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SINGLE SPECIES POPULATION DYNAMICS IN SEASONAL ENVIRONMENT WITH SHORT REPRODUCTION PERIOD

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Abstract. We present a periodic nonlinear scalar delay differential equation model for a population with short reproduction period. By transforming the equation to a discrete dynamical system, we reduce the infinite dimensional problem to one dimension. We determine the basic reproduction number not merely as the spectral radius of an operator, but as an explicit formula and show that is serves as a threshold parameter for the stability of the trivial equilibrium and for permanence.

1. Introduction.

The mating season of several animal species is limited to a short period each year. This phenomenon, called seasonal breeding, helps the survival of juveniles as the timing of breeding season allows to optimize factors as ambient temperature, nutrition availability, predation by other species. Sexual interest and behaviour of both sexes are expressed and accepted only in this period. As examples we might mention most of the bird species or the rut, i.e. the mating season of ruminant animals such as deer, elks, antelopes etc. For example, the rut of the white-tailed deer lasts approximately three weeks, that of the elk between 20 and 45 days. Sexual maturation of females may depend on population density. To model this type of reproduction behaviour, several studies (see e.g. [1, 7]) considered hybrid discrete–continuous models in which they assume that birth occurs at discrete time instants while death occurs throughout the whole year. To study the population dynamics of such a species, we propose the nonlinear scalar delay differential equation

$$x'(t) = -a(t)x(t) + f(t, x(t-1)), \tag{1}$$

with $f\colon \mathbb{R}\times[0,\infty)\to[0,\infty)$ satisfying

$$\begin{cases} f(t,x) = 0, & \text{if } kP \le t \le kP + L,\ k = 0,1,2,\dots, \\ f(t,x) > 0, & \text{elsewhere,} \end{cases}$$

where we assume $1 \le L < P < L+1$. That is, we denote by P the period of the seasonally changing environment and $P - L$ the length of the mating season. We note that P is usually equal to one year, however, in this work, for mathematical convenience, we set the maturation delay to be 1. The definition of f corresponds

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to the short mating season: there is no reproduction outside this period. The assumptions $1 \leq L < P < L+1$ are biologically realistic, as $P < L+1$ means that mating period is shorter than maturation period, which is in accordance with the above examples for seasonal breeders. The mortality rate $a(t)$ is a nonnegative, P-periodic continuous function, while is the density-dependent reproduction function, P-periodic in the first variable. We assume $f(t,0) = 0$ for all $t \in \mathbb{R}$.

2. Stability of the zero equilibrium of (1).

Our main goal in this section is to determine a formula for the asymptotic stability of the zero equilibrium of (1). In general, a stability condition for periodic delay differential equations cannot be given as an explicit formula [5, 8]. In order to find an explicit condition in the case of (1), we will first transcribe the equation to a discrete dynamical system. Considering the properties of $f(t,x)$, we can see that the equation $x'(t) = -a(t)x(t) + f(t, x(t-1))$ given in (1) can be written as $x'(t) = -a(t)x(t)$ on the interval $[0, L]$, hence, the solution of (1) on this interval can be obtained as

$$x(t) = x_0 e^{-\int_0^t a(u)\,\mathrm{d}u}. \tag{2}$$

Specially, for $t = L$, one has

$$x(L) = x_0 e^{-\int_0^L a(u)\mathrm{d}u}.$$

Substituting the right-hand side of (2) taken at time $t-1$ into the last term of (1), we get that for $L \leq t \leq P$, the equation takes the form

$$x'(t) = -a(t)x(t) + f\big(t, x_0 e^{-\int_0^{t-1} a(u)\,\mathrm{d}u}\big),$$

hence, on $[L, P]$ we obtain that the solution started from x_0 at $t = 0$ can be written as

$$x(t) = e^{-\int_L^t a(u)\,\mathrm{d}u} \left(x_0 e^{-\int_0^L a(u)\,\mathrm{d}u} + \int_L^t e^{\int_L^s a(u)\mathrm{d}u} f\big(s, x_0 e^{-\int_0^{s-1} a(u)\,\mathrm{d}u}\big)\,\mathrm{d}s \right),$$

and substituting $t = P$, this formula gives

$$x(P) = e^{-\int_L^P a(u)\,\mathrm{d}u} \left(x_0 e^{-\int_0^L a(u)\,\mathrm{d}u} + \int_L^P e^{\int_L^s a(u)\mathrm{d}u} f\big(s, x_0 e^{-\int_0^{s-1} a(u)\,\mathrm{d}u}\big)\,\mathrm{d}s \right),$$

yielding an explicit formula for the value of the solution evaluated at the end of the period.

Let us consider the discrete dynamical system induced by the function $\mathcal{F}\colon \mathbb{R} \to \mathbb{R}$, $x_0 \mapsto x(P; x_0)$, where $x(t; x_0)$ denotes the solution of (1) started from x_0 at $t = 0$. (We note that because of the special form of f, it is enough to set an initial value x_0 instead of an initial function.) The condition for the asymptotic stability of the zero equilibrium of the discrete system is $|\mathcal{F}'(0)| < 1$, i.e. the condition can be written as

$$\gamma := e^{-\int_0^P a(u)\,\mathrm{d}u} + e^{-\int_L^P a(u)\,\mathrm{d}u} \int_L^P e^{\int_L^s a(u)\mathrm{d}u} b(t) e^{-\int_0^{s-1} a(u)\,\mathrm{d}u}\,\mathrm{d}s < 1, \tag{3}$$

with $b(t) = D_2 f(t, 0)$, which yields us a necessary and sufficient condition for the asymptotic stability of the zero equilibrium of (1).

Proceeding the other way around, i.e. linearizing (1) first to obtain

$$x'(t) = -a(t)x(t) + b(t)x(t-1), \tag{4}$$

and then solving the linearized equation in an analogous way as it was done for (1), we obtain the same formula (3). To show that this condition also implies local asymptotic stability of the continuous system (4), see [3, Theorem 2.1 (iii)]. The above calculations show that the stability condition for the discrete dynamical system induced by $\mathcal{F}$ and that for the delay equation are the same. Based on general theory of linearized stability for delay differential equations, this condition serves as an explicit formula to determine the local asymptotic stability of the zero equilibrium of (1).

Note that the discrete dynamical system induced by $\mathcal{F}$ is closely related to Clark's equation [2].

We can easily obtain the following simple conditions for the global asymptotic stability of the zero solution of (1).

Proposition 1. *Let* $\gamma < 1$.

a) In case $\mathcal{F}$ *does not have any nontrivial fixed points* ($\mathcal{F}(x) < x$ *for all* x), *the trivial solution is also globally asymptotically stable.*

b) Let $f(t,x) \le b(t)x$ *hold for all* t, x. *Then the zero equilibrium of* (1) *is globally asymptotically stable.*

2.1. **Permanence for $\gamma > 1$ and bounded reproduction function.** In the previous subsection we have shown that for $\gamma < 1$, the zero equilibrium of (1) is locally asymptotically stable. The next result states that in the opposite case, the species is permanent for bounded f.

Proposition 2. *Suppose that* f *is bounded, let* $\max_{(t,x)} f(t,x) = M$. *If* $\gamma > 1$, *then the species is permanent, i.e. there exist* $\mathcal{m}, \mathcal{M} > 0$ *such that* $\mathcal{m} \le \liminf_{t\to\infty} x(t) \le \limsup_{t\to\infty} x(t) \le \mathcal{M}$ *for all initial value* $x_0 > 0$.

Proof. Let us suppose that $\gamma > 1$ holds.

Introducing the notation $\mathcal{I} = e^{-\int_0^P a(u)\,\mathrm{d}u} < 1$, we can give the following estimation for $\mathcal{F}$:

$$\begin{aligned} x_0 \mapsto x_1 &= \mathcal{I}x_0 + \int_L^P e^{-\int_s^P a(u)\,\mathrm{d}u} f(s, x_0 e^{-\int_0^{s-1} a(u)\,\mathrm{d}u})\,\mathrm{d}s \\ &\le \mathcal{I}x_0 + \int_L^P f(s, x_0 e^{-\int_0^{s-1} a(u)\,\mathrm{d}u})\,\mathrm{d}s \le \mathcal{I}x_0 + (P-L)M. \end{aligned}$$

By iterating $\mathcal{F}$, we obtain similarly that

$$\mathcal{F}^n(x_0) =: x_n \le \mathcal{I}^n x_0 + \sum_{k=0}^{n-1} (P-L)M\mathcal{I}^k = \mathcal{I}^n x_0 + (P-L)M\frac{\mathcal{I}^{n-1} - 1}{\mathcal{I} - 1}.$$

Let $\mathfrak{M} > \frac{(P-L)M}{1-\mathcal{I}}$. Then, for n large enough, $\mathcal{F}^n(x_0) < \mathfrak{M}$. As $\gamma > 1$, there exists a minimal $\delta > 0$ such that $\mathcal{F}(\delta) = \delta$. Let $\mathfrak{m} := \min_{\delta \le x \le \mathfrak{M}} \mathcal{F}(x)$. We obtain from the above that, for n large enough, $\mathcal{F}^n(x_0) < \mathfrak{M}$, while it follows from the properties of δ and $\mathfrak{m}$ that if $x \in [\delta, \mathfrak{M}]$, then $\mathcal{F}(x) \in [\mathfrak{m}, \mathfrak{M}]$, hence, we have that $\mathcal{F}^n(x_0) \in [\mathfrak{m}, \mathfrak{M}]$ for n large enough.

Now, applying an argumentation analogous to the one in the proof of [3, Theorem 2.1 (iii)], we prove that the permanence of the continuous model follows from that of the discrete dynamical system.

Let us define

$$m_k := \min_{kP \le t \le (k+1)P} x(t; x_0) \quad \text{and} \quad M_k := \max_{kP \le t \le (k+1)P} x(t; x_0), \qquad k = 0, 1, 2, \ldots$$

and denote by t_{m_k} and t_{M_k} the time instants when these values are attained, respectively. Using the comparison method from [6, Theorem 3.6], and the simple estimation $x'(t) \geq -a(t)x(t)$, we get that for any $t_2 \geq t_1$,

$$x(t_2) \geq x(t_1)e^{-\int_{t_1}^{t_2}} a(u)\,\mathrm{d}u.$$

Specially, we have

$$\begin{aligned} m_{k+1} &\geq x(kP)e^{-\int_{kP}^{t_{m_{k+1}}} a(u)\,\mathrm{d}u} \geq x(kP)e^{-\int_{kP}^{(k+1)P} a(u)\,\mathrm{d}u} \\ &= x(kP)e^{-\int_0^P a(u)\,\mathrm{d}u} \geq \mathfrak{m}\, e^{-\int_0^P a(u)\,\mathrm{d}u} =: \mathscr{m} \end{aligned}$$

and

$$x(kP) \geq M_k e^{-\int_{t_{M_k}}^{kP} a(u)\,\mathrm{d}u} \geq M_k e^{-\int_{(k-1)P}^{kP} a(u)\,\mathrm{d}u} = M_k e^{-\int_{(k-1)P}^{kP} a(u)\,\mathrm{d}u},$$

the latter inequality yielding

$$M_k \leq \mathfrak{M}\, e^{\int_0^P a(u)\,\mathrm{d}u} =: \mathcal{M}.$$

Hence, we have shown that for the solution $x(t;t_0,x_0)$ of (1) started from x_0 there exist $\mathscr{m}, \mathcal{M} > 0$ such that $\mathscr{m} \leq \liminf_{t\to\infty} x(t) \leq \limsup_{t\to\infty} x(t) \leq \mathcal{M}$, i.e. the species is permanent if $\gamma > 1$. ☐

3. Existence and stability of positive equilibrium.

As we have seen above, the zero equilibrium of the nonlinear model (1) loses its local stability when $\gamma > 1$. If this condition holds, the existence of a bounded nontrivial sequence of (1) implies the existence of a nontrivial equilibrium.

If $\gamma > 1$ holds, it is clearly a sufficient condition for the existence of a positive periodic solution of (1) if there exists $\tilde{x} > 0$ such that $\mathcal{F}(\tilde{x}) < \tilde{x}$ as this implies the existence of a positive equilibrium of $\mathcal{F}(x)$. Let us introduce the notations

$$K := e^{-\int_0^P a(u)\,\mathrm{d}u}$$

and

$$\mathcal{H}(x) := e^{-\int_L^P a(u)\,\mathrm{d}u} \int_L^P e^{\int_L^s a(u)\mathrm{d}u} f\left(s, xe^{-\int_0^{s-1} a(u)\,\mathrm{d}u}\right) \mathrm{d}s,$$

with these notations we can formulate condition $\mathcal{F}(\tilde{x}) < \tilde{x}$ as $\mathcal{H}(\tilde{x}) < (1-K)\tilde{x}$. A sufficient condition for the existence of a positive equilibrium of $\mathcal{F}$ is that there exists a ξ_0 such that $f(s,\xi) < \frac{\xi}{1-K}$ for all s if $\xi > \xi_0$.

Proposition 3. *Let $\gamma > 1$.*

a) Suppose (1) has a positive equilibrium $\bar{x}$. If the condition

$$-2 < \mathcal{B}(\bar{x}) := -\frac{\mathcal{H}(\bar{x})}{\bar{x}} + \mathcal{H}'(\bar{x}) < 0 \tag{5}$$

holds then $\bar{x}$ is locally asymptotically stable

b) Suppose that for f, the conditions

$$\frac{\partial f}{\partial x}(t,x) \geq 0 \quad \text{and} \quad \frac{\partial^2 f}{\partial x^2}(t,x) \leq 0$$

hold. Then (1) has a positive equilibrium $\bar{x}$ which is globally attractive.

Proof. The proof of a) is straightforward.

From the two assumpitons of b) we have that $\mathcal{F}'(x) > 0$ and $\mathcal{F}''(x) < 0$, which, in turn, imply the existence of a unique positive fixed point of $\mathcal{F}$. From this, the statement b) follows.

$\square$

4. **Applications.**

4.1. **Periodic Ricker-type birth function.** We consider (1) with the periodic Ricker-type birth function

$$f(t, x(t)) = \alpha(t)x(t)e^{-\beta(t)x(t)},$$

where $\alpha(t)$ and $\beta(t)$ are P-periodic real functions. Here we choose

$$\alpha(t) = \alpha \left(\cos\left(\left(t - \tfrac{L+P}{2}\right) 2\pi/P\right) - \cos\left(\left(L - \tfrac{L+P}{2}\right) 2\pi/P\right)\right)$$

with $\hat{\alpha} \in \mathbb{R}^+$ and $\beta(t) \equiv 5$. Let $P = 1.7$, $L = 1.5$ and $a(t) = \sin(2\pi t/P + 0.1) + 1.1$. The function $f(t, x)$ for various values of x is shown in Fig. 1.

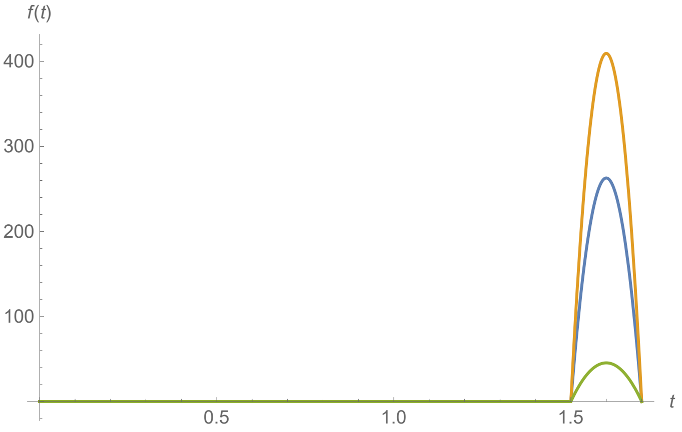
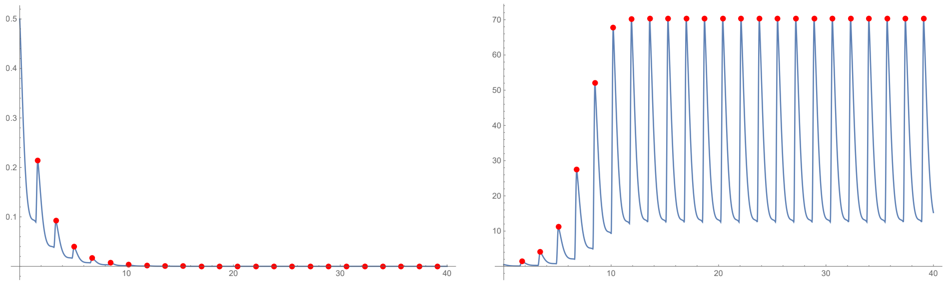
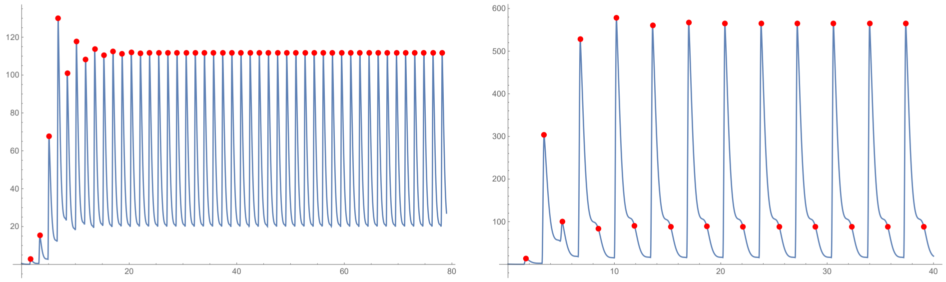


FIGURE 1. The function $f(t, x)$ for $x \in \{5, 10, 100\}$ and $\hat{\alpha} = 1000$

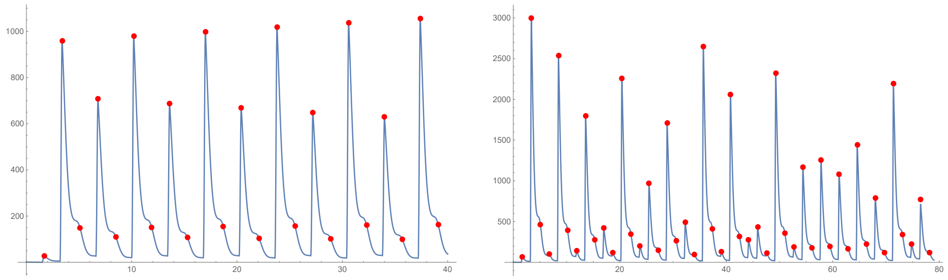
Figure 2 shows the solutions of (1) and the iterates of the corresponding discrete dynamical system for various values of $\hat{\alpha}$. For $\hat{\alpha} = 100$ (see Figure 2(a)), the value γ can be calculated as $\gamma = 0.430605$ which implies the local asymptotic stability of the zero equilibrium of (1), while from Proposition 1 b), we obtain that the trivial equilibrium is also globally asymptotically stable. As we increase $\hat{\alpha}$, we can observe that at $\hat{\alpha} \approx 305.944$, γ passes through 1, showing that the zero equilibrium loses its stability and a periodic solution of (1) arises (correspondingly, one can observe the arisal of a positive equilibrium of the discrete dynamical system). Figure 2(b) shows this situation at $\hat{\alpha} = 1000$. For this value of our parameter, we can calculate that (5) holds as $\mathcal{B}(70.290454) \approx -1.05279$ in the equilibrium 70.290454 of the discrete dynamical system, implying the asymptotic stability of this equilibrium, and thus that of the periodic solution of (1). Simulations for larger values of $\hat{\alpha}$ are shown in Figures 2(c)–2(f), suggesting that further increasing this parameter results in periodic orbits of the discrete dynamical system and later in orbits which seem to be chaotic.



(a) $\hat{\alpha} = 100$ (b) $\hat{\alpha} = 1000$



(c) $\hat{\alpha} = 2000$ (d) $\hat{\alpha} = 10000$



(e) $\hat{\alpha} = 20000$ (f) $\hat{\alpha} = 50000$

FIGURE 2. Solutions of (1) with periodic Ricker-type birth function for different values of parameter $\hat{\alpha}$.

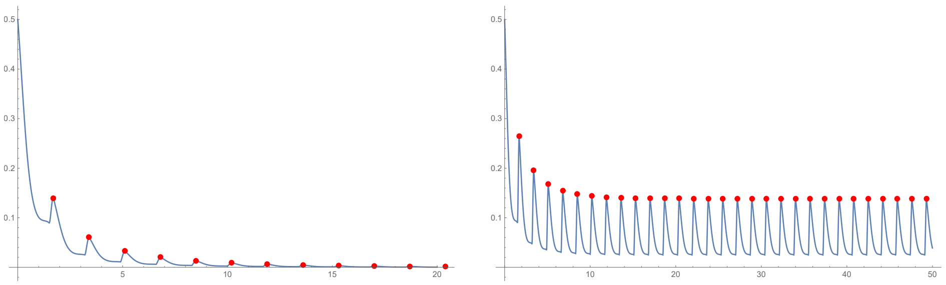
4.2. **Periodic Beverton–Holt-type birth function.** In this subsection we consider model (1) with the periodic Beverton–Holt-type birth function

$$f(t, x(t)) = \frac{\alpha(t)x(t)}{\beta(t) + x(t)}, \tag{6}$$

where $\alpha(t), \beta(t)$ are P-periodic real functions. In this example, we choose these functions as

$$\beta(t) = \cos\left(\left(t - \tfrac{L+P}{2}\right) 2\pi/P\right) - \cos\left(\left(L - \tfrac{L+P}{2}\right) 2\pi/P\right)$$

while $\alpha(t)$, P, L and $a(t)$ are chosen as in the previous example. One can easily obtain that $\mathcal{F}'(x) > 0$ and $\mathcal{F}''(x) < 0$. Hence, in accordance with Proposition 3 b), two possible cases may arise, depending on the threshold parameter γ and for the model (6), γ provides a threshold parameter for global stability. If $\gamma \leq 1$, the zero equilibrium is globally asymptotically stable (here we can again apply Proposition 1 b)), while if $\gamma > 1$, a unique positive periodic solution is a global attractor as in the latter case $\mathcal{F}'(x) > 0$ and $\mathcal{F}''(x) < 0$ imply that there is a unique positive fixed point of $\mathcal{F}$. Figure 3(a) shows the case $\hat{\alpha} = 10$. Here, $\gamma = 0.772551$, showing the local asymptotic stability of the zero equilibrium. Increasing $\hat{\alpha}$, the value of γ passes through 1 at $\hat{\alpha} \approx 13.6779$ Figure 3(b) shows the case $\hat{\alpha} = 30$, where $\gamma = 2.00941$, thus, the zero equilibrium is unstable in this case.



(a) $\hat{\alpha} = 10$ (b) $\hat{\alpha} = 20$

FIGURE 3. Solutions of (1) with periodic Beverton–Holt-type birth function for different values of parameter $\hat{\alpha}$.

5. Discussion.

We established a model for a population with short reproduction period in a periodic environment, given by a scalar nonlinear delay equation, where time delay stands for maturation. Mortality rate and the density-dependent reproduction function are assumed to be periodic. Usually, for periodic models, a threshold parameter for the persistence of a species or a disease can be determined as the spectral radius of a linear operator on a space of periodic functions [4, 8]. However, for the periodic model established here, we were able to determine an explicit formula for this parameter and showed that is serves as a threshold for the stability of the trivial equilibrium and for permanence.

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