

The phenomenon of asynchronous exponential growth is also recognized by mathematical demographers in linear models of age-structured human populations. These models predict dispersion of any initial age distribution to a stable age distribution even as the population grows exponentially to infinity. This dispersion proceeds in such a way that the proportion of the population within any age range converges to a limiting value independent of the initial age distribution. Demographers call this kind of behavior strong ergodicity and it is commonly observed in human populations with fertility and mortality rates unaffected by crowding. Many mathematical researchers have analyzed asynchronous exponential growth in linear age-structured population dynamics [4, 16, 18, 22–25, 30, 32, 35].

It is the purpose of this paper to study the phenomenon of asynchronous exponential growth in nonlinear models of population growth. The inclusion of nonlinearities in population models is usually designed to halt exponential growth and force convergence to stable equilibria or stable cycles. The role of nonlinearities in these models is to account for crowding effects and to stabilize population growth. For some models of population growth nonlinearities play a different role. Their role is not to control unlimited and unstabilized growth, but to control dispersion and interaction of subpopulations. Such models allow exponential growth to infinity, but still describe population behavior as nonlinearities become important before crowding effects become dominant. An example of such a model is tumor cell population growth with proliferating and quiescent cell subpopulations. It is not expected that a tumor will grow until it stabilizes to equilibrium, but that it will simply grow. The importance of nonlinearities in this model lies in the increasing inclination of proliferating cells to become quiescent as tumor size increases. Clinicians describe this phenomenon as the diminishing growth fraction, which is just the decreasing proportion of proliferating tumor cells as the tumor grows. This type of growth is analogous to asynchronous exponential growth found in linear models of population dynamics.

To formulate a nonlinear version of asynchronous exponential growth we will view a nonlinear model of an exponentially growing population as being asymptotically linear. We thus require that the nonlinear processes in the model converge to linear processes as the population becomes large. The abstract nonlinear differential equation describing this growth has the form

$$z'(t) = Az(t) + F(z(t)), \qquad t \geq 0, \quad z(0) = x \in X,$$

where X is a Banach space, A is a linear operator in X, and F is a nonlinear operator in X. We hypothesize that $\|F(z)\| \leq f(\|z\|)\, \|z\|$, where $f\colon \mathbb{R}_+ \to \mathbb{R}_+$ satisfies $\int^\infty (f(r)/r)\, dr < \infty$. We also hypothesize that A is the infinitesimal generator of a strongly continuous semigroup $T(t)$, $t \geq 0$ of bounded linear operators in X. We require that $T(t)$, $t \geq 0$ has asynchronous exponential growth with intrinsic growth constant $\lambda > 0$. This means that $\lim_{t\to\infty} e^{-\lambda t} T(t) = P$, where P is a rank one projection in X. We will provide sufficient conditions to establish that for $x \in X$, $\lim_{t\to\infty} e^{-\lambda t} z(t)$ exists, is nonzero, and lies in the range of P. The solutions will therefore exhibit nonlinear asynchronous exponential growth in the sense that after multiplication by an exponential factor in time they converge to a nonzero limit lying in the range of P.

Our analysis of the nonlinear problem is a linearization about infinity. Our hypotheses will guarantee that as the solutions become infinite they inherit the properties of solutions of the linearized problem $\hat{z}'(t) = A\hat{z}(t)$. In particular, the solutions of the nonlinear problem will have the property that proportions of the population converge to a limit independent of the initial data. That is, if $k_1, k_2 \in X^*$, then the ratio $\langle z(t), k_1 \rangle / \langle z(t), k_2 \rangle$ converges to a limit independent of $z(0)$ as t approaches infinity. This convergence of proportions is characteristic of age-structured or size-structured populations during their growth phase.

The organization of this paper is as follows: In Section 1 we state and prove our main results for the nonlinear semigroup of operators associated with the abstract nonlinear differential equation. In Section 2 we extend these results using the duality theory of semigroup theory. In Section 3 we illustrate the results with examples.

1. Main Results

Let X be a Banach space, let X^* be its dual space, and let $B(X)$ be the space of bounded linear operators in X. If X is also an ordered Banach space, let X_+, X^*_+, and $B(X)_+$ be the positive cones of X, X^*, and $B(X)$, respectively.

DEFINITION 1.1. A *strongly continuous semigroup* is a family of mappings $T(t)$, $t \geq 0$ in X such that (i) for every $t \geq 0$, $T(t)$ is a continuous (possibly nonlinear) operator from X into X, (ii) $T(0)x = x$ for $x \in X$, (iii) $T(t+s)x = T(t)\,T(s)x$ for $s, t \geq 0$, $x \in X$, and (iv) $T(t)x$ is continuous in t for $x \in X$. If $T(t) \in B(X)$ for $t \geq 0$, then the semigroup is called *linear* and if $T(t)(X_+) \subset X_+$ for $t \geq 0$, then the semigroup is called *positive*.

DEFINITION 1.2. $T(t)$, $t \geq 0$ has *asynchronous exponential growth* if and only if there exists a positive constant $\lambda > 0$ and a nonzero (possibly nonlinear) operator P in X such that $R(P)$ is contained in a one-dimensional subspace of X and for each $x \in X$, $\lim_{t \to \infty} e^{-\lambda t} T(t)x = Px$. The constant λ is called the *intrinsic growth constant* (it is uniquely determined, since P is nonzero). In the linear case P is a projection called the *spectral projection*. The asynchronous exponential growth is called *uniform* if and only if $\lim_{t \to \infty} e^{-\lambda t} T(t)x = Px$ uniformly for x in bounded sets of X. It is *exponential* if and only if there exists $M > 0$ and $\delta > 0$ such that $\|e^{-\lambda t} T(t)x - Px\| \leq M e^{-\delta t} \|x\|$ for all x in X. If X is an ordered Banach space, $Y \subset X_+$, and $Px \geq 0$, $Px \neq 0$ for all $x \in Y - \{0\}$, then the asynchronous exponential growth is *strictly positive* on Y. If, in addition, Px is a quasi-interior point of X_+ for all $x \in Y - \{0\}$, then the asynchronous exponential growth is *ergodic* on Y (x is a quasi-interior point of X_+ if and only if $x \in X_+$ and $\langle x, x^* \rangle > 0$ whenever $x^* \in X^*_+ - \{0\}$).

Remark 1.1. In the linear case it is known that the linear semigroup $T(t)$, $t \geq 0$ with infinitesimal generator A has uniform asynchronous exponential growth with intrinsic growth constant $\lambda > 0$ if and only if (1) λ is a simple eigenvalue of A, (2) $\lambda > \operatorname{Re} \lambda_1$ for any $\lambda_1 \neq \lambda$ in $\sigma(A)$, and (3) $\lim_{t \to \infty} (1/t) \log(\alpha[T(t)]) < \lambda$, where $\alpha[T(t)]$ is the measure of noncompactness (see [24, Proposition 3.1; 36, Proposition 2.3]). In the linear case uniform asynchronous exponenal growth is necessarily exponential (see [36, Proposition 2.3]) and uniform asynchronous exponential growth is ergodic on X_+ provided that $T(t)$, $t \geq 0$ is irreducible; that is, if $x \in X_+ - \{0\}$, $x^* \in X^*_+ - \{0\}$, there exists $t \geq 0$ such that $\langle T(t)x, x^* \rangle > 0$ (see [10, Theorem 9.11]). Example 3.1 in Section 3 shows that for a linear semigroup strictly positive asynchronous exponential growth in X_+ need not be uniform or ergodic. Example 3.2 shows that for a linear semigroup uniform asynchronous exponential growth need not be ergodic in X_+.

Consider the abstract semilinear differential equation in X

$$z'(t) = Az(t) + F(z(t)), \qquad t \geq 0, \quad z(0) = x \in X. \tag{1.1}$$

We require the following hypotheses:

(H.1) A is the infinitesimal generator of a strongly continuous linear semigroup $T(t)$, $t \geqslant 0$ in X and there exists $\lambda > 0$ such that for each $x \in X$, $Px := \lim_{t \to \infty} e^{-\lambda t} T(t)x$ exists (P is necessarily in $B(X)$ and is a projection on X).

(H.2) F maps X into X and is Lipschitz continuous on each bounded set of X.

(H.3) There is a nonincreasing function f from $\mathbb{R}_+$ into $\mathbb{R}_+$ such that $\|F(x)\| \leqslant f(\|x\|)\, \|x\|$ for all $x \in X$.

(H.4) $\int_{r_0}^{\infty} (f(r)/r)\, dr < \infty$ for all $r_0 > 0$.

The hypotheses (H.1)–(H.3) guarantee the existence of a unique mild solution to (1.1), that is, a continuous function $z\colon \mathbb{R}_+ \to X$ satisfying

$$z(t) = T(t)x + \int_0^t T(t-s)\, F(z(s))\, ds, \qquad t \geqslant 0. \tag{1.2}$$

Furthermore, the solutions of (1.2) form a strongly continuous semigroup $S(t)$, $t \geqslant 0$ in X by the formula $S(t)x := z(t)$ (see [27, Chap. 8]). (We note that the full strength of the hypotheses (H.1)–(H.3) is not needed for the existence of solutions to (1.2) and in particular the asynchronous exponential growth of $T(t)$, $t \geqslant 0$ is not needed.)

THEOREM 1.1. *Let* (H.1)–(H.4) *hold. If* $x \in X$, *then* $\lim_{t \to \infty} e^{-\lambda t} S(t)x$ *exists and is* $Qx := P(x + \int_0^{\infty} e^{-\lambda s} F(S(s)x)\, ds)$. *If the convergence of* $e^{-\lambda t} T(t)x$ *to* Px *is uniform on bounded sets of* $x \in X$, *then the convergence of* $e^{-\lambda t} S(t)x$ *to* Qx *is also uniform on bounded sets of* $x \in S$.

Proof. From (H.1) and the Principle of Uniform Boundedness there exists a constant C_1 such that

$$e^{-\lambda t}\, \|T(t)\| \leqslant C_1 \qquad \text{for} \quad t \geqslant 0. \tag{1.3}$$

From (1.2) we obtain

$$e^{-\lambda t} S(t)x = e^{-\lambda t} T(t)x + \int_0^t e^{-\lambda(t-s)}\, T(t-s) e^{-\lambda s} F(S(s)x)\, ds, \qquad x \in X, \quad t \geqslant 0, \tag{1.4}$$

$$e^{-\lambda t}\, \|S(t)x\| \leqslant C_1\, \|x\| + C_1 f(0) \int_0^t e^{-\lambda s}\, \|S(s)x\|\, ds, \qquad x \in X, \quad t \geqslant 0. \tag{1.5}$$

By Gronwall's lemma

$$e^{-\lambda t}\,\|S(t)x\| \leqslant C_1\,\|x\|\,e^{C_1 f(0)t}, \qquad x\in X, \quad t\geqslant 0. \tag{1.6}$$

Let $c>0$ and let $B_c := \{x\in X : \|x\|\leqslant c\}$. We claim

There exists a constant K_c such that $e^{-\lambda t}\,\|S(t)x\|\leqslant K_c$ for $x\in B_c$ and $t\geqslant 0$. (1.7)

Let $0<\delta<\lambda$ and use (H.4) to choose t_1 such that $\int_{c\exp[\delta t_1]}^{\infty}(f(r)/r)\,dr<(\delta/2C_1)\cdot$ Let $x\in B_c$, $t>t_1$, and define $\Omega := \{s\in[t_1,t] : e^{-\delta s}\,\|S(s)x\|\leqslant c\}$. From (1.4) and (H.3)

$$e^{-\lambda t}\,\|S(t)x\|\leqslant e^{-\lambda t}\,\|T(t)x\| + \left[\int_0^{t_1}+\int_\Omega+\int_{[t_1,t]-\Omega}\right] C_1 f(\|S(s)x\|)e^{-\lambda s}\,\|S(s)x\|\,ds, \qquad t_1\leqslant t. \tag{1.8}$$

By (1.6) the first integral in (1.8) is bounded by a constant independent of $t\geqslant t_1$ and $x\in B_c$. The second integral in (1.8) is bounded by $\int_{t_1}^{t} C_1 f(0)e^{-(\lambda-\delta)s}c\,ds<C_1 cf(0)/(\lambda-\delta)$. The third integral in (1.8) is bounded by $\int_{t_1}^{t} C_1 f(ce^{\delta s})e^{-\lambda s}\,\|S(s)x\|\,ds\leqslant(\sup_{t_1\leqslant s\leqslant t}e^{-\lambda s}\,\|S(s)x\|)(C_1/\delta)\int_{c\exp[\delta t_1]}^{\infty}(f(r)/r)\,dr$. The claim (1.7) now follows.

We next claim that for $c>0$

$$\lim_{t\to\infty}\int_0^t e^{-\lambda s}F(S(s)x)\,ds \qquad \text{exists uniformly for} \quad x\in B_c. \tag{1.9}$$

Let $0\leqslant t_1<t$ and let Ω be as before. Then (1.9) follows from

$$\left\|\int_{t_1}^{t} e^{-\lambda s}F(S(s)x)\,ds\right\|\leqslant\left[\int_\Omega+\int_{[t_1,t]-\Omega}\right] f(\|S(s)x\|)e^{-\lambda s}\,\|S(s)x\|\,ds$$
$$\leqslant f(0)\,ce^{-(\lambda-\delta)t_1}/(\lambda-\delta)+\frac{K_c}{\delta}\int_{c\exp[\delta t_1]}^{\infty}\frac{f(r)}{r}\,dr. \tag{1.10}$$

To prove the claims of Theorem 1.1 let $0\leqslant t_1<t$, let $x\in B_c$, let Ω be as before, and observe that

$$\|e^{-\lambda t}S(t)x-Qx\|\leqslant\|e^{-\lambda t}T(t)x-Px\|+\left[\int_0^{t_1}+\int_\Omega+\int_{[t_1,t]-\Omega}+\int_t^\infty\right]\times\|(e^{-\lambda(t-s)}T(t-s)-P)\,e^{-\lambda s}F(S(s)x)\|\,ds.$$

The claims of Theorem 1.1 now follow using arguments similar to the ones above. ∎

In the following theorem we establish some properties of Q.

THEOREM 1.2. *Let* (H.1)–(H.4) *hold.*

$$Qx = e^{-\lambda t} QS(t)x$$

and (1.11)

$$Qx = P\left[e^{-\lambda t} S(t)x + \int_t^\infty e^{-\lambda s} F(S(s)x)\, ds\right] \textit{for } x \in X, \quad t \geqslant 0.$$

Q is uniformly continuous on bounded sets of X. (1.12)

$Qx = Px + o(\|x\|)$ *as* $\|x\| \to \infty$

(*that is, if* $\varepsilon > 0$ *there exists* $M_\varepsilon > 0$ *such that if* $\|x\| > M_\varepsilon$,

then $\|Qx - Px\| < \varepsilon \|x\|$). (1.13)

$$\lim_{r \to \infty} \frac{1}{r} Q(rx) = Px \textit{ for } x \in X. \quad (1.14)$$

If $Px \neq 0$, then $Q(rx) \neq 0$ for r sufficiently large. (1.15)

Let $x \in X$ and let there exist a sequence $t_n \to \infty$ such that $\|S(t_n)x\| \to \infty$. If $Qx = 0$, then $\lim_{n \to \infty} PS(t_n)x/\|S(t_n)x\| = 0$. If $Qx \neq 0$, then $\lim_{n \to \infty} PS(t_n)x/\|S(t_n)x\| = Qx/\|Qx\|$. (1.16)

Proof. Claim (1.11) follows from Theorem 1.1 and the fact that $Qx = e^{-\lambda t} \lim_{s \to \infty} e^{-\lambda(s-t)} S(s-t)\, S(t)x$. We next claim

If $c > 0$ and $t > 0$ there exists a constant $C(c, t)$ such that $e^{-\lambda t} \|S(t)x_1 - S(t)x_2\| \leqslant C(c, t) \|x_1 - x_2\|$ for $x_1, x_2 \in B_c$. (1.17)

By (H.2) and (1.6) there exists $C' > 0$ such that for $0 \leqslant s \leqslant t$, $x_1, x_2 \in B_c$, $\|F(S(s)x_1) - F(S(s)x_2)\| \leqslant C' \|S(s)x_1 - S(s)x_2\|$. Then (1.4) implies (with C_1 as in (1.3))

$$e^{-\lambda t} \|S(t)x_1 - S(t)x_2\| \leqslant C_1 \|x_1 - x_2\| + C_1 C' \int_0^t e^{-\lambda s} \|S(s)x_1 - S(s)x_2\|\, ds$$

and Gronwall's Lemma yields (1.17) with $C(c, t) = C_1 e^{C_1 C' t}$. To prove (1.12) let $0 < \delta < \lambda$, let $c > 0$, let $\varepsilon > 0$, and let $t_1 > 0$ such that $\int_{e^{\delta t_1}}^\infty (f(r)/r)\, dr < \varepsilon/4K_c$ (where K_c is as in (1.7)) and $f(0)e^{-(\lambda-\delta)t_1}/(\lambda - \delta) <$

$\varepsilon/4$. Let $x_1, x_2 \in B_c$ and let $\Omega_i := \{s \geqslant t_1 : e^{-\delta s} \|S(s)x_i\| \leqslant 1\}$, $i = 1, 2$. From (1.11) and (1.17) we obtain

$$\|Qx_1 - Qx_2\| \leqslant \|P\| \Bigg[e^{-\lambda t_1} \|S(t_1)x_1 - S(t_1)x_2\| + \sum_{i=1}^{2} \left[\int_{\Omega_i} + \int_{[t_1, \infty) - \Omega_i} \right] e^{-\lambda s} \|F(S(s)x_i)\| \, ds \Bigg] \leqslant \|P\| \, [C(c, t_1) \|x_1 - x_2\| + \varepsilon].$$

and claim (1.12) follows.

We next claim there exists $C > 0$ and $M > 0$ such that

$$e^{-\lambda t} \|S(t)x\| \leqslant C \|x\| \qquad \text{for} \quad \|x\| \geqslant M, \quad t \geqslant 0. \tag{1.18}$$

Let $0 < \delta < \lambda$ and choose M such that $(1/\delta) \int_M^\infty (f(r)/r) \, dr < \frac{1}{2}$. Let $x \in X$ be such that $\|x\| \geqslant M$, and let $\Omega := \{s \geqslant 0 : \|S(s)x\| \leqslant e^{\delta s} \|x\|\}$. Then for $t \geqslant 0$

$$\begin{aligned} e^{-\lambda t} \|S(t)x\| &\leqslant e^{-\lambda t} \|T(t)x\| + \left[\int_{\Omega} + \int_{[0, t] - \Omega} \right] f(\|S(s)x\|) \, e^{-\lambda s} \|S(s)x\| \, ds \\ &\leqslant C_1 \|x\| + f(0) \|x\|/(\lambda - \delta) \\ &\quad + \left(\max_{0 \leqslant s \leqslant t} e^{-\lambda s} \|S(s)x\| \right) \frac{1}{\delta} \int_{\|x\|}^{\infty} \frac{f(r)}{r} \, dr \end{aligned}$$

which implies (1.18). Let $\varepsilon > 0$, let $\|x\| \geqslant M$, and let $\Omega_\varepsilon := \{s \geqslant 0 : \|S(s)x\| \leqslant \varepsilon e^{\delta s} \|x\|\}$. From (1.18) we obtain

$$\begin{aligned} \|Qx - Px\| &\leqslant \|P\| \left[\int_{\Omega_\varepsilon} + \int_{[0, \infty) - \Omega_\varepsilon} \right] f(\|S(s)x\|) \, e^{-\lambda s} \|S(s)x\| \, ds \\ &\leqslant \|P\| \left[f(0) \, \varepsilon \, \|x\|/(\lambda - \delta) + \frac{C \|x\|}{\delta} \int_{\varepsilon \|x\|}^{\infty} \frac{f(r)}{r} \, dr \right] \end{aligned}$$

which implies (1.13), and then (1.14) and (1.15) follow immediately from (1.13).

To prove (1.16) let $x \in X$ and let there exist a sequence t_n such that $t_n \to \infty$ and $\|S(t_n)x\| \to \infty$. Let $\varepsilon > 0$ and let M_ε be as in (1.13). If $\|S(t_n)x\| > M_\varepsilon$, then

$$\left\| \frac{QS(t_n)x}{\|S(t_n)x\|} - \frac{PS(t_n)x}{\|S(t_n)x\|} \right\| < \varepsilon.$$

By (1.11) $QS(t_n)x/\|S(t_n)x\| = Qx/\|e^{-\lambda t_n} S(t_n)x\|$ and (1.16) then follows. ∎

Remark 1.2. If X is an ordered Banach space, $S(t)X_+ \subset X_+$ for $t \geqslant 0$, $Px \in X_+ - \{0\}$ for $x \in X_+ - \{0\}$, $x \in X_+ - \{0\}$, and there is a sequence $t_n \to \infty$ such that $\|S(t_n)x\| \to \infty$ and $S(t_n)x/\|S(t_n)x\|$ converges, then $Qx \neq 0$. This claim follows from (1.16), since if $S(t_n)x/\|S(t_n)x\| \to z$, then $z \in X_+$, $\|z\| = 1$, $z \neq 0$, and $PS(t_n)x/\|S(t_n)x\| \to Pz \neq 0$. If X is finite dimensional, then $S(t_n)x/\|S(t_n)x\|$ has a convergent subsequence, and thus $Qx \neq 0$ if $\|S(t_n)x\| \to \infty$.

THEOREM 1.3. *Let* (H.1)–(H.4) *hold. If* $T(t)$, $t \geqslant 0$ *has* (*uniform*) *asynchronous exponential growth, then* $S(t)$, $t \geqslant 0$ *has* (*uniform*) *asynchronous exponential growth.*

Proof. If $P \neq 0$, then $Q \neq 0$ by (1.14). If $R(P)$ is one-dimensional, then $R(Q)$ lies in a one-dimensional subspace by Theorem 1.1. If the convergence of $e^{-\lambda t}T(t)$ to Px is uniform on bounded sets, then the convergence of $e^{-\lambda t}S(t)x$ to Qx is uniform on bounded sets by Theorem 1.2. ▮

Remark 1.3. A useful consequence of asynchronous exponential growth is that ratios determined by linear functionals converge to a limit independent of initial data. For the nonlinear semigroup $S(t)$, $t \geqslant 0$ corresponding to (1.1) we make the following observation: Let (H.1)–(H.4) hold, let $k_1, k_2 \in X^*$, let $T(t)$, $t \geqslant 0$ have asynchronous exponential growth, and let $Y = \{x \in X: \langle Qx, k_2 \rangle \neq 0$, and $\langle Px, k_2 \rangle \neq 0\}$. Since $R(P)$ is one-dimensional, there exists $x_0 \in X$ and $k \in X^*$ such that $Px = \langle x, k \rangle x_0$ for all $x \in X$. Let $x \in Y$ and let $y := x + \int_0^\infty e^{-\lambda s} F(S(s)x)\, ds$. Then $\lim_{t \to \infty} \langle S(t)x, k_1 \rangle / \langle S(t)x, k_2 \rangle = \langle Qx, k_1 \rangle / \langle Qx, k_2 \rangle = \langle Py, k_1 \rangle / \langle Py, k_2 \rangle = \langle x_0, k_1 \rangle / \langle x_0, k_2 \rangle = \langle Px, k_1 \rangle / \langle Px, k_2 \rangle = \lim_{t \to \infty} \langle T(t)x, k_1 \rangle / \langle T(t)x, k_2 \rangle$. Thus, the limit of the ratio determined by k_1 and k_2 with $S(t)$, $t \geqslant 0$ is the same as with $T(t)$, $t \geqslant 0$ and is independent of $y \in Y$.

Additional information concerning the set on which Q is nonzero can be obtained in the setting of an ordered Banach space.

THEOREM 1.4. *Let X be an ordered Banach space, let* (H.1)–(H.4) *hold, and let $Y \subset X_+$ be such that*

(H.5) $PF(S(t)x) \geqslant 0$ *for* $x \in Y$, $t \geqslant 0$.

If $T(t)$, $t \geqslant 0$ has asynchronous exponential growth strictly positive (*ergodic*) *on Y, then $S(t)$, $t \geqslant 0$ has asynchronous exponential growth strictly positive* (*ergodic*) *on Y.*

Proof. The claims of the theorem follow immediately from Theorem 1.1 and the fact that $Qx \geqslant Px$ for all $x \in Y$. ▮

THEOREM 1.5. *Let X be an ordered Banach space, let* (H.1)–(H.4) *hold, and*

(H.6) *There exists $L \in B(X)$ and a constant $M_L \geq 0$ such that $A - L$ is the infinitesimal generator of a positive linear semigroup $T_L(t)$, $t \geq 0$ in X having asynchronous exponential growth strictly positive on X_+ with intrinsic growth constant λ_L, spectral projection P_L, and satisfying $Lx + F(x) \geq 0$ for all $x \in X_+$ such that $\|x\| \geq M_L$.*

(H.7) *There exists $c > 0$ such that $\|Px\| \geq c\,\|x\|$ for all $x \in X_+$.*

Then, $S(t)$, $t \geq 0$ has asynchronous exponential growth strictly positive on $Y = \{x \in X_+ : \|S(t)x\| \geq M_L$ and $S(t)x \in X_+ - \{0\}$ for t sufficiently large$\}$.

Proof. Let $x \in Y$. There exists t_1 such that $\|S(t)x\| \geq M_L$ for $t \geq t_1$. Let $x_1 := S(t_1)x$. For $t \geq 0$

$$S(t)x_1 = T_L(t)x_1 + \int_0^t T_L(t-s)\,[LS(s)x_1 + F(S(s)x_1)]\,ds \geq T_L(t)x_1,$$

which means $e^{-\lambda_L t}S(t)\,x_1 - e^{-\lambda_L t}T_L(t)x_1 \in X_+$ for all $t \geq 0$. By (H.6) $\lim_{t\to\infty} e^{-\lambda_L t}T_L(t)x_1 = P_L x_1 \in X_+ - \{0\}$. Since X_+ is norm closed and proper (see [10, p. 265]), there exists $d > 0$ such that $e^{-\lambda_L t}\,\|S(t)x_1\| \geq d$ for all $t \geq 0$. Thus, $\lim_{t\to\infty} \|S(t)x\| = \infty$, and the conclusion of the theorem follows from (H.7) and (1.16). ∎

2. ASYNCHRONOUS EXPONENTIAL GROWTH OF SEMIGROUPS ON DUAL BANACH SPACES

Many concrete problems that arise in applications, most notably models of structured populations and functional differential equations, can be formulated abstractly as Cauchy problems of the form (1.1) with the exception that the function F takes values, not in $B(X)$ but in $B(X, Z)$, where Z is a superspace of X. For instance, age dependent population problems with nonlinearities in the birth rate cannot be treated as abstract Cauchy problems in L^1 within the framework of the previous section. If, on the other hand, one lets the nonlinear terms take on values in the bigger space M of Borel measures, then the problem can at least formally be written as an equation of type (1.1). This is due to the fact that all neonates enter the population with age zero; thus the source term describing the birth process is a measure concentrated at the origin and not an L^1-density (see [5]).

It is the purpose of this section to show that the results of the previous sections hold, *mutatis mutandis* in the case where the nonlinear part takes on values in a superspace. Of course, this problem does not even make sense if the semigroup generated by the linear part cannot be extended to the bigger space. We will therefore start by looking at the linear problem in the spirit of the theory of weakly $*$ continuous semigroups and the perturbation theory of dual semigroups as developed in [5–9, 12, 13] which provides a means of such an extension and a functional analytic framework for the nonlinear theory.

Typically, the solutions to a linear population problem define an integral w^*-semigroup $T^\times(t)$, $t \geq 0$ of bounded linear operators on a dual Banach space X^*. This means, by definition, that in addition to the properties $T^\times(0) = I$, $T^\times(t+s) = T^\times(t)\, T^\times(s)$, $t, s \geq 0$, $T^\times(t)$, $t \geq 0$ satisfies

$$\langle x, T^\times(t)x^* - x^* \rangle \to 0 \qquad \text{as } t \downarrow 0 \text{ for all } x \in X \text{ and all } x^* \in X^*, \tag{2.1}$$

$$T^\times(t) \int_0^s T^\times(\tau)x^*\, d\tau = \int_0^s T^\times(t+\tau)x^*\, d\tau, \qquad t, s \geq 0. \tag{2.2}$$

The integrals in (2.2) are w^*-Riemann integrals. The semigroup $T^\times(t)$, $t \geq 0$ is generated by an operator $A^\times$ on X^* in the following sense

$x^* \in D(A^*)$ and $A^\times x^* = y^*$ if and only if

$$\frac{d}{dt} \langle x, T^\times(t)x^* \rangle = \langle x, T^\times(t)y^* \rangle, \; x \in X, \; t \geq 0. \tag{2.3}$$

For all $x^* \in X^*$, $t \geq 0$, $\int_0^t T^\times(\tau)x^*\, d\tau \in D(A^\times)$ and

$$A^\times \int_0^t T^\times(\tau)x^*\, d\tau = T^\times(t)x^* - x^*. \tag{2.4}$$

The subspace $X^\odot := \overline{D(A^\times)}$ of X^* is the maximal subspace on which $T^\times(t)$, $t \geq 0$ is strongly continuous. $T^\odot(t) := T^\times(t)|_{X^\odot}$ is a C_0-semigroup with infinitesimal generator $A^\odot$—the part of $A^\times$ in $X^\odot$. In age dependent population problems $X^\odot$ can be identified with $L^1[0, \infty)$ and the C_0-semigroup $T^\odot(t)$, $t \geq 0$ is the usual solution semigroup on this space. The semigroup $T^\times(t)$, $t \geq 0$ acting on the bigger space $X^* \cong M[0, \infty)$ is then obtained by some sort of extension procedure, for instance by using the following duality framework.

Let $T^{\odot *}(t)$, $t \geq 0$ be the dual semigroup on the dual space $X^{\odot *}$ of $X^\odot$ and let $T^{\odot\odot} := T^{\odot *}|_{X^{\odot\odot}}$, where $X^{\odot\odot} := \overline{D(A^{\odot *})}$ is the maximal subspace of strong continuity of $T^{\odot *}(t)$, $t \geq 0$. The infinitesimal generator $A^{\odot\odot}$ of $T^{\odot\odot}(t)$, $t \geq 0$ is the part of $A^{\odot *}$ in $X^{\odot\odot}$. There is a pairing [,] between $X^{\odot\odot}$ and X^*, which satisfies

$$|[x^{\odot\odot}, x^*]| \leq M\, \|x^\odot\|\, \|x^*\|, \qquad x^\odot \in X^\odot, \; x^* \in X^* \tag{2.5}$$

for some constant $M < \infty$. The pairing is canonical in the sense that whenever the ordinary duality pairing is defined (i.e., if either $x^{\odot\odot} \in X$ or $x^* \in X^{\odot}$) then the [,]-pairing coincides with the ordinary one. It was shown in [8] that although $T^{\times}(t)$, $t \geq 0$ is in general not the adjoint of any strongly continuous semigroup on X, it is always the adjoint of $T^{\odot\odot}(t)$, $t \geq 0$ with respect to the pairing [,], that is

$$[T^{\odot\odot}(t)x^{\odot\odot}, x^*] = [x^{\odot\odot}, T^{\times}(t)x^{**}], \qquad t \geq 0. \tag{2.6}$$

Moreover,

$$[A^{\odot\odot}x^{\odot\odot}, x^*] = [x^{\odot\odot}, A^{\times}x^*], \qquad x^{\odot\odot} \in D(A^{\odot\odot}), x^* \in D(A^{\times}). \tag{2.7}$$

We refer the reader to [8] for more details.

In the previous section we proved results stating that if the linear problem had asynchronous exponential growth, then the same was true of the nonlinear problem. When the nonlinear perturbation takes on values in a bigger space we need to know that the linear semigroup $T^{\times}(t)$, $t \geq 0$ acting on the bigger space has asynchronous exponential growth. In practical problems the semigroup $T^{\odot}(t)$, $t \geq 0$ acting on the smaller space can usually be obtained by a constructive procedure (successive approximations) and it is often a relatively easy task to determine whether $T^{\odot}(t)$, $t \geq 0$ has anynchronous exponential growth or not. The following theorem which states that $T^{\times}(t)$, $t \geq 0$ has asynchronous exponential growth provided $T^{\odot}(t)$, $t \geq 0$ has (the converse is almost trivial) is therefore of importance for the nonlinear problem although it has some intrinsic interest as well. Since we do not want to introduce yet another concept of asynchronous exponential growth (corresponding to the weak topology on X^* induced by $X^{\odot\odot}$) we will restrict ourselves to at least uniform asynchronous exponential growth.

THEOREM 2.1. *Let $T^{\times}(t)$, $t \geq 0$ be an integral w*-semigroup with generator $A^{\times}$ (in the sense of (2.3), (2.4)). $T^{\times}(t)$, $t \geq 0$ has uniform asynchronous exponential growth if and only if $T^{\odot}(t)$, $t \geq 0$ has. If this is the case, they have the same intrinsic growth constant λ and there exists an eigenvector $e^{\odot}$ of $A^{\odot}$ and an eigenvector $e^{\odot\odot}$ of $A^{\odot\odot}$, both corresponding to the eigenvalue λ, such that the spectral projection $P^{\times}$ of $T^{\times}(t)$, $t \geq 0$ is given by*

$$P^{\times}x^* = [e^{\odot\odot}, x^*]e^{\odot}. \tag{2.8}$$

The spectral projection $P^{\odot}$ of $T^{\odot}(t)$, $t \geq 0$ is the restriction of $P^{\times}$ to $X^{\odot}$. Moreover, both $T^{\odot *}(t)$, $t \geq 0$ and $T^{\odot\odot}(t)$, $t \geq 0$ have uniform asynchronous exponential growth with intrinsic growth constant λ and spectral projections $P^{\odot *}$ and $P^{\odot\odot} := P^{\odot *}|_{X^{\odot\odot}}$, respectively.

Proof. Let $T^\times(t)$, $t \geqslant 0$ have uniform asynchronous exponential growth with intrinsic growth constant λ and spectral projection $P^\times$. Since $P^\times$ is of rank one, it is of the form

$$P^\times x^* = \langle x^*, e^{**} \rangle e^* \tag{2.9}$$

for some $e^{**} \in X^{**}$, $e^* \in X^*$. Since $P^\times$ is a projection we must have $\langle e^*, e^{**} \rangle = 1$. The defining property $P^\times := \lim_{t \to \infty} e^{-\lambda t} T^\times(t)$ implies

$$P^\times T^\times(t) = T^\times(t) P^\times = e^{\lambda t} P^\times.$$

Thus $t \to e^{\lambda t} T^\times(t) P^\times x^*$ is even strongly differentiable for all $x^* \in X^*$ with derivative $\lambda T^\times(t) P^\times x^*$. It follows from the definition of the generator $A^\times$ that $P^\times x^* \in D(A^\times) \subset X^\odot$ and $A^\times P^\times x^* = \lambda P^\times x^*$. Since $A^\odot$ is the part of $A^\times$ in $X^\odot$, it follows that in fact $P^\times x^* \in D(A^\odot)$. In particular, $e^* =: e^\odot \in \mathscr{D}(A^\odot) \subset X^\odot$ is an eigenvector of $A^\odot$ corresponding to the eigenvalue λ and

$$P^\times x^* = \langle x^*, e^{**} \rangle e^\odot. \tag{2.11}$$

It is now obvious that $T^\odot(t)$, $t \geqslant 0$ has uniform asynchronous exponential growth with spectral projection

$$P^\odot x^\odot = \langle x^\odot, e^{\odot *} \rangle e^\odot, \tag{2.12}$$

where $e^{\odot *}$ is the restriction of e^{**} to $X^\odot$.

Assume now that $T^\odot(t)$, $t \geqslant 0$ has uniform asynchronous exponential growth with intrinsic growth constant λ. The spectral projection is then necessarily of the form (2.12). Since taking adjoints preserves the operator norm, it is clear that $T^{\odot *}(t)$, $t \geqslant 0$ has uniform asynchronous exponential growth with the same intrinsic growth constant and spectral projection

$$P^{\odot *} x^{\odot *} = \langle x^{\odot *}, e^\odot \rangle e^{\odot *}. \tag{2.13}$$

Exactly as we above concluded that $e^* =: e^\odot$ is an eigenvector of $A^\odot$, we now conclude that $e^{\odot *} =: e^{\odot\odot} \in \mathscr{D}(A^{\odot\odot}) \subset X^{\odot\odot}$ is an eigenvector of $A^{\odot\odot}$ corresponding to the eigenvalue λ. In particular $T^{\odot\odot}(t)$, $t \geqslant 0$ has uniform asynchronous exponential growth with spectral projection

$$P^{\odot\odot} x^{\odot\odot} = \langle x^{\odot\odot}, e^\odot \rangle e^{\odot\odot}. \tag{2.14}$$

From expression (2.14) it is clear that $P^{\odot\odot}$ is continuous with respect to the weak topology on $X^{\odot\odot}$ induced by X^* through the pairing [,]. $P^{\odot\odot}$ thus has a unique adjoint $P^\times$ with respect to this pairing. Obviously $P^\times$ is given by

$$P^\times x^* = [e^{\odot\odot}, x^*] e^\odot. \tag{2.15}$$

Taking adjoints with respect to the pairing [,] does not preserve norms, but by (2.5)

$$\|e^{-\lambda t}T^{\times}(t)-P^{\times}\| \leqslant M\,\|e^{-\lambda t}T^{\odot\odot}(t)-P^{\odot\odot}\|. \tag{2.16}$$

Thus $T^{\times}(t)$, $t\geqslant 0$ has uniform asynchronous exponential growth with intrinsic growth constant λ and spectral projection $P^{\times}$ defined by (2.15). ∎

We now turn to the nonlinear problem. As mentioned above we shall assume that $T^{\times}(t)$, $t\geqslant 0$ satisfies the following modified version of (H.1):

(H.1)′ $T^{\times}(t)$, $t\geqslant 0$ is an integral ω^* semigroup with generator $A^{\times}$ having uniform asynchronous exponential growth with spectral projection $P^{\times}$ and intrinsic growth constant λ.

Hypothesis (H.2) is replaced by

(H.2)′ F maps $X^{\odot}$ into X^* and is Lipschitz continuous on bounded subsets of $X^{\odot}$.

By (H.3)′ we simply mean (H.3) where $x\in X$ is replaced by $x^{\odot}\in X^{\odot}$.

Consider the abstract Cauchy problem

$$z'(t)=A^{\times}z(t)+F(z(t)), \qquad t\geqslant 0, \quad z(0)=x^{\odot}\in X^{\odot}. \tag{2.17}$$

Observe that we restrict our attention to initial values in $X^{\odot}$.

THEOREM 2.2. *Let* (H.1)′–(H.3)′ *hold. The variation of constants formula*

$$S(t)x^{\odot}=T^{\odot}(t)x^{\odot}+\int_0^t T^{\times}(t-s)\,F(S(s)x^{\odot})\,ds \tag{2.18}$$

uniquely determines a strongly continuous semigroup of nonlinear operators $S(t)$, $t\geqslant 0$ *on* $X^{\odot}$, *where* $z(t)=S(t)x^{\odot}$ *is the unique mild solution to* (2.17).

For a proof of Theorem 2.2 see [7, 8]. As in the corresponding result of Section 1, asynchronous exponential growth of $T^{\times}(t)$, $t\geqslant 0$ is irrelevant in Theorem 2.2. The proof of Theorem 2.2 depends on the following lemma.

LEMMA 2.3. *Let* $T^{\times}(t)$, $t\geqslant 0$ *be as above and let* $g:\mathbb{R}^+\to X^*$ *be continuous. Let* $M\geqslant 1$, $w\in\mathbb{R}$ *be chosen such that* $\|T^{\times}(t)\|\leqslant Me^{wt}$. *Then*

(i) *The mapping* $t\to\int_0^t T^{\times}(t-s)\,g(s)\,ds$ *is continuous with values in* $X^{\odot}$.

(ii) *There exists a constant* $M_1\geqslant M$ *such that* $\|\int_0^t T^{\times}(t-s)\,g(s)\,ds\|\leqslant M_1((e^{wt}-1)/w)\,\sup_{0\leqslant s\leqslant t}\|g(s)\|$.

Part (i) of Lemma 2.3 shows that the variation of constants formula (2.18) makes sense in $X^\odot$ and part (ii) shows that (2.18) can be solved by successive approximations in the standard manner. Lemma 2.3 also shows that all the estimates in the proofs of Theorem 1.1–1.5 hold *verbatim* in this more general situation. For instance we have the following analogues of Theorems 1.1 and 1.3.

THEOREM 2.4. *Let* (H.1)′–(H.3)′ *and* (H.4) *hold. If* $x^\odot \in X^\odot$, *then* $Qx^\odot := \lim_{t\to\infty} e^{-\lambda t} S(t) x^\odot$ *exists and*

$$Qx^\odot = P^\times \left(x^\odot + \int_0^\infty e^{-\lambda s} F(S(x) x^\odot)\, ds \right). \tag{2.19}$$

Moreover, the convergence of $e^{-\lambda t} S(t) x^\odot$ *to* $Qx^\odot$ *is uniform on bounded sets of* $X^\odot$, *and hence* $S(t)$, $t \geq 0$ *has uniform asynchronous exponential growth.*

It is immediately clear that the operator $Q: X^\odot \to X^\odot$ has all the properties proved in Theorem 1.2 provided that $x \in X$ is replaced by $x^\odot \in X^\odot$ and P is replaced by $P^\odot$ (or by $P^\times$ in (1.11)). Theorem 1.4 and 1.5 have analogues, too. Since these results depend on the order structure of the spaces we recall that if X is an ordered Banach space, then so are X^* and $X^\odot$. One has $X^\odot_+ = X^\odot \cap X^*_+$. The proof of the following theorem is as obvious as its analogue Theorem 1.4.

THEOREM 2.5. *Let X be an ordered Banach space, let* (H.1)′–(H.3)′ *and* (H.4) *hold, and let* $Y \subset X^\odot_+$ *be such that*

(H.5)′ $P^\times F(S(t) x^\odot) \geq 0$ for $x^\odot \in Y$, $t \geq 0$.

If $T^\times(t)$, $t \geq 0$ *as asynchronous exponential growth strictly positive (ergodic) on* Y, *then* $S(t)$, $t \geq 0$ *has asynchronous exponential growth strictly positive (ergodic) on* Y.

For the sake of completeness we close this section by stating the analogue of Theorem 1.5.

THEOREM 2.6. *Let X be an ordered Banach space, let* (H.1)′–(H.3)′, (H.4) *hold, and*

(H.6)′ *There exists* $L \in \mathscr{B}(X^\odot, X^*)$ *and a constant* $M_L \geq 0$ *such that* $A^\times - L$ *is the generator of a positive integral w*-semigroup* $T^\times_L(t)$, $t \geq 0$ *having uniform asynchronous exponential growth strictly positive on* $X^\odot_+$ *with intrinsic growth constant* λ_L, *spectral projection* $P^\times_L$, *and satisfying* $Lx^\odot + F(x^\odot) \geq 0$ *for all* $x^\odot \in X^\odot_+$ *such that* $\|x^\odot\| \geq M_L$.

(H.7)′ *There exists* $c > 0$ *such that* $\|P^\odot x^\odot\| \geq c\,\|x^\odot\|$ *for all* $x^\odot \in X^\odot_+$.

Then, $S(t)$, $t \geqslant 0$ has uniform asynchronous exponential growth strictly positive on $Y = \{x^{\odot} \in X_+^{\odot}: \|S(t)x^{\odot}\| \geqslant M_L$ and $S(t)x^{\odot} \in X_+^{\odot} - \{0\}$ for t sufficiently large$\}$.

3. EXAMPLES

The examples below illustrate linear and nonlinear asynchronous exponential growth. An additional example of nonlinear asynchronous exponential growth for a size-structured cell model of tumor growth with proliferating and quiescent classes is given in [21].

EXAMPLE 3.1. Let $X = l_1$, $\|\bar{x}\| := \sum_{k=1}^{\infty} |x_k|$ for $\bar{x} = \{x_k\} \in X$. Define $A: X \to X$ by $(A\bar{x})_1 := \sum_{k=1}^{\infty} x_k/k$, $(A\bar{x})_k := ((k-1)/k)x_k$, $k = 2, 3, \ldots$. It is easily seen that A is the infinitesimal generator of a linear semigroup $T(t)$, $t \geqslant 0$ given by $(T(t)\bar{x})_1 := e^t(x_1 + \sum_{k=2}^{\infty}(1 - e^{-t/k})x_k)$, $(T(t)\bar{x})_k := e^{(k-1)t/k}x_k$, $k = 2, 3, \ldots$. Obviously, $\lim_{t\to\infty} e^{-t}T(t)\bar{x} = P\bar{x}$, where $(P\bar{x})_1 := \sum_{k=1}^{\infty} x_k$, $(P\bar{x})_k := 0$, $k = 2, 3, \ldots$. Further, for $\bar{x} \in X$

$$\|e^{-t}T(t)\bar{x} - P\bar{x}\| = 2\sum_{k=2}^{\infty} e^{-t/k}|x_k|.$$

Then, for $\bar{x} \in X$, $\lim_{t\to\infty} e^{-t}T(t)\bar{x} = P\bar{x}$, but $\|e^{-t}T(t) - P\| = 2$ for all $t \geqslant 0$. Consequently, $T(t)$, $t \geqslant 0$ has asynchronous exponential growth with intrinsic growth constant 1 and spectral projection P, but the asynchronous exponential growth is not uniform. Notice that the asynchronous exponential growth is strictly positive on X_+, but not ergodic, and $T(t)$, $t \geqslant 0$ is not irreducible.

EXAMPLE 3.2. Let $X = L^1(0, \infty; \mathbb{R})$ and consider the following linear model of age-structured population dynamics (see [16, Remark 2.5; 35, Theorem 4.10]):

$$\begin{aligned} z_t(a,t) + z_a(a,t) &= -\mu(a)\,z(a,t), \qquad a > 0, \quad t > 0, \\ z(0,t) &= \int_0^{\infty} \beta(a)\,z(a,t)\,da, \qquad t > 0, \\ z(a,0) &= \phi(a), \qquad a > 0. \end{aligned} \tag{3.1}$$

The age density of the population at time t is $z(a, t)$ (the total population in the age range $[a_1, a_2]$ at time t is $\int_{a_1}^{a_2} z(a,t)\,da$). It is assumed that $\mu \in L_+^{\infty}(0, \infty; \mathbb{R})$, $0 < \operatorname{ess\,inf}_{a>0} \mu(a)$, $\beta \in L_+^{\infty}(0, \infty; \mathbb{R})$, and $\phi \in X$. The *mortality modulus* μ has the interpretation that $\Pi(a_1, a_2) := \exp[-\int_{a_1}^{a_2} \mu(a)\,da]$

is the probability of survival from age a_1 to age a_2. The *fertility modulus* β has the interpretation that $\int_0^\infty \beta(a)\, z(a, t)\, da$ is the *birth rate* at time t. The (generalized) solutions of (3.1) yield a linear semigroup of positive operators in X given by $(T(t)\phi)(a) = z(a, t)$. The infinitesimal generator of $T(t)$, $t \geq 0$ is $A\phi := -\phi' - \mu\phi$, $D(A) := \{\phi \in X : \phi' \in X$ and $\phi(0) = \int_0^\infty \beta(a)\, \phi(a)\, da\}$. This semigroup has uniform asynchronous exponential growth if the *net reproductive rate* $\int_0^\infty \beta(a)\, \Pi(a, 0)\, da$ is positive. The intrinsic growth constant is then the unique real (necessarily positive) solution λ of the *characteristic equation* $1 = \int_0^\infty e^{-\lambda a} \beta(a)\, \Pi(a, 0)\, da$. The spectral projection P is given by $(P\phi)(a) = e^{-\lambda a}\, \Pi(a, 0)\, R_\lambda(\phi)/M_\lambda$, where

$$R_\lambda(\phi) := \int_0^\infty \beta(a)\, e^{-\lambda a} \left(\int_0^a e^{-\lambda b}\, \Pi(a, b)\, \phi(b)\, db \right) da$$

is the *natural reproductive value* of the initial age distribution ϕ and

$$M_\lambda := \int_0^\infty \beta(a)\, a e^{-\lambda a}\, \Pi(a, 0)\, da$$

is the *mean age of childbirth*. It is easily seen that $T(t)$, $t \geq 0$ is ergodic on X_+ if and only if $T(t)$, $t \geq 0$ is irreducible if and only if there exists no $a_0 \geq 0$ such that $\beta(a)$ vanishes a.e. on (a_0, ∞). If $\beta(a)$ does vanish a.e. on (a_0, ∞) for some $a_0 > 0$, then $T(t)$, $t \geq 0$ is ergodic on $Y := \{\phi \varepsilon X_+ : \phi$ is not 0 a.e. on $(0, a_0)\}$.

EXAMPLE 3.3. Let $X = \mathbb{R}$ and consider the scalar ordinary differential equation

$$z'(t) = \left(\frac{a + bz(t)}{c + dz(t)} \right) z(t), \qquad t \geq 0, \quad z(0) = x, \tag{3.2}$$

where a, b, c, $d > 0$, $ad \neq bc$. Take $Ax = (b/d)x$ and $F(z) = ((ad - bc)/(d(c + dz)))z$ and (3.2) has the form (1.1). Obviously, (H.1) is satisfied with $\lambda = b/d$, $Px = x$, and (H.2)–(H.4) are satisfied with $f(r) = (ad - bc)/(d(c + dr))$. If $ad > bc$, then (H.5) holds. If $ad < bc$, then (H.6) and (H.7) hold with $Lx = (b/d - a/c)x$, $\lambda_L = a/c$, $P_L x = x$, and $M_L = 0$. Consequently, Theorems 1.1–1.5 apply and the solutions of (3.2) have asynchronous exponential growth strictly positive on $\mathbb{R}^+$ with intrinsic growth constant $\lambda = b/d$. Separation of variables of (3.2) yields

$$e^{-(b/d)t} z(t) = x \left[\frac{e^{-(b/d)t}(a + bz(t))}{a + bx} \right]^{1 - ad/bc}, \qquad Qx = x^{bc/ad} \left(\frac{b}{a + bx} \right)^{bc/ad - 1}.$$

If $a = 0$ in (3.2), then choose A, λ, P, f as above and (H.6) is satisfied with

$Lx = lx$, $l \in (0, b/d)$, $\lambda_L = b/d - l$, $P_L x = x$, $M_L = (c/ld)(b/d - l)$. Theorem 1.5 now applies to show that the solutions of (3.2) (with $a = 0$) have asynchronous exponential growth strictly positive on $\mathbb{R}_+$ with intrinsic growth constant $\lambda = b/d$. Separation of variables in this case yields

$$e^{-(b/d)t} z(t) = x e^{(c/d)[1/z(t) - 1/x]}, \quad Qx = x e^{-c/dx}.$$

EXAMPLE 3.4. Let $X = \mathbb{R}$ and consider the scalar ordinary differential equation

$$z'(t) = \left(a + \frac{b}{z(t)^p}\right) z(t), \qquad t \geqslant 0, \quad z(0) = x, \tag{3.3}$$

where $a > 0$, $b \in \mathbb{R}$, $p > 0$. Take $Ax = ax$ and $F_\varepsilon(x) = bx/x^p$ for $x \geqslant \varepsilon$ and $F_\varepsilon(x) = bx/\varepsilon^p$ for $0 \leqslant r < \varepsilon$ (where $\varepsilon > 0$). Then (H.1) is satisfied with $\lambda = a$, $Px = x$, and (H.2)–(H.4) are satisfied with $f_\varepsilon(r) = b/r^p$ for $r \geqslant \varepsilon$ and $f_\varepsilon(r) = b/\varepsilon^p$ for $0 \leqslant r < \varepsilon$. If $b > 0$, then (H.5) is satisfied. If $b < 0$, then (H.6) and (H.7) are satisfied with $Lx = lx$, $0 < l < a$, $\lambda_L = a - l$, $M_L = \varepsilon = (-b/l)^{1/p}$. Thus, the solutions of (3.3) have asynchronous exponential growth with intrinsic growth constant a strictly positive on $\mathbb{R}^+$ if $b > 0$ and on $Y = ((-b/a)^{1/p}, \infty)$ if $b < 0$. The following formulas are easily verified:

$$z(t) = \left[\left(x^p + \frac{b}{a}\right) e^{pat} - \frac{b}{a}\right]^{1/p}, \qquad t \geqslant 0, \quad Qx = \left(x + \frac{b}{a}\right)^{1/p}.$$

EXAMPLE 3.5. Let $X = \mathbb{R}$ and consider the equation

$$z'(t) = \left(1 - \frac{1}{\log(z(t))}\right) z(t), \qquad t \geqslant 0, \quad z(0) = x. \tag{3.4}$$

Take $Ax = x$, $F(x) = -x/\log(x)$ for $x \geqslant e$ and $F(x) = x$ for $0 \leqslant x < e$ and (3.4) has the form (1.1). Separation of variables yields

$$e^{-t} z(t) = \frac{x(\log(x) - 1)}{\log(z(t)) - 1}, \qquad x \geqslant e, \quad t \geqslant 0.$$

Since $\lim_{t \to \infty} z(t) = \infty$ for $x > e$, $\lim_{t \to \infty} e^{-t} z(t) = 0$ for $x > e$. Thus, the solutions of (3.4) do not have strictly positive asynchronous exponential growth on $Y = (e, \infty)$. Notice that (H.4) is not satisfied, since $\int^\infty (1/r \log(r))\, dr = \infty$.

Consider also the equation

$$z'(t) = \left(1 + \frac{1}{\log(z(t))}\right) z(t), \qquad t > 0, \quad z(0) = x. \tag{3.5}$$

If $x > 1$, then $z(t)$ is increasing. Since $(e^{-t}z(t))' = e^{-t}z(t)/\log(z(t))$, $e^{-t}z(t)$ is also increasing for $x > 1$. Assume $e^{-t}z(t) < M$ for some $M > 1$. Then $e^{-t}z(t)/\log(z(t)) > x/(\log(M) + t)$, which implies $e^{-t}z(t) \to \infty$, since

$$e^{-t}z(t) = x + \int_0^t e^{-s}z(s)/\log(z(s))\, ds.$$

Thus, the solutions of (3.5) do not have asynchronous exponential growth.

Example 3.6. Let $X = \mathbb{R}^2$ with norm $\|[x_1, x_2]\| = |x_1| + |x_2|$ and consider the system

$$\begin{aligned} p'(t) &= (\beta_p - \mu_p - r_p(n(t)))\, p(t) + r_q(n(t))\, q(t), \\ q'(t) &= r_p(n(t))\, p(t) - (r_q(n(t)) + \mu_q)\, q(t), \\ n(t) &= p(t) + q(t), \qquad p(0) = x_1,\ q(0) = x_2. \end{aligned} \tag{3.6}$$

This system describes a population of tumor cells with proliferating cell subpopulation p and quiescent cell subpopulation q (see [20]). $\beta_p > 0$ is the division rate of proliferating cells, $\mu_p \geqslant 0$, $\mu_q \geqslant 0$ are the mortality rates of proliferating and quiescent cells, respectively, $r_p(n) \geqslant 0$ is the (nonlinear) transition rate from the proliferating class to the quiescent class, and $r_q(n) \geqslant 0$ is the (nonlinear) transition rate from the quiescent class to the proliferating class. For this tumor population we suppose that $r_p(n)$ is nondecreasing in n and $r_q(n)$ is nonincreasing in n. We suppose that $r_p(n)$ and $r_q(n)$ are Lipschitz continuous on bounded sets of n in $\mathbb{R}_+$, $r_p(\infty) := \lim_{n\to\infty} r_p(n) < \infty$, $r_q(\infty) := \lim_{n\to\infty} r_q(n) \geqslant 0$, $\int_{r_0}^{\infty} |r_p(\infty) - r_p(n)|/n\, dn < \infty$, and $\int_{r_0}^{\infty} |r_q(\infty) - r_q(n)|/n\, dn < \infty$ for $r_0 > 0$.

Define $a = \beta_p - \mu_p - r_p(\infty)$, $b = r_q(\infty)$, $c = r_p(\infty)$, $d = -(r_q(\infty) + \mu_q)$, $A[x_1, x_2] = [ax_1 + bx_2, cx_1 + dx_2]$, $f(n)[x_1, x_2] = [(r_p(\infty) - r_p(n))\, x_1 + (r_q(n) - r_q(\infty))x_2, (r_p(n) - r_p(\infty))x_1 + (r_q(\infty) - r_q(n))x_2]$ and then (3.6) has the form (1.1) with $F([x_1, x_2]) = f(\|[x_1, x_2]\|)[x_1, x_2]$. We require that $a > 0$, $b > 0$, $c > 0$. The eigenvalues of A are $\lambda_\pm := (a + d \pm [(a-d)^2 + 4bc]^{1/2})/2$. Further, $\lambda_+ > 0$ and $A[1, u_+] = \lambda_+[1, u_+]$, $A[1, u_-] = \lambda_-[1, u_-]$, where $u_\pm = (d - a \pm [(a-d)^2 + 4bc]^{1/2})/2b$, $u_+ > 0$, $u_- < 0$. The hypothesis (H.1) is satisfied with $\lambda = \lambda_+$ and $P[x_1, x_2] = (x_2 - x_1 u_-)/(u_+ - u_-)[1, u_+]$. The hypotheses (H.2)–(H.4) are satisfied, as well as (H.5), since $P[1, -1] = (1 + u_-)/(u_+ - u_-)[1, u_+] \in X_+ - \{0\}$. By Theorem 1.4 the solutions of (3.6) have asynchronous exponential growth strictly positive on $\mathbb{R}^2_+$ with intrinsic growth constant $\lambda = \lambda_+$. Notice that if $a > 0$ then no nontrivial equilibria of (3.6) exist in X_+. The case that $a < 0$ and $\mu_q > 0$ (so that equilibria exist in $X_+ - \{0\}$) is considered in [20].

EXAMPLE 3.7. Let $X = L^1(0, 1; \mathbb{R})$ and consider the nonlinear diffusion problem

$$\begin{aligned} &z_t(x, t) = z_{xx}(x, t) + f(x, \|z(\cdot, t)\|)\, z(x, t), \\ &z_x(0, t) = z_x(1, t) = 0, \qquad t > 0, \\ &z(x, 0) = \phi(x), \qquad 0 \leqslant x \leqslant 1. \end{aligned} \tag{3.7}$$

We require that $f\colon [0, 1] \times \mathbb{R}_+ \to \mathbb{R}_+$, f is Lipschitz continuous on bounded sets of $[0, 1] \times \mathbb{R}_+$, and there exists a continuous function $a(x)$ on $[0, 1]$, $a \not\equiv 0$, such that $\lim_{r \to \infty} f(x, r) = a(x)$ uniformly for $x \in [0, 1]$. We require also that $a \geqslant 0$ and

$$\sup_{0 \leqslant x \leqslant 1} \int_{r_0}^{\infty} \frac{|f(x, r) - a(x)|}{r}\, dr < \infty, \qquad r_0 > 0.$$

We consider two cases—Case 1: $f(x, r)$ is nonincreasing in r for $x \in [0, 1]$, and Case 2: $f(x, r)$ is nondecreasing in r for $x \in [0, 1]$. Define $(A\phi)(x) := \phi''(x) + a(x)\, \phi(x)$, $D(A) := \{\phi \in X\colon \phi'' \in X, \phi'(0) = \phi'(1) = 0\}$. It can be shown that A is the infinitesimal generator of a linear semigroup $T(t)$, $t \geqslant 0$ in X having asynchronous exponential growth ergodic in X with intrinsic growth constant $\lambda > 0$ and spectral projection P. Further, $P\phi = \langle \phi, \phi_0^* \rangle \phi_0$, where $A\phi_0 = \lambda\phi_0$, $A^*\phi_0^* = \lambda\phi_0^*$, ϕ_0 and ϕ_0^* are strictly positive on $[0, 1]$, and P satisfies (H.7). Hypotheses (H.1)–(H.4) are satisfied and (3.7) can be written abstractly as

$$z'(t) = Az(t) + (f(\|z(t)\|) - a)\, z(t), \qquad z(0) = \phi \in X.$$

In Case 1 (H.5) is satisfied and the nonlinear semigroup $S(t)$, $t \geqslant 0$ for (3.7) $(S(t)\phi = z(\cdot, t))$ has asynchronous exponential growth ergodic on X_+ with intrinsic growth constant λ. In Case 2 choose $l \in (0, \lambda)$, define $L\phi = l\phi$, and choose M_L such that if $\phi \in X_+$ and $\|\phi\| \geqslant M_L$ then $l + f(x, \|\phi\|) - a(x) \geqslant 0$. Then (H.6) is satisfied and the nonlinear semigroup $S(t)$, $t \geqslant 0$ has asynchronous exponential growth strictly positive on $Y = \{\phi \in X_+ :$ $\|S(t)\phi\| \geqslant M_L$ for t sufficiently large$\}$. In case 2 there may exist nontrivial equilibria for (3.7), since for sufficiently small positive r, $f(x, r)$ could be identically 0.

EXAMPLE 3.8. Consider the following nonlinear k-state age-structured demographic model in $L^1(0, \alpha; \mathbb{R}^k)$:

$$\begin{aligned} n_t(a,t)+n_a(a,t) &= R(a,N(t))\,n(a,t), \qquad a>0, \quad t>0,\\ n(0,t) &= \int_0^\alpha B(a,N(t))\,n(a,t)\,da, \qquad t>0,\\ n(a,0) &= \phi(a), \qquad a>0,\\ N(t) &= \|n(\cdot,t)\|_1. \end{aligned} \tag{3.8}$$

Here $n(a,t)=(n_1(a,t),...,n_k(a,t))^t$, $n_i(a,t)$, $1\leqslant i\leqslant k$, is the ith-subpopulation density function at time t. $R(a,N)$ is the density dependent state-transition rate matrix whose ijth entry $r_{ij}(a,N)\geqslant 0$, $i\neq j$, is the transition rate at age a from state j to state i when the total population is N, and whose diagonal entries are $r_{ii}(a,N)=-\mu_i(a)-\sum_{j\neq i} r_{ji}(a,N)$, where $\mu_i(a)\geqslant 0$ is the (density-independent) natural mortality in the ith state, $B(a,N)$ is the fertility matrix whose ijth entry $b_{ij}(a,N)$ is the average number of offspring in state i per unit time produced by an individual at age a in state j when the total population is N, α is the maximum reproductive age, and $\phi\in L^1_+(0,\alpha;\mathbb{R}^k)$ is the initial population distribution.

We require that each r_{ij} and b_{ij} is Lipschitz continuous in N on bounded sets of $[0,\alpha]\times\mathbb{R}_+$ either nondecreasing or nonincreasing in N, and that the limits $r_{ij}(a,\infty):=\lim_{N\to\infty} r_{ij}(a,N)$ and $b_{ij}(a,\infty):=\lim_{N\to\infty} b_{ij}(a,N)$ are finite and exist uniformly for $a\in[0,\alpha]$ with

$$\max_{a\in[0,\alpha]}\int_{r_0}^\infty (|r_{ij}(a,N)-r_{ij}(a,\infty)|/N)\,dN<\infty,$$

$$\max_{a\in[0,\alpha]}\int_{r_0}^\infty (|b_{ij}(a,N)-b_{ij}(a,\infty)|/N)\,dN<\infty, \qquad r_0>0.$$

Let $Q(a)$ be the matrix with entries $q_{ij}(a)=r_{ij}(a,\infty)$, $i\neq j$, $q_{ii}(a)=-\mu_i(a)-\sum_{i\neq j} r_{ji}(a,\infty)$ and let $M(a)$ be the matrix with entries $m_{ij}(a)=b_{ij}(a,\infty)$. We require that $\mu_i, q_i\in C_+[0,\alpha;\mathbb{R}]$ and $m_{ij}\in L^\infty_+(0,\alpha;\mathbb{R})$. Finally define $h(a,N)$ as the matrix with entries $h_{ij}(a,N)=r_{ij}(a,N)-r_{ij}(a,\infty)$, $i\neq j$, and $h_{ii}(a,N)=-\sum_{j\neq i}[r_{ji}(a,N)-r_{ji}(a,\infty)]$ and define $g(a,N)$ as the matrix with entries $g_{ij}(a,N)=b_{ij}(a,N)-b_{ij}(a,\infty)$. The model (3.8) can now be written as a perturbed linear system

$$\begin{aligned} n_t(a,t)+n_a(a,t) &= Q(a)\,n(a,t)+h(a,N(t))\,n(a,t),\\ n(0,t) &= \int_0^\alpha M(a)\,n(a,t)\,da+\int_0^\alpha g(a,N(t))\,n(a,t)\,da,\\ n(a,0) &= \phi(a),\\ N(t) &= \|n(\cdot,t)\|_1. \end{aligned} \tag{3.9}$$

The linear system $(h \equiv 0, g \equiv 0)$ has been analyzed by Inaba [24]. He showed that the operator $A^{\odot}$ defined by $(A^{\odot}\phi)(a) = -\phi(a) + Q(a)\,\phi(a)$, $\mathscr{D}(A^{\odot}) = \{\phi \in L^1(0, \alpha; \mathbb{R}^k) : \phi$ is absolutely continuous, $\phi(0) = \int_0^\alpha M(a)\,\phi(a)\,da\}$ is the infinitesimal generator of a strongly continuous semigroup $T^{\odot}(t)$, $t \geq 0$ of positive linear operators in $L^1(0, \alpha, \mathbb{R}^k)$ (the reason for the use of the symbol $\odot$ will become clear below). Following Inaba we define $\psi(\lambda) = \int_0^\alpha e^{-\lambda a} M(a)\,J(a)\,da$, where $J(a)$ is the solution of the matrix differential equation $J'(a) = Q(a)\,J(a)$, $J(0) = I$ ($\psi(0)$ is the net reproductive matrix). We suppose that $\psi(0)$ is indecomposable (that is, there do not exist two subsets K and H of integers such that $K \cap H = \phi$, $K \cup H = \{1, ..., k\}$, and $\psi_{ij} = 0$ for $i \in K$, $j \in H$) and that its Frobenius root is greater than 1. Consequently $T^{\odot}(t)$, $t \geq 0$ has uniform asynchronous exponential growth ergodic in $L^1_+(0, \alpha; \mathbb{R}^k)$ with intrinsic growth constant $\lambda > 0$ (λ is the unique real root of the equation $G(\lambda) = 1$, where $G(\lambda)$ is the Frobenius root of $\psi(\lambda)$) (see [24, Propositions 3.2, 3.3]).

The semigroup $T^{\odot}(t)$, $t \geq 0$ could also have been obtained using perturbation theory of dual semigroups (see [5]). In this way one obtains an integral w^*-semigroup $T^{\times}(t)$, $t \geq 0$ on $X^* = M([0, \alpha); \mathbb{R}^k)$ with generator $A^{\times}\phi = -\phi' + Q(\cdot)\phi + \int_0^\alpha M(a)\,\phi(a)\,da\,\delta$, $\mathscr{D}(A^{\times}) = \{\phi$ is an absolutely continuous measure and $-\phi' + Q(\cdot)\phi \in M([0, a); \mathbb{R}^k)\}$. Here δ is the Dirac measure concentrated at the origin. In this case $T^{\times}(t)$, $t \geq 0$ is actually a dual semigroup $T^*(t)$, $t \geq 0$ since $X = C_0([0, \alpha); \mathbb{R}^k)$ is sun-reflexive (cf. [5]). Moreover, $X^{\odot} = \overline{\mathscr{D}(A^{\times})}$ can be identified with $L^1(0, \alpha; \mathbb{R}^k)$ and $T^{\odot}(t)$, $t \geq 0$ and $A^{\odot}$ are exactly the semigroup and generator found in [24]. The model (3.9) can now be written abstractly as a semilinear Cauchy problem of the form (2.17) with $F: X^{\odot} \to X^*$ defined by

$$F(\phi) = h(\cdot, \|\phi\|)\phi + \int_0^\alpha g(a, \|\phi\|)\,\phi(a)\,da\,\delta.$$

In the first term on the right the L^1-density ϕ is interpreted as an absolutely continuous measure (recall the Radon–Nikodym isometry between L^1 and the absolutely continuous measures).

By the assumptions made it is obvious that F satisfies (H.2)′, (H.3)′, and (H.4). By Theorem 2.1 $T^{\times}(t)$, $t \geq 0$ satisfies (H.1)′ and thus we conclude from Theorem 2.2 that the nonlinear semigroup $S(t)$, $t \geq 0$ on $X^{\odot}$ associated with (3.9) also has uniform asynchronous exponential growth.

Next we show using Theorem 2.6 that the uniform asynchrononous exponential growth of $S(t)$, $t \geq 0$ is strictly positive on $X^{\odot}_+$. By [24, Proposition 3.2], (H.7)′ holds. We have to define L such that (H.6)′ is satisfied. First note that $h_{ij}(a, N) \geq 0$ if and only if $r_{ij}(a, N)$ is nonincreasing in N $(i \neq j)$ and $g_{ij}(a, N) \geq 0$ if and only if $b_{ij}(a, N)$ is nonincreasing in N. Define for $i \neq j$, $l^h_{ij}(a) = -[r_{ij}(a, 0) - r_{ij}(a, \infty)]$ if $r_{ij}(a, N)$ is nondecreasing in N and $l^h_{ij}(a)=0$ otherwise. Define $l^h_{ii}(a)=\sum[r_{ji}(a,0)-r_{ji}(a,\infty)]$, where the sum is taken over all j for which $r_{ji}(a,N)$ is nonincreasing. Define $l^g_{ij}(a)=-[b_{ij}(a,0)-b_{ij}(a,\infty)]$ if $b_{ij}(a,N)$ is nondecreasing in N and $l^g_{ij}(a)=0$ otherwise. These definitions determine matrix valued functions l^h and l^g. Define the bounded linear operator $L\colon X^{\odot}\to X^*$ by

$$L\phi=l^h\phi+\int_0^\alpha l^g(a)\,\phi(a)\,da\,\delta.$$

By the definitions made above $L\phi+F(\phi)\geqslant 0$ for all $\phi\in X^{\odot}_{+}$. Moreover, the generator $A^{\odot}_L$ (the part of $A^{\times}-L$ in $X^{\odot}$) defines a strongly continuous linear semigroup $T^{\odot}_L(t)$, $t\geqslant 0$ on $X^{\odot}$ associated with the problem

$$\begin{aligned} n_t(a,t)+n_a(a,t)&=\hat{Q}(a)\,n(a,t).\\ n(0,t)&=\int_0^\alpha \hat{M}(a)\,n(a,t)\,da, \qquad (3.10)\\ n(a,0)&=\phi(a), \end{aligned}$$

where $\hat{q}_{ij}(a)$ is either $r_{ij}(a,\infty)$ or $r_{ij}(a,0)$ depending on whether $r_{ij}(a,N)$ is nonincreasing on nondecreasing in N $(i\neq j)$ and $\hat{q}_{ii}(a)=-\mu_i(a)-\sum_{j\neq i}\hat{q}_{ji}(a)$, and $\hat{m}_{ij}(a)=b_{ij}(a,\infty)$ if $b_{ij}(a,N)$ is nonincreasing and $\hat{m}_{ij}(a)=b_{ij}(a,0)$ otherwise. Thus problem (3.10) is of exactly the same type as the unperturbed version of (3.9) and we may conclude exactly as above that $T^{\odot}_L(t)$, $t\geqslant 0$ is a positive semigroup having uniform asynchronous exponential growth strictly positive on $X^{\odot}_{+}$. Thus we may apply Theorem 2.6.

The ijth entry $q_{ij}(a)$ of $Q(a)$ represents the rate at which an individual born in the jth state will survive and be in the ith state at age a. Indecomposibility of the net reproduction rate matrix $\psi(0)$ means there does not exist $K\cup H=\{1,\ldots,k\}$ such that $K\cap H=\phi$ and $\sum_k m_{ik}(a)\,q_{kj}(a)=0$ for $i\in K$, $j\in H$, $a\in[0,\alpha]$; that is, no proper set K of population states is closed with respect to self-reproduction in the sense that individuals in K can only be reproduced by individuals from K (see [24]). Indecomposibility of $\hat{\psi}(0)$ means that no proper set K of population states is closed with respect to self-reproduction when the total population is sufficiently large.

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