



## Note on stability conditions for structured population dynamics models

*Dedicated to Professor Tibor Krisztin on the occasion of his 60th birthday*

Yukihiko Nakata 

Department of Mathematics, Shimane University, Nishikawatsu-cho 1060, Matsue, 690-8504, Japan

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**Abstract.** We consider a characteristic equation to analyze asymptotic stability of a scalar renewal equation, motivated by structured population dynamics models. The characteristic equation is given by

$$1 = \int_0^{\infty} k(a)e^{-\lambda a} da,$$

where  $k : \mathbb{R}_+ \rightarrow \mathbb{R}$  can be decomposed into positive and negative parts. It is shown that if delayed negative feedback is characterized by a convex function, then all roots of the characteristic equation locate in the left half complex plane.

**Keywords:** structured population dynamics model, stability, characteristic equation.

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### 1 Introduction

Structured population models describe population dynamics incorporating certain variability at the individual level such as age or body size. To describe dynamics of heterogeneous population, the physiological process at the individual level is an essential modelling ingredient [18, 30]. The incorporation of population heterogeneity leads to infinite dimensional dynamical systems. Structured population models are traditionally formulated by hyperbolic partial differential equations [30, 39].

Alternatively, many structured population models can be formulated by delay equations: a system of renewal equations (Volterra type integral equations) and delay differential equations [11, 18]. See [14] for a consumer-resource model and [1, 15] for a cell population dynamical model. In the papers [32, 33] we formulated an epidemic model, where infective population is structured by age-since-infection, by a system of delay equations and derive its characteristic equation to study stability of an endemic equilibrium. Due to the infinite-dimensional nature

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 Email: ynakata@riko.shimane-u.ac.jp

of the structured population dynamical model, stability analysis is a challenging task. In particular, when one analyzes (in)stability of a positive equilibrium, where population of interest persists, often a complicated characteristic equation arises. In [6, 7, 35] numerical approaches are proposed to study stability of structured population models.

In this paper we analyze a characteristic equation, corresponding to a scalar renewal equation

$$y(t) = \int_0^\infty k(a)y(t-a)da, \quad (1.1)$$

where  $k : \mathbb{R}_+ \rightarrow \mathbb{R}$  satisfies certain conditions (see Section 3 of [12], see also Section 3 of this paper). For some  $\rho > 0$  let  $L_\rho^1(\mathbb{R}_-; \mathbb{R})$  be the space consisting of all equivalence classes of measurable functions  $\phi : \mathbb{R}_- \rightarrow \mathbb{R}$  such that the weighted integral with respect to the function  $a \mapsto e^{-\rho a}$ ,  $a \in \mathbb{R}_+$  is finite i.e.,

$$\int_0^\infty |\phi(-a)| e^{-\rho a} da < \infty.$$

Initial condition for (1.1) is given as  $y(\theta) = \psi(\theta)$ ,  $\theta \leq 0$  with  $\psi \in L_\rho^1(\mathbb{R}_-; \mathbb{R})$ . Exponential stability of the trivial solution of (1.1) is determined by the location of complex roots in  $\mathbb{C}$  of the characteristic equation:

$$1 = \int_0^\infty k(a)e^{-\lambda a} da, \quad \operatorname{Re} \lambda > -\rho. \quad (1.2)$$

If all the roots of the characteristic equation (1.2) have negative real part, then the trivial solution of (1.1) is exponentially stable, while if there exists at least one root with positive real part then the trivial solution is unstable, see Theorem 3.15 in [12]. See also [11] for the finite delay case.

In Section 2 of this paper we introduce some structured population models formulated by the following scalar nonlinear delay equation:

$$x(t) = F(x_t), \quad (1.3)$$

where  $F$  is a mapping from  $L_\rho^1(\mathbb{R}_-; \mathbb{R}) \rightarrow \mathbb{R}$ . We here use a standard notation from the theory of functional differential equations [16, 28]

$$x_t : \mathbb{R}_- \rightarrow \mathbb{R}$$

defined by the relation  $x_t(\theta) = x(t+\theta)$ ,  $\theta \leq 0$ . Assuming that there exists a constant solution  $\bar{x}$  for (1.3), we can linearize the nonlinear equation (1.3) around the constant solution, if  $F$  is continuously differentiable. Linearized equation is given by (1.1) with

$$DF(\bar{x})\psi = \int_0^\infty k(a)\psi(-a)da.$$

In [11, 12] the principle of linearized stability is established, so it is now rigorously shown that distribution of complex roots of (1.2) characterizes exponential stability and instability of a constant solution of the nonlinear delay equation (1.3).

Stability analysis for the positive equilibrium is often our interest when we analyze structured population dynamics models, but complexity of the characteristic equation is an obstacle and either simplification [1, 32, 33] or numerical approaches [6, 35] are required. Linearization of (1.3) around the trivial state  $\bar{x} = 0$  leads, in many examples, (1.1) with  $k(a) \geq 0$  for all  $a$ . We thus get Lotka's characteristic equation (1.2). It is well known that if  $\int_0^\infty k(a)da < 1$  then

the trivial state is exponentially stable while if  $\int_0^\infty k(a)da > 1$  then it is unstable. The quantity  $\int_0^\infty k(a)da$ , called as the basic reproduction number, determines population extinction and growth [17]. However, linearizing the equation (1.1) around a *positive* equilibrium, one often obtains linear equation (1.1) with positive and negative feedback. In this situation, differently from Lotka's characteristic equation, our understanding of the location of roots for (1.2) is still limited.

Characteristic equations derived from delay differential equations are closely related to the equation (1.2). In [28, 36] several types of transcendental equations have been studied. When delay is distributed, the stability analysis is quite involved [2, 3, 8, 21, 27, 31, 38]. In [3] the authors consider a differential equation with distributed delay and show that the variation of the delay distribution promotes stability. In [27, 31] the authors pay attention to symmetry of distributed delays and obtain stability conditions.

The paper is organized as follows. In Section 2 we introduce two structured population dynamics models, which can be formulated by the nonlinear renewal equation (1.3). We compute the characteristic equation for the positive equilibrium. In Section 3, motivated by examples shown in Section 2, we analyze the characteristic equation (1.2), assuming that  $k$  has both positive and negative parts. We derive some sufficient conditions for nonexistence of roots in the right half complex plane. In Section 5 we discuss our results.

## 2 Structured population dynamics models

In this section we introduce structured population dynamics models, which can be expressed by a nonlinear scalar renewal equation (1.3). We then show that the characteristic equation for the positive equilibrium is given by (1.2).

### 2.1 Epidemic model with waning immunity

Let  $S(t)$  denotes the number of susceptible population at time  $t$  and  $\Lambda(t)$  be the force of infection at time  $t$ . In [32] we formulate an epidemic model with waning immunity:

$$S'(t) = -S(t)\Lambda(t) + \int_0^\infty S(t-a)\Lambda(t-a)\mathcal{G}(a)da, \quad (2.1a)$$

$$\Lambda(t) = \int_0^\infty \beta(a)S(t-a)\Lambda(t-a)\mathcal{F}(a)da, \quad (2.1b)$$

where  $\beta(a)$  denotes the age-specific transmission coefficient of infected individuals whose infection-age is  $a$ ,  $\mathcal{F}$  is a probability function, for an infected individual, to be infectious until his or her infection-age becomes  $a$  and  $\mathcal{G}$  denotes a probability per unit of time to obtain susceptibility after infection. We assume that  $\beta$ ,  $\mathcal{F}$  and  $\mathcal{G}$  are positive functions from  $\mathbb{R}_+$  to  $\mathbb{R}_+$ . From the interpretation,  $\mathcal{F}$  is a decreasing function with  $\mathcal{F}(0) = 1$  and  $\int_0^\infty \mathcal{G}(a)da = 1$  holds. We also refer to [33] for the formulation of an epidemic model by delay equations.

Infective population  $I(t)$  and summation of infective and recovered population  $I(t) + R(t)$  at time  $t$  are respectively given as

$$I(t) = \int_0^\infty S(t-a)\Lambda(t-a)\mathcal{F}(a)da, \quad (2.2)$$

$$I(t) + R(t) = \int_0^\infty S(t-a)\Lambda(t-a)\mathcal{L}(a)da, \quad (2.3)$$

where

$$\mathcal{L}(a) := 1 - \int_0^a \mathcal{G}(s) ds$$

is the probability for individuals who was infected not to obtain susceptibility since the last infection.

To compute the characteristic equation we derive a scalar nonlinear renewal equation (1.3). Since demography is ignored in (2.1), we can assume that

$$S(t) + I(t) + R(t) = S(t) + \int_0^\infty S(t-a)\Lambda(t-a)\mathcal{L}(a)da = 1 \quad (2.4)$$

holds for any  $t$  (here 1 is a total population, or one may interpret  $S, I$  and  $R$  as population fraction). Denote by  $b(t)$  newly infectives per unit time:  $b(t) = S(t)\Lambda(t)$ . From (2.4) and (2.1b) we see that

$$\begin{aligned} S(t) &= 1 - \int_0^\infty b(t-a)\mathcal{L}(a)da, \\ \Lambda(t) &= \int_0^\infty \beta(a)b(t-a)\mathcal{F}(a)da. \end{aligned}$$

So we obtain a scalar renewal equation for  $b$ :

$$b(t) = \left(1 - \int_0^\infty b(t-a)\mathcal{L}(a)da\right) \int_0^\infty \beta(a)b(t-a)\mathcal{F}(a)da. \quad (2.5)$$

In [19] the authors consider a special case of (2.5). The basic reproduction number  $R_0$  ([17]) for (2.5) is computed as

$$R_0 := \int_0^\infty \beta(a)\mathcal{F}(a)da$$

and if  $R_0 > 1$  then there exists a unique endemic equilibrium

$$b = \frac{R_0 - 1}{\int_0^\infty \mathcal{L}(a)da}.$$

The characteristic equation for the endemic equilibrium can be computed as

$$1 = \frac{\int_0^\infty \beta(a)\mathcal{F}(a)e^{-\lambda a}da}{\int_0^\infty \beta(a)\mathcal{F}(a)da} - (R_0 - 1) \frac{\int_0^\infty \mathcal{L}(a)e^{-\lambda a}da}{\int_0^\infty \mathcal{L}(a)da}, \quad (2.6)$$

after linearization of (2.5) around the endemic equilibrium. We therefore obtain the characteristic equation (1.2) with

$$k(a) = \frac{\beta(a)\mathcal{F}(a)}{\int_0^\infty \beta(a)\mathcal{F}(a)da} - (R_0 - 1) \frac{\mathcal{L}(a)}{\int_0^\infty \mathcal{L}(a)da}.$$

## 2.2 Gurtin and McCamy model

Here we present a special case of age structured population model formulated by Gurtin and McCamy in the famous paper [23]:

$$(\partial_t + \partial_a) n(t, a) = -\gamma(a)n(t, a), \quad (2.7a)$$

$$n(t, 0) = \int_0^\infty \beta(a, P(t))n(t, a)da, \quad (2.7b)$$

with

$$P(t) = \int_0^{\infty} n(t, a) da.$$

Here  $\beta(\cdot, P) \in L^\infty(\mathbb{R}_+; \mathbb{R}_+)$  denotes the fecundity rate and  $\gamma \in L^\infty(\mathbb{R}_+; \mathbb{R}_+)$  is the mortality rate.

The Gurtin–McCamy model (2.7) can be alternatively formulated by the following scalar delay equation. See also Section 3.5 in [11].

$$b(t) = \int_0^{\infty} \beta(a, J(b_t)) b(t-a) e^{-\int_0^a \gamma(s) ds} da, \quad (2.8)$$

where  $J : L^1(\mathbb{R}_-; \mathbb{R}_+) \rightarrow \mathbb{R}_+$  is defined as

$$J(\phi) = \int_0^{\infty} \phi(-a) e^{-\int_0^a \gamma(s) ds} da.$$

In [23] Gurtin and McCamy also formulated a system of integral equations.

Assume that there exists a positive constant equilibrium of (2.8) satisfying

$$1 = \int_0^{\infty} \beta(a, J(\bar{b})) e^{-\int_0^a \gamma(s) ds} da,$$

where  $\bar{b}$  is a constant solution and is positive. The characteristic equation for the positive equilibrium can be given as (1.2) with

$$k(a) = \beta(a, J(\bar{b})) e^{-\int_0^a \gamma(s) ds} - c \frac{e^{-\int_0^a \gamma(s) ds}}{\int_0^{\infty} e^{-\int_0^a \gamma(s) ds} da},$$

where

$$c = -b \int_0^{\infty} \partial_2 \beta(a, J(\bar{b})) e^{-\int_0^a \gamma(s) ds} da \int_0^{\infty} e^{-\int_0^a \gamma(s) ds} da.$$

### 3 Stability criterion

We consider the characteristic equation (1.2), motivated by examples in Section 2. It is assumed that  $k$  has both negative and positive parts:

$$k(a) = p(a) - Q(a),$$

where  $p, Q : \mathbb{R}_+ \rightarrow \mathbb{R}_+$ . To apply the principle of linearized stability established in Theorem 3.15 in [12], we assume that

$$\begin{aligned} \int_0^{\infty} p(a) e^{\rho a} da < \infty, & \quad \text{ess sup}_{a \in \mathbb{R}_+} p(a) e^{\rho a} < \infty, \\ \int_0^{\infty} Q(a) e^{\rho a} da < \infty, & \quad \text{ess sup}_{a \in \mathbb{R}_+} Q(a) e^{\rho a} < \infty \end{aligned}$$

hold for some  $\rho > 0$ . Population dynamics models in Section 2 motivate us to put

**Assumption 3.1.** It holds that

$$\int_0^{\infty} p(a) da = 1 \quad (3.1)$$

and that  $Q$  is a non-increasing function.

The first assumption (3.1) amounts to that one individual produces exactly one individual in the entire life time when population reaches the positive equilibrium. Since  $Q$  can be associated to survival probability functions, we can assume the monotonicity.

Let us put

$$q(a) := \frac{Q(a)}{\int_0^\infty Q(a) da}$$

and then define

$$c := \int_0^\infty Q(a) da > 0.$$

The characteristic equation (1.2) is now given as

$$1 = \int_0^\infty p(a)e^{-\lambda a} da - c \int_0^\infty q(a)e^{-\lambda a} da, \quad \operatorname{Re} \lambda > -\rho. \quad (3.2)$$

Our first step is to show that there is no root with  $\operatorname{Re} \lambda > 0$  if  $c > 0$  is small enough.

**Proposition 3.1.** *Equation (3.2) has a root  $\lambda = 0$  if and only if  $c = 0$ . If  $c > 0$  is small enough, (3.2) has no root  $\lambda$  with  $\operatorname{Re} \lambda \geq 0$ .*

*Proof.* It is easy to see that (3.2) has no root with positive real part and that  $\lambda = 0$  is a root when  $c = 0$  holds. To show that the root  $\lambda = 0$  moves to the left half complex plane as  $c$  increases, we apply the implicit function theorem. We compute

$$\lambda'(c) = -\frac{-\int_0^\infty q(a)e^{-\lambda a} da}{-\int_0^\infty ap(a)e^{-\lambda a} da + c \int_0^\infty aq(a)e^{-\lambda a} da}.$$

For  $\lambda = \lambda(c)$  with  $\lambda(0) = 0$  we have

$$\operatorname{Re} \lambda'(0) = -\frac{\int_0^\infty q(a) da}{\int_0^\infty ap(a) da} < 0.$$

Thus we obtain the conclusion. □

Next we show that

**Lemma 3.2.** *Let  $\lambda$  be a root of (3.2) with  $\operatorname{Re} \lambda = \mu > 0$ . Then*

$$|\lambda| \leq \frac{2q(0)c}{1 - \int_0^\infty p(a)e^{-\mu a} da} \quad (3.3)$$

*holds.*

*Proof.* By partial integration we compute that

$$\int_0^\infty q(a)e^{-\lambda a} da = \frac{1}{\lambda} \left( q(0) + \int_0^\infty e^{-\lambda a} dq(a) \right),$$

noting that  $q$  is a decreasing function, thus it is a bounded variation function such that  $\int_0^\infty dq(a) = -q(0)$ . We can rewrite (3.2) as

$$\lambda = -c \frac{q(0) + \int_0^\infty e^{-\lambda a} dq(a)}{1 - \int_0^\infty p(a)e^{-\lambda a} da}.$$

Assume that  $\operatorname{Re} \lambda = \mu > 0$  holds. Since  $|\int_0^\infty p(a)e^{-\lambda a} da| \leq \int_0^\infty p(a)e^{-\mu a} da$  holds, we get

$$\left| 1 - \int_0^\infty p(a)e^{-\lambda a} da \right| \geq 1 - \int_0^\infty p(a)e^{-\mu a} da > 0.$$

It also holds

$$\left| q(0) + \int_0^\infty e^{-\lambda a} dq(a) \right| \leq 2q(0).$$

Therefore we obtain the estimation as in (3.3).  $\square$

In Lemma 3.2 we obtain a priori bounds for roots, in the right half complex plane, of the characteristic equation (3.2). Note that

$$\lambda \mapsto 1 - \int_0^\infty p(a)e^{-\lambda a} da + c \int_0^\infty q(a)e^{-\lambda a} da$$

is an analytic function for  $\operatorname{Re} \lambda > -\rho$ , see e.g. Chapter 6 of [20]. By the application of Rouché's theorem, see Lemma 2.8 in Chapter XI of [16], roots can enter or leave the right half complex plane only through the imaginary axis, varying the parameter.

Let us increase the parameter  $c$  and see if roots cross the imaginary axis and move to the right half complex plane. To consider this situation, we assume that there exists  $c > 0$  such that (3.2) has a conjugate pair of imaginary roots. Substituting  $\lambda = i\omega$ ,  $\omega \in \mathbb{R}_+ \setminus \{0\}$  we get

$$1 = \int_0^\infty p(a) \cos(\omega a) da - c \int_0^\infty q(a) \cos(\omega a) da, \quad (3.4)$$

$$0 = \int_0^\infty p(a) \sin(\omega a) da - c \int_0^\infty q(a) \sin(\omega a) da. \quad (3.5)$$

Let us state an implicit stability criterion.

**Lemma 3.3.** *If*

$$\int_0^\infty q(a) \cos(\omega a) da \geq 0 \quad (3.6)$$

*holds for any  $\omega \geq 0$ , then (3.2) has no root  $\lambda$  with  $\operatorname{Re} \lambda \geq 0$ .*

*Proof.* Since

$$1 - \int_0^\infty p(a) \cos(\omega a) da > 0,$$

holds for any  $\omega > 0$  from Assumption 3.1, equality in (3.4) does not hold. Hence there is no  $c$  such that  $\lambda = \pm i\omega$  is a conjugate pair of roots of (3.2). From Proposition 3.1, for sufficiently small  $c$ , (3.2) has no root  $\lambda$  with  $\operatorname{Re} \lambda \geq 0$ . By way of Rouché's theorem (see Lemma 2.8 in Chapter XI of [16]), (3.2) has no root  $\lambda$  with  $\operatorname{Re} \lambda \geq 0$  for every  $c > 0$ . Thus we obtain the conclusion.  $\square$

To obtain an explicit condition for  $q$  such that (3.6) holds, we introduce a result of positivity of Fourier transforms from [37]. Let us assume that  $\nu \in L^1(\mathbb{R}_+; \mathbb{R}_+)$  and that  $\nu$  is a non-increasing function. It holds

$$\int_0^\infty \nu(a) \sin(\omega a) da = \sum_{j=0}^{\infty} \int_{\frac{2\pi j}{\omega}}^{\frac{2\pi(j+1)}{\omega}} \nu(a) \sin(\omega a) da.$$

For  $j \in \mathbb{N}_+$  we have

$$\begin{aligned} & \int_{\frac{2\pi j}{\omega}}^{\frac{2\pi(j+1)}{\omega}} v(a) \sin(\omega a) da \\ &= \int_{\frac{2\pi j}{\omega}}^{\frac{2\pi j + \pi}{\omega}} v(a) \sin(\omega a) da + \int_{\frac{2\pi j + \pi}{\omega}}^{\frac{2\pi(j+1)}{\omega}} v(a) \sin(\omega a) da \\ &= \int_{\frac{2\pi j}{\omega}}^{\frac{2\pi j + \pi}{\omega}} v(a) \sin(\omega a) da - \int_{\frac{2\pi j}{\omega}}^{\frac{2\pi j + \pi}{\omega}} v\left(a + \frac{\pi}{\omega}\right) \sin(\omega a) da. \end{aligned}$$

Let

$$g(a) := v(a) - v\left(a + \frac{\pi}{\omega}\right), \quad a \in \mathbb{R}_+.$$

Since  $v$  is non-increasing,  $g(a) \geq 0$  holds for any  $a$ . Therefore, we obtain that

$$\int_0^\infty v(a) \sin(\omega a) da = \sum_{j=0}^\infty \int_{\frac{2\pi j}{\omega}}^{\frac{2\pi j + \pi}{\omega}} g(a) \sin(\omega a) da \geq 0.$$

We summarize the result above, which can be found in [37].

**Lemma 3.4.** *Let  $v \in L^1(\mathbb{R}_+; \mathbb{R}_+)$ . If  $v$  is a non-increasing function then*

$$\int_0^\infty v(a) \sin(\omega a) da \geq 0$$

for any  $\omega \geq 0$ .

We say that  $\kappa : \mathbb{R}_+ \rightarrow \mathbb{R}$  is a convex function if for any  $a_1, a_2 \in \mathbb{R}_+$  and for any  $h \in [0, 1]$

$$\kappa(ha_1 + (1-h)a_2) \leq h\kappa(a_1) + (1-h)\kappa(a_2)$$

holds.

**Theorem 3.5.** *Let us assume that  $q$  is a convex function. Then (3.2) has no root  $\lambda$  with  $\operatorname{Re} \lambda \geq 0$ .*

*Proof.* To apply Lemma 3.3 we show that (3.6) holds. Since  $q : \mathbb{R}_+ \rightarrow \mathbb{R}_+$  is absolutely continuous, there exists  $d \in L^1_{\text{loc}}$  such that  $-q'(a) = d(a)$ . We compute

$$\int_0^\infty q(a) \cos(\omega a) da = \frac{1}{\omega} \int_0^\infty d(a) \sin(\omega a) da.$$

Since  $d$  is a decreasing function, see also Chapter 3 in [40], from Lemma 3.4 we obtain (3.6). By Lemma 3.3 we get the conclusion.  $\square$

Convexity of distribution of delay is used to study a characteristic equation derived from a delay differential equation in [38]. See also [22] for stability analysis of a difference equation. See also Propositions 4.3 and 4.4 in Chapter IV of [26] for similar results if  $q$  is differentiable.

We note that the convexity is not a necessary condition for Lemma 3.3. Indeed there is an important example for  $q$  such that (3.6) holds but it is not a convex function, see Appendix A for the proof.

**Example 3.6.** Let

$$q(a) = \frac{e^{-\alpha_1 a} + \alpha_1 \int_0^a e^{-\alpha_2 s - \alpha_1(a-s)} ds}{\frac{1}{\alpha_1} + \frac{1}{\alpha_2}}$$

where  $\alpha_1, \alpha_2 > 0$ . One sees that  $q$  is a decreasing function and that (3.6) holds, but  $q$  is not convex for small  $a$ .



We can also deduce another stability condition.

**Theorem 3.7.** *Let us assume that  $p = q$  holds, then (3.2) has no root  $\lambda$  with  $\operatorname{Re} \lambda \geq 0$ .*

*Proof.* Assuming that  $\lambda = \pm i\omega$ ,  $\omega > 0$  is a purely imaginary root, from (3.4) and (3.5), we have

$$1 = (1 - c) \int_0^\infty q(a) \cos(\omega a) da, \quad (3.7)$$

$$0 = \int_0^\infty q(a) \sin(\omega a) da. \quad (3.8)$$

Observe that

$$\int_0^\infty q(a) \sin(\omega a) da = \frac{1}{\omega} \left( q(0) + \int_0^\infty dq(a) \cos(\omega a) \right) = 0,$$

thus  $\int_0^\infty dq(a) \cos \omega a = -q(0)$  holds. On the other hand,

$$\left( \int_0^\infty dq(a) \cos(\omega a) \right)^2 + \left( \int_0^\infty dq(a) \sin(\omega a) \right)^2 \leq q(0)^2$$

holds, thus

$$\int_0^\infty q(a) \cos(\omega a) da = \frac{1}{\omega} \int_0^\infty dq(a) \sin(\omega a) = 0$$

follows, which is a contradiction to (3.7). Thus there is no  $c$  such that  $\lambda = \pm i\omega$  is a conjugate pair of roots of (3.2). Repeating the same argument in the proof of Lemma 3.3, we can conclude that, for every  $c > 0$ , (3.2) has no root  $\lambda$  with  $\operatorname{Re} \lambda \geq 0$ . Thus we obtain the conclusion.  $\square$

## 4 Discussion

The motivation of this paper comes from studies of characteristic equations in [1, 14, 19, 32, 33]. In the papers [1, 32, 33] we formulate structured population dynamics models by delay equations and derive characteristic equations to study stability of equilibria. The characteristic equations are not easy to handle due to multiple Laplace transforms, thus we simplify the characteristic equation to proceed the analysis. In the paper [33] we show that the assumption of waning immunity add complexity to the characteristic equation, compared to one of the epidemic model with permanent immunity (instability is actually possible due to the waning immunity, see also [24, 32, 34]). Our aim in this paper is to perform a systematic analysis of a class of characteristic equations and to obtain insights into roles of distributed positive and negative feedback (i.e., two distributed delays) in the position of complex roots of the characteristic equation.

In Section 2, we show that some structured population models can be expressed by a *scalar* nonlinear renewal equation (in terms of population birth rate) (1.3). As one can see in the examples in Section 2, the kernel  $k$  can be decomposed into positive and negative parts, corresponding to the reproduction of individuals and negative environmental feedback. In fact the positive equilibrium emerges as a balance of positive and negative feedback [13].

Using the results in Section 3, we can derive stability conditions for the endemic equilibrium of the model given in Section 2.1. For example, applying the result in Theorem 3.7 to the characteristic equation (2.6), we get

**Proposition 4.1.** *Let  $\beta(a) = \beta$  (constant) and  $\mathcal{F}(a) = \mathcal{L}(a)$ . Then the endemic equilibrium is asymptotically stable.*

This result is also given as a corollary of Theorem 5.1 of [24] (when the recovery period is zero), see also [25]. In the paper [25] the same condition was proposed but with a step function  $\mathcal{F}$ .

Let us consider a situation that both immunity and infectious periods are exponentially distributed. Then  $\mathcal{L}$  is given as

$$\mathcal{L}(a) = \mathcal{F}(a) - \int_0^a \mathcal{P}(a-s) d\mathcal{F}(s),$$

with

$$\mathcal{F}(a) = e^{-\alpha_1 a}, \quad \mathcal{P}(a) = e^{-\alpha_2 a},$$

where  $\alpha_1$  is the recovery rate and  $\alpha_2$  is the rate of immunity loss, see also [32]. It is indeed the case of Example 3.6. Thus it is shown that the endemic equilibrium is asymptotically stable. See also Theorem 3.6 in [33] for a similar result.

Analysis of the characteristic equation is a challenging issue in the study of structured population models [1, 4, 5, 14, 19, 32, 33]. It is known that stability analysis is much more involved when delay is *distributed*, rather than it is given in a single point [2, 3, 27, 28]. Indeed the distribution of the delay influences stability, see [2, 3, 27, 31, 38]. In this paper we aim to relate the delay distribution and stability property, since the distribution has an obvious biological meaning, such as survival probability and fecundity function, in the structured population models. Stability analysis of differential equation with multiple discrete delay is still challenging, see [29] and references therein.

## Appendix A Convolution of exponential functions

Let

$$\mathcal{F}(a) = e^{-\alpha_1 a}, \quad \mathcal{P}(a) = e^{-\alpha_2 a}, \quad a \in \mathbb{R}_+,$$

where  $\alpha_1, \alpha_2 > 0$ . Consider a function  $\mathcal{L}$  defined as

$$\mathcal{L}(a) = \mathcal{F}(a) - \int_0^a \mathcal{P}(a-s) d\mathcal{F}(s), \quad a \in \mathbb{R}_+.$$

From direct computations we get

$$\begin{aligned} \frac{d}{da} \mathcal{L}(a) &= -\alpha_1 \alpha_2 \int_0^a e^{-\alpha_2(a-s) - \alpha_1 s} ds, \\ \frac{d^2}{da^2} \mathcal{L}(a) &= -\alpha_1 \alpha_2 e^{-\alpha_1 a} + \alpha_1 \alpha_2^2 \int_0^a e^{-\alpha_2(a-s) - \alpha_1 s} ds. \end{aligned}$$

Thus one can see that  $\mathcal{L}$  is a decreasing function, but it is not convex for small  $a$ . The map  $q$  in Example 3.6 is obtained by

$$q(a) = \frac{\mathcal{L}(a)}{\int_0^\infty \mathcal{L}(a) da} = \frac{\mathcal{L}(a)}{\frac{1}{\alpha_1} + \frac{1}{\alpha_2}}.$$

For  $\lambda \in \mathbb{C}$ ,  $\text{Re } \lambda > -\alpha_{1,2}$  let us compute

$$\int_0^\infty \mathcal{L}(a) e^{-\lambda a} da = \int_0^\infty \mathcal{F}(a) e^{-\lambda a} da - \int_0^\infty \mathcal{P}(a) e^{-\lambda a} da \int_0^\infty e^{-\lambda a} d\mathcal{F}(a).$$

One can see that

$$\int_0^\infty \mathcal{F}(a)e^{-\lambda a} da = \frac{1}{\lambda + \alpha_1},$$

$$- \int_0^\infty \mathcal{P}(a)e^{-\lambda a} da \int_0^\infty e^{-\lambda a} d\mathcal{F}(a) = \frac{1}{\lambda + \alpha_2} \frac{\alpha_1}{\lambda + \alpha_1}.$$

Therefore we get

$$\int_0^\infty \mathcal{L}(a)e^{-\lambda a} da = \frac{\lambda + \alpha_1 + \alpha_2}{(\lambda + \alpha_1)(\lambda + \alpha_2)}. \quad (\text{A.1})$$

We now substitute  $\lambda = i\omega$  into (A.1) to get

$$\int_0^\infty \mathcal{L}(a) \cos(\omega a) da = \operatorname{Re} \frac{i\omega + \alpha_1 + \alpha_2}{(i\omega + \alpha_1)(i\omega + \alpha_2)}$$

$$= \frac{(\alpha_1 + \alpha_2) \alpha_1 \alpha_2}{(\alpha_1 \alpha_2 - \omega^2)^2 + \omega^2 (\alpha_1 + \alpha_2)}$$

$$> 0.$$

Therefore we obtain

$$\int_0^\infty q(a) \cos(\omega a) da = \frac{\int_0^\infty \mathcal{L}(a) \cos \omega a da}{\int_0^\infty \mathcal{L}(a) da} > 0.$$

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