

STABILITY AND PERSISTENCE IN ODE MODELS FOR POPULATIONS WITH MANY STAGES

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ABSTRACT. A model of ordinary differential equations is formulated for populations which are structured by many stages. The model is motivated by ticks which are vectors of infectious diseases, but is general enough to apply to many other species. Our analysis identifies a basic reproduction number that acts as a threshold between population extinction and persistence. We establish conditions for the existence and uniqueness of nonzero equilibria and show that their local stability cannot be expected in general. Boundedness of solutions remains an open problem though we give some sufficient conditions.

1. Introduction. Individual characteristics affect the development of populations and, to take this into account, structured population models are a golden middle ground between unstructured models of total densities and very detailed individual based models (see [6, 22, 24, 39], e.g.).

In many mammalian and other species, development occurs in a rather continuous way and can best be traced along age or size structure leading to systems of

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partial differential and/or integral equations (see [1, 4, 5, 9, 11, 12, 14, 16, 29, 35, 36, 38, 41], e.g., and the literature cited there).

Stage-structured models are a very natural choice when the life cycle of a species is divided into well distinguishable discrete stages each of which may have their specific climatic and nutritional requirements and their specific vulnerabilities to predators or human control measures. Such models typically lead to systems of ordinary and/or delay differential equations and of difference equations [7, 16, 17]. An example par excellence is the tick *Ixodes Scpularis* that has four main stages: eggs, larvae, nymphs, and adults [27, 28]. All stages except the egg stage have questing, feeding and engorged substages (or phases) with the adults having an additional egg-laying phase and larvae having an additional hardening phase (a total of twelve stages). Adult ticks mainly feed on deer, while nymphs and larvae mainly feed on rodents, and only feeding ticks are able to contract and transmit the infectious diseases like Lyme disease [18, 28]. Questing activity is temperature dependant with adults being active at quite cooler temperatures than larvae and nymphs [26, Fig.3]. Only a stage-structured model can hope to catch the impact of these abiotic and biotic factors on the dynamics of a tick population. Density-dependent negative feedback is also stage-specific. Feeding ticks induce an immune reaction of their hosts that increases their mortality, slows down their development, and decreases their fertility with the latter effect being postponed to the egg-laying phase [26, 28].

The model in this manuscript is mainly motivated by tick dynamics, notably by the computer model in [26], but will be formulated general enough to apply to a wide range of stage structured populations. Similarly to [21, 43, 44], it is a model of many ordinary differential equations (Section 2); for a model of delay-differential equations focussing on ticks see [13]. Our model also applies to epidemic models with many disease stages [20, 30] provided that the equations for susceptible and/or vaccinated individuals can be eliminated. The model incorporates density-dependent feedbacks between the stages that affect mortality, stage-transition, and procreation rates. Our analysis, after establishing uniqueness and global existence of solutions (Section 3), identifies reproduction numbers in a biologically meaningful way and establishes the basic reproduction number as a threshold deciding about extinction or persistence of the population (Sections 4 and 5). We discuss the boundedness of solutions (Section 7) which is a difficult problem if density-dependent negative feedback is exclusively interstage. For this reason, existence of nonzero equilibria is not derived as a consequence of permanence ([23], [34, Ch.6], [45]), but via fixed point theorems in conical shells [8] (Section 6). Since the systems are large, uniqueness and stability of nonzero equilibria become a challenge (Sections 6.2 and 8). We give an example where a nonzero equilibrium is unstable while the negative feedback is of a very simple nature (Section 8). If a system has several feedbacks, for instance both on stage transition and procreation, then even models with only two stages can show multiple nonzero equilibria and a plethora of complicated bifurcations [2]. We take the difficulties of proving boundedness of solutions as an indication that a literal translation of the computer model in [26] into ordinary differential equations may not capture the negative feedback from adult feeding to adult egg-laying via host immunity or resistance in the right way. We therefore suggest an alternative model formulation in the epilog (Section 9).

2. The model. Let $2 \leq n \in \mathbb{N}$ and consider a system modeling a population structured by n stages,

$$\left. \begin{aligned} x'_1 &= g(x) - (\gamma_1(x) + \mu_1(x))x_1 \\ x'_j &= \gamma_{j-1}(x)x_{j-1} - (\gamma_j(x) + \mu_j(x))x_j \end{aligned} \right\} \quad x = (x_1, \dots, x_n). \quad (2.1)$$

Here x_j is the size of the j^{th} stage of the population (eggs or other forms of offspring and various larval, pupal, and adult stages). The vector $x = (x_1, \dots, x_n)$, comprising all stage sizes, gives the population state, here the stage distribution. The first stage contains the offspring with $g(x)$ being the rate at which offspring enters the stage if the stage distribution is $x \in \mathbb{R}_+^n$, $g(0) = 0$. $\mu_j(x) \geq 0$ are the per capita mortality rates in stage j at population state x . $\gamma_j(x) \geq 0$ are the per capita transition rates from stage j to stage $j + 1$ at stage distribution x .

Our system is potentially very large. The tick models in [21, 43, 44] have 12 ordinary differential equations (ODEs) and could possibly contain more. They are pure ODE versions of the computer model in [26] where some of the terms have delays. Since, analytically, it is not much more difficult to handle 24 rather than 12 ODEs, it is an attractive alternative to mimic the delay differential equations by subsystems of ODEs (linear chain trick) leading to even larger systems [6, 24, 29, 32].

2.1. A leaner model. Since the systems are large, it is important to use a lean notation. So we introduce the per capita stage exit rates,

$$\left. \begin{aligned} \eta_j(x) &= \gamma_j(x) + \mu_j(x), \quad j = 1, \dots, n - 1 \\ \eta_n(x) &= \mu_n(x) \end{aligned} \right\} \quad x \in \mathbb{R}_+^n. \quad (2.2)$$

The system (2.1) then takes the form,

$$\left. \begin{aligned} x'_1 &= g(x) - \eta_1(x)x_1 \\ x'_j &= \gamma_{j-1}(x)x_{j-1} - \eta_j(x)x_j \end{aligned} \right\} \quad x = (x_1, \dots, x_n). \quad (2.3)$$

We have more flexibility if we formulate our overall assumptions in terms of system (2.3).

Overall Assumptions. All functions $g, \gamma_j, \eta_j : \mathbb{R}_+^n \rightarrow \mathbb{R}_+$ are Lipschitz continuous on bounded subsets of \mathbb{R}_+^n ,

$$\eta_j(x) \geq \gamma_j(x) \geq 0, \quad j = 1, \dots, n - 1, \quad x \in \mathbb{R}_+^n. \quad (2.4)$$

The population birth rate $g : \mathbb{R}_+^n \rightarrow \mathbb{R}_+$ is differentiable at 0. □

The partial derivatives at 0,

$$\partial_j g(0) =: \beta_j, \quad j = 1, \dots, n, \quad (2.5)$$

can be interpreted as the per capita birth rates of individuals in the j^{th} stage if there is no competition. The numbers

$$p_j(x) = \frac{\gamma_j(x)}{\eta_j(x)} \in [0, 1], \quad j = 1, \dots, n - 1, \quad (2.6)$$

provide the probabilities of getting through the j^{th} stage alive if the stage distribution of the population is x . Indeed, $\frac{1}{\eta_j(x)}$ is the mean sojourn time in the j^{th} stage (counting death) and $\gamma_j(x)$ is the per capita rate of leaving the stage alive. See [36, Sec.13.6] for a more systematic exposition.

2.2. Cyclic stage models. A special case is the cyclic stage model in which only the last stage produces offspring,

$$\left. \begin{aligned} x'_1 &= \gamma_n(x)x_n - \eta_1(x)x_1 \\ x'_j &= \gamma_{j-1}(x)x_{j-1} - \eta_j(x)x_j \\ &\quad j = 2, \dots, n \end{aligned} \right\} x = (x_1, \dots, x_n). \quad (2.7)$$

While we keep the assumptions $\gamma_j(x) \leq \eta_j(x)$ for all $j = 1, \dots, n-1$, no such assumption is made for γ_n because γ_n is the per capita reproduction rate and not a transition rate. The models considered in [21] and [43] fit into this framework by assuming

$$\begin{aligned} \gamma_n(x) &= \tilde{\gamma}_n(x_{n-2}), & \gamma_j(x) &= \tilde{\gamma}_j, & j &= 1, \dots, n-1, \\ \eta_j(x) &= \tilde{\gamma}_j + \tilde{\mu}_j(x_j), & j &= 1, \dots, n, \end{aligned} \quad (2.8)$$

with some of the $\tilde{\mu}_j$ being constant. Here x_n is interpreted as the (number of) egg-laying adult ticks, x_{n-1} engorged adult ticks, and x_{n-2} feeding adult ticks. There is good reason to let $\gamma_j(x)$ depend on x because hosts can develop immunity or resistance to ticks that do not only lead to weight reduction in engorged ticks and to reduced tick fecundity but also to prolonged feeding times [42]. It is also suggestive to consider a more general dependence of μ_j on x than x_j : If host immunity or resistance which are triggered by feeding ticks increase the per capita mortality rate of feeding ticks, then they may also increase the per capita mortality rate of engorged ticks, i.e., μ_{n-1} could depend on x_{n-2} .

3. Solutions. Let $f : \mathbb{R}_+^n \rightarrow \mathbb{R}^n$ be the vector field given by the right hand side of (2.3) and let f_j denote the components of f , $j = 1, \dots, n$. The assumptions mentioned before imply that the vector field is Lipschitz continuous on bounded subsets of \mathbb{R}_+^n . By standard ODE theory, solutions to initial values in \mathbb{R}_+^n exist on open intervals containing 0 and are uniquely determined by and continuously depend on those initial values.

To show that solutions that start in \mathbb{R}_+^n stay in \mathbb{R}_+^n in forward time as long as they exist, we use [33, Prop.B.7] (see also [36, Prop.A.1]). We only need to check the following:

If $x \in \mathbb{R}_+^n$ and $x_1 = 0$, then $f_1(x) = g(x) \geq 0$.

If $j = 2, \dots, n$, $x \in \mathbb{R}_+^n$ and $x_j = 0$, then $f_j(x) = \gamma_{j-1}(x)x_{j-1} \geq 0$.

To show that no solution blows up in finite forward time, we consider the total population size

$$y(t) = \sum_{j=1}^n x_j(t).$$

We add the equations in (2.3),

$$y' = g(x) - \eta_1(x)x_1 + \sum_{j=2}^n [\gamma_{j-1}(x)x_{j-1} - \eta_j(x)x_j].$$

We regroup and change the index of summation in one sum,

$$y' = g(x) + \sum_{j=1}^{n-1} [\gamma_j(x) - \eta_j(x)]x_j - \eta_n(x)x_n.$$

Since the solution is non-negative, by (2.4),

$$y' \leq g(x).$$

We make the following assumption.

Assumption 3.1. *There exists some $c > 0$ such that $g(x) \leq c\|x\|$ for all $x \in \mathbb{R}_+^n$.*

Here $\|\cdot\|$ is your favorite norm on \mathbb{R}^n . Then there exists some \tilde{c} such that $y' \leq \tilde{c}y$ and $y(t) \leq y(0)e^{\tilde{c}t}$ for all $t \geq 0$ for which the solution exists.

Theorem 3.2. *Let Assumption 3.1 be satisfied. Then, for each $x^\circ \in \mathbb{R}_+^n$, there exists a unique solution $x : \mathbb{R}_+ \rightarrow \mathbb{R}_+^n$ with $x(0) = x^\circ$.*

4. Stability of the extinction equilibrium. Since we have assumed that $g(0) = 0$, the origin is an equilibrium of (2.3) that represents a steady state at which the population is extinct (extinction equilibrium). We will analyze the stability of the origin in a way that does not require writing down huge matrices and right away leads to an expression for the reproduction number \mathcal{R}_0 that is readily interpretable.

Since g is also assumed to be differentiable at 0, the vector field f is differentiable at 0 and

$$\left. \begin{aligned} f'_1(0)x &= g'(0)x - \eta_1(0)x_1 \\ f'_j(0)x &= \gamma_{j-1}(0)x_{j-1} - \eta_j(0)x_j \\ &\qquad j = 2, \dots, n \end{aligned} \right\} x = (x_1, \dots, x_n) \in \mathbb{R}_+^n. \quad (4.1)$$

We make another assumption.

Assumption 4.1. $\gamma_j(0) > 0$ for all $j = 1, \dots, n - 1$ and $\eta_j(x) > 0$ for all $j = 1, \dots, n$ and $x \in \mathbb{R}_+^n$.

These assumptions are reasonable because, without competition, transition to the next stage should always be possible and exit from a stage should occur under all stage distributions at a positive rate by either transition or death. Since the system is large, we do our stability analysis ab ovo (from scratch) starting from eigenvalues and eigenvectors (cf. [36, Sec.23.3] and [43]).

Let $\lambda \in \mathbb{C}$ be an eigenvalue of $f'(0)$ and $x \in \mathbb{C}^n$, $x \neq 0$, an associated eigenvector. Then

$$\begin{aligned} \lambda x_1 &= g'(0)x - \eta_1(0)x_1, \\ \lambda x_j &= \gamma_{j-1}(0)x_{j-1} - \eta_j(0)x_j, \quad j = 2, \dots, n. \end{aligned}$$

This gives us a recursive relation for the coordinates of x ,

$$\begin{aligned} x_1 &= \frac{g'(0)x}{\lambda + \eta_1(0)}, \\ x_j &= \frac{\gamma_{j-1}(0)x_{j-1}}{\lambda + \eta_j(0)}, \quad j = 2, \dots, n. \end{aligned}$$

We solve,

$$x_k = \prod_{j=2}^k \frac{\gamma_{j-1}(0)}{\lambda + \eta_j(0)} x_1, \quad k = 2, \dots, n. \quad (4.2)$$

We notice that $x \neq 0$ implies $x_j \neq 0$ for all $j = 1, \dots, n$. We substitute these expression into the first equation, notice that $g'(0)x = \sum_{k=1}^n \beta_k x_k$ with the per capita reproduction rates β_k from (2.5) and divide by $x_1 \neq 0$. After some regrouping, we obtain the characteristic equation

$$1 = \sum_{k=1}^n \frac{\beta_k}{\lambda + \eta_k(0)} \prod_{j=1}^{k-1} \frac{\gamma_j(0)}{\lambda + \eta_j(0)} =: \chi(\lambda).$$

Here $\prod_{j=1}^0 := 1$. Notice that

$$\chi(0) = \sum_{k=1}^n \frac{\beta_k}{\eta_k(0)} q_k =: \mathcal{R}_0, \quad q_k = \prod_{j=1}^{k-1} \frac{\gamma_j(0)}{\eta_j(0)} = \prod_{j=1}^{k-1} p_j(0) \quad (4.3)$$

has the interpretation of a basic reproduction number. Since p_j is the probability of surviving the j^{th} stage, q_k is the probability of making it to the k^{th} stage, while $1/\eta_k(0)$ is the expected length of the k^{th} stage and β_k is the per capita reproduction rate during the k^{th} stage (all without competition). So $\chi(0)$ is the expected amount of offspring an average newborn (or newly laid egg) can produce during its lifetime if there is no competition.

Assume that $\mathcal{R}_0 = \chi(0) > 1$. Since χ is strictly decreasing in $\lambda \geq 0$ and $\chi(\lambda) \rightarrow 0$ as $\lambda \rightarrow \infty$ and χ is continuous, by the intermediate value theorem there exists some $\lambda > 0$ such that $\chi(\lambda) = 1$. Working backwards and defining x by (4.2) with $x_1 = 1$, we see that this λ is an eigenvalue of $f'(0)$ associated with an eigenvector $x \in (0, \infty)^n$. This implies that the origin is unstable.

Now assume that $\mathcal{R}_0 = \chi(0) < 1$. Then $\chi(\lambda) < 1$ for all $\lambda \geq 0$ and there are no eigenvalues λ of $f'(0)$ with $\lambda \geq 0$. Suppose there is an eigenvalue $\lambda \in \mathbb{C}$ with $\Re \lambda \geq 0$. We apply absolute values to the characteristic equation, use the triangle inequality and the multiplicity of the absolute value,

$$1 \leq \sum_{k=1}^n \frac{\beta_k}{|\lambda + \eta_k(0)|} \prod_{j=1}^{k-1} \frac{\gamma_j(0)}{|\lambda + \eta_j(0)|}.$$

Since

$$|\lambda + \eta_j(0)| \geq \Re \lambda + \eta_j(0),$$

we have

$$1 \leq \chi(\Re \lambda) \leq \chi(0) < 1,$$

a contradiction. This shows that all eigenvalues have negative real parts if $\mathcal{R}_0 < 1$. We summarize.

Theorem 4.2. *Let the Assumptions 4.1 be satisfied. Then the origin is locally asymptotically stable if $\mathcal{R}_0 < 1$ and unstable if $\mathcal{R}_0 > 1$.*

In order to explore the possible global stability of the origin if $\mathcal{R}_0 < 1$, we introduce a Lyapunov function to-be,

$$V(x) = \sum_{j=1}^n \alpha_j x_j, \quad x \in \mathbb{R}_+^n, \quad (4.4)$$

with $\alpha_j > 0$, $\alpha_1 = 1$. Let x be a solution of (2.3). Then

$$(d/dt)V(x) = \sum_{k=1}^n \alpha_k x'_k = g(x) - \eta_1(x)x_1 + \sum_{j=2}^n \alpha_j [\gamma_{j-1}(x)x_{j-1} - \eta_j(x)x_j].$$

We regroup, change the summation index in one sum and regroup again,

$$(d/dt)V(x) = g(x) - \alpha_n \eta_n(x)x_n + \sum_{j=1}^{n-1} [\alpha_{j+1} \gamma_j(x) - \alpha_j \eta_j(x)]x_j.$$

We assume that $g(x) \leq \sum_{j=1}^n \beta_j x_j$ for all $x \in \mathbb{R}_+^n$ and $\eta_n(x) \geq \eta_n(0)$. Then

$$(d/dt)V(x) \leq [\beta_n - \alpha_n \eta_n(0)]x_n + \sum_{j=1}^{n-1} [\beta_j + \alpha_{j+1} \gamma_j(x) - \alpha_j \eta_j(x)]x_j.$$

We choose the coefficients α_j recursively as

$$\alpha_{j+1} = \frac{\alpha_j \eta_j(0) - \beta_j}{\gamma_j(0)} = \frac{\alpha_j}{p_j(0)} - \frac{\beta_j}{\gamma_j(0)}. \tag{4.5}$$

Then

$$\begin{aligned} (d/dt)V(x) &\leq [\beta_n - \alpha_n \eta_n(0)]x_n + \sum_{j=1}^{n-1} \beta_j \left(1 - \frac{\gamma_j(x)}{\gamma_j(0)}\right)x_j \\ &\quad + \sum_{j=1}^{n-1} \alpha_j \left(\frac{\eta_j(0)\gamma_j(x)}{\gamma_j(0)} - \eta_j(x)\right)x_j. \end{aligned} \tag{4.6}$$

The finite recursion (4.5) is solved by

$$\begin{aligned} \alpha_1 &= 1, \quad \alpha_2 = \frac{1}{p_1(0)} - \frac{\beta_1}{\gamma_1(0)}, \\ \alpha_j &= \frac{1}{p_{j-1}(0) \cdots p_1(0)} - \sum_{k=1}^{j-2} \frac{1}{p_{j-1}(0) \cdots p_{k+1}(0)} \frac{\beta_k}{\gamma_k(0)} - \frac{\beta_{j-1}}{\gamma_{j-1}(0)}. \end{aligned} \tag{4.7}$$

By (2.6) and (4.3), this can be rewritten as

$$\alpha_j = q_j^{-1} \left(1 - \sum_{k=1}^{j-1} q_k \frac{\beta_k}{\eta_k(0)}\right) \geq q_j^{-1} (1 - \mathcal{R}_0), \quad j = 2, \dots, n. \tag{4.8}$$

In particular,

$$\alpha_n = q_n^{-1} \left(1 + q_n \frac{\beta_n}{\eta_n(0)} - \mathcal{R}_0\right) \tag{4.9}$$

and

$$\beta_n - \alpha_n \eta_n(0) = q_n^{-1} \eta_n(0) (\mathcal{R}_0 - 1). \tag{4.10}$$

We substitute the last formula into (4.6),

$$\begin{aligned} (d/dt)V(x) &\leq q_n^{-1} \eta_n(0) (\mathcal{R}_0 - 1)x_n + \sum_{j=1}^{n-1} \beta_j \left(1 - \frac{\gamma_j(x)}{\gamma_j(0)}\right)x_j \\ &\quad + \sum_{j=1}^{n-1} \alpha_j \left(\frac{\eta_j(0)\gamma_j(x)}{\gamma_j(0)} - \eta_j(x)\right)x_j. \end{aligned} \tag{4.11}$$

We assume that $\mathcal{R}_0 < 1$ or $\mathcal{R}_0 = 1$ and $\beta_n > 0$. Then $\alpha_j > 0$ for $j = 1, \dots, n$.

In order to enforce that $(d/dt)V(x) \leq 0$, we make the following assumptions. Recall (2.6), the probabilities of surviving the j^{th} stage at stage distribution x , $p_j(x) = \frac{\gamma_j(x)}{\eta_j(x)}$.

- Assumption 4.3.** (a) If $j \in \{1, \dots, n - 1\}$, $x \in \mathbb{R}_+^n$, then $p_j(x) \leq p_j(0)$.
 (b) If $j \in \{1, \dots, n - 1\}$ and $\beta_j > 0$, then $\gamma_j(x) \geq \gamma_j(0)$ for all $x \in \mathbb{R}_+^n$.

Assumption (a) is very plausible stating that stage survival is larger without than with intraspecific competition. Assumption (b) may seem counterintuitive at the first glance. Notice, however, that it is trivially satisfied, if reproduction only occurs in the last stage or if the transition rates are constant. It can also be plausible if there are several reproductive stages and the later stages are less reproductive than the earlier ones. Then intraspecific competition would move reproductive individuals faster into the less reproductive stages.

Theorem 4.4. *Let the Assumptions 4.1 and 4.3 be satisfied and either $\mathcal{R}_0 < 1$ or $\mathcal{R}_0 = 1$ and $\beta_n > 0$. Then the origin is globally stable in the sense that there exists some $c > 0$ such that*

$$\sum_{j=1}^n x_j(t) \leq c \sum_{j=1}^n x_j(0), \quad t \geq 0,$$

for all solutions with $x(0) \in \mathbb{R}_+^n$.

Proof. By our assumptions $(d/dt)V(x(t)) \leq 0$ and $V(x(t))$ is a decreasing function of $t \geq 0$. In view of our choice of V in (4.4), set $c = \frac{\max \alpha_j}{\min \alpha_j}$. \square

Theorem 4.5. *Let the Assumptions 4.1 and 4.3 be satisfied and $\mathcal{R}_0 < 1$. Then the origin is globally asymptotically stable.*

Proof. By Theorem 4.4, every solution starting in \mathbb{R}_+ is bounded in forward time and has a nonempty ω -limit set ω . Since V introduced in (4.4) is a Lyapunov function, V is constant on ω . Let $x \in \omega$. Since ω is invariant, there exists a solution $y : \mathbb{R} \rightarrow \omega$ with $y(0) = x$. By (4.11) and Assumption 4.3,

$$\begin{aligned} 0 &= (V \circ y)'(0) \\ &\leq q_n^{-1} \eta_n(0)(\mathcal{R}_0 - 1)x_n + \sum_{j=1}^{n-1} \alpha_j \left(\frac{\eta_j(0)\gamma_j(x)}{\gamma_j(0)} - \eta_j(x) \right) x_j \\ &\leq q_n^{-1} \eta_n(0)(\mathcal{R}_0 - 1)x_n + \alpha_{n-1} \left(\frac{\eta_{n-1}(0)\gamma_{n-1}(x)}{\gamma_{n-1}(0)} - \eta_{n-1}(x) \right) x_{n-1}. \end{aligned} \quad (4.12)$$

Since $\mathcal{R}_0 < 1$, $x_n = 0$. Further, if $\gamma_{n-1}(x) = 0$, then $x_{n-1} = 0$.

So, for all $x \in \omega$, we have $x_n = 0$ and, if $\gamma_{n-1}(x) = 0$, then $x_{n-1} = 0$.

Now let $x \in \omega$ and $\gamma_{n-1}(x) > 0$. Since ω is invariant, there again exists a solution $y : \mathbb{R} \rightarrow \omega$ with $y(0) = x$. By our previous consideration, $y_n(t) = 0$ for all $t \in \mathbb{R}$ and, from the differential equation for the last stage,

$$0 = y_n'(0) = \gamma_{n-1}(x)x_{n-1} - \eta_n(x)x_n = \gamma_{n-1}(x)x_{n-1}.$$

Thus, again, $x_{n-1} = 0$. So, for all $x \in \omega(x)$, $x_{n-1} = 0$.

Continuing this way, we obtain that $x = 0$. So $\omega = \{0\}$. Since the ω -limit set attracts the solution, all solutions converge to the origin as time tends to infinity. \square

Theorem 4.6. *Let the Assumptions 4.1 and 4.3 be satisfied and $\mathcal{R}_0 = 1$. Further assume that there is some $k \in \{1, \dots, n-1\}$ with the following properties:*

- $p_k(x) < p_k(0)$ if $x \in \mathbb{R}_+^n$ and $x_k > 0$,
- η_j is bounded away from 0 for $j = k+1, \dots, n$.

Then the origin is globally asymptotically stable.

Proof. Let ω be the ω -limit set of a solution. Let $x \in \omega$. Then there exists a solution $y : \mathbb{R} \rightarrow \omega$ with $y(0) = x$. Since V is constant on ω , $\frac{d}{dt}V(y) = 0$. Let k be as specified in the assumption. By (4.12), $x_k = 0$. So $x_k = 0$ for all $x \in \omega$.

As in the proof of Theorem 4.5, we obtain $x_j = 0$ for $j = 1, \dots, k$ and all $x \in \omega$.

Let $x \in \omega$ again. As before, there exists a solution $y : \mathbb{R} \rightarrow \omega$ with $y(0) = x$. By our previous results, $y_k(t) = 0$ for all $t \in \mathbb{R}$. So

$$y'_{k+1} = -\eta_{k+1}(y)y_{k+1}.$$

If $y_{k+1}(r) > 0$ for some $r \in \mathbb{R}$, then $y_{k+1}(t) \rightarrow \infty$ as $t \rightarrow -\infty$ because η_{k+1} is bounded away from 0. This contradicts the boundedness of y . So $y_{k+1}(t) = 0$ for all $t \in \mathbb{R}$. Continuing this argument, we successively obtain that $y_j(t) = 0$ for all $j = k, \dots, n, t \in \mathbb{R}$. Thus $x = y(0) = 0$ and $\omega = \{0\}$. Since a solution is attracted by its ω -limit set, all solutions converges to 0 as time tends to infinity. \square

5. Persistence. We strive for persistence results that do not require any dissipativity of the model system. Even boundedness of solutions will not be required because it would need more restrictive assumptions than we would like to make (Section 7). The Assumptions 3.1 and 4.1 are supposed to hold throughout this section. We make another assumption.

Assumption 5.1. *The per capita transition rates γ_j are bounded and the exit rates η_j are bounded away from 0. Further, for any $\delta \in (0, 1)$, there exists some $\epsilon > 0$ such that*

$$g(x) \geq (1 - \delta) \sum_{j=1}^n \beta_j x_j, \quad x \in \mathbb{R}_+^n, \|x\| \leq \epsilon.$$

Example 5.2. Let

$$g(x) = \sum_{j=1}^n b_j(x)x_j, \quad x = (x_1, \dots, x_n) \in \mathbb{R}_+^n,$$

where the $b_j : \mathbb{R}_+^n \rightarrow \mathbb{R}_+$ are Lipschitz continuous on bounded subsets on \mathbb{R}_+^n . $b_j(x)$ can be interpreted as the per capita birth (or egg-laying) rate during stage j at stage distribution x . Then g satisfies the Assumptions 5.1. Further g is differentiable at 0 and $\partial_j g(0) = b_j(0) = \beta_j$.

Theorem 5.3. *Let Assumption 5.1 be satisfied. If $\mathcal{R}_0 > 1$, there exists some $\epsilon > 0$ such that*

$$\limsup_{t \rightarrow \infty} x_1(t) \geq \epsilon$$

for all solutions x with $x(0) \in \mathbb{R}_+^n, x_1(0) > 0$.

Proof. In the following let $\|\cdot\|$ denote the sum-norm. Suppose the claim is not true. Let $\delta > 0$ be arbitrary. Since η_j and γ_j are continuous and $\eta_j(x) > 0$, there exists some $\epsilon > 0$ such that

$$\left. \begin{aligned} \gamma_j(x) &\geq (1 - \delta)\gamma_j(0) \\ \eta_j(x) &\leq (1 + \delta)\eta_j(0) \end{aligned} \right\}, \quad x \in \mathbb{R}_+^n, \|x\| \leq \epsilon. \tag{5.1}$$

Further, by assumption,

$$g(x) \geq (1 - \delta) \sum_{j=1}^n \beta_j x_j, \quad x \in \mathbb{R}_+^n, \|x\| \leq \epsilon.$$

Since we have assumed that the claim is false, for any $\tilde{\epsilon} > 0$ there exists a solution x (which depends on $\tilde{\epsilon}$) such that $x(0) \in \mathbb{R}_+^n$, $x_1(0) > 0$, and $\limsup_{t \rightarrow \infty} x_1(t) < \tilde{\epsilon}$. This implies that x_2 is bounded. By the fluctuation lemma [19] [36, Prop.A.22], there exists a sequence $t_k \rightarrow \infty$ such that

$$x_2(t_k) \rightarrow x_2^\infty := \limsup_{t \rightarrow \infty} x_2(t), \quad x_2'(t_k) \rightarrow 0.$$

From the differential equation for x_2 ,

$$x_2^\infty \leq \frac{\sup \gamma_1}{\inf \eta_2} x_1^\infty.$$

We apply the fluctuation lemma multiple times and find some $c \geq 1$ which only depends on the η_j and γ_j such that $\limsup_{t \rightarrow \infty} \|x(t)\| < c\tilde{\epsilon}$. Further $x_1(t) > 0$ for all $t \geq 0$. After a forward shift in time, we can assume that $\|x(t)\| < c\tilde{\epsilon}$ and $x_1(t) > 0$ for all $t \geq 0$, $j = 1, \dots, n$. Choose $\tilde{\epsilon} = \epsilon/c$. Then

$$\begin{aligned} x_1' &\geq (1 - \delta) \sum_{j=1}^n \beta_j x_j - (1 + \delta) \eta_1(0) x_1, \\ x_j' &\geq (1 - \delta) \gamma_{j-1}(0) x_{j-1} - (1 + \delta) \eta_j(0) x_j, \quad j = 2, \dots, n. \end{aligned}$$

For $\lambda > 0$, let $\hat{x}_j(\lambda) = \int_0^\infty e^{-\lambda t} x_j(t) dt$ denote the Laplace transform of x_j . Notice that $\hat{x}(\lambda)$ exists for $\lambda > 0$ and $\hat{x}(\lambda) \leq \epsilon/\lambda$,

$$\begin{aligned} \lambda \hat{x}_1(\lambda) &\geq (1 - \delta) \sum_{j=1}^n \beta_j \hat{x}_j(\lambda) - (1 + \delta) \eta_1(0) \hat{x}_1(\lambda), \\ \lambda \hat{x}_j(\lambda) &\geq (1 - \delta) \gamma_{j-1}(0) \hat{x}_{j-1}(\lambda) - (1 + \delta) \eta_j(0) \hat{x}_j(\lambda), \quad j = 2, \dots, n. \end{aligned}$$

We reorganize

$$\begin{aligned} \hat{x}_1(\lambda) &\geq \frac{(1 - \delta) \sum_{j=1}^n \beta_j \hat{x}_j(\lambda)}{\lambda + (1 + \delta) \eta_1(0)}, \\ \hat{x}_j(\lambda) &\geq \frac{(1 - \delta) \gamma_{j-1}(0) \hat{x}_{j-1}(\lambda)}{\lambda + (1 + \delta) \eta_j(0)}. \end{aligned}$$

We solve these recursive inequalities,

$$\hat{x}_j(\lambda) \geq (1 - \delta)^{j-1} \prod_{k=2}^j \frac{\gamma_{k-1}(0)}{\lambda + (1 + \delta) \eta_k(0)} \hat{x}_1(\lambda).$$

We substitute these formulas into the one for $\hat{x}_1(\lambda)$ and divide by $\hat{x}_1(\lambda)$, which is positive, and reorganize,

$$1 \geq \sum_{j=1}^n \frac{(1 - \delta)^j \beta_j}{\lambda + (1 + \delta) \eta_j(0)} \prod_{k=1}^{j-1} \frac{\gamma_k(0)}{\lambda + (1 + \delta) \eta_k(0)}.$$

Notice that this inequality no longer contains any terms belonging to the solution x (which depends on δ) and thus holds for any $\delta \in (0, 1)$ and $\lambda > 0$. So we can take the limit as $\delta, \lambda \rightarrow 0$ and obtain $1 \geq \mathcal{R}_0$ (recall (4.3)), a contradiction. \square

Unfortunately, it seems to be difficult to turn the uniform weak persistence result in Theorem 5.3 into a uniform persistence result. So we try the next approach as well.

The linear map $f'(0)$ on \mathbb{R}^n can be written as

$$f'(0) = B + C, \tag{5.2}$$

with $B = (B_1, \dots, B_n)$ and $C = (C_1, \dots, C_n)$ and $B_j, C_j : \mathbb{R}^n \rightarrow \mathbb{R}$,

$$\begin{aligned} B_1x &= -\eta_1(0)x_1, \\ B_jx &= \gamma_{j-1}(0)x_{j-1} - \eta_j(0)x_j, \quad j = 2, \dots, n, \end{aligned} \tag{5.3}$$

and

$$\left. \begin{aligned} C_1x &= \sum_{j=1}^n \beta_j x_j \\ C_jx &= 0, \quad j = 2, \dots, n \end{aligned} \right\} x = (x_1, \dots, x_n). \tag{5.4}$$

The eigenvalues of B are $-\eta_1(0), \dots, -\eta_n(0)$, and so B has a negative spectral bound. Further B is quasipositive and C is positive. So the spectral bound of $f'(0)$ has the same sign as $\mathbf{r}(C(-B)^{-1}) - 1$ with \mathbf{r} denoting the spectral radius. See [10], [37, Thm.3.5], [40]; the map $C(-B)^{-1}$ can be interpreted as a next generation map (or matrix).

Let λ be an eigenvalue of $C(-B)^{-1}$ and y be an associated eigenvector. By the form of C , we have $y_j = 0$ for $j = 2, \dots, n$ and, without loss of generality, $y_1 = 1$. Then $x = (-B)^{-1}y$ can be found by solving the system

$$\eta_1(0)x_1 = 1, \quad \eta_j(0)x_j - \gamma_{j-1}(0)x_{j-1} = 0, \quad j = 2, \dots, n, \tag{5.5}$$

for $x \in \mathbb{R}^n$. This leads to the recursion

$$x_1 = \frac{1}{\eta_1(0)}, \quad x_j = \frac{\gamma_{j-1}(0)}{\eta_j(0)}x_{j-1}, \quad j = 2, \dots, n. \tag{5.6}$$

This recursion is solved by (recall (4.3))

$$x_j = \frac{q_j}{\eta_j(0)}, \quad j = 1, \dots, n. \tag{5.7}$$

By (5.4), $\lambda = \sum_{j=1}^n \beta_j x_j = \mathcal{R}_0$ and \mathcal{R}_0 is the spectral radius of $C(-B)^{-1}$.

We can now prove the following result.

Theorem 5.4. *Let $\mathcal{R}_0 > 1$ and $\beta_n = \partial_n g(0) > 0$. Then there exists some $\epsilon > 0$ such that*

$$\liminf_{t \rightarrow \infty} \sum_{j=1}^n x_j(t) \geq \epsilon$$

for all solutions x of (2.3) in \mathbb{R}_+^n with $x(0) \neq 0$.

The assumptions of this theorem and those of Theorem 5.3 are not comparable, but if it comes to applications the assumption $\beta_n = \partial_n g(0) > 0$ will be more restrictive than those of Theorem 5.3.

Proof. By the preceding consideration, the spectral bound of $f'(0)$ is positive. Since $\beta_n > 0$ and $\gamma_j(0) > 0$ for $j = 1, \dots, n - 1$, $f'(0)$ is irreducible. By consequences of the Perron-Frobenius theory (see [36, Thm.A.45], e.g.), there exist $\lambda > 0$ and $v \in (0, \infty)^n$ such that v is a left eigenvector of the matrix associated with $f'(0)$,

$$\langle v, f'(0)x \rangle = \lambda \langle v, x \rangle, \quad x \in \mathbb{R}^n, \tag{5.8}$$

with $\langle \cdot, \cdot \rangle$ denoting the Euclidean inner product on \mathbb{R}^n . Since $v \in (0, \infty)^n$,

$$\|x\|_0 = \sum_{j=1}^n v_j |x_j|, \quad x \in \mathbb{R}^n,$$

is a norm on \mathbb{R}^n which is equivalent to the sum-norm (and any other norm on \mathbb{R}^n). We define

$$\rho(x) = \|x\|_0 = \langle v, x \rangle, \quad x \in \mathbb{R}_+^n.$$

We claim that the semiflow induced by (2.3) is uniformly weakly ρ -persistent, i.e., there exists some $\epsilon > 0$ such that $\limsup_{t \rightarrow \infty} \rho(x(t)) \geq \epsilon$ for all solutions with $\rho(x(0)) > 0$.

Let $\delta \in (0, \lambda)$. Since f is differentiable and $f(0) = 0$, there exists some $\epsilon > 0$ such that

$$\|f(x) - f'(0)x\|_0 \leq \delta \|x\|_0, \quad x \in \mathbb{R}_+^n, \|x\|_0 < \epsilon. \quad (5.9)$$

Suppose that the semiflow is not uniformly weakly ρ -persistent. Then there exists some solution $x : \mathbb{R}_+ \rightarrow \mathbb{R}_+^n$ with $x(0) \neq 0$ such that

$$\limsup_{t \rightarrow \infty} \rho(x(t)) < \epsilon.$$

It follows from the form of the equations, that $x_j(t) > 0$ for $j = 1, \dots, n$ and $t > 0$. Shifting forward in time, we can assume that $x_j(t) > 0$ for $j = 1, \dots, n$ and $t \geq 0$ and

$$\|x(t)\|_0 < \epsilon, \quad t \geq 0.$$

Then $\rho(x(t)) > 0$ for $t \geq 0$ and

$$\frac{d}{dt} \rho(x(t)) = \langle v, f'(0)x(t) \rangle + \langle v, f(x(t)) - f'(0)x(t) \rangle.$$

By (5.8) and (5.9),

$$\begin{aligned} \frac{d}{dt} \rho(x(t)) &\geq \lambda \langle v, x(t) \rangle - \|f(x(t)) - f'(0)x(t)\|_0 \\ &\geq \lambda \rho(x(t)) - \delta \|x(t)\|_0 = (\lambda - \delta) \rho(x(t)). \end{aligned}$$

Since $\lambda - \delta > 0$ and $\rho(x(t)) > 0$, $\rho(x(t)) \rightarrow \infty$, a contradiction.

This proves that the semiflow induced by (2.3) is uniformly weakly ρ -persistent. By [36, Thm.A.32] or [34, Thm.4.13], the semiflow is uniformly ρ -persistent. Notice that any ρ -ring $\{\epsilon_1 \leq \rho(x) \leq \epsilon_2\}$, $0 < \epsilon_1 < \epsilon_2 < \infty$, is compact. The statement of the theorem now follows from the equivalence of the sum norm and $\|\cdot\|_0$. \square

Remark 5.5. We could have used the relation between \mathcal{R}_0 and the spectral bound of $f'(0)$ to prove a global stability result for the origin as in [21, Thm.2] if $\mathcal{R}_0 < 1$. This would require $f(x) \leq f'(0)x$ for all $x \in \mathbb{R}_+^n$ which would in turn require $\gamma_j(x) \leq \gamma_j(0)$ and $\eta_j(x) \geq \eta_j(0)$. While the first assumption is suggestive and has been made in Assumption 4.3 (though only for those j for which $\beta_j > 0$), the second assumption is less suggestive. Recall that $\eta_j = \gamma_j(x) + \mu_j(x)$. Again, it is suggestive to assume that $\mu_j(x) \geq \mu_j(0)$, but this does not imply $\eta_j(x) \geq \eta_j(0)$. However,

$$p_j(x) = \frac{\gamma_j(x)}{\eta_j(x)} \leq p_j(0),$$

as assumed in Assumption 4.1, does follow. Further, we would not obtain a globally asymptotic stability result for $\mathcal{R}_0 = 1$ (Theorem 4.6) this way.

6. Persistence equilibria. A vector $x \in \mathbb{R}_+^n$ is an equilibrium of (2.3) if and only if it satisfies the fixed point system

$$\left. \begin{aligned} x_1 &= \frac{g(x)}{\eta_1(x)} && =: F_1(x) \\ x_j &= \frac{\gamma_{j-1}(x)}{\eta_j(x)} x_{j-1} && =: F_j(x) \\ &&& j = 2, \dots, n \end{aligned} \right\} x = (x_1, \dots, x_n). \tag{6.1}$$

We choose this reformulation because of the wealth of fixed point theorems available in the literature. Since 0 is a fixed point of $F = (F_1, \dots, F_n) : \mathbb{R}_+^n \rightarrow \mathbb{R}_+^n$, fixed point theorems in conical shells are particularly useful [8, Sec.20.2].

In this section, we assume that

$$g(x) = \sum_{j=1}^n b_j(x)x_j, \quad x \in \mathbb{R}_+^n. \tag{6.2}$$

Here $b_j(x)$ is the per capita birth (or egg-laying) rate in stage j at stage distribution x . Analogously to (4.3), we define the reproduction number at stage distribution x by

$$\mathcal{R}(x) = \sum_{j=1}^n \frac{b_j(x)}{\eta_j(x)} q_j(x), \quad q_j(x) = \prod_{\ell=1}^{j-1} \frac{\gamma_\ell(x)}{\eta_\ell(x)}, \quad x \in \mathbb{R}_+^n. \tag{6.3}$$

Solving the recursive equations in (6.1) and substituting the solutions into the first equation shows that any nonzero equilibrium x satisfies $\mathcal{R}(x) = 1$.

We deal with the existence and the uniqueness of persistence equilibria separately because they hold under quite different assumptions.

6.1. Existence of persistence equilibria. We specialize [8, Thm.20.1] to our situation.

Proposition 6.1. *Let $F : \mathbb{R}_+^n \rightarrow \mathbb{R}_+^n$ be continuous. Let $0 < r_1 < r_2 < \infty$ and*

- (a) $F(x) \neq \lambda x$ for all $\lambda > 1$ and $x \in \mathbb{R}_+^n$ with $\|x\| = r_2$;
- (b) there exists some $u \in \mathbb{R}_+^n$, $u \neq 0$, such that $x - F(x) \neq \alpha u$ for all $\alpha > 0$ and all $x \in \mathbb{R}_+^n$ with $\|x\| = r_1$.

Then there exists some $x \in \mathbb{R}_+^n$ with $r_1 \leq \|x\| \leq r_2$ and $F(x) = x$.

Theorem 6.2. *Assume that the functions b_j are bounded on \mathbb{R}_+^n and the functions η_j are bounded away from 0. Assume that $\mathcal{R}_0 = \mathcal{R}(0) > 1$ and there exists some $c > 0$ such that*

$$\mathcal{R}(x) < 1, \quad x \in \mathbb{R}_+^n, \|x\| \geq c.$$

Then there exists an equilibrium in $(0, \infty)^n$.

Proof. We choose $\|\cdot\|$ as the sum norm on \mathbb{R}^n . Suppose that assumption (a) in Proposition 6.1 is not satisfied for any $r_2 > 1$. Then there exist sequences (x^k) in \mathbb{R}_+^n and (λ_k) in $(1, \infty)$ such that $\|x^k\| \rightarrow \infty$ and $F(x^k) = \lambda_k x^k$. By the definition

of F in (6.1),

$$\left. \begin{aligned} x_1^k &= \frac{g(x^k)}{\lambda_k \eta_1(x^k)} \\ x_j^k &= \frac{\gamma_{j-1}(x^k)}{\lambda_k \eta_j(x^k)} x_{j-1}^k \\ j &= 2, \dots, n \end{aligned} \right\} x^k = (x_1^k, \dots, x_n^k).$$

By iteration,

$$x_j^k = \prod_{\ell=2}^j \frac{\gamma_{\ell-1}(x^k)}{\lambda_k \eta_\ell(x^k)} x_1 = \frac{q_j(x^k) \eta_1(x^k)}{\lambda_k^{j-1} \eta_j(x^k)} x_1^k. \tag{6.4}$$

We conclude that $x_1^k \neq 0$. We substitute these equations into the equation for x_1^k and divide by x_1^k ,

$$1 = \sum_{j=1}^n b_j(x^k) \frac{q_j(x^k)}{\lambda_k^j \eta_j(x^k)} \leq \mathcal{R}(x^k). \tag{6.5}$$

Our assumptions imply that $\mathcal{R}(x^k) < 1$ for sufficiently large k contradicting (6.5).

So assumption (a) of Proposition 6.1 is satisfied with some $r_2 > 1$.

Now suppose that assumption (b) of Proposition 6.1 is not satisfied for any $r_1 \in (0, 1)$ with $u = (1, \dots, 1)$. Then there exists a sequence (x^k) in \mathbb{R}^n and some sequence (α_k) in $(0, \infty)$ such that $0 \neq \|x^k\| \rightarrow 0$ and $x^k - F(x^k) = \alpha_k u$. Since $F(0) = 0$ and F is continuous, $\alpha_k \rightarrow 0$. Set $y^k = \frac{x^k}{\|x^k\|}$. Then

$$y^k - \frac{F(x^k)}{\|x^k\|} \in \mathbb{R}_+^n.$$

Since F is differentiable at 0,

$$0 = \lim_{k \rightarrow \infty} \frac{F(x^k) - F'(0)x^k}{\|x^k\|} = \lim_{k \rightarrow \infty} \left(\frac{F(x^k)}{\|x^k\|} - F'(0)y^k \right).$$

After choosing a subsequence, we can assume that $y^k \rightarrow y \in \mathbb{R}_+^n$ with $\|y\| = 1$ and $\frac{F(x^k)}{\|x^k\|} \rightarrow F'(0)y$. Then $y - F'(0)y \in \mathbb{R}_+^n$ and

$$\left. \begin{aligned} y_1 &\geq \frac{g'(0)y}{\eta_1(y)} \\ y_j &\geq \frac{\gamma_{j-1}(0)}{\eta_j(0)} y_{j-1} \\ j &= 2, \dots, n \end{aligned} \right\} y = (y_1, \dots, y_n). \tag{6.6}$$

A similar consideration as before implies that $\mathcal{R}_0 \leq 1$, a contradiction.

So assumption (b) of Proposition 6.1 is satisfied and there exists a nonzero fixed point x of F in \mathbb{R}_+^n . Then $x \in (0, \infty)^n$. □

Theorem 6.2 does not cover the models in [21, 43] because not all exit rates are density-dependent.

Therefore, we establish an existence result that is tailored to the cyclic model (2.7). For this model, the reproduction rate at stage distribution x is

$$\mathcal{R}(x) = \prod_{j=1}^n \frac{\gamma_j(x)}{\eta_j(x)}, \quad x \in \mathbb{R}_+^n.$$

So $\|x\| \rightarrow \infty$ could mean that $x_1 \rightarrow \infty$ and $x_j = 0$ for $j = 2, \dots, n$. Since γ_1/η_1 is assumed constant in [21, 43], $\mathcal{R}(x) = \mathcal{R}(0)$ as $\|x\| \rightarrow \infty$ is possible.

Theorem 6.3. *Assume that the functions γ_j are bounded and the functions η_j are bounded away from 0 on \mathbb{R}_+^n , $j = 1, \dots, n$. Assume that $\mathcal{R}_0 = \mathcal{R}(0) > 1$ and that there exists some $c > 0$ such that*

$$\mathcal{R}(x) < 1 \quad \text{for all } x \in \mathbb{R}_+^n \text{ with } \min_{j=1}^n x_j \geq c.$$

Then there exists an equilibrium of (2.7) in $(0, \infty)^n$.

Proof. Suppose that assumption (a) in Proposition 6.1 is not satisfied for any $r_2 > 1$. Then there exist sequences (x^k) in \mathbb{R}_+^n and (λ_k) in $(1, \infty)$ such that $\|x^k\| \rightarrow \infty$ and $F(x^k) = \lambda_k x^k$. Then

$$\left. \begin{aligned} x_1^k &= \frac{\gamma_n(x^k)}{\lambda_k \eta_1(x^k)} x_n^k \\ x_j^k &= \frac{\gamma_{j-1}(x^k)}{\lambda_k \eta_j(x^k)} x_{j-1}^k \\ & \qquad \qquad \qquad j = 2, \dots, n \end{aligned} \right\} \quad x^k = (x_1^k, \dots, x_n^k). \tag{6.7}$$

By iteration,

$$x_j^k = \prod_{\ell=2}^j \frac{\gamma_{\ell-1}(x^k)}{\lambda_k \eta_\ell(x^k)} x_1 = \frac{q_j(x^k) \eta_1(x^k)}{\lambda_k^{j-1} \eta_j(x^k)} x_1^k, \quad j = 2, \dots, n.$$

We conclude that $x_1^k \neq 0$. We substitute these equations into the equation for x_1^k and divide by x_1^k ,

$$1 = \frac{1}{\lambda_k^n} \prod_{j=1}^n \frac{\gamma_j(x^k)}{\eta_j(x^k)} \leq \mathcal{R}(x^k). \tag{6.8}$$

This implies that the sequence (λ_k) is bounded.

Assume that the sequence (x_n^k) is bounded. Then, by (6.7), since the γ_j are bounded and the η_j are bounded away from 0, all sequences $(x_j^k)_{k \in \mathbb{N}}$ are bounded contradicting that $\|x^k\| \rightarrow \infty$. So (x_n^k) is unbounded and converges to ∞ after choosing subsequences. Again by (6.7), all sequences $(x_j^k)_{k \in \mathbb{N}}$ converge to ∞ .

Our assumptions imply that $\mathcal{R}(x^k) < 1$ for sufficiently large k contradicting (6.8).

So assumption (a) of Proposition 6.1 is satisfied with some $r_2 > 1$.

Assumption (b) of Proposition 6.1 follows in the same way as in the proof of Theorem 6.2. □

6.2. Uniqueness of persistence equilibria. Any positive equilibrium $x = (x_1, \dots, x_n)$ satisfies

$$\begin{aligned} 1 = \mathcal{R}(x) &= \sum_{k=1}^n \frac{b_k(x)}{\eta_k(x)} q_k(x), & q_k &= \prod_{j=1}^{k-1} \frac{\gamma_j(x)}{\eta_j(x)}, \\ \eta_j(x) x_j &= \gamma_{j-1}(x) x_{j-1}, & j &= 2, \dots, n. \end{aligned} \tag{6.9}$$

Let \leq denote the componentwise ordering in \mathbb{R}^n , $x \leq \tilde{x}$ (equivalently $\tilde{x} \geq x$) if and only if $x_j \leq \tilde{x}_j$ for $j = 1, \dots, n$. We write $x < \tilde{x}$ if $x \leq \tilde{x}$ and $x \neq \tilde{x}$, and $x \ll \tilde{x}$ if $x_j < \tilde{x}_j$ for $j = 1, \dots, n$.

Assumption 6.4. *The rate functions γ_j and η_j and the reproduction number function \mathcal{R} have the following monotonicity properties:*

- (a) *If $x, \tilde{x} \in \mathbb{R}_+^n$, $j \in \{1, \dots, n-1\}$ and $x_j < \tilde{x}_j$, then $\gamma_j(x)x_j < \gamma_j(\tilde{x})\tilde{x}_j$.*
- (b) *If $x, \tilde{x} \in \mathbb{R}_+^n$, $j \in \{2, \dots, n\}$, and $x_\ell < \tilde{x}_\ell$ for $\ell = j, \dots, n$, then $\eta_j(x)x_j < \eta_j(\tilde{x})x_j$.*
- (c) *If $x, \tilde{x} \in \mathbb{R}_+^n$ and $x \ll \tilde{x}$, then $\mathcal{R}(x) > \mathcal{R}(\tilde{x})$.*

Remark 6.5. (a) Assumption 6.4 (a) implies that $\gamma_j(x)$ only depends on x_j .
 (b) Assumption 6.4 (b) implies that $\eta_j(x)$ does not depend on $x_1 \dots x_{j-1}$, $j = 2, \dots, n$.
 (c) $\mathcal{R}(x) \geq \mathcal{R}(\tilde{x})$ if $x \ll \tilde{x}$ in Assumption 6.4 (c) is satisfied if the functions η_j are increasing and the functions γ_j and b_j are decreasing. To get a strict inequality, $q_j(y) > 0$ for all $y \geq 0$, $j = 1, \dots, n-1$, and some appropriate monotonicities must be strict. For instance, for some $k \in \{1, \dots, n\}$, $b_k(x) > b_k(\tilde{x})$ if $x, \tilde{x} \in \mathbb{R}_+^n$ and $x \ll \tilde{x}$.

Theorem 6.6. *If Assumption 6.4 holds, there is at most one nonzero equilibrium.*

Proof. Let $x, \tilde{x} \in \mathbb{R}_+^n$ be two equilibria. Without loss of generality we can assume that $x_n \leq \tilde{x}_n$. By Assumption 6.4 (b), $\eta_n(x)x_n \leq \eta_n(\tilde{x})\tilde{x}$ with the inequality being strict if and only if $x_n < \tilde{x}_n$. Since $\eta_n(x)x_n = \gamma_{n-1}(x)x_{n-1}$ and the same equation holds with \tilde{x} replacing x , it follows from Assumption 6.4 (a) that $x_{n-1} \leq \tilde{x}_{n-1}$ with the inequality being strict if and only if $x_n < \tilde{x}_n$.

Assumption 6.4 (b) now implies that $\eta_{n-1}(x)x_{n-1} \leq \eta_{n-1}(\tilde{x})\tilde{x}_{n-1}$ with strict inequality if and only if $x_n < \tilde{x}_n$. Since $\eta_{n-1}(x)x_{n-1} = \gamma_{n-2}(x)x_{n-2}$ and the same equation holds with \tilde{x} replacing x , it follows from Assumption 6.4 (a) that $x_{n-2} \leq \tilde{x}_{n-2}$ with the inequality being strict if and only if $x_n < \tilde{x}_n$.

Proceeding this way, we find that $x_j \leq \tilde{x}_j$ for $j = 1, \dots, n$, with equality holding for all j if $x_n = \tilde{x}_n$, and strict inequality holding for all j if $x_n < \tilde{x}_n$. Suppose that $x_n < \tilde{x}_n$. Then $x \ll \tilde{x}$ and $\mathcal{R}(x) > \mathcal{R}(\tilde{x})$, a contradiction because $\mathcal{R}(x) = 1 = \mathcal{R}(\tilde{x})$. So $x_n = \tilde{x}_n$ and $x = \tilde{x}$. □

7. Boundedness and dissipativity for cyclic stage structure. We consider the system (2.7).

Assumption 7.1. *The functions γ_j are bounded, and the functions η_j are bounded away from 0.*

We define

$$\nu_j(y) = \inf\{\eta_j(x); x \in \mathbb{R}_+^n; x_j \geq y\}, \quad y \geq 0, \quad j = 1, \dots, n. \tag{7.1}$$

These properties of ν_j follow directly from the definition and from Assumption 7.1.

Lemma 7.2. *For all $x \in \mathbb{R}_+^n$, $\eta_j(x) \geq \nu_j(x_j) > 0$. Further ν_j is increasing (not necessarily strictly) on \mathbb{R}_+ .*

We set $\Gamma_j = \sup_{x \in \mathbb{R}_+^n} \gamma_j(x)$. From (2.7), (7.1) and our assumptions, we have the following system of differential inequalities,

$$\left. \begin{aligned} x'_1 &\leq \Gamma_n x_n - \nu_1(x_1)x_1 \\ x'_j &\leq \Gamma_{j-1}x_{j-1} - \nu_j(x_j)x_j \\ &\qquad\qquad\qquad j = 2, \dots, n \end{aligned} \right\} x = (x_1, \dots, x_n). \tag{7.2}$$

Let $j = 1, \dots, n$, and $T > 0$. We define

$$x_j^T = \max_{0 \leq t \leq T} x_j(t). \tag{7.3}$$

Let $j \geq 2$ and assume $x_j^T > x_j(0)$. Then x_j^T is taken at some $t \in (0, T]$,

$$x_j(t) = x_j^T, \quad x_j'(t) \geq 0.$$

By the differential inequality for x_j ,

$$x_j^T \leq \frac{\Gamma_{j-1}}{\nu_j(x_j^T)} x_{j-1}^T. \tag{7.4}$$

Without assuming $x_j^T > x_j(0)$,

$$x_j^T \leq \max \left\{ x_j(0), \frac{\Gamma_{j-1}}{\nu_j(x_j^T)} x_{j-1}^T \right\}, \quad j = 2, \dots, n. \tag{7.5}$$

Similarly, we derive that

$$x_1^T \leq \max \left\{ x_1(0), \frac{\Gamma_n}{\nu_1(x_1^T)} x_n^T \right\}. \tag{7.6}$$

Theorem 7.3. *Let Assumption 7.1 be satisfied and $\Gamma_j := \sup_{x \in \mathbb{R}_+^n} \gamma_j(x)$.*

Assume that there exists some $c > 0$ and $\xi \in (0, 1)$ such that

$$\prod_{j=1}^n \frac{\Gamma_j}{\eta_j(x^j)} \leq \xi \quad \text{for all vectors } x^1, \dots, x^n \in \mathbb{R}_+^n \text{ with } x_j^j \geq c.$$

Then all solutions of (2.3) are bounded. Further the system is dissipative: There exists some $\tilde{c} > 0$ such that $x_j^\infty := \limsup_{t \rightarrow \infty} x_j(t) \leq \tilde{c}$ for all solutions of (2.3). Finally $\min_{j=1}^n x_j^\infty \leq c$.

Proof. Let $c > 0$ be as in the assumptions of the theorem. Since the ν_j are increasing,

$$1 > \xi \geq \prod_{j=1}^n \frac{\Gamma_j}{\nu_j(c)} \geq \prod_{j=1}^n \frac{\Gamma_j}{\nu_j(\infty)}. \tag{7.7}$$

Suppose that x_n is not bounded. Then $x_n^T \rightarrow \infty$ as $T \rightarrow \infty$. It follows from (7.5) that $x_j^T \rightarrow \infty$ as $T \rightarrow \infty$. So, for sufficiently large T , (7.4) holds for $j = 2, \dots, n$. We solve (7.4) recursively, substitute the result into (7.6) and divide by x_1^T to obtain

$$1 \leq \prod_{j=1}^n \frac{\Gamma_j}{\nu_j(x_j^T)}.$$

We take the limit as $T \rightarrow \infty$ and obtain

$$1 \leq \prod_{j=1}^n \frac{\Gamma_j}{\nu_j(\infty)},$$

a contradiction to (7.7).

Thus x_n is bounded. By (7.6), x_1 is bounded and then the x_j are bounded for $j = 1, \dots, n$.

Now we can apply the fluctuation method [19] [36, Prop.A.22]. Let

$$x_j^\infty = \limsup_{t \rightarrow \infty} x_j(t).$$

There exists a sequence (t_k) in \mathbb{R}_+ with $t_k \rightarrow \infty$, $x_j(t_k) \rightarrow x_j^\infty$, and $x'_j(t_k) \rightarrow 0$. By (7.2),

$$0 \leq \Gamma_{j-1}x_{j-1}^\infty - \nu_j(x_j^\infty)x_j^\infty$$

and so

$$x_j^\infty \leq \frac{\Gamma_{j-1}}{\nu_j(x_j^\infty)}x_{j-1}^\infty.$$

Similarly

$$x_1^\infty \leq \frac{\Gamma_n}{\nu_1(x_1^\infty)}x_n^\infty.$$

We solve the first set of inequalities recursively and substitute it into the last,

$$x_1^\infty \leq \prod_{j=1}^n \frac{\Gamma_j}{\nu_j(x_j^\infty)}x_1^\infty.$$

Without loss of generality we can assume that $x_1^\infty > 0$ and divide by it. Since the ν_j are increasing,

$$1 \leq \prod_{j=1}^n \frac{\Gamma_j}{\nu_j(\tilde{x}^\infty)}, \quad \tilde{x}^\infty = \min_{j=1}^n x_j^\infty,$$

and, by (7.7), we have $\tilde{x}^\infty \leq c$. Since $x_j^\infty \leq \frac{\Gamma_{j-1}}{\nu_j(0)}x_{j-1}^\infty$ and $x_1^\infty \leq \frac{\Gamma_n}{\nu_1(0)}x_n^\infty$, we find a $\tilde{c} > 0$ that only depends on Γ_j and $\nu_j(0)$ such that $x_j^\infty \leq \tilde{c}$. \square

7.1. Back to persistence. In dynamical systems language, the result of Theorem 7.3 means that the semiflow induced by system (2.7) is point-dissipative. Since our state space is \mathbb{R}_+^n , the semiflow is asymptotically smooth [34, Rem.2.26]. The following persistence result follows from Theorem 5.4 and [34, Cor.4.22] (or results in [45]).

Theorem 7.4. *Let the Assumptions 4.1 and 7.1 be satisfied. Set $\Gamma_j = \sup \gamma_j(\mathbb{R}_+^n)$. Assume that there exists some $c > 0$ and $\xi \in (0, 1)$ such that*

$$\prod_{j=1}^n \frac{\Gamma_j}{\eta_j(x^j)} \leq \xi, \quad \text{for all vectors } x^1, \dots, x^n \in \mathbb{R}_+^n \text{ with } x_j^j \geq c.$$

Further let

$$1 < \mathcal{R}_0 = \prod_{j=1}^n \frac{\gamma_j(0)}{\eta_j(0)}.$$

Then there exists some $\epsilon > 0$ such that

$$\liminf_{t \rightarrow \infty} x_j(t) \geq \epsilon, \quad j = 1, \dots, n$$

for any solution x of (2.7) in \mathbb{R}_+^n with $x(0) \neq 0$.

Proof. We apply [34, Cor.4.22] with $\rho(x) = \sum_{j=1}^n x_j$ and $\tilde{\rho}(x) = \min_{j=1}^n x_j$. By Theorem 5.4, the semiflow induced by (2.7) is uniformly ρ -persistent.

Now let $x : \mathbb{R} \rightarrow \mathbb{R}^n$ be a total trajectory, i.e. in our case, just a solution of (2.7), x bounded, and $\rho(x(t)) > 0$ for all $t \in \mathbb{R}$. By our assumptions, $x_j(t) > 0$ for all $t \in \mathbb{R}$, $j = 1, \dots, n$. In particular, $\tilde{\rho}(x(0)) > 0$. By [34, Cor.4.22], there exists some $\epsilon > 0$ such that

$$\liminf_{t \rightarrow \infty} \tilde{\rho}(x(t)) \geq \epsilon,$$

for all solutions x in \mathbb{R}_+^n with $\rho(x(0)) > 0$, i.e., $x(0) \neq 0$. \square

Example 7.5. We consider the cyclic stage structured system

$$\left. \begin{aligned} x'_1 &= \gamma_n(x)x_n - \eta_1(x_1)x_1 \\ x'_j &= \gamma_{j-1}(x)x_{j-1} - \eta_j(x_j)x_j \\ & \quad j = 2, \dots, n \end{aligned} \right\} x = (x_1, \dots, x_n) \tag{7.8}$$

Assume that $\gamma_j(x) \leq \gamma_j(0)$ for all $x \in \mathbb{R}_+^n$, that all η_j are bounded away from 0, $j = 1, \dots, n$, and that $\eta_j(s) \rightarrow \infty$ as $s \rightarrow \infty$ for at least one $j \in \{1, \dots, n\}$.

Then there exists a bounded set that attracts all solutions. If $\mathcal{R}_0 > 1$, the population is uniformly persistent.

8. Local stability studies in a special case. The purpose of this section is to illustrate that it may be very difficult to show general stability results for the persistence equilibrium in the models in [21, 43].

We consider the case that only one particular stage exerts a negative feedback on procreating adults. Let $n \geq 3$, $\ell \in \{1, \dots, n\}$, and

$$\left. \begin{aligned} x'_1 &= h(x_\ell)x_n - \eta_1x_1, \\ x'_j &= \gamma_{j-1}x_{j-1} - \eta_jx_j, \quad j = 2, \dots, n. \end{aligned} \right\} \tag{8.1}$$

Here $\eta_j \geq \gamma_j > 0$, $j = 1, \dots, n - 1$, $\eta_n > 0$. Further $h : \mathbb{R}_+ \rightarrow \mathbb{R}_+$ is decreasing and differentiable, $h(0) > 0 \geq h'(0)$. For $\ell = n - 2$, this is a special case of the ODE version of [26] investigated in [21, 43].

Notice that, for $\ell < n$, Theorem 7.3 does not provide any useful condition for the boundedness of solutions because its assumptions would imply that $\mathcal{R}_0 \leq 1$. Notice that $\gamma_n(x) = h(x_\ell)$. So boundedness of solutions is an open problem for this system. Here we focus on the stability of persistence equilibria.

After scaling time, we can assume that

$$h(0) = 1. \tag{8.2}$$

If $h'(0) < 0$, we can also assume that $h'(0) = -1$ by scaling the dependent variables. In this special case, we obtain from Section 6 that

$$\mathcal{R}_0 = \frac{q}{\eta_n}, \quad q = q_n = \prod_{j=1}^{n-1} \frac{\gamma_j}{\eta_j}, \tag{8.3}$$

and, if $\mathcal{R}_0 > 1$, there is a unique persistence equilibrium $x \in (0, \infty)^n$ determined by

$$1 = \mathcal{R}(x_\ell) = h(x_\ell) \frac{q}{\eta_n}. \tag{8.4}$$

We will also need the relation

$$x_n = x_\ell \frac{\prod_{k=\ell}^{n-1} \gamma_k}{\prod_{k=\ell+1}^n \eta_k}. \tag{8.5}$$

The variational system (linearization about the equilibrium) is

$$\left. \begin{aligned} y'_1 &= h'(x_\ell)x_ny_\ell + h(x_\ell)y_n - \eta_1y_1, \\ y'_j &= \gamma_{j-1}y_{j-1} - \eta_jy_j, \quad j = 2, \dots, n. \end{aligned} \right\} \tag{8.6}$$

Eigenvectors v of the right hand side with associated eigenvalues satisfy

$$\left. \begin{aligned} \lambda v_1 &= h'(x_\ell)x_nv_\ell + h(x_\ell)v_n - \eta_1v_1, \\ \lambda v_j &= \gamma_{j-1}v_{j-1} - \eta_jv_j, \quad j = 2, \dots, n. \end{aligned} \right\} \tag{8.7}$$

This is rewritten as

$$\begin{aligned} v_1 &= \frac{h'(x_\ell)x_n v_\ell + h(x_\ell)v_n}{\lambda + \eta_1}, \\ v_j &= \frac{\gamma_{j-1}v_{j-1}}{\lambda + \eta_j}, \quad j = 2, \dots, n. \end{aligned} \quad (8.8)$$

So

$$v_j = \frac{\prod_{k=1}^{j-1} \gamma_k}{\prod_{k=2}^j (\lambda + \eta_k)} v_1, \quad j = 2, \dots, n.$$

We substitute this into the first equation and divide by v_1 ,

$$1 = h'(x_\ell)x_n \frac{\prod_{k=1}^{\ell-1} \gamma_k}{\prod_{k=1}^\ell (\lambda + \eta_k)} + h(x_\ell) \frac{\prod_{k=1}^{n-1} \gamma_k}{\prod_{k=1}^n (\lambda + \eta_k)}. \quad (8.9)$$

We substitute (8.5) and (8.4),

$$1 = \frac{h'(x_\ell)x_\ell}{h(x_\ell)} \frac{\prod_{k=1}^\ell \eta_k}{\prod_{k=1}^\ell (\lambda + \eta_k)} + \frac{\prod_{k=1}^n \eta_k}{\prod_{k=1}^n (\lambda + \eta_k)}.$$

Assume that $h'(x_\ell) < 0$. We rewrite this equation as

$$1 = -\psi(x_\ell) \prod_{k=1}^\ell \frac{\eta_k}{\lambda + \eta_k} + \prod_{k=1}^n \frac{\eta_k}{\lambda + \eta_k} \quad (8.10)$$

with

$$\psi(x_\ell) = -\frac{h'(x_\ell)x_\ell}{h(x_\ell)} > 0. \quad (8.11)$$

Then this equation, whatever ℓ , has no solutions $\lambda \geq 0$. We explore several cases for ℓ .

8.1. Negative feedback from the first stage to itself. Let $\ell = 1$. Then we can reorganize equation (8.10) as

$$1 + \psi(x_\ell) \frac{\eta_1}{\lambda + \eta_1} = \prod_{k=1}^n \frac{\eta_k}{\lambda + \eta_k}.$$

We observe that, if the real part of λ is nonnegative, the absolute value of the left hand side is greater than 1, and the absolute value of the right hand side is at most 1. So there are no roots with nonnegative real parts. Alternatively we can argue that the linearized system is quasipositive and the eigenvalue with leading real part is actually real. So the persistence equilibrium is locally asymptotically stable.

8.2. Negative feedback from the last stage. Let $\ell = n$. Then equation (8.10) becomes

$$1 = (1 - \psi(x_\ell)) \prod_{k=1}^n \frac{\eta_k}{\lambda + \eta_k}. \quad (8.12)$$

We take absolute values and find that there are no roots with nonnegative real part if

$$\psi(x_\ell) \leq 2.$$

In fact, one can show that the persistence equilibrium is globally asymptotically stable if h is strictly decreasing and $s^2 h(s)$ is an increasing function of s . This is done by deriving a single integral equation for x_n and combining Theorem B.40 and Corollary 9.9 in [36] (see also [13]).

Suppose that

$$\psi(x_\ell) > 2.$$

Set all η_k equal, $\eta_k = \eta$. Then (8.12) amounts to solving

$$\left(\frac{\lambda}{\eta} + 1\right)^n = \alpha := 1 - \psi(x_\ell),$$

with $\alpha < -1$. For sufficiently large n , it is possible to find a solution λ with positive real part.

Set $z = \frac{\lambda}{\eta} + 1$ and search for z in polar coordinates $z = re^{i\theta}$. This leads to $r = |\alpha|^{1/n}$ and $n\theta = -\pi$, i.e., $z = r(\cos(-\pi/n) + i \sin(-\pi/n))$. Since $r > 1$, $r \cos(-\pi/n) > 1$ for large enough n . So

$$\lambda = \eta(z - 1)$$

has a positive real part independently of how $\eta > 0$ is chosen.

8.3. Negative feedback from an intermediate stage. Let $1 < \ell < n$. We bring (8.10) to the standard form of a characteristic polynomial,

$$\chi(\lambda) = \prod_{k=1}^n (\lambda + \eta_k) + \psi(x_\ell) \prod_{k=1}^{\ell} \eta_k \prod_{k=\ell+1}^n (\lambda + \eta_k) - \prod_{k=1}^n \eta_k. \tag{8.13}$$

Choose $\eta_n = 0$ and $\eta_1 = \dots = \eta_\ell$. Then the characteristic equation has the solution $\lambda = 0 = \eta_n$ and the solutions $\lambda = -\eta_k$ for $k = \ell + 1, \dots, n - 1$ and the solutions λ of

$$0 = \left(\frac{\lambda}{\eta_1} + 1\right)^\ell + \psi(x_\ell).$$

By our previous consideration, this equation has a solution λ with positive real part if $\psi(x_\ell) > 1$ and ℓ is large enough. By Rouché’s theorem [32, A.3], the original equation has a solution λ with positive real part if $\psi(x_\ell) > 1$ and ℓ is large enough and η_n is small enough.

We need to make sure that our choices are feasible. Recall $\eta_n/q = h(x_\ell)$, q independent of η_n . If h is strictly decreasing with limit 0 at infinity, then $x_\ell \rightarrow \infty$ as $\eta_n \rightarrow 0$. For our purposes so far, we needed to have that $\psi(x_\ell) > 1$ which we can achieve if $\psi(\infty) = \lim_{s \rightarrow \infty} \psi(s) > 1$ and $\eta_n > 0$ is chosen sufficiently small.

Example 8.1. Recall that we assumed $h(0) = 1$ and $1 = -h'(0)$ if $h'(0) \neq 0$ to reduce degrees of freedom that do not really exist.

(a) $h(y) = e^{-y}$. Then $\psi(y) = y \rightarrow \infty$ as $y \rightarrow \infty$.

(b) $h(y) = \frac{\alpha}{\alpha + y^\alpha}$ with $\alpha > 0$. Then $\psi(y) \rightarrow \alpha$ as $y \rightarrow \infty$ and $\psi(\infty)$ can be taken as large as wanted by choosing α large.

Let us consider the cases $n = 5$ and $n = 6$ and $\ell = n - 2$. For $n \geq 5$,

$$\chi(\lambda) = \sum_{j=0}^n a_{n-j} \lambda^j$$

with $a_0 = 1$,

$$\begin{aligned} a_1 &= \sum_{k=1}^n \eta_k = b_1 + \eta_n, \\ a_j &= b_j + \phi_j(\eta_n), \quad j = 2, \dots, n-3, \\ a_{n-2} &= b_{n-2} + \phi_{n-2}(\eta_n) + \psi(x_{n-2}) \prod_{k=1}^{n-2} \eta_k, \\ a_{n-1} &= b_{n-1} + \phi_{n-1}(\eta_n) + \psi(x_{n-2}) \prod_{k=1}^{n-2} \eta_k (\eta_n + \eta_{n-1}) \\ a_n &= \psi(x_{n-2}) \prod_{k=1}^n \eta_k, \end{aligned}$$

where $\phi_j(\eta_n) \rightarrow 0$ as $\eta_n \rightarrow 0$. We assume that

$$h(y) \rightarrow 0, \quad \frac{-h'(y)y}{h(y)} \rightarrow \psi(\infty), \quad y \rightarrow \infty. \quad (8.14)$$

Then $x_{n-2} \rightarrow \infty$ as $\eta_n \rightarrow 0$ and

$$\psi(x_{n-2}) \rightarrow \psi(\infty).$$

Case. $n = 5$.

Then, as $\eta_5 \rightarrow 0$,

$$\begin{aligned} a_1 a_2 - a_3 &= (b_1 + \eta_5)(b_2 + \phi_2(\eta_5)) - b_3 - \phi_3(\eta_5) - \psi(x_3) \eta_1 \eta_2 \eta_3 \\ &\rightarrow (b_1 + \eta_5) b_2 - b_3 - \psi(\infty) \eta_1 \eta_2 \eta_3 < 0 \end{aligned}$$

if $\psi(\infty)$ is large enough. By the Routh-Hurwitz criterion (see (36') in XV.§6 of [15]), the equilibrium is unstable.

Case. $n = 6$.

The equilibrium is unstable (see (36') in XV.§6 of [15]) if

$$0 > \begin{vmatrix} a_1 & 1 & 0 \\ a_3 & a_2 & a_1 \\ a_5 & a_4 & a_3 \end{vmatrix} = -a_1(a_1 a_4 - a_5) + a_3(a_1 a_2 - a_3).$$

As $\eta_6 \rightarrow 0$, the second summand remains bounded and a_1 remains bounded away from 0, while

$$\begin{aligned} a_1 a_4 - a_5 &= [a_1 - (\eta_5 + \eta_6)] \psi(x_4) \prod_{k=1}^4 \eta_k + \theta(\eta_6) \\ &= \left(\sum_{k=1}^4 \eta_k \right) \psi(x_4) \prod_{k=1}^4 \eta_k + \theta(\eta_6), \end{aligned}$$

where $\theta(\eta_6)$ remains bounded as $\eta_6 \rightarrow 0$. As $\psi(x_4) \rightarrow \psi(\infty)$ as $\eta_6 \rightarrow 0$ and $\psi(\infty)$ can be made as large as wanted, $a_1 a_4 - a_5$ can be made as large as wanted as $\eta_6 \rightarrow 0$.

So the persistence equilibrium is unstable for sufficiently small $\eta_6 > 0$.

9. Epilog: A modified model. We developed a model for populations with many discrete stages. We obtained satisfactory results concerning the persistence and extinction of the population and the existence and uniqueness of positive equilibria. Some special cases of these models, however, present substantial difficulties for proving the boundedness of solutions and the stability of positive equilibria. In particular, we are not able to show boundedness of solutions for the system

$$\begin{aligned} x'_1 &= h(x_\ell)x_n - \eta_1x_1, \\ x'_j &= \gamma_{j-1}x_{j-1} - \eta_jx_j, \quad j = 2, \dots, n, \end{aligned} \tag{9.1}$$

with $n \geq 3$ and $1 < \ell < n$. Here $\eta_j \geq \gamma_j > 0$, $j = 1, \dots, n - 1$, $\eta_n > 0$ and $h : \mathbb{R}_+ \rightarrow \mathbb{R}_+$ is strictly decreasing. (9.1) is a special case of the models in [21, 43] with $\ell = n - 2 = 10$, but we are not even able to prove boundedness of solutions if $n = 3$ and $\ell = 2$. This is quite disturbing because one feels that a strong immune response or resistance of the hosts which is triggered when the adult ticks feed on them (represented by x_ℓ) and reduces the fertility of the ticks when they lay their eggs later (represented by x_n) should be able to keep tick numbers bounded even if there are no other overcrowding effects present.

Sometimes mathematical difficulties can be a sign that something is wrong with the model [35], in our case with modeling the negative feedback of feeding adults on the fertility of egg-laying adults. A first observation is that, if the negative feedback is due to an immune reaction caused by feeding adults which only plays out during egg-laying, then the fertility reduction of egg-laying adults is caused by the ticks that were feeding at the same time as the egg-laying adults were, i.e., at some moment in the past. In a model of ordinary differential equations, where stage lengths are exponentially distributed, it is difficult to model the appropriate delay in a consistent way. In a model with discrete delays where stage lengths are the same for all individuals in the stage, this is possible in a more satisfactory way though it does not remove the mathematical difficulties [13].

Here we suggest an alternative model formulation within the framework of ordinary differential equations.

Let x_1 be the amount of eggs, x_j ($j = 2, \dots, n - 3$) the amount of ticks in various larval, nymph, and adult stages, x_{n-2} the amount of feeding adult ticks, x_{n-1} the reproductive potential of engorged adult ticks, and x_n the reproductive potential of egg-laying adult ticks. Then

$$\begin{aligned} x'_1 &= \beta_nx_n - (\tau_1(x_1) + \mu_1(x_1))x_1, \\ x'_j &= \tau_{j-1}(x_{j-1})x_{j-1} - (\tau_j(x_j) + \mu_j(x_j))x_j, \quad j = 2, \dots, n - 2, \\ x'_{n-1} &= \theta(x_{n-2})\tau_{n-2}(x_{n-2})x_{n-2} - (\tau_{n-1}(x_{n-1}) + \mu_{n-1}(x_{n-1}))x_{n-1}, \\ x'_n &= \tau_{n-1}(x_{n-1})x_{n-1} - \mu_n(x_n)x_n. \end{aligned} \tag{9.2}$$

Here $\tau_{j-1}(x_{j-1}) \geq 0$ is the per capita transition rate from the $(j - 1)^{th}$ stage to the j^{th} stage, $\mu_j(x_j) \geq 0$ the per capita mortality in the j^{th} stage, and $\theta_{n-2}(x_{n-2}) \in [0, 1]$ the fertility reduction factor due to the immunity or resistance that the host develops as response to the number of feeding ticks.

For $x = (x_1, \dots, x_n)$, we set

$$\begin{aligned} \eta_j(x) &= \tau_j(x_j) + \mu_j(x_j), \quad j = 1, \dots, n - 1, \\ \eta_n(x) &= \mu_n(x_n), \\ \gamma_j(x) &= \tau_j(x_j), \quad j = 1, \dots, n - 3, \quad j = n - 1, \end{aligned}$$

$$\begin{aligned}\gamma_{n-2}(x) &= \theta(x_{n-2})\tau_{n-2}(x_{n-2}), \\ \gamma_n(x) &= \beta_n,\end{aligned}$$

and this modified model is a special case of (2.7) and (2.3) satisfying (2.4). All results from Sections 2 to 6 apply.

Boundedness of solutions can now simply be enforced by assuming that $y\tau_{n-2}(y)\theta(y)$ is a bounded function of $y \geq 0$ which can be achieved by assuming that θ decreases sufficiently fast as a function of y .

Global stability of the persistence equilibrium can be enforced by assuming that the function $y\theta(y)\tau_{n-2}(y)$ is increasing in $y \geq 0$ and $\theta(y)\tau_{n-2}(y)$ is strictly decreasing in $y > 0$ and that the functions $y\tau_j(y)$ are increasing in $y \geq 0$ while τ_j is decreasing and θ strictly decreasing. Further $\mu_j(x_j)$ should be increasing in x_j . Then the system induces a monotone semiflow [31] with at most one nonzero equilibrium (Section 6.2). This is a bit of a balancing act because $y\theta(y)\tau_{n-2}(y)$ should be both increasing and bounded as a function of y . Hopefully, some of these assumptions can be weakened.

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