An alternative delayed population growth difference equation model

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Received: 12 October 2020 / Revised: 13 May 2021 / Accepted: 18 July 2021 / Published online: 7 August 2021
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Abstract
We propose an alternative delayed population growth difference equation model based on a modification of the Beverton–Holt recurrence, assuming a delay only in the growth contribution that takes into account that those individuals that die during the delay, do not contribute to growth. The model introduced differs from a delayed logistic difference equation, known as the delayed Pielou or delayed Beverton–Holt model, that was formulated as a discretization of the Hutchinson model. The analysis of our delayed difference equation model identifies a critical delay threshold. If the time delay exceeds this threshold, the model predicts that the population will go extinct for all non-negative initial conditions. If the delay is below this threshold, the population survives and its size converges to a positive globally asymptotically stable equilibrium that is decreasing in size as the delay increases. We show global asymptotic stability of the positive equilibrium using two different techniques. For one set of parameter values, a contraction mapping result is applied, while the proof for the remaining set of parameter values, relies on showing that the map is eventually componentwise monotone.

Keywords Single species growth models · Logistic growth · Beverton–Holt model · Delayed Beverton–Holt/Pielou model · Delay difference equation · Discretization · Global stability · Extinction threshold · Componentwise monotonicity

Mathematics Subject Classification 39A60 · 39A30 · 92D25 · 92B05

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1 Introduction

The logistic growth model is a well studied differential equation, introduced by Verhulst (1838) in the context of modelling population growth. A discretization of the Verhulst model can be obtained by applying the Euler method to the logistic differential equation and is often referred to as the logistic difference equation, see for example (May 2001; Smith 1968). Robert May (1974) popularized this discrete version of the Verhulst model, also known as the logistic map, which contributed significantly to the mathematical study of chaos. This model was however criticized biologically as solutions can become negative and also because of its potential for chaotic behavior, not possible in the continuous logistic model. Hence, referring to it as the “discrete counterpart” does not seem appropriate. To overcome the possible negativity of solutions, a recurrence derived under the assumption that the fraction of surviving individuals is given by an exponential function is considered to be the appropriate discretization by some authors (MacFadyen 1963; May 1974). In this work however, we modify yet another discretization of the logistic model in order to include the effect of delay on growth, namely the Beverton–Holt model, also known as the Pielou equation. We refer to this new model as a delayed logistic difference equation, since the Beverton–Holt model was originally derived in Beverton and Holt (1957) under the assumption of an underlying logistic growth model, and authors such as Bohner et al. (2010), Brauer and Castillo-Chavez (2001), Pielou (1969), Pielou and Gordon (1974) argue that the Beverton–Holt model is a discretization of the logistic differential equation, since it preserves most of its properties.

Despite its simplicity, the Beverton–Holt equation is used in resource management to model populations, especially in fisheries science (Freeman et al. 2014; Haddon 2011; Hilborn and Walters 1992; Sharma et al. 2005). Naturally, simple mathematical models often inherit implicit assumptions on processes. For example, they may assume aspects of the population are homogeneous. As these assumptions are not necessarily satisfied in real-world systems, model predictions should be interpreted carefully, dependent on the level of violation of these assumptions. There are however benefits in applying simple models. One reason is that these models are usually more tractable. As well, if data is limited, simple population models such as the Beverton–Holt model are preferred in assessing the species size (Dichmont et al. 2016; Froese et al. 2017; Punt et al. 2015; Rosenberg et al. 2018; Winker et al. 2018; Worm et al. 2009). Furthermore, more complex models are frequently constructed using such simple models as building blocks. For example, age-structure population models often use the Beverton–Holt model as the recruitment function (Haddon 2011).

To improve a model, one may start to refine assumptions, one by one, to capture more realistic features. Simple continuous population models assume instantaneous population changes and discrete population models assume that either generations do not overlap or that the recruitment into the breeding population occurs within the first generation of the life span. The formulation of delay differential equations offers a mathematical tool to model non-instantaneous reaction times and a time lag in breeding. An example of a population where such a delay model seems appropriate is Daphnia, since the future population size is determined by the food availability at the time the eggs are formed rather than when they hatch (Arino et al. 2007). Another early
example of the application of a delay differential equations model is the Nicholson’s blowfly model. Data on Australian sheep-blowfly, collected by Nicholson (1954), was fit to a delayed Hutchinson model. Later, in Gurney et al. (1980), a delayed exponential growth model was fit to obtain a more satisfactory quantitative fit to the collected time history.

A natural extension for difference equation models is consideration of age-structure. While age-structured population models may make more precise predictions, they require following the age distribution of the population through time and their implementation requires the collection of specific age dependent data that is not always economically or biologically feasible (Hilborn and Walters 1992). The formulation of delay difference equations is an attractive compromise between a higher dimensional difference equation model and a simple population model as it can account for an underlying age-structure in populations while preserving a relatively simple structure. Newly recruited individuals may not contribute to the recruitment in the following breeding season but rather have to reach a certain age-class to be a member of the breeding population. The formulation of delay difference equations allows for such a delay in joining the breeding population, as also outlined by Clark (1976) and later Deriso (1980). Clark’s formulation of a delay difference equation was motivated by a study on Antarctic fin whales by Allen in Allen (1963), who noticed a maturation period greater than one spawning season in the stock-recruitment relation. From data and discussions by Allen, for example in Allen (1963), Allen (1966), Clark calculated that it took on average 5 seasons before a newborn baleen whale joined the breeding population and hence employed a delay of 5 seasons in his model. Motivated by Allen’s and Clark’s work, a delay difference equation model was implemented to predict the sei whale population size, see (Twenty-sixth annual report of the international commission on whaling 1976; Twenty-eighth annual report of the international commission on whaling 1978) and (Beddington 1978). Motivated by Deriso’s work on delay difference equations in Deriso (1980), the author’s in Fournier and Doonan (1987), Schnute (1985), Schnute (1987) provide details of a generic stock-assessment with an underlying delay difference equation model. While the simplicity of the model structure is preserved in these delay models, the contribution of different age classes to the change in biomass can be considered without keeping track of the precise age distribution.

The above arguments led to the inclusion of delay in continuous and discrete population models. A popular modification of the Verhulst model is the delay logistic differential equation (Hutchinson or Wright model). The Hutchinson model has been extensively studied by several authors, see for example (Cushing 1977; Gopalsamy 1992; Jaquette et al. 2017; MacDonald 1978; Nisbet and Gurney 1982; van den Berg and Jaquette 2018), despite certain questionable properties. More precisely, the size of the equilibrium of the Hutchinson model is independent of the delay and is globally asymptotically stable if and only if the product of the growth rate and the time delay is bounded by the rather unintuitive bound of \( \frac{\pi}{2} \), see (van den Berg and Jaquette 2018). For parameter values that do not satisfy this bound, solutions of the Hutchinson model exhibit another unreasonable property. In particular, nontrivial periodic solutions persist and hence the population avoids extinction, independent of the length of the delay.
While the Hutchinson model was derived assuming a delay in the per-capita growth rate, the alternative delay differential equation formulated in Arino et al. (2006) includes a delay solely in the growth process and takes into consideration the fact that those individuals that die during the delay, do not contribute to growth. The authors in Arino et al. (2006) show that their model predicts that the population dies out if the delay exceeds a certain threshold and converges to a globally asymptotically stable equilibrium with size that decreases as the delay increases. This behavior seems more reasonable for populations in natural ecosystems. The recurrence introduced in this work is derived using the same assumptions as in Arino et al. (2006) and exhibits similar properties. It can therefore be considered as the discrete analogue of Arino et al. (2006).

Considering delay in the Beverton–Holt model, interpreted as a discrete delay logistic model, has been addressed by several authors. A popularized delay logistic difference equation with an underlying Beverton–Holt structure, known as the delay Pielou logistic recurrence is,
\[ x_{t+1} = x_t f(x_{t-\tau}), \]
with
\[ f(w) = \left( \alpha + \beta w \right)^{-1}. \]
This recurrence was introduced in Pielou (1969) as a discretization of Hutchinson’s model and discussed by many authors, including (Camouzis and Ladas 2007; Kocić 2010, 2011; Kocić and Ladas 1993; Kocić et al. 2004; Kulenović and Merino 2007; Levin and May 1976; Pielou 1969; Pielou and Gordon 1974). This delayed Beverton–Holt/Pielou model can be criticized for the same reasons as Hutchinson’s model, because it exhibits the same questionable behavior described above, see Garab et al. (2019), Kocić and Ladas (1993), Kulenović and Ladas (2001), Kuruklis and Ladas (1992)). For example, it can be shown that if \( (1 - \alpha)^{-1} \) is bounded by the unintuitive bound of \( 2 \cos \left( \frac{k\pi}{2k+1} \right) \), then the delay-independent equilibrium \( \frac{1}{\beta} \) is asymptotically stable (Kuruklis and Ladas 1992) and if the delay \( \tau \) remains below \( (1 - \alpha)^{-1} \), then this equilibrium is globally asymptotically stable (Kocić and Ladas 1992). The model introduced in this work also differs from another delayed Beverton–Holt model introduced in Bohner et al. (2018), where the delay is only on the left-hand side, i.e., \( x_{t+\tau} = x_t f(x_t) \), with the same \( f \) as mentioned above. Solutions of that model with constant parameters are shown to converge to a unique constant that is again independent of the delay \( \tau \). In contrast, we not only derive a delay discrete model based on first principles, but the solutions of our proposed model exhibit more realistic behavior. More precisely, based on the existence of a positive equilibrium, we identify a critical threshold for the delay. We continue our analysis of the proposed model with the local stability of the trivial and the unique positive equilibria followed by studying the global dynamical behavior. We prove that for positive initial conditions, if the delay exceeds the critical threshold, then the trivial equilibrium is globally asymptotically stable. Instead, if the delay falls below the threshold, then the population survives and converges to a positive equilibrium that decreases in size as the delay increases.

The paper is organized as follows. In Sect. 2, we derive the discrete delay model by modifying the classical Beverton–Holt model considering a delay only in the growth contribution and requires individuals to survive the delay period to contribute to growth. This model differs from existing models mentioned above. In Sect. 3, we discuss the global dynamics. The behavior of our discrete model mirrors most of the qualitative behavior predicted by the continuous delay model in Arino et al. (2006). The
main difference between the predictions of these two models is that in the continuous model, if the initial data is either entirely above or entirely below the positive equilibrium, solutions converge to the equilibrium monotonically. We provide numerical simulations to show that this is not the case for the discrete model. Another simulation illustrates how the dynamics differ for certain choices of parameters, and hence show why a different technique was needed to prove the global stability of the positive equilibrium. Finally, in the conclusion in Sect. 4, we summarize our results and highlight the differences between the dynamical behavior of our modified Beverton–Holt model and two related models: its continuous analogue introduced in Arino et al. (2006) and its underlying submodel, the Beverton–Holt model.

2 Derivation of a discrete delay growth model

In this section, we derive a delayed logistic growth model by identifying the growth and decline contributions in the Beverton–Holt model before incorporating a time lag in the growth component, taking into consideration that those that die during the delay do not contribute to growth. A similar technique was applied in the derivation of the logistic delay differential equation introduced in Arino et al. (2006). The classical Beverton–Holt model is given by

\[ y_{t+1} = \frac{\rho K y_t}{K + (\rho - 1)y_t}, \]

with \( K \in \mathbb{R}^+ \), representing the carrying capacity, \( \rho > 1 \), the proliferation rate, and \( y_t \), the population at time \( t \). Recurrence (1) was obtained in Beverton and Holt (1957) by solving the logistic growth model and relating the solution evaluated at time \( t + T \) to the solution at time \( t \). The parameter \( \rho \) was introduced by substituting \( \rho = e^{rT} \) for \( r > 0 \), resulting in \( \rho > 1 \), as outlined in Beverton and Holt (1957). The recurrence (1) can be normalized using the variable transformation \( z_t = \frac{y_t}{K} \) resulting in

\[ z_{t+1} = \frac{z_t}{\rho + (\rho - 1)\frac{z_t}{\rho}} = p_t z_t, \]

where

\[ p_t := \frac{1}{\rho + (\rho - 1)z_t}, \]

can be interpreted as the survival probability. Following the reasoning in Arino et al. (2006), we assume that the survival probability depends on growth, death, and intraspecific competition. Then, (3) reveals that the term \( \frac{\rho - 1}{\rho} \) determines the decline due to intraspecific competition and \( \frac{1}{\rho} < 1 \) is the sum of the death and growth contribution. This sum can generally be expressed as \( \frac{1}{\rho} = 1 + b - a \), where \( a > 0 \) is the growth component and \( b > 0 \) the death component. Since \( \rho > 1 \), this implies that
\( a - b \in (0, 1) \), i.e., the value of the actual growth component exceeds the value of the death component.

To highlight each of the three components: growth, death, and intraspecific competition, we express the survival probability (3) as

\[
p_t = \frac{1}{1 - (a - b) + cz_t}.
\]

Expression (4) is decreasing in \( b \) and \( c \), due to death and competition, and is increasing in \( a \), representing the growth contribution. We note that the distinction of intraspecific competition, growth, and death follows the approach in Arino et al. (2006), where the authors consider these three components before implementing a delay solely in the growth component. In this work, we proceed similarly and consider a delay only in the growth contribution.

The motivation for such a delay is that in simple species models, such as (1), there is the implicit assumption that a newly born individual at breeding event \( t \) reaches maturity and is therefore able to reproduce at the next breeding event \( t + 1 \). In Deriso (1980), Deriso justified the use of delay models to describe the dynamics of species where recruitment to the mature stock occurs after several breeding events. This is the case, for example, when newborn individuals do not contribute to reproduction after only one breeding cycle, but rather reach fecundity after \( \tau \) breeding cycles such as for baleen whales (Allen 1963, 1966; Clark 1976). Then, the group of fecund individuals at time \( t + 1 \) not only depends on the fecund individuals at time \( t \), but also on individuals that reach fecundity for the first time at time \( t + 1 \).

Based on the survival probability in (4), the individuals exposed to death and competition follow the recursion

\[
w_{t+1} = \frac{1}{1 + b + cw_t} w_t.
\]

This can be solved in the same way as the Beverton–Holt model, i.e., by multiplying both sides by the denominator to obtain

\[
w_{t+1} + bw_{t+1} + cw_t w_{t+1} = w_t,
\]

and hence

\[
\Delta w_t = w_{t+1} - w_t = -w_{t+1} (b + cw_t).
\]

Substituting \( v_t = \frac{1}{w_t} \) (for \( w_t \neq 0 \)) to obtain

\[
\Delta v_t = -\frac{\Delta w_t}{w_t w_{t+1}} = bv_t + c,
\]
yields a first order linear difference equation with the solution given in Kelley and Peterson (1991) by

\[ \nu_t = (1 + b)^{t-t_0} \nu_{t_0} + \sum_{i=t_0}^{t-1} (1 + b)^{t-i-1} c, \]

\[ = (1 + b)^{t-t_0} \nu_{t_0} + \frac{c(1 + b)^t}{1+b} \sum_{i=t_0}^{t-1} \left( \frac{1}{1+b} \right)^i. \]

Using the formula for the sum of a geometric series,

\[ \nu_t = (1 + b)^{t-t_0} \nu_{t_0} + \frac{c(1 + b)^t}{1+b} \left\{ \frac{1 - \frac{1}{(1+b)^{t-t_0}}}{1 - \frac{1}{1+b}} - \frac{1 - \frac{1}{(1+b)^{t-1}}}{1 - \frac{1}{1+b}} \right\}, \]

\[ = (1 + b)^{t-t_0} \left( \nu_{t_0} + \frac{c}{b} \right) - \frac{c}{b}. \]

Returning to \( w_t \), yields

\[ w_t = \frac{b w_{t_0}}{(1+b)^{t-t_0} (b + c w_{t_0}) - c w_{t_0}}. \]

Setting \( t_0 = t - \tau \), the fraction of individuals at time \( t - \tau \) that survive to time \( t \) is given by

\[ w_t = \frac{b w_{t-\tau}}{(1+b)^{t} (b + c w_{t-\tau}) - c w_{t-\tau}} := F(w_{t-\tau}). \] (5)

The surviving fraction is now used in the recurrence

\[ z_{t+1} = p_t z_t = \frac{1}{1 + b + c z_t - a} z_t, \]

where \( b + c z_t \) determines the decay and \( a \) the growth. Rearranging, we obtain

\[ z_{t+1} (1 + b + c z_t) - a z_{t+1} = z_t. \] (6)

Recalling that \( a \) is the growth rate, we identify \( a z_{t+1} \) as the growth contribution of the Beverton–Holt recurrence. If, for example, fecundity is reached after \( \tau > 1 \) reproductive cycles, it is reasonable to consider a delay in the growth contribution. We therefore assume that the growth contribution is proportional to the (fecund) population at time \( t - \tau \) that survive until time \( t + 1 \). Thus, we replace \( a z_{t+1} \) in (6) by \( a F(z_{t+1-\tau}) \), where \( F \) determines the fraction of \( z_{t-\tau+1} \) that survives \( \tau \) units, given in (5), to obtain

\[ z_{t+1} (1 + b + c z_t) - a F(z_{t+1-\tau}) = z_t. \]
Solving this for $z_{t+1}$ yields the delay difference recurrence

$$z_{t+1} = \frac{1}{1 + b + cz_t} (z_t + aF(z_{t-\tau+1})).$$

The fecund individuals at time $t+1$, denoted by $z_{t+1}$, is therefore given by the sum of the surviving fecund individuals $z_t$ and the surviving individuals reaching fecundity for the first time, expressed by $aF(z_{t-\tau+1})$. The surviving probability $1/m(z_t)$, then multiplies the sum $z_t + aF(z_{t-\tau+1})$.

By (5), the recurrence we obtain is

$$z_{t+1} = \frac{1}{m(z_t)} \left\{ z_t + \frac{ab z_{t-\tau+1}}{M(z_{t-\tau+1})} \right\} =: H(z_t, z_{t-\tau+1}), \quad t \geq \tau - 1, \quad (7)$$

with

$$m(x) := 1 + b + cx, \quad M(x) := b\beta + (\beta - 1)cx, \quad \text{and} \quad \beta := (1 + b)^T, \quad (8)$$

and initial condition $z_0 \in \mathbb{R}^\tau$ with components $z_i \geq 0, \ i = 0, 1, \ldots, \tau - 1$. We note that the derived model (7) depends explicitly on the delay because $\beta = (1 + b)^T$.

The recurrence (7) differs from existing delay population models since it is of the form $z_{t+1} = \frac{1}{m(z_t)} (z_t + H_1(z_{t-\tau+1}))$ with $H_1(z) = \frac{abz}{M(z)}$. Thus, $\frac{1}{m(z_t)}$ multiplies both terms of the sum and therefore is different from the nonlinear delay difference equation studied by Clark (1976), $z_{t+1} = \lambda z_t + F(z_{t-k})$, where $\lambda \in \mathbb{R}$ is the survival coefficient and $F(z_{t-k})$ represents the recruitment into the breeding population by those born $k$ years ago. Clark’s recurrence has been analysed by several authors, see for example (Botsford 1992; Clark 1976; El-Morshedy and Liz 2006; Fisher 1984; Goh 1980). Instead, (7) considers a density-dependent survival coefficient $\lambda(z_t) = \frac{1}{m(z_t)}$ that is applied at the end of the period and therefore applied to both terms that contribute the breeding population, i.e., $z_{t+1} = \lambda(z_t) (z_t + F(z_{t-k}))$. Model (7) also is different from the delayed Pielou/Beveryton–Holt model with the general form $z_{t+1} = z_t H_2(z_{t-\tau})$, see for example (Levin and May 1976; Pielou 1969; Pielou and Gordon 1974), and the delayed Beverton–Holt model of the form $z_{t+\tau} = z_t H_2(z_t)$, discussed in Bohner et al. (2018), where $H_2$ is the reciprocal of a linear function.

Although recurrence (7) differs from existing delay models, if $\tau = 0$, our recurrence reduces to the classical Beverton–Holt model, since

$$z_{t+1} = \frac{z_t}{1 + b + cz_t} + \frac{a}{1 + b + cz_t} z_{t+1},$$

which, after rearranging terms, yields

$$z_{t+1} = \frac{z_t}{1 + b - a + cz_t}.$$

This is the equation used to derive the model, which is by (2)–(4) an equivalent expression for the normalized Beverton–Holt model when $1 + b - a = \frac{1}{\rho}$ and $c = \frac{\rho - 1}{\rho}$.
This recurrence is well established and these models and generalizations have been extensively studied, see for example Beverton and Holt (1957), Bohner et al. (2010), Haddan (2011), Kocić and Ladas (1993), Pielou (1969), Pielou and Gordon (1974). In fact, the explicit solution of the normalized Beverton–Holt model can be easily obtained by a variable transformation and is given by $z_t = \frac{z_0}{z_0 + (1 - z_0)\rho^{-t}}$ for $t_0 = 0$. For $z_0 > 0$ and $\rho > 1$, $\lim_{t \to \infty} z_t = 1$ and if $0 < \rho < 1$, $\lim_{t \to \infty} z_t = 0$. Therefore, throughout this paper, we assume $\tau > 0$. Although, in the derivation of (7) certain relationships between the parameters $a$, $b$, $c$ were assumed, the recurrence remains valid for arbitrary parameter choices of $a$, $b$, $c \geq 0$. For this reason, we consider the dynamics of (7) with (8) in the following sections and only require that $a$, $b$, $c \geq 0$. This is consistent with the study of the Beverton–Holt model. Even though the derivation by Beverton and Holt in 1957 lead to specific domains for the model parameters (Beverton and Holt 1957), the recurrence remains valid for arbitrary positive parameters. Thus, the Beverton–Holt model under the assumption of arbitrary positive parameter values, also known as the Pielou equation, became the focus of many studies.

3 Dynamics of the discrete delay difference equation

In this section, we present results concerning the dynamics of the discrete delay recurrence equation (7) for $t, \tau \in \mathbb{N} = \{1, 2, 3, \ldots\}$, $t \geq \tau > 0$, and initial conditions $z_0 = (z_0, z_1, \ldots, z_{\tau-1})$ with $z_i \geq 0$ for $i = 0, 1, \ldots, \tau - 1$.

We consider (7) with (8) and $a, b, c > 0$, unless explicitly stated otherwise. We justify the focus on $a, b, c > 0$ by noting that if $a = 0$ or $b = 0$ or $c = 0$, no positive equilibrium exists unless $a = b\beta$, in which case all values are equilibria.

We start our analysis with some basic results about the existence of fixed points, before continuing to the discussion of their local and global stability. The proofs are given in the appendix.

We define the critical delay $\tau_c \in \mathbb{R}$ as

$$\tau_c := \frac{\log(\frac{a}{b})}{\log(1+b)}$$

and remind the reader that for recurrences, $\tau \in \mathbb{N} = \{1, 2, \ldots, \}$. Therefore, the inequality $\tau \geq \tau_c$ is understood as $\tau \in [\tau_c, \infty) \cap \mathbb{N}_0$, which we express henceforth by $\tau \geq [\tau_c] = \min\{n \geq \tau_c : n \in \mathbb{Z}\}$ for $\tau_c \in \mathbb{R}$. Similarly, the inequality $\tau < \tau_c$ is expressed as $\tau < [\tau_c]$. We point out that for $\tau \in \mathbb{N}$

$$\tau \geq [\tau_c] \iff \tau \geq \tau_c \iff a \leq b\beta$$

for $\beta$ defined in (8). The equivalence (10) implies that for $\tau \in \mathbb{N}$, the inequality $\tau < [\tau_c]$ is equivalent to $\tau < \tau_c$, which is equivalent to $a > b\beta$. This relation is extensively exploited in proofs of the claims in this section.
We also point out that if $\tau_c \in (0, 1]$, then $\tau < \lceil \tau_c \rceil$ is only satisfied for $\tau = 0$, in which case (7) reduces to the classical Beverton–Holt model.

The first result addresses the positivity of solutions as formulated in the proceeding lemma.

**Lemma 3.1** Let $z_t$ be a solution of (7). If $z_i = 0$, $i = 0, 1, \ldots, \tau - 1$, then $z_i = 0$ for all $i \in N_0 = \{0, 1, 2, \ldots\}$. If $z_s > 0$ for at least one $s \in \{0, 1, \ldots, \tau - 1\}$, then $z_t > 0$ for all $t \geq \tau + s$.

**Theorem 3.2** If $\tau \geq \lceil \tau_c \rceil$, then $\tilde{z}_0 \equiv 0$ is the only non-negative equilibrium. If $\tau < \lceil \tau_c \rceil$, then there also exists a unique positive equilibrium

$$
\tilde{z}_+ = \frac{-b(2\beta - 1) + \sqrt{(b(2\beta - 1))^2 + 4b(a - b\beta)(\beta - 1)}}{2c(\beta - 1)}.
$$

(11)

Equation (11) reveals the importance of $a > b\beta$, which is by (10) equivalent to $\tau < \tau_c$ that assures the positivity of $\tilde{z}_+$. A positive equilibrium can therefore only exist if the delay is below a critical upper bound, otherwise the population is doomed to go extinct. Since $\beta$ depends on $\tau$, the positive equilibrium $\tilde{z}_+$ is a function of the delay. In fact, $\tilde{z}_+$ is monotone decreasing in the delay, which ultimately yields an upper bound, as formulated below.

**Lemma 3.3** Let $\tau < \lceil \tau_c \rceil$. Then $\tilde{z}_+$ given in (11) is decreasing in $\tau$ and $\tilde{z}_+ \leq \frac{a - b}{c}$.

As in the continuous delay logistic model in Arino et al. (2006), the unique positive equilibrium is decreasing in size as the delay increases. This dependency of the equilibrium on the delay also highlights a difference with the existing discrete delay Beverton–Holt model in Pielou (1969), in which the equilibrium is independent of the delay.

**Theorem 3.4** Consider (7).

a) The trivial equilibrium, $\tilde{z}_0$, is

i) locally asymptotically stable if $\tau \geq \lceil \tau_c \rceil$, and is

ii) unstable if $\tau < \lceil \tau_c \rceil$.

b) Whenever the positive equilibrium, $\tilde{z}_+$, exists, i.e., $\tau < \lceil \tau_c \rceil$, it is locally asymptotically stable.

An alternative method to that given in the Appendix for proving the local asymptotic stability of $\tilde{z}_0$ if $\tau > \lceil \tau_c \rceil$ and of $\tilde{z}_+$ if $\tau < \lceil \tau_c \rceil$ can be obtained by exploiting the structure of the Jacobian, which is a companion matrix. An explicit formula of powers of the Jacobian can be used to obtain the matrix $\infty$-norm that provides a bound on the spectral radius

\[1\]

The interested reader is referred to arXiv:2010.04378v1 (Version 1) and welcome to contact the corresponding author for more information.
**Theorem 3.5** If \( \tau \geq \lceil \tau_c \rceil \), then \( \tilde{z}_0 \) is globally asymptotically stable for solutions with non-negative initial conditions.

Hence, if the positive equilibrium does not exist, that is, if the delay equals or exceeds the critical delay \( \tau_c \), then the population goes extinct over time. This is reasonable recalling that the delay determines the growth contribution and therefore, if the time span to reach fecundity is longer than the critical time \( \tau_c \), the decline component dominates and leads to the species’ extinction. We point out that this is consistent with the corresponding continuous model in Arino et al. (2006), where the trivial equilibrium is globally asymptotically stable if the delay exceeds the critical delay.

It remains to discuss the case when \( \tau < \tau_c \) and the unique positive equilibrium exists. For \( \tau < \tau_c \), we distinguish between \( c\tilde{z}_+ > 1 \) and \( c\tilde{z}_+ \leq 1 \) and use a different technique for each case to discuss global stability. The case of \( c\tilde{z}_+ \leq 1 \) is in fact related to the derivation of model (7) because the recurrence was derived in Sect. 2 for \( a - b = \frac{1}{\rho} \) for \( \rho > 1 \), which implies that \( a - b \in (0, 1) \). By Lemma 3.3, \( \tilde{z}_+ \leq \frac{a - b}{c} \), and thus for \( a - b \in (0, 1) \), \( \tilde{z}_+ \leq \frac{1}{c} \). In that case, when \( c\tilde{z}_+ \leq 1 \), solutions have specific properties. As formally stated below, solutions with initial conditions that are all below \( \tilde{z}_+ \) remain below \( \tilde{z}_+ \) and solutions with initial conditions all above \( \tilde{z}_+ \) remain above \( \tilde{z}_+ \). This property also holds for the classical Beverton–Holt model (1) for \( \rho > 1 \) (i.e., \( \tau = 0 \)). On the other hand, if some of the \( \tau \) initial conditions are above and some are below \( \tilde{z}_+ \), then solutions of (7) can oscillate about the equilibrium \( \tilde{z}_+ \) but are bounded by the minimum and maximum value of the initial conditions. We will show that these properties ultimately lead to the global asymptotic stability of \( \tilde{z}_+ \) if \( \tau < \tau_c \).

We emphasize that the case of \( c\tilde{z}_+ \leq 1 \) corresponds in general to the following parameter relation.

**Proposition 3.6**

\[
c\tilde{z}_+ \leq 1 \quad \iff \quad a \leq \frac{1 + b}{b} (b\beta + \beta - 1)
\]  

**Lemma 3.7** Let \( \tau < \lceil \tau_c \rceil \) and \( c\tilde{z}_+ \leq 1 \). If \( z_i \leq \tilde{z}_+ \) for \( i = 0, 1, \ldots, \tau - 1 \), then \( z_t \leq \tilde{z}_+ \) for all \( t \geq 0 \). If \( z_i \geq \tilde{z}_+ \) for \( i = 0, 1, \ldots, \tau - 1 \), then \( z_t \geq \tilde{z}_+ \) for all \( t \geq 0 \).

**Lemma 3.8** Let \( \tau < \lceil \tau_c \rceil \) and \( c\tilde{z}_+ \leq 1 \). If \( z_i > 0 \) for \( i = 0, 1, \ldots, \tau - 1 \), then

\[
\min\{z_0, z_1, \ldots, z_{\tau - 1}, \tilde{z}_+\} \leq z_t \leq \max\{z_0, z_1, \ldots, z_{\tau - 1}, \tilde{z}_+\}, \quad \text{for all} \quad t \geq 0.
\]  

**Theorem 3.9** Let \( \tau < \lceil \tau_c \rceil \). If \( c\tilde{z}_+ \leq 1 \), then \( \tilde{z}_+ \) is globally asymptotically stable for solutions with initial conditions \( z_0 \neq 0 \).

Figure 1 illustrates the dynamic behavior of solutions of (7) for three different initial conditions in the case when \( c\tilde{z}_+ \leq 1 \). If \( \tau \in \mathbb{N} \) is chosen to be less than \( \tau_c \), then solutions with at least one positive initial condition converge to the positive equilibrium \( \tilde{z}_+ \), as per Theorem 3.9. This coincides with the global behavior for the continuous
Fig. 1 Behavior of three solutions for different parameters with $c \tilde{z}_+ \leq 1$. Top panel: $a = 0.272$, $b = 0.105$, $c = 0.142$, $\tau = 9$. Middle panel: $a = 0.508$, $b = 0.177$, $c = 0.663$, $\tau = 6$. Bottom panel: $a = 0.884$, $b = 0.209$, $c = 0.905$, $\tau = 7$. The values on the left of the vertical dashed line are the initial conditions. The solid horizontal line is $\tilde{z}_+$. The solutions convergence to the solid line $y = \tilde{z}_+$ in all three panels but is very slow in the top and middle panels.

model in Arino et al. (2006). However, unlike the corresponding continuous model, solutions of (7) can be non-monotone, independent on whether all initial conditions are above $\tilde{z}_+$ (top panel in Fig. 1), below $\tilde{z}_+$ (middle panel in Fig. 1), or on either side (bottom panel in Fig. 1). Note that all of the figures in this paper were produced using the software package R (R Core Team 2013). The non-monotone behavior of solutions differs from the behavior of those of the classical Beverton–Holt model for $\rho > 1$, where solutions monotonically increase (decrease) to the positive equilibrium $K$ for initial conditions below (above) $K$.

Figure 2 demonstrates that Lemma 3.7 can not be extended to the case when $c \tilde{z}_+ > 1$. Solutions with all initial conditions below $\tilde{z}_+$ can exceed $\tilde{z}_+$ eventually (left panel). Similarly, solutions with initial conditions that are all above $\tilde{z}_+$ can obtain values below $\tilde{z}_+$ (right panel).

Theorem 3.9 exploits the contraction mapping theorem but this technique fails if $c \tilde{z}_+ > 1$. Instead, if $c \tilde{z}_+ > 1$, the global asymptotic stability of $\tilde{z}_+$ if $\tau < \tau_c$ can be obtained using Theorem 1.15 in Grove and Ladas (2004), stated in the appendix for completeness. For the application of this theorem, we require some preliminary work.

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Fig. 2 Solutions for parameter values when $c \tilde{z}_+ > 1$, hence violating the assumption in Lemma 3.7. The solid line represents the positive equilibrium. The dotted line identifies the last initial condition. Left panel: $a = 38.72$, $b = 0.227$, $c = 0.498$, $\tau = 5$, $z_0 = (2.226, 3.274, 2.861, 2.269, 0.956)$. Right panel: $a = 137.78$, $b = 0.640$, $c = 0.417$, $\tau = 5$, $z_0 = (7.368, 7.985, 8.934, 9.572, 21.444)$. Although the initial conditions are all below $\tilde{z}_+$ (left panel), subsequent iterates can be above $\tilde{z}_+$. Similarly on the right, although all initial conditions are above $\tilde{z}_+$, subsequent iterates can fall below $\tilde{z}_+$.

Proposition 3.10 Let $\tau < \tau_c$. If $c \tilde{z}_+ > 1$, then there exists $T \in \mathbb{N}$ such that for $t \geq T$,

$$z_t \geq \chi := \frac{b(1 + b)\beta}{c(ab - (\beta - 1)(1 + b))}$$

(14)

and $H(z_t, z_{t+1})$ is decreasing in the first variable.

Proposition 3.10 implies that if $z_t \geq \chi$ for all $t$, then $\frac{\partial}{\partial u} H(u, v) < 0$. Also $\frac{\partial}{\partial v} H(u, v) > 0$, see (18). Therefore, if $z_t \geq \chi$ for all $t$, the partial derivatives of $H$ with respect to each variable do not change sign, i.e., $H$ is componentwise monotone.

Proposition 3.11 Consider $H$ defined in (7) and $\chi$ defined in (14). There exists $U^* > \tilde{z}_+$, such that for all $U \geq U^*$, $H : [\chi, U] \times [\chi, U] \rightarrow [\chi, U]$.

Propositions 3.10 and 3.11 are fundamental in the proof of the global asymptotic stability of the positive equilibrium. In particular, Proposition 3.11 implies that there exists $T \geq 0$ such that $z_t \geq \chi$ for all $t \geq T$. By the statement following Proposition 3.10, $H$ is eventually componentwise monotone.

Theorem 3.12 Let $\tau < \tau_c$. If $c \tilde{z}_+ > 1$, then $\tilde{z}_+$ is globally asymptotically stable for initial conditions $z_0 \neq 0$.

Figure 3 illustrates Proposition 3.10 and Theorem 3.12.

Theorems 3.5, 3.9, and 3.12 combined, prove the global asymptotic stability of the non-negative equilibria. Consequently, the positive equilibrium $\tilde{z}_+$ is globally asymptotically stable whenever it exists, otherwise the trivial solution is globally asymptotically stable.
Fig. 3 Behavior of three solutions for parameter combinations where $c\tilde{z}_+ > 1$ for $a = 38.118, b = 0.557, c = 0.313, \tau = 5, \tilde{z}_+ = 3.258$. The vertical dashed line separates the initial conditions from the iterations. The solid horizontal line is $\tilde{z}_+$. The dotted horizontal line is at $\chi = 2.9819$ on the vertical axis. The figure illustrates a crucial result used in the proof of the global stability of $\tilde{z}_+$, namely that solutions are eventually above $\chi$. In that case, $H$ is componentwise monotone, decreasing in the first variable and increasing in the second variable.

4 Conclusion

In this paper, we introduced an alternative delayed Beverton–Holt model that can be viewed as the discretization of the delayed logistic model in Arino et al. (2006). Starting from the (classical) Beverton–Holt model (1), the survival probability was assumed to depend on three components: growth, death, and intraspecific competition. To account for a time delay in the growth, created for example by a time lag in reaching fecundity, the recurrence was rearranged to identify the growth term. The model takes into consideration the fact that those individuals that die during the delay, do not contribute to growth. This method is consistent with the approach in Arino et al. (2006), where an alternative delayed logistic differential equations model was formulated. Even though in the derivation of the delay recurrence model, we made certain restrictions on the parameter values, we studied the recurrence for arbitrary positive parameters, since the recurrence model remains mathematically valid. Since the model reduces to the classical Beverton–Holt model in the case of no delay, we focused on the model analysis when the delay $\tau > 0$, that is $\tau \in \{1, 2, 3, \ldots\}$.

We began the analysis of our delayed Beverton–Holt model by finding a critical threshold of the delay, i.e., an extinction threshold. If the delay is larger than this threshold, the trivial equilibrium is the only non-negative equilibrium and it is globally asymptotically stable. If the delay is smaller than this threshold a unique positive equilibrium also exists and it is globally asymptotically stable with respect to all solutions with positive initial conditions. For the parameter values assumed in the derivation of our model, we proved the global asymptotic stability of the survival equilibrium if the delay is below the threshold using a contraction mapping argument. We used a different technique to prove the global asymptotic stability of the positive equilibrium in the case of arbitrary positive parameter values that relies on componentwise monotonicity.
Some of the properties of the delay Beverton–Holt model (7) that we introduced are similar to those of the classical Beverton–Holt model. More specifically, for parameter values consistent with the derivation of our model in Sect. 2, solutions with initial conditions above (below) the unique positive equilibrium remain above (below) the equilibrium. In contrast, solutions of our model do not always converge monotonically even for parameter values consistent with the derivation of the model. This non-monotone behavior of solutions of our model was illustrated with simulations. However, the corresponding figures also seem to indicate an eventual monotonic convergence to the positive equilibrium.

We justified that our recurrence (7) is an appropriate discretization of the delay logistic model introduced in Arino et al. (2006). Both models separate the net-growth rate into three components: growth, death, and intraspecific competition and consider a time lag only in the growth contribution and take into consideration that those members of the population that die during the delay period do not contribute to growth. Further, both models exhibit similar dynamics dependent on a critical threshold. If the delay is below the critical threshold, solutions of both models converge to a positive equilibrium that decreases in size for increasing delay values, and converge to the trivial solution, otherwise. We think that these model properties are reasonable for natural ecosystems and differ from the properties of the other discrete and continuous delay logistic models already mentioned in this paper. There are however, slight variations in the dynamic behavior between the solutions of the continuous and the discrete models. In contrast to the continuous counterpart, the solutions of the discrete model do not always converge monotonically, even if the initial distribution is entirely above or entirely below the positive equilibrium, but rather can display damped oscillations about the positive equilibrium, as demonstrated in Figs. 1, 2 and 3.

Acknowledgements The research of Gail S. K. Wolkowicz was partially supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery grant with accelerator supplement. We also thank both of the referees for their helpful suggestions.

Appendix: Proofs

Proof of Lemma 3.1 Clearly, if all of the components of the initial condition \( z_0 \) equal zero, then \( z_i = 0 \) for all \( i \in \mathbb{N}_0 \). If on the other hand, there exists at least one \( s \in \{0, 1, \ldots, \tau - 1\} \) such that \( z_s > 0 \), then, since the right hand side of (7) is always non-negative, \( z_{s+\tau} = \frac{z_{s+\tau-1}}{m(z_{s+\tau-1})} + \frac{a}{m(z_{s+\tau-1})} b\tilde{z} \geq 0 \). Thus \( z_{s+\tau+1} \geq \frac{z_{s+\tau}}{m(z_{s+\tau})} > 0 \). Similarly, \( z_{s+\tau+i} > 0 \) for \( i \geq 1 \).

Proof of Theorem 3.2 By (7) with (8), a positive equilibrium \( \tilde{z}_+ \) satisfies the equation

\[
\tilde{z}_+ = \frac{\tilde{z}_+}{1 + b + c\tilde{z}_+} + \frac{a}{1 + b + c\tilde{z}_+} \cdot \frac{b\tilde{z}_+}{\beta + (\beta - 1)c\tilde{z}_+}.
\]
Rearranging and using the fact that $\tilde{z}_+ \neq 0$, it follows that $\tilde{z}_+$ must satisfy the quadratic equation

$$(\beta - 1)(c\tilde{z}_+)^2 + (b\beta + b(\beta - 1))c\tilde{z}_+ + b(\beta - a) = 0.$$ 

By the Routh–Hurwitz condition, since $\beta > 1$ for $\tau \geq 1$, there are no roots with positive real parts unless $a > b\beta$, and in this case there are two real roots, one positive and one negative. Solving the quadratic equation, the positive real root, $\tilde{z}_+$, is given by (11). \quad \square

**Proof of Lemma 3.3** By (10), $a > \beta b > b$ and by (7), if $\tau < \tau_c$, then $\tilde{z}_+$ exists and satisfies

$$\tilde{z}_+ = \frac{\tilde{z}_+}{m(\tilde{z}_+)} + \frac{b\tilde{z}_+}{m(\tilde{z}_+)M(\tilde{z}_+)}.$$ 

Rearranging, we obtain

$$(b + c\tilde{z}_+)(b\beta + (\beta - 1)c\tilde{z}_+) = ab.$$ 

We note that by (7), $\tilde{z}_+$ depends on $\beta$ and therefore on $\tau$. Hence, $f(\tau) = \tilde{z}_+$ solves

$$(b + cf(\tau))(b\beta + (\beta - 1)cf(\tau)) = ab. \quad (15)$$ 

Taking the difference of (15) evaluated at $\tau + 1$ and $\tau$, we have

$$(b + cf(\tau + 1))(b\beta(1 + b) + c(\beta(1 + b) - 1)f(\tau + 1))$$

$$- (b + cf(\tau))(b\beta + (\beta - 1)cf(\tau)) = 0,$$

i.e., with $\Delta f = f(\tau + 1) - f(\tau)$,

$$b^3 \beta + bc(\beta - 1) (\Delta f) + \beta b^2 cf(\tau + 1) + cb\beta (\Delta f) + cb^2 \beta f(\tau + 1)$$

$$+ c^2 (\beta - 1) (\Delta f) (f(\tau + 1) + f(\tau)) + b\beta c^2 f^2(\tau + 1) = 0,$$

i.e.,

$$\Delta f = -\frac{b^3 \beta + bc(\beta - 1)(\Delta f) + \beta b^2 cf(\tau + 1) + cb\beta (\Delta f) + cb^2 \beta f(\tau + 1)}{bc(\beta - 1) + cb\beta + c^2 (\beta - 1) (f(\tau + 1) + f(\tau))} < 0$$

for $f(\tau), f(\tau + 1) \geq 0$. Therefore, $f(\tau) = \tilde{z}_+$ is decreasing and $\tilde{z}_+$ evaluated at $\tau = 0$ is an upper bound for $\tilde{z}_+$. To obtain this upper bound, we note that for $\tau = 0$ and $\beta = 1$, (7) becomes

$$z_{t+1} = \frac{z_t}{1 + b + cz_t} + \frac{az_{t+1}}{1 + b + cz_t}.$$ 

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Rearranging terms yields

\[ z_{t+1} \left[ 1 - \frac{a}{1 + b + cz_t} \right] = \frac{z_t}{1 + b + cz_t}, \]

which is of the Beverton–Holt type, defined earlier,

\[ z_{t+1} = \frac{z_t}{1 + b + cz_t - a}, \]

that has the nontrivial equilibrium, \( \tilde{z} = \frac{a-b}{c} \), that is therefore the upper bound for \( \tilde{z}_+ \).

\[ \square \]

**Proof of Theorem 3.4** Linearizing \((7)\), we obtain the linear difference equation

\[ w_{t+1} - \tilde{z} = \frac{\partial H(u, v)}{\partial u} \bigg|_{u=v=\tilde{z}} (w_t - \tilde{z}) + \frac{\partial H(u, v)}{\partial v} \bigg|_{u=v=\tilde{z}} (w_{t-\tau+1} - \tilde{z}), \quad (16) \]

with

\[ \frac{\partial}{\partial u} H(u, v) = \frac{1 + b}{m^2(u)} - \frac{abcv}{m^2(u)M(v)}, \]
\[ \frac{\partial}{\partial v} H(u, v) = \frac{ab^2 \beta}{m(u)M^2(v)}, \]

where \( \beta, m, M \) are defined in \((8)\).

\( a) \) At \( E_0, \frac{\partial}{\partial u} H(0, 0) = \frac{1}{1+b} \) and \( \frac{\partial}{\partial v} H(0, 0) = \frac{a}{\beta(1+b)}. \)

\( i) \) First, we consider the case \( \tau > \lceil \tau_c \rceil \geq \tau_c \) and therefore as pointed out in \((10)\), \( a < b \beta. \) Thus

\[ \frac{\partial}{\partial u} H(0, 0) + \frac{\partial}{\partial v} H(0, 0) = \frac{1}{1+b} + \frac{a}{\beta(1+b)} = \frac{1}{1+b} + \frac{b}{1+b} = 1. \]

By a result in Clark (1976) and its reformulation in Kocić and Ladas (1993, Theorem 1.3.7), we obtain the local asymptotic stability of \( \tilde{z}_0 \).

Next we consider the case, \( \tau = \tau_c. \) Then \( a = b \beta. \) Select any \( \epsilon > 0. \) If \( z_i \in [0, \epsilon] \) for \( i = 0, 1, \ldots, \tau - 1, \) then

\[ 0 \leq z_{t+1} \leq \frac{z_t}{1 + b + cz_t} + \frac{b z_{t-\tau+1}}{1 + b + cz_t} \leq \frac{1 + b}{1 + b + cz_t} \epsilon \leq \epsilon. \]

Hence, \( z_{t+1} \in [0, \epsilon], \) for all \( t \geq 0. \) This implies not only that \( \tilde{z}_0 \) is stable, but also that the sequence \( z_t \) is bounded. By Lemma 3.1, \( \liminf_{t \to \infty} z_t \geq 0. \) To
prove that \( \bar{z}_0 \) is attractive, we proceed using proof by contradiction. Suppose that 
\[
\bar{z} = \limsup_{t \to \infty} z_t > 0. \quad \text{Since } a = b\beta, \]
\[
\frac{\partial H(u, v)}{\partial u} = \frac{1 + b}{(1 + b + cu)^2} - \frac{b^2c\beta v}{(1 + b + cu)^2[\beta + (\beta - 1)cv]} \geq \frac{1}{(1 + b + cu)^2}(1 + b - bcv), \quad (17)
\]
\[
\frac{\partial H(u, v)}{\partial v} = \frac{b^3\beta^2}{(1 + b + cu)(\beta + (\beta - 1)cv)^2} > 0. \quad (18)
\]

If \( \epsilon < \frac{1 + b}{bc}, \) then \( \frac{\partial H(u, v)}{\partial u} > 0 \) for \( v \in [0, \epsilon]. \) Therefore, \( H \) is monotone increasing in both variables for \( u, v \in [0, \epsilon] \) and

\[
\bar{z} = \limsup z_{t+1} = \limsup H(z_t, z_{t-\tau+1}) \leq H(\limsup z_t, \limsup z_{t-\tau+1})
\]

\[
H(\bar{z}, \bar{z}) = \frac{\bar{z}}{1 + b + c\bar{z}} + \frac{b^2\beta\bar{z}}{(1 + b + c\bar{z})(b\beta + (\beta - 1)c\bar{z})} = \frac{b\beta(1 + b + (\beta - 1)c\bar{z}) + b(b - 1)c\bar{z} + c\bar{z}b\beta + c^2\bar{z}^2(\beta - 1)}{b\beta(1 + b) + (\beta - 1)c\bar{z}} < \bar{z},
\]

contradicting \( \bar{z} > 0. \) Hence, \( \bar{z}_0 \) is locally asymptotically stable.

a) ii) Next, we prove that \( \bar{z}_0 \) is unstable when \( \tau < \lceil \tau_c \rceil, \) and hence as pointed out in (10), \( a > b\beta. \) Since the characteristic equation of (16) evaluated at \( \bar{z}_0 \) is given by

\[
P(\lambda) = \lambda - \frac{1}{1 + b} \lambda^{\tau-1} - \frac{a}{\beta(1 + b)} = 0
\]

and \( P(1) < 0, \) but, since \( \tau > 0, \lim_{\lambda \to \infty} P(\lambda) = \infty, \) there is a real root \( \lambda > 1, \) and therefore \( \bar{z}_0 \) is unstable.

b) Let \( \tau < \lceil \tau_c \rceil. \) By (10), \( a > b\beta. \) By Lemma 3.2, \( \bar{z}_+ \) exists and is unique. Since \( \bar{z}_+ \) is an equilibrium of (7), we obtain

\[
ab = (b + c\bar{z}_+)(b\beta + (\beta - 1)c\bar{z}_+) = (m(\bar{z}_+) - 1)M(\bar{z}_+). \quad (19)
\]

The linearization evaluated at \( \bar{z}_+ \) is then of the form (16) with

\[
\frac{\partial H(\bar{z}_+, \bar{z}_+)}{\partial u} = \frac{1 + b}{m^2(\bar{z}_+)} - \frac{c\bar{z}_+}{m^2(\bar{z}_+)} \geq \frac{ab}{b\beta + (\beta - 1)c\bar{z}_+} \geq \frac{1 + b}{m^2(\bar{z}_+)} - \frac{c\bar{z}_+}{m^2(\bar{z}_+)}(b + c\bar{z}_+) = \frac{1 - c\bar{z}_+}{m(\bar{z}_+)}, \quad (19)
\]

and

\[
\frac{\partial H(\bar{z}_+, \bar{z}_+)}{\partial v} = \frac{ab^2\beta}{m(\bar{z}_+)M^2(\bar{z}_+)} \geq \frac{\beta(b + c\bar{z}_+)^2}{am(\bar{z}_+)} = \frac{\beta(m(\bar{z}_+) - 1)^2}{am(\bar{z}_+)}.
\]
Note that \( \frac{\partial}{\partial u} H(\tilde{z}_+, \tilde{z}_+) > 0 \).

We show that

\[
\left| \frac{\partial}{\partial u} H(\tilde{z}_+, \tilde{z}_+) \right| + \left| \frac{\partial}{\partial v} H(\tilde{z}_+, \tilde{z}_+) \right| = \left| 1 - c\tilde{z}_+ \right| + \left| \frac{\beta(m(\tilde{z}_+ - 1)^2}{am(\tilde{z}_+)} \right| < 1, \quad (20)
\]

since then, by the formulation of Clark (1976) in Kocić and Ladas (1993, Theorem 1.3.7), \( \tilde{z}_+ \) is locally asymptotically stable.

Firstly, if \( c\tilde{z}_+ = 1 \), then \( \frac{\partial}{\partial u} H(\tilde{z}_+, \tilde{z}_+) = 0 \) and

\[
\frac{\partial}{\partial u} H(\tilde{z}_+, \tilde{z}_+) = \frac{\beta(m(\tilde{z}_+ - 1)^2}{am(\tilde{z}_+)} < 1.
\]

Secondly, assume that \( 0 < c\tilde{z}_+ < 1 \). Then, \( \frac{\partial}{\partial u} H(\tilde{z}_+, \tilde{z}_+) \) is also positive and the inequality in (20) is equivalent to

\[
\beta \frac{(m(\tilde{z}_+ - 1)^2}{a} < m(\tilde{z}_+) - 1 + c\tilde{z}_+.
\]

Since, \( m(\tilde{z}_+) - 1 = b + c\tilde{z}_+ \), using (19), this inequality can be rewritten as

\[
\beta \frac{(m(\tilde{z}_+ - 1)b}{[b\beta + (\beta - 1)c\tilde{z}_+]} < m(\tilde{z}_+) - 1 + c\tilde{z}_+,
\]

or equivalently,

\[
\beta(m(\tilde{z}_+) - 1)b < (m(\tilde{z}_+) - 1)[b\beta + (\beta - 1)c\tilde{z}_+] + c\tilde{z}_+[b\beta + (\beta - 1)c\tilde{z}_+].
\]

Since this is clearly satisfied, it follows that when \( c\tilde{z}_+ < 1 \), (20) also holds.

Thirdly, if \( c\tilde{z}_+ > 1 \), then \( -\frac{\partial}{\partial u} H(\tilde{z}_+, \tilde{z}_+) > 0 \) and

\[
\frac{\partial}{\partial u} H(\tilde{z}_+, \tilde{z}_+) = \frac{\beta(m(\tilde{z}_+ - 1)^2}{am(\tilde{z}_+)} = \frac{a(c\tilde{z}_+ - 1) + \beta(m(\tilde{z}_+) - 1)^2}{am(\tilde{z}_+)}.
\]

To show (20) holds, we show

\[
a(c\tilde{z}_+ - 1) + \beta(m(\tilde{z}_+) - 1)^2 < am(\tilde{z}_+) = a(1 + b) + ac\tilde{z}_+.
\]

Cancelling terms and recalling that \( m(\tilde{z}_+) - 1 = b + c\tilde{z}_+ \), we have the equivalent form

\[
\beta(b + c\tilde{z}_+)^2 < a(2 + b) \quad (19) \quad \frac{(2 + b)}{b}(b + c\tilde{z}_+)(b\beta + (\beta - 1)c\tilde{z}_+).
\]
Simplifying this inequality yields
\[
\left( \frac{2 + b}{b} \right) c \tilde{z}_+ < \beta (b + c \tilde{z}_+) \left( \frac{2 + b}{b} - 1 \right).
\]
Further simplification results in
\[
(2 + b)c \tilde{z}_+ < 2\beta (b + c \tilde{z}_+) = 2(1 + b)^\tau (b + c \tilde{z}_+).
\]
Since
\[
2(1 + b)^\tau (b + c \tilde{z}_+) \geq 2(1 + b)(b + c \tilde{z}_+) > (2 + b)c \tilde{z}_+.
\]
(20) holds.
Therefore, in all three cases, (20) holds independent of the sign of \(c \tilde{z}_+ - 1\) and so by Kocić and Ladas (1993, Theorem 1.3.7), \(\tilde{z}_+\) is locally asymptotically stable.

Proof of Theorem 3.5  
By (7), for \(u, v \geq 0\),
\[
|H(u, v)| = \left| \frac{u}{1 + b + cu} + \frac{a}{1 + b + cu} \cdot \frac{bv}{b\beta + (\beta - 1)cv} \right| \leq \left| \frac{u}{1 + b + cu} \right| + \left| \frac{a}{1 + b + cu} \cdot \frac{bv}{b\beta + (\beta - 1)cv} \right| \leq \left| \frac{u}{1 + b} \right| + \left| \frac{a}{1 + b} \right| \cdot \left| \frac{bv}{b\beta} \right| \leq \alpha \|u\|_\infty,
\]
with \(\alpha = \frac{1}{1 + b} + \frac{a}{(1 + b)\beta}\) and \(\|u\|_\infty = \max\{u, v\}\). Since \(\tau > \lceil \tau_c \rceil \geq \tau_c\), \(a < b\beta\) by (10) and therefore \(\alpha < 1\). By the contraction mapping theorem (Theorem 2 in Liz and Ferreiro 2002), \(\tilde{z}_0\) is globally asymptotically stable.

If \(\tau = \tau_c\), then \(a = b\beta\). By the proof in Theorem 3.4 a) ii), the solutions remain bounded since \(\epsilon > 0\) was chosen arbitrarily and not required to be small. In the same proof, \(H\) was shown to be increasing in the second variable. However, that argument did require \(\epsilon\) to be sufficiently small. In this case, \(H\) is not necessarily always increasing in the first variable. Nevertheless, due to the boundedness and positivity of \(z_t\), there exists a finite \(\tilde{z} = \limsup z_t \geq 0\). To show that \(\tilde{z} = \tilde{z}_0\) and therefore \(\tilde{z}_0\) is attractive, we proceed using proof by contradiction. Suppose \(\tilde{z} > 0\). Then
\[
\tilde{z} = \limsup z_{t+1} = \limsup H(z_t, z_{t-\tau+1}) \leq \limsup H(z_t, \tilde{z})
\]
\[
= \limsup \left\{ \frac{z_t}{1 + b + cz_t} + \frac{b^2 \beta \tilde{z}}{(1 + b + cz_t)\beta + (\beta - 1)c\tilde{z}} \right\}
\]
\[
\leq \limsup \left\{ \frac{z_t}{1 + b + cz_t} + \frac{b^2 \beta \tilde{z}}{(1 + b)\beta + (\beta - 1)c\tilde{z}} \right\}
\]
contradicting the assumption that $\bar{z} > 0$. Therefore, $0 \leq \lim \inf z_t \leq \lim \sup z_t = 0$, and hence $\lim_{t \to \infty} z_t = 0$. \hfill \Box

**Proof of Proposition 3.6** By (11),

\[
c\tilde{z} + 1 \iff -b(2\beta - 1) + \sqrt{b^2(2\beta - 1)^2 - 4b(b\beta - a)(\beta - 1)} \leq 2(\beta - 1)
\]

\[
\iff -b(2\beta - 1) + \sqrt{b(b + 4a(\beta - 1))} \leq 2(\beta - 1)
\]

\[
\iff 4ab(\beta - 1) + b^2 \leq (2(\beta - 1) + b(2\beta - 1))^2
\]

\[
\iff 4ab(\beta - 1) \leq 4(\beta - 1)^2
\]

\[
+ 4b(\beta - 1)(2\beta - 1) + b^2(4\beta(\beta - 1) + 1) - b^2
\]

\[
\iff ab \leq (\beta - 1) + b(2\beta - 1) + b^2 \beta
\]

\[
\iff ab \leq (1 + b)(\beta - 1 + b\beta),
\]

and the result follows. \hfill \Box

**Proof of Lemma 3.7** Define $w_t := z_t - \tilde{z}+$, then

\[
w_{t+1} = H(z_t, z_{t-\tau+1}) - \tilde{z}+ = H(z_t, z_{t-\tau+1}) - H(\bar{z}, \bar{z}+).
\]

Let $u := z_t$ and $v := z_{t-\tau+1}$. Then

\[
w_{t+1} = \frac{(1 + b)(u - \tilde{z}+)}{m(u)m(\tilde{z}+)}
\]

\[
+ \frac{ab(b \beta (1 + b)(v - \tilde{z}+) + b \beta c \tilde{z}+(v - u) + (\beta - 1)c^2 \tilde{z}+(v - u))}{m(u)M(v)m(\tilde{z}+)}
\]

\[
= \left\{ \begin{array}{l}
(1 + b) \frac{m(u)M(v)m(\tilde{z}+)}{m(u)m(\tilde{z}+)} - ab \frac{b \beta c \tilde{z}+(v - \bar{z}+)}{m(u)M(v)m(\tilde{z}+)} = b \beta m(\tilde{z}+)
+ ab \frac{b \beta (1 + b) + b \beta c \tilde{z}+}{m(u)M(v)m(\tilde{z}+)}
\end{array} \right.
\]

\[
= \left\{ \begin{array}{l}
1 + b \frac{m(u)M(v)m(\tilde{z}+)}{m(u)m(\tilde{z}+)} - \frac{abc \tilde{z}+}{m(u)m(\tilde{z}+)}
+ \frac{ab^2 \beta}{m(u)M(v)m(\tilde{z}+)}
\end{array} \right.
\]

\[
(u - \tilde{z}+) + \frac{ab^2 \beta}{m(u)M(v)m(\tilde{z}+)}(v - \tilde{z}+)
\]
\begin{equation}
(19) \quad \frac{1 \nolimits - c \tilde{z}_+}{m(u)} (u - \tilde{z}_+) + \frac{b \beta (m(\tilde{z}_+) - 1)}{m(u) M(v)} (v - \tilde{z}_+) = d_1 w_t + d_2 w_{t-\tau + 1},
\end{equation}

where

\begin{equation}
d_1 = \frac{1 \nolimits - c \tilde{z}_+}{m(\tilde{z}_+ + w_t)} \quad \text{and} \quad d_2 = \frac{b \beta (m(\tilde{z}_+) - 1)}{m(\tilde{z}_+ + w_t) M(\tilde{z}_+ + w_{t-\tau + 1})}.
\end{equation}

Since \( 0 < c \tilde{z}_+ \leq 1 \) and \( m(\tilde{z}_+) - 1 = b \nolimits + c \tilde{z}_+ > 0 \), \( d_1, d_2 > 0 \). Hence, if \( \text{sign}(w_t) = \text{sign}(w_{t-\tau + 1}) \), then \( \text{sign}(w_{t+1}) = \text{sign}(w_t) \). Consequently, \( z_{t+1} \geq \tilde{z}_+ \) for \( z_t, z_{t-\tau + 1} \geq \tilde{z}_+ \). Similarly, if \( z_t, z_{t-\tau + 1} \leq \tilde{z}_+ \), then \( z_{t+1} \{z}_+ \). \( \square \)

**Proof of Lemma 3.8** As before, define \( w_t := z_t - \tilde{z}_+ \). To show that (13) holds, it suffices to show that

\[
\min\{w_0, w_1, \ldots, w_{\tau-1}, 0\} \leq w_t \leq \max\{w_0, w_1, \ldots, w_{\tau-1}, 0\} \quad \text{for all} \quad t \geq \tau.
\]

(23)

First we consider the lower bound. For any \( t \geq \tau \), let \( u = z_{t-1} \) and \( v = z_{t-\tau} \). Then by (21) and the fact that \( d_1 \geq 1 + b > 0 \) and \( d_2 \geq b \beta > 0 \), where \( d_1 \) and \( d_2 \) are defined in (22), we have

\[
w_t = d_1 w_{t-1} + d_2 w_{t-\tau} \geq (d_1 + d_2) \min\{w_{t-1}, w_{t-\tau}, 0\} \nolimits \\
\geq \left| \frac{1 \nolimits - c \tilde{z}_+}{1 + b} + \frac{b \beta (m(\tilde{z}_+) - 1)}{(1 + b)b \beta} \right| \min\{w_{t-1}, w_{t-\tau}, 0\} \\
= |1| \min\{w_{t-1}, w_{t-\tau}, 0\} \geq \min\{w_{t-1}, w_{t-2}, \ldots, w_{t-\tau}, 0\}.
\]

Hence, the lower bound in (23) holds for \( t = \tau \). Arguing inductively, it then also holds for all \( t \geq \tau \). The argument to show the upper bound in (23) is similar. Hence, the result follows. \( \square \)

**Proof of Theorem 3.9** As in Lemma 3.8, define \( w_t := z_t - \tilde{z}_+ \). Let \( \bar{w} = \lim \sup w_t \) and \( \underline{w} = \lim \inf w_t \). Then, by Lemma 3.8, both \( \bar{w} \) and \( \underline{w} \) are finite. Recalling that \( u = z_t \) and \( v = z_{t-\tau + 1} \) in (21), we define \( \tilde{H} \) as follows

\[
w_{t+1} = H(z_t, z_{t-\tau + 1}) - H(\tilde{z}_+, \tilde{z}_+) = \frac{1 \nolimits - c \tilde{z}_+}{m(\tilde{z}_+ + w_t)} w_t \\
+ \frac{b \beta (m(\tilde{z}_+) - 1)}{m(\tilde{z}_+ + w_t) M(\tilde{z}_+ + w_{t-\tau + 1})} w_{t-\tau + 1} := \tilde{H}(w_t, w_{t-\tau + 1}).
\]

Then

\[
\frac{\partial \tilde{H}}{\partial w_{t-\tau + 1}} = \frac{b \beta (m(\tilde{z}_+) - 1)(b \beta + (\beta - 1)c \tilde{z}_+)}{(1 + b + c(\tilde{z}_+ + w_t))(b \beta + (\beta - 1)c(\tilde{z}_+ + w_{t-\tau + 1}))^2} > 0.
\]
We proceed using proof by contradiction. Suppose $\bar{w} > 0$. Then

$$\bar{w} = \limsup w_{t+1} \leq \limsup \tilde{H}(w_t, \bar{w}) = \limsup \frac{1 - c\tilde{z}_+}{1 + b + cz_t} w_t$$

$$+ \frac{b\beta(m(\tilde{z}_+ - 1))}{(1 + b + cz_t)(b\beta + (\beta - 1)c(\tilde{z}_+ + \bar{w}))} \frac{\bar{w}}{w}$$

$$\leq \limsup \frac{1 - c\tilde{z}_+}{1 + b + cz_t} w + \frac{b\beta(m(\tilde{z}_+ - 1))}{(1 + b)(b\beta + (\beta - 1)c(\tilde{z}_+ + \bar{w}))} \frac{\bar{w}}{w}$$

$$\leq \left( \frac{1 - c\tilde{z}_+}{1 + b} + \frac{b\beta(m(\tilde{z}_+ - 1))}{(1 + b)(b\beta + (\beta - 1)c(\tilde{z}_+ + \bar{w}))} \frac{\bar{w}}{w} \right)$$

$$< \bar{w},$$

contradicting the assumption that $\bar{w} > 0$. Hence, $\bar{w} \leq 0$ and therefore $w \leq 0$.

Next we show that $\underline{w} = 0$. Since $z_t \geq 0$, $\underline{w} \geq -\tilde{z}_+$. Again we proceed using proof by contradiction. Suppose $\underline{w} = -\tilde{z}_+$. Then there must exist a subsequence $w_{t_j}$ converging to $-\tilde{z}_+$. By Lemma 3.1 for $z_0 \neq 0$, we can assume, without loss of generality, that $z_i > 0$, i.e., $w_i > -\tilde{z}_+$ for $i = 0, 1, \ldots, \tau - 1$. By Lemma 3.8, $w_i \geq \min\{w_0, w_1, \ldots, w_{\tau-1}, 0\} > -\tilde{z}_+$, violating the assumption that the subsequence decreases to $-\tilde{z}_+$. Suppose therefore $-\tilde{z}_+ < \underline{w} < 0$. Then

$$\underline{w} = \liminf w_{t+1} \geq \liminf \tilde{H}(w_t, \underline{w}) = \liminf \frac{1 - c\tilde{z}_+}{1 + b + cz_t} w_t$$

$$+ \frac{b\beta(b + c\tilde{z}_+)}{(1 + b + cz_t)(b\beta + (\beta - 1)c(\tilde{z}_+ + \underline{w}))} \underline{w}$$

$$\geq \liminf \frac{1 - c\tilde{z}_+}{1 + b + cz_t} \underline{w} + \frac{b\beta(b + c\tilde{z}_+)}{(1 + b)(b\beta + (\beta - 1)c(\tilde{z}_+ + \underline{w}))} \underline{w}$$

$$\underline{w} < 0$$

$$\geq \left( \frac{1 - c\tilde{z}_+}{1 + b} + \frac{b\beta(b + c\tilde{z}_+)}{(1 + b)(b\beta + (\beta - 1)c(\tilde{z}_+ + \underline{w}))} \underline{w} \right) \underline{w}$$

$$= \frac{b\beta(1 + b) + (1 - c\tilde{z}_+)(\beta - 1)c(\tilde{z}_+ + \underline{w})}{(1 + b)(b\beta + (\beta - 1)c(\tilde{z}_+ + \underline{w}))} \underline{w} > \underline{w},$$

because $c\tilde{z}_+ \in (0, 1]$. This violates the assumption that $\underline{w} < 0$. Therefore, $\underline{w} = 0 = \bar{w}$, completing the proof. \hfill \square

For the reader’s convenience, we state the following theorem from Grove and Ladas (2004) that we will use to prove Theorem 3.12, i.e., the global asymptotic stability of the positive equilibrium.
Theorem 1.15 in Grove and Ladas (2004) Let \( g : [a, b]^{k+1} \to [a, b] \) be a continuous function, where \( k \) is a positive integer and \([a, b]\) is an interval of real numbers. Consider

\[
x_{n+1} = g(x_n, x_{n-1}, \ldots, x_{n-k}), \quad n = 0, 1, \ldots
\]

Assume that \( g \) satisfies the following conditions:

1. For each integer \( i \) with \( 1 \leq i \leq k + 1 \), the function \( g(z_1, z_2, \ldots, z_{k+1}) \) is weakly monotonic in \( z_i \) for fixed \( z_j, j \neq i \).
2. If \((r, R) \in \mathbb{R}^2\) is a solution of the system

\[
\begin{align*}
r &= g(r_1, r_2, \ldots, r_{k+1}), \\
R &= g(R_1, R_2, \ldots, R_{k+1}),
\end{align*}
\]

where for each \( i = 1, 2, \ldots, k + 1 \), we set

\[
R_i = \begin{cases} 
R & \text{if } g \text{ is non-decreasing in } z_i \\
r & \text{if } g \text{ is non-increasing in } z_i
\end{cases}
\]

and

\[
r_i = \begin{cases} 
R & \text{if } g \text{ is non-decreasing in } z_i \\
r & \text{if } g \text{ is non-increasing in } z_i
\end{cases}
\]

and \( r = R \), then there exists exactly one equilibrium \( \bar{x} \) and every solution converges to \( \bar{x} \).

Note that we call weakly monotonic in the statement of the Theorem 1.15 in Grove and Ladas (2004) componentwise monotone. In order to apply this theorem, we first need to prove Propositions 3.10 and 3.11.

Proof of Proposition 3.10 Differentiating \( H(z_t, z_{t-\tau+1}) \) with respect to \( z_t \) is given by (17). Simplifying yields

\[
\frac{\partial H}{\partial z_t}(z_t, z_{t-\tau+1}) = \frac{b\beta(1+b) + c((\beta - 1)(1+b) - ab)z_{t-\tau+1}}{(1 + b + cz_t)^2(b\beta + (\beta - 1)c(z_{t-\tau+1})^2).}
\]

Since the denominator is positive,

\[
\frac{\partial H}{\partial z_t}(z_t, z_{t-\tau+1}) > 0 \iff P(z_{t-\tau+1}) = a_0 + a_1 z_{t-\tau+1} > 0,
\]

where

\[
a_0 = b\beta(1+b), \quad a_1 = c((\beta - 1)(1+b) - ab) \\
= c((\beta - 1)(1+b) - (b + cz)(\beta b + (\beta - 1)c(z_+))),
\]

(24)
and $ab$ was replaced by (19). Clearly, $a_0 > 0$ and since we are assuming that $c\bar{z}_+ > 1$, it follows that $a_1 < 0$, since

\[
\begin{align*}
a_1 &= c((\beta - 1)(1 + b) - (b + c\bar{z}_+)(b\beta + (\beta - 1)c\bar{z}_+)) \\
&< c((\beta - 1)(1 + b) - (b + 1)(\beta(b + 1) - 1)) \\
&= -cb\beta(1 + b) < 0.
\end{align*}
\]  

(25)

Therefore,

\[
\frac{\partial H}{\partial z_t} \begin{cases} 
> 0 & z_{t-\tau+1} < \chi := \frac{a_0}{(-a_1)}, \\
< 0 & z_{t-\tau+1} > \chi, \\
= 0 & z_{t-\tau+1} = \chi.
\end{cases}
\]  

(26)

Since $c\bar{z}_+ > 1$,

\[
\beta b < c\bar{z}_+(1 + b)(\beta - 1)(c\bar{z}_+ - 1)
\]

and therefore,

\[
\begin{align*}
\beta b(1 + b) &< c\bar{z}_+(1 + b)(b\beta + (\beta - 1)(c\bar{z}_+ - 1)) \\
&< c\bar{z}_+(1 + b)(b\beta + (\beta - 1)c\bar{z}_+) - (\beta - 1)(1 + b) \\
&< c\bar{z}_+((b + c\bar{z}_+)(b\beta + (\beta - 1)c\bar{z}_+) - (\beta - 1)(1 + b)).
\end{align*}
\]

Dividing by the right-hand side yields

\[
\chi = \frac{\beta b(1 + b)}{c((b + c\bar{z}_+)(b\beta + (\beta - 1)c\bar{z}_+) - (\beta - 1)(1 + b))} < \bar{z}_+.
\]

(27)

Further, since $\chi = \frac{a_0}{-a_1}$, by (24),

\[
c\chi < 1 \iff c\left[\frac{\beta b(1 + b)}{c((b + \bar{z}_+)(\beta b + (\beta - 1)c\bar{z}_+) - (\beta - 1)(1 + b))} < 1
\]

\[
\iff \frac{b\beta(1 + b)}{(b + \bar{z}_+)(\beta b + (\beta - 1)c\bar{z}_+) - (\beta - 1)(1 + b))} < 1
\]

\[
\iff \beta b(1 + b) < (b + \bar{z}_+)(\beta b + (\beta - 1)c\bar{z}_+) - (\beta - 1)(1 + b)
\]

\[
\iff \beta b(1 + b) + (\beta - 1)(1 + b) < (b + \bar{z}_+)(\beta b + (\beta - 1)c\bar{z}_+).
\]

The last inequality holds, since for $c\bar{z}_+ > 1$

\[
(b + 1)(\beta - 1) < (b + c\bar{z}_+)(\beta b + (\beta - 1)) < (b + c\bar{z}_+)(\beta b + (\beta - 1)c\bar{z}_+).
\]

Combining this with (27), we have

\[
c\chi < 1 \quad \text{and} \quad \chi < \bar{z}_+.
\]  

(28)
We now claim that

$$z_{t+1} = H(z_t, z_{t-\tau+1}) > \begin{cases} \chi & \text{if } z_{t-\tau+1} \geq \chi, \\ \min\{z_t, z_{t-\tau+1}\} & \text{if } z_{t-\tau+1} < \chi. \end{cases} \quad (29)$$

Firstly, we show that if $z_{t-\tau+1} \geq \chi$, then $z_{t+1} > \chi$. Since

$$\lim_{Z \to \infty} H(Z, \chi) = \lim_{Z \to \infty} \frac{Z M(\chi) + (m(\tilde{z}_+) - 1) M(\tilde{z}_+) \chi}{(1 + b + c Z) M(\chi)} = \frac{1}{c} > \chi,$$

and by (26), $H$ is non-increasing in the first variable, so for any $Z > z_t$, we have

$$\chi < \frac{1}{c} \leq H(Z, \chi) \leq H(z_t, \chi) \leq H(z_t, z_{t-\tau+1}),$$

where the last inequality holds, because $H$ is increasing in the second variable.

Secondly, if $z_{t-\tau+1} < \chi$, we show that (29) holds by showing that

$$z_{t+1} > z_m, \quad \text{where } z_m = \min\{z_t, z_{t-\tau+1}\}.$$  

This inequality is satisfied, since for $z_{t-\tau+1} < \chi < \tilde{z}_+$, $H$ is strictly increasing in both variables, and therefore

$$z_{t+1} = H(z_t, z_{t-\tau+1}) \geq H(z_m, z_m) = \frac{M(z_m) + (m(\tilde{z}_+) - 1) M(\tilde{z}_+) z_m}{m(z_m) M(z_m)} z_m > \frac{M(z_m) + (m(z_m) - 1) M(z_m)}{m(z_m) M(z_m)} z_m = z_m,$$

resulting in (29).

We now define

$$z_{m_i} := \min\{z_t | i \tau \leq t \leq (i + 1) \tau - 1\}, \quad i = 0, 1, 2, \ldots, \quad (30)$$

and use (28) and (29) to prove that $z_t > \chi$ for all sufficiently large $t$. We proceed using proof by contradiction. Suppose this is not true. Then for every fixed $t \geq 0$, there exists $\tilde{T} > t$ such that $z_{\tilde{T}} \leq \chi$. By (29), this implies that $z_{m_i} < \chi$ for all $i$. Since the sequence $\{z_{m_i}\}$ is also increasing, there exists $z^*$ such that

$$z^* = \lim_{i \to \infty} z_{m_i} \leq \chi. \quad (31)$$

Then, for each $\epsilon > 0$ there exists $j(\epsilon)$ such that $z^* - \epsilon < z_{m_{j(\epsilon)}} \leq z^*$. By (30), this also implies that

$$z^* - \epsilon < z_t \quad \text{for all } t \geq j(\epsilon) \tau$$

(32)
and

\[ S_i = \{ z_t \mid z_t \leq z^* , \ t \geq i \tau \} \neq \emptyset , \ \text{for all } i \geq j(\epsilon) . \] (33)

By (29), if \( z_\chi , z_{s+t-1} \notin S_i , \) then \( z_{s+t} \notin S_i . \) Let \( z_s \in S_i , \) for some fixed but arbitrary \( i \geq j(\epsilon) . \) Then \( z_\tau \leq z^* , \) and by (32), \( z^* - \epsilon < z_s , z_{s+t-1} . \) Since \( z_s \leq z^* \leq \chi , \) \( H \) is non-decreasing in both variables and we obtain

\[ z_{s+t} = H(z_{s+t-1}, z_s) \geq H(z^* - \epsilon , z^* - \epsilon) . \]

We obtain a contradiction to (33) by showing that there exists \( \epsilon \in (0, z^*) \) such that \( H(z^* - \epsilon , z^* - \epsilon) > z^* , \) since then \( z_{s+t} > z^* , \) and this implies that \( S_i = \emptyset \) for \( i > j(\epsilon) + 1 . \) To show the existence of such an \( \epsilon \in (0, \tilde{z}_+ ) , \) note that \( H(z^* - \epsilon , z^* - \epsilon) - z^* \) is of the form

\[ H(z^* - \epsilon , z^* - \epsilon) - z^* = \frac{\alpha_2 \epsilon^2 + \alpha_1 \epsilon + \alpha_0}{m(z^* - \epsilon)M(z^* - \epsilon)} . \]

Since the denominator is positive and

\[ \alpha_0 = cz^*(\tilde{z}_+ - z^*)[b(2\beta - 1) + c(\beta - 1)(\tilde{z}_+ + z^*)] > 0 , \]

there exists \( \delta > 0 \) such that for \( \epsilon \in (0, \delta) , \) \( \alpha_2 \epsilon^2 + \alpha_1 \epsilon + \alpha_0 > 0 . \) Hence, there exists \( \epsilon \in (0, z^*) \) such that \( H(z^* - \epsilon , z^* - \epsilon) > z^* \). Therefore, we have obtained a contradiction and so there exists \( T \) such that \( z_t \geq \chi \) for all \( t \geq T . \) \( \Box \)

**Proof of Proposition 3.11** By Proposition (3.10), there exists \( T \) such that \( z_t \geq \chi \) for all \( t \geq T . \) Without loss of generality, let \( T = 0 . \) We prove that there exists \( U > \tilde{z}_+ \) such that \( z_{t+1} \in [\chi , U] \) for \( z_t , z_{t-\tau +1} \in [\chi , U] . \) Since \( H \) is increasing in the second variable, and by Proposition (3.10), \( z_t \geq \chi \) for all \( t \geq 0 , \) it follows by (26) that \( H \) is decreasing in the first variable. Therefore, if such a \( U \) exists, then

\[ z_{t+1} = H(z_t, z_{t-\tau +1}) \leq H(\chi , U) , \quad z_t , z_{t-\tau +1} \in [\chi , U] . \]

Hence, to prove the existence of such a \( U , \) it suffices to show that \( H(\chi , U) \leq U \) for some \( U > \tilde{z}_+ . \)

\[ H(\chi , U) - U = \frac{Q(U)}{(1 + b)cm(\tilde{z}_+ )M(U)(b\beta + (\beta - 1)(c\tilde{z}_+ - 1))} , \] (34)

where \( Q(U) \) is a second-order polynomial of the form \( q_2 U^2 + q_1 U + q_0 , \) with

\[ q_2 = -c^2(1 + b)(\beta - 1)m(\tilde{z}_+ )(b\beta + (\beta - 1)(c\tilde{z}_+ - 1)) < 0 . \]

Therefore, there exists \( U^* > \tilde{z}_+ > \chi \) such that \( Q(U^*) \leq 0 \) and therefore, since the denominator in (34) is positive, \( H(\chi , U) \leq U , \) for all \( U \geq U^* , \) completing the proof. \( \Box \)
Proof of Theorem 3.12 Let $z_0 \neq 0$. Then, by Proposition 3.10, there exists $T$ such that $z_t \geq \chi$ for all $t \geq T$. By Proposition 3.11, there exists $U > \tilde{z}_+$ such that $z_t \in [\chi, U]$ for $t \geq T$. Without loss of generality, we therefore assume $z_s \in [\chi, U]$ for $s = 0, 1, \ldots, \tau - 1$, and $H : [\chi, U] \times [\chi, U] \to [\chi, U]$. In that case, $H$ is decreasing in the first variable and strictly increasing in the second variable, hence satisfying 1. in (Grove and Ladas 2004, Theorem 1.15).

Next we show that 2. in Grove and Ladas (2004, Theorem 1.15) also holds to obtain the result. Consider now $r, R \in [\chi, U]$ such that

$$r = H(R, r) = \frac{R}{m(R)} + \frac{abr}{m(R)M(r)} \quad (35)$$

$$R = H(r, R) = \frac{r}{m(r)} + \frac{abR}{m(r)M(R)}. \quad (36)$$

In what follows, we show that $r = R = \tilde{z}_+$ is the only solution to (35)–(36) in $[\chi, U]$. To find all possible solutions of (35)–(36), we multiply (35) by its denominator and obtain

$$rM(r)m(R) = RM(r) + abr. \quad (37)$$

Solving for $M(r)$, we obtain

$$M(r) = \frac{abr}{r(1 + b) + R(cr - 1)}. \quad (38)$$

If $cr = 1$, then (38) reduces to

$$b\beta + (\beta - 1) = \frac{ab}{1 + b},$$

violating (12), since $c\tilde{z}_+ > 1$. Therefore, $cr \neq 1$. In this case, we solve (37) for $R$ and obtain

$$R = r \frac{ab - M(r)(1 + b)}{(cr - 1)M(r)}. \quad (39)$$

If $cr < 1$, or equivalently $r < 1/c$, then, by (12),

$$(1 + b)M(r) \leq (1 + b)M(1/c) = (1 + b)(b\beta + (\beta - 1)) < ab.$$

This results in a negative value on the right-hand side of (39), violating the condition that $R \in [\chi, U]$. The only possibility that remains is that

$$cr > 1. \quad (40)$$
Next we find the solutions of (35)–(36). Rearranging terms in (36) and solving for \( R \) yields

\[
R_m(r)M(R) = rM(R) + abR
\]

\[
\iff Rb\beta m(r) + c(\beta - 1)m(r)R^2 = rb\beta + (\beta - 1)crR + abR
\]

\[
\iff R^2[c(\beta - 1)m(r)] + R\{b\beta m(r) - (\beta - 1)cr - ab\} - rb\beta = 0.
\]

Since \( c(\beta - 1)m(r) > 0 \) and \( r\beta b > 0 \), there exists exactly one positive root given by

\[
R_+ = \frac{(\beta - 1)cr + ab - b\beta m(r) + \sqrt{[b\beta m(r) - (\beta - 1)cr - ab]^2 + 4r\beta bc(\beta - 1)m(r)}}{2c(\beta - 1)m(r)}.
\]

Since the values of \( R \) in (39) and (41) must be equal \( R - R_+ = 0 \), and hence

\[
0 = R - R_+ = \frac{P(r)}{2c(\beta - 1)(cr - 1)m(r)M(r)} \iff P(r) = 0,
\]

where \( P(r) = 0 \) if and only if

\[
(r\{ab - M(r)(1 + b)\}) 2c(\beta - 1)m(r) - (cr - 1)M(r)\{(\beta - 1)cr + ab - b\beta m(r)\}
\]

\[
= (cr - 1)M(r)\sqrt{[b\beta m(r) - (\beta - 1)cr - ab]^2 + 4r\beta bc(\beta - 1)m(r)}.
\]

If there exists \( r \) such that this equality is satisfied, then \( r \) also solves

\[
(r\{ab - M(r)(1 + b)\}) 2c(\beta - 1)m(r) - (cr - 1)M(r)\{(\beta - 1)cr + ab - b\beta m(r)\})^2
\]

\[
-(cr - 1)^2M^2(r)\left([b\beta m(r) - (\beta - 1)cr - ab]^2 + 4r\beta bc(\beta - 1)m(r)\right) = 0.
\]

Since \( m(r) \) and \( M(r) \) are linear functions in \( r \), the left-hand side can be expressed as a sixth order polynomial in \( r \), namely

\[
\hat{P}(r) = \sum_{i=0}^{6} \alpha_i r^i \quad \text{with}
\]

\[
\alpha_0 = 0
\]

\[
\alpha_1 = 4eb^3\beta (1 + b)(\beta - 1)(a^2 - 2a\beta(1 + b) + b^2(2 + b))
\]

\[
\alpha_2 = -4b^2c^2(\beta - 1)(a^2(2 + b^2 - 3b(\beta - 1) - 2\beta)
\]

\[
- a\beta(1 + b)(4 + 2b^2 + b(7 - 8\beta) - 4\beta)
\]

\[
+ b\beta^2(2 + b)(3 + b^2 + b(4 - 5\beta) - 4\beta))
\]

\[
\alpha_3 = -4bc^3(\beta - 1)(a^2b(-2\beta + 2 + b)
\]

\[
+ b\beta(2 + b)(3 + 2b^2 - 5b(\beta - 1) - 3\beta)(2\beta - 1)
\]
\[ + a(b^3(2 - 5\beta) + 2(\beta - 1)^2 + b^2(7 - 21\beta + 12\beta^2) + b(\beta - 1)(-7 + 12\beta)) \]

\[ \alpha_4 = 4bc^4(\beta - 1)(a(-4(\beta - 1)^2 - 8b(\beta - 1)^2) + b^2(-3 + 4\beta) - (2 + b)(-\beta - 1)^2(-1 + 4\beta) + b^2(1 - 6\beta + 6\beta^2) + b(2 - 13\beta + 21\beta^2 - 10\beta^3)) \]

\[ \alpha_5 = 4c^5(\beta - 1)^2(b^3(2(1 - 2\beta) - b(7 + 2a - 11\beta)(\beta - 1) + 2(\beta - 1)^2 + b^2(7 + a - 16\beta + 5\beta^2)) \]

\[ \alpha_6 = 4(2 + b)(\beta - (1 + b))(\beta - 1)^3c^6. \]

The first three roots are easily found as equilibria of (7). The other roots are obtained using the symbolic computing environment in MAPLE (2019) and can be checked analytically:

\[ r_1 = 0, \quad r_2 = \tilde{z}_+, \quad r_3 = \tilde{z}_-, \quad r_4 = \frac{-(1 + b)}{c} \quad r_5 = \frac{\gamma_1 + \sqrt{\gamma_2}}{\gamma_3}, \quad r_6 = \frac{\gamma_1 - \sqrt{\gamma_2}}{\gamma_3}, \]

where

\[ \gamma_3 = -2c^2(2 + b)(\beta - (1 + b))(\beta - 1) < 0, \]

\[ \gamma_1 = c \left[ -(c\tilde{z}_+)^2(\beta - 1)(2\beta - 2 - b) + (c\tilde{z}_+)([(\beta - 1)(b + 2(1 - 2\beta)) + b\beta] + 2b\beta[2\beta - 2 - b]) \right], \]

\[ \gamma_2 = \gamma_1^2 + 4b\beta c^2(2 + b)(\beta - 1 - b)(\beta - 1)(c\tilde{z}_+[(\beta - 1)c\tilde{z}_+ - b] + 2b\beta(c\tilde{z}_+ - 1)). \]

Clearly, \( r_1, r_3, r_4 \not\in [\chi, U] \), since they are negative. We next show that \( r_5 \) and \( r_6 \) are also both not feasible. Interpreting \( \gamma_1 \) as a function of \( c\tilde{z}_+ \),

\[ \gamma_1 = \gamma_1(c\tilde{z}_+) = \hat{a}_2(c\tilde{z}_+)^2 + \hat{a}_1(c\tilde{z}_+) + \hat{a}_0, \quad \hat{a}_0 = 2b\beta c(2\beta - 2 - b) > 0. \]

Since \( \hat{a}_2 = -c(\beta - 1)(2\beta - 2 - b) < 0 \), there exists exactly one positive root and one negative root of the equation \( \gamma_1 = 0 \). This root lies in the interval \((0, 1)\), because

\[ \gamma_1(0) = \hat{a}_0 > 0 \quad \text{and} \quad \gamma_1(1) = -c(\beta - 1 - b)(2\beta - 2 - b) < 0, \]

and so \( \gamma_1 < 0 \) for all \( c\tilde{z}_+ > 1 \). Also, since \( \gamma_3 < 0 \), the roots \( r_5 \) and \( r_6 \) can be expressed as

\[ r_5 = \frac{|\gamma_1| - \sqrt{\gamma_2}}{|\gamma_3|} \quad \text{and} \quad r_6 = \frac{|\gamma_1| + \sqrt{\gamma_2}}{|\gamma_3|}. \quad (42) \]

It follows that \( r_5 \) is negative and hence not feasible, since

\[ \gamma_2 = \gamma_1^2 + 4b(2 + b)(\beta - 1 - b)(\beta - 1)b c^2(c\tilde{z}_+[(\beta - 1)c\tilde{z}_+ - b] \]

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and $\beta > 1 + b$, $c_z + > 1$ and $(\beta - 1)c_z + - b > (\beta - 1) - b > 0$.

Next we show that although $r_6$ and the corresponding $R_6$ value solve (35)–(36), if $r_6 \in [\chi, U]$, then $R_6 \leq 0$ and hence not feasible. We proceed using proof by contradiction. If $r_6 \in [\chi, U]$, then by (40) $cr_6 > 1$. By (39) and (42), $R_6 > 0$ if and only if

$$ab > (1 + b)M(r_6) \iff (m(z_+ - 1)M(z_+) > (1 + b)M(r_6)$$

$$\iff (b + c_z +)(\beta b + (\beta - 1)c_z + ) > (1 + b)[\beta b + (\beta - 1)c |\gamma_1| + \sqrt{\gamma_2} |\gamma_3|]$$

$$\iff \frac{|\gamma_3|^2}{c^2} [(b + c_z +)(\beta b + (\beta - 1)c_z + ) - (1 + b)\beta b]^2 + (1 + b)^2(\beta - 1)^2|\gamma_1|^2$$

$$- 2(1 + b)(\beta - 1)|\gamma_1| |\gamma_3| [(b + c_z +)(\beta b + (\beta - 1)c_z + ) - (1 + b)\beta b]$$

$$> (1 + b)^2(\beta - 1)^2\gamma_2$$

$$\iff Q(c_z + ) := b_0 + b_1(c_z + ) + b_2(c_z + )^2 + b_3(c_z + )^3 + b_4(c_z + )^4 > 0,$$

(43)

where

$$b_0 = 4b^3\beta^2c^2(2 + b)(\beta - 1)^2[(\beta - 1)^2(1 + 2b) - b^2(2\beta - 1)]$$

$$b_1 = 4b^2\beta c^2(2 + b)(\beta - 1)^2[2(\beta - 1)^2(1 + 2b) + b^3\beta - b^2(-1 + \beta + \beta^2)]$$

$$b_2 = 4b\beta c^2(2 + b)(\beta - 1)^2[3(\beta - 1)^3(1 + 2b)$$

$$+ b^2\beta(-3 + 8\beta - 5\beta^2) + b^3(1 + 5\beta(\beta - 1))]$$

$$b_3 = -8b^2\beta c^2(2 + b)(\beta - 1)^3(\beta - 1 - b)(2\beta - 1)$$

$$b_4 = -4b^2\beta c^2(2 + b)(\beta - 1)^4(\beta - 1 - b).$$

Interpreting the left-hand side of (44) as a function of $c_z +$, it is a polynomial of order four. Its four roots, obtained by Maple and easily verifiable, are given by

$$(c_z + )_1 = 1, \quad (c_z + )_2 = -b, \quad (c_z + )_3 = \frac{-b\beta}{\beta - 1}, \quad (c_z + )_4 = \frac{-(\beta(2b + 1) - (1 + b))/\beta - 1).$$

The largest positive root is $(c_z + )_4 = 1$. Since $b_4 < 0$, $Q(c_z + ) < 0$ for all $c_z + > 1$. This violates (44), since $c_z + > 1$. 

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Finally, \( r_2 = \tilde{z}_+ \), a fixed point of the system, and hence \( R_2 = \tilde{z}_+ \). Therefore, \( r_2 = R_2 \in [\chi, U] \) and is the only feasible solution of (35)–(36). By (Grove and Ladas 2004, Theorem 1.15), \( \tilde{z}_+ \) is attractive and by Theorem 3.4, \( \tilde{z}_+ \) is locally asymptotically stable. Therefore, \( \tilde{z}_+ \) is globally asymptotically stable. □

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