An Evolutionary Beverton-Holt Model

J.M. Cushing

Abstract The classic Beverton-Holt (discrete logistic) difference equation, which arises in population dynamics, has a globally asymptotically stable equilibrium (for positive initial conditions) if its coefficients are constants. If the coefficients change in time, then the equation becomes nonautonomous and the asymptotic dynamics might not be as simple. One reason the coefficients can change in time is their evolution by natural selection. If the model coefficients are functions of a heritable phenotypic trait subject to natural selection then, by standard methods for modeling evolution, the model becomes a planar system of coupled difference equations, consisting of a Beverton-Holt type equation for the population dynamics and a difference equation for the dynamics of the mean phenotypic trait. We consider a case when the trait equation uncouples from the population dynamic equation and obtain criteria under which the evolutionary system has globally asymptotically stable equilibria or periodic solutions.

1 Introduction

The well-known difference equation

$$x_{t+1} = b\frac{1}{1+cx_t}x_t, \qquad b, c > 0 \tag{1}$$

arose historically in population dynamics as a discrete analog of logistic growth [6] (also see [7–10]). It has been used as a basic model in many studies in population, ecological and evolutionary dynamics in the same way that the logistic differential

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equation is used as a starting point for innumerable differential equation models in these fields. The equation has been used, for example, in the fisheries industry where it is known as the Beverton-Holt equation, a name that is now widely used for the equation.

The dynamics of (1) are well known. For $x_0 > 0$ the equilibrium $x^e = 0$ (which we will refer to as the *extinction equilibrium*) is globally asymptotically stable (GAS) if $b < 1$. If $b > 1$ then $x = 0$ is unstable and the *survival equilibrium* $x^e = (b-1)/c$ is GAS. Moreover, solution sequences are monotone (and hence the strong analogy with the logistic differential equation).

There are numerous biological reasons to consider the coefficients b and c in Eq. (1) not to be constants. For example, these parameters might change in time due to changing environmental conditions, to physiological cycles, etc. Their fluctuations might be stochastic or deterministically regular, even periodic (modeling seasonal, monthly, or daily environmental oscillations). These fluctuations in (1) give rise respectively to a stochastic, a nonautonomous, and a periodically forced difference equation. The mathematical literature on the latter case has, for both (1) and for more general scalar difference equations, grown considerably in the last decade.

Another biological reason for which parameters in population dynamic models might change is time is evolutionary adaptation. In this case, the coefficients b and/or c in (1) are assumed to be functions of a phenotypic trait or several phenotypic traits that are subject to Darwinian evolution through natural selection and hence that change in time. If a scalar v represents a quantified phenotypic trait (e.g. body size, age, color, metabolic rate, aggressiveness, etc.) whose value affects and determines the values of b and c experienced by an individual that inherits the trait v (or by a mutant or an invader with trait v), then we write $b = b(v)$ and $c = c(v)$. It is up to the modeler to assign specific properties to these two functions that reflect the biological situation of interest. It can be the case that these parameters are not only affected by the trait value v of the individual, but by the traits of other individuals in the population (for example, through competition for resources). One way to model this case (called frequency dependence) is to assume that b and/or c also depend on the mean trait u of the population and to write

$$b = b(v, u), \quad c = c(v, u).$$

A method for modeling the change in the mean trait u over time, as subject to evolution, is by means of the equations

$$x_{t+1} = b(v, u_t) \left. \frac{1}{1 + c(v, u_t) x_t} \right|_{v=u_t} x_t \tag{2}$$

$$u_{t+1} = u_t + \sigma^2 \left. \frac{\partial \ln r(x, v, u_t)}{\partial v} \right|_{v=u_t} \tag{3}$$

where

$$r\left(x, v, u\right) := b\left(v, u\right)\frac{1}{1 + c\left(v, u\right)x}$$

[1, 4, 5, 11]. The equation for u_t (the trait dynamics) states that change in the mean trait is proportional to the fitness gradient where here fitness is defined as $\ln r\left(x, v, u\right)$. The parameter σ^2 (the constant of proportionality in the assumed evolution law) has different biological interpretations that depend on the assumptions made in modeling evolution [1]. Generally, however, σ^2 is proportional to the variance of the trait in the population, which is assumed constant over time. In any case, σ^2 measures how fast evolution occurs, and we refer to it as the *speed of evolution*.

The model equations (2) constitute a planar system of difference equations in which the population dynamics of x_t and the evolutionary dynamics of u_t are in general coupled. A method known as adaptive dynamics uncouples the trait equation from the population dynamic equation by making the assumption that evolutionary and population dynamics occur on (infinitely) different time scales [1, 4]. In this paper, we consider a (fairly general) case in which the trait dynamics uncouple from the population dynamics without the necessity of this strong assumption about differing time scales.

We will assume that b depends only on v (i.e., only on the trait inherited by the individual and not on the traits of others in the population). We also assume that c, which is surrogate for intraspecific competition, is a function of the difference $v - u$; that is to say, the amount of competition felt by an individual depends on how different its trait is from that of others, as represented by the mean u. Letting R and R^+ denote the real numbers and positive real numbers respectively, we make the following assumption:

$$b = b\left(v\right) \text{ and } c = c\left(v - u\right) \text{ where } b, c \in C^2\left(R, R^+\right) \quad \text{and} \quad c'(0) = 0. \tag{4}$$

The ecological reason for the assumption $c'(0) = 0$ is that it is often assumed in evolutionary game theory models that an individual experiences maximum competition when its trait equals the population mean, i.e. the competition coefficient c is maximized when $v = u$. In this case, the evolutionary Beverton-Holt model (2) becomes

$$x_{t+1} = b\left(u_t\right)\frac{1}{1 + c_0 x_t}x_t \tag{5}$$

$$u_{t+1} = u_t + \sigma^2\frac{b'\left(u_t\right)}{b\left(u_t\right)} \tag{6}$$

where $c_0 = c\left(0\right) > 0$. The prime denotes differentiation: $b'\left(u_t\right) = \partial b\left(v\right)/\partial v|_{v=u_t}$. Note that (6) is uncoupled from Eq. (5), but not vice versa.

The evolutionary models (2) and (3) are included in the general models studied in [3]. The theorems in [3] extend the fundamental bifurcation theorem for general population models that occurs as extinction states destabilize. These theorems apply to the evolutionary Beverton-Holt model (5)–(6) and provide criteria under which equilibrium states are locally stable or unstable. However, in this paper we will obtain a more general, independent analysis (including global dynamics) of (5)–(6) by taking advantage of the fact that (6) is uncoupled from (5) and of the fact that the global dynamics of (5) are well-known if evolution does not take place (i. e. $\sigma^2 = 0$ and u_t remains constant at u_0 for all time).

2 Asymptotic Dynamics of the Evolutionary Beverton-Holt Model

A *critical trait (mean)* u is one for which $b'(u) = 0$. Note that critical traits are equilibria of the scalar trait equation (5). Also note that (x^e, u^e) is an equilibrium of (5)–(6) if and only if u^e is a critical trait. If u^e is a critical trait, there exist two equilibria, one with $x^e = 0$ and another with $x^e = (b(u^e) - 1)/c_0$. We call the equilibrium $(0, u^e)$ an *extinction equilibrium*. We define a *survival equilibrium* (x^e, u^e) of the system (5)–(6) to be an equilibrium associated with trait u^e for which $x^e > 0$. The survival equilibria of (5)–(6) are

$$\left(x_+^e, u^e\right) = \left(\frac{b(u^e) - 1}{c_0}, u^e\right) \tag{7}$$

where u^e is any critical trait that satisfies

$$b\left(u^e\right) > 1.$$

Let $U \subseteq R$. We say that an equilibrium (x^e, u^e), $x^e \geq 0$, is *globally attracting on* $R^+ \times U$ if $(x_0, u_0) \in R^+ \times U$ implies $\lim_{t\to+\infty}(x_t, u_t) = (x^e, u^e)$. If, in addition, (x^e, u^e) is a locally asymptotically stable equilibrium of (5)–(6), then we say it is *globally asymptotically stable (GAS) on* $R^+ \times U$.

Note that because (6) is uncoupled from (5), the local asymptotic stability of an equilibrium (x^e, u^e) of (5)–(6) implies that u^e is a locally asymptotically stable equilibrium of (6).

Theorem 1 *Assume (4) and that* u^e *is a critical trait. We have the following facts about the extinction equilibrium* $(\hat{0}, u^e)$ *and the survival equilibrium (7) of the evolutionary system (5)–(6).*

(a) (Extinction equilibria). If $b(u^e) > 1$ *or if*

$$\left|1 + \sigma^2 \frac{b''(u^e)}{b(u^e)}\right| > 1 \tag{8}$$

then the extinction equilibrium $(\hat{0}, u^e)$ *is unstable.*

If $b\left(u^{e}\right) < 1$ *and*

$$\left|1+\sigma^{2}\frac{b''\left(u^{e}\right)}{b\left(u^{e}\right)}\right| < 1 \tag{9}$$

then there exists an open neighborhood U *of* u^{e} *such that the extinction equilibrium* $(\hat{0}, u^{e})$ *is GAS on* $R^{+} \times U$.

(b) (Survival equilibria) If $b\left(u^{e}\right) > 1$ *and (8) hold, then the survival equilibrium (7) is unstable.*

If $b\left(u^{e}\right) > 1$ *and (9) hold, then there exists an open neighborhood* U *of* u^{e} *such that the survival equilibrium (7) is GAS on* $R^{+} \times U$.

Note that the instability inequality (8) holds if $b''(u^{e}) > 0$.

Proof The Jacobian $J\left(x, u\right)$ of (5)–(6), when evaluated at any equilibrium (x^{e}, u^{e}), namely

$$J\left(x^{e}, u^{e}\right) = \begin{pmatrix} b\left(u^{e}\right)\frac{1}{\left(1+c_{0}x^{e}\right)^{2}} & 0 \\ 0 & 1+\sigma^{2}\frac{b''\left(u^{e}\right)}{b\left(u^{e}\right)} \end{pmatrix} \tag{10}$$

has eigenvalues

$$\lambda_{1} = b\left(u^{e}\right)\frac{1}{\left(1+c_{0}x^{e}\right)^{2}}, \quad \lambda_{2} = 1+\sigma^{2}\frac{b''\left(u^{e}\right)}{b\left(u^{e}\right)}.$$

(a) The instability assertions follow from the linearization principle when either λ_1 or λ_2 have absolute value greater than one. By the linearization principle, the extinction equilibrium $(0, u^{e})$ is locally asymptotically stable when both λ_1 or λ_2 have absolute value less than one. What remains to show, in this case, is its global asymptotic stability when $b\left(u^{e}\right) < 1$. Since u^{e} is a locally asymptotically stable equilibrium of the trait equation (6), we can find a $\delta > 0$ be such that $|u_0 - u^{e}| < \delta$ implies $\lim_{t\to+\infty} u_t = u^{e}$. Let (x_t, u_t) be any solution of (5) with an initial condition (x_0, u_0) that satisfies $x_0 > 0$ and $|u_0 - u^{e}| < \delta$. We need to show that

$$\lim_{t\to+\infty}\left(x_t, u_t\right) = (0, u^{e}). \tag{11}$$

Since we already know that $\lim_{t\to+\infty} u_t = u^{e}$, we need only show $\lim_{t\to+\infty} x_t = 0$. Since $b\left(u^{e}\right) < 1$ we can choose a real number β satisfying $b\left(u^{e}\right) < \beta < 1$ and, since $\lim_{t\to+\infty} u_t = u^{e}$, there exists a $T > 0$ such that $t \geq T$ implies $b\left(u_t\right) \leq \beta$. From (5) we have

$$0 \leq x_{t+1} = b\left(u_t\right)\frac{1}{1+c_0x_t}x_t \leq \beta x_t$$

for all $t \geq T$. It follows that $\lim_{t\to+\infty} x\left(t\right) = 0$, i.e. (11) holds.

(b) For a survival equilibrium (7) we have

$$0 < \lambda_1 = \frac{1}{b\,(u^e)} < 1.$$

When (8) holds, instability follows because $|\lambda_2| > 1$.

On the other hand, when (9) holds, then $|\lambda_2| < 1$ and the survival equilibrium is locally asymptotic stability. What remains to prove, in this case, is its global stability. Since u^e is a locally asymptotically stable equilibrium of the trait equation (6), we can find a $\delta > 0$ be such that $|u_0 - u^e| < \delta$ implies $\lim_{t\to+\infty} u_t = u^e$. Let (x_t, u_t) be any solution of (5)–(6) with an initial condition (x_0, u_0) that satisfies $x_0 > 0$ and $|u_0 - u^e| < \delta$. We need to show

$$\lim_{t\to+\infty} (x_t, u_t) = (x^e, u^e). \tag{12}$$

Since we already know that $\lim_{t\to+\infty} u_t = u^e$, we need only show $\lim_{t\to+\infty} x_t = x^e_+$. The sequence x_t is positive for all t and satisfies the asymptotically autonomous equation (5). A straightforward calculation shows that $y_t := 1/x_t$ satisfies the linear, asymptotically autonomous equation

$$0 < y_{t+1} = \frac{1}{b\,(u_t)} y_t + \frac{c_0}{b\,(u_t)}.$$

Lemma 1 in the Appendix implies

$$\lim_{t\to+} y_t = \frac{c_0}{b\,(u^e) - 1}$$

from which we obtain

$$\lim_{t\to+} x_t = \frac{b\,(u^e) - 1}{c_0} = x^e$$

and hence (12) holds. This completes the proof.

With regard to evolutionary convergence (i.e. the stability of a survival equilibrium), Theorem 1b requires (9) hold. For this inequality to hold it is necessary that $b''(u^e) < 0$ and

$$\sigma^2 < -2\frac{b\,(u^e)}{b''\,(u^e)}, \tag{13}$$

that is to say, that the speed of evolution be not too fast. The open neighborhood U in Theorem 1(b) can be taken to be the basin (interval) of attraction of u^e as a stable equilibrium of the trait equation (6).

If the inequality (13) is reversed, that is to say, if the speed of evolution is too fast, then Theorem 1(a) implies the survival equilibrium is unstable and the expected exchange of stability between equilibrium branches as $b\,(u^e)$ increases through 1 does not occur. This destabilization of the survival equilibrium is due to a period doubling bifurcation in the trait equation (6) as σ^2 increases through the critical value $-2b\left(u^e\right)/b''\left(u^e\right)$ where the derivative of

$$u+\sigma^2\frac{b'\left(u\right)}{b\left(u\right)}$$

equals -1 at $u=u^e$. In such a case, the uncoupled trait equation (5) can have locally asymptotically stable periodic cycles. In this case we have the following theorem for the dynamics of the evolutionary system (5). We say that a p-periodic solution $\left(\xi_t,\upsilon_t\right)$ of the system (5)–(6) is a *survival* p-periodic solution if $\xi_t>0$ for all t.

Theorem 2 *Assume (4). Suppose υ_t is a hyperbolic, locally asymptotic p-periodic solution of the trait equation (6). If*

$$\prod_{t=0}^{p-1}b\left(\upsilon_t\right)>1 \tag{14}$$

then there exists a survival p-periodic solution $\left(\xi_t,\upsilon_t\right)$ of the evolutionary system (5)–(6) which is globally asymptotically stable on $R^+\times U$ for some open neighborhood U of υ_0.

Proof The x_t component of a solution pair $\left(x_t,u_t\right)$ of (5)–(6) satisfies the nonautonomous equation

$$x_{t+1}=b\left(u_t\right)\frac{1}{1+c_0x_t}x_t,\quad x_0>0 \tag{15}$$

where u_t satisfies the uncoupled trait equation (6). Suppose u_t approaches the p-periodic solution υ_t as $t\to+\infty$. Then the nonautonomous equation (15) is asymptotically periodic with limiting equation

$$x_{t+1}=b\left(\upsilon_t\right)\frac{1}{1+c_0x_t}x_t,\quad x_0>0. \tag{16}$$

Defining $y_t=1/x_t$ we obtain the linear, asymptotically periodic equation

$$y_{t+1}=\frac{1}{b\left(u_t\right)}y_t+\frac{c_0}{b\left(u_t\right)},\quad y_0>0. \tag{17}$$

By Theorem 1 in [2] the periodically forced limiting equation

$$y_{t+1}=\frac{1}{b\left(\upsilon_t\right)}y_t+\frac{c_0}{b\left(\upsilon_t\right)} \tag{18}$$

has a unique, positive p-periodic solution θ_t.

To show the periodic solution θ_t is attracting, we consider the p-fold composite equation of (17), which is a linear (asymptotically autonomous) equation of the form (21) in Lemma 1 in the Appendix, namely,

$$y_{t+1} = \alpha_t y_t + \beta_t$$

with

$$\alpha_t = \frac{1}{\prod_{i=0}^{p-1} b\left(u_t\right)} \to \alpha^e = \frac{1}{\prod_{i=0}^{p-1} b\left(\upsilon_i\right)} < 1$$

and a sequence $\beta_t > 0$ (a formula for which we do not need) which approaches a limit β^e as $t \to \infty$. By Lemma 1, inequality (14) implies the solution of the p-fold composite with initial condition $y_0 > 0$ approaches as $t \to \infty$ the equilibrium $\beta^e / \left(1 - \alpha^e\right)$ of the limiting equation of the composite. This limit is, in fact, the first point θ_0 in the p-periodic solution θ_t. Repeating this argument using y_i, $1 \leq i \leq p-1$, as a starting point, we find that the solution of the composite approaches the ith point θ_i in the p-periodic solution θ_t.

All of this is to say that the solution of (17) approaches the periodic solution θ_t of the limiting equation (18), which in turns implies the solution x_t of (15) approaches the periodic solution $\xi_t = 1/\theta_t$ of the limiting equation (16). All that remains to prove is that p-periodic solution (ξ_t, υ_t) of (5)–(6) is locally asymptotically stable. This is done by investigating the eigenvalues of the Jacobian of the p-fold composite map arising from (5)–(6). This Jacobian is equal to the product $\Pi_{i=0}^{p-1} J\left(\xi_t, \upsilon_t\right)$ where

$$J\left(x, u\right) = \begin{pmatrix} \lambda_1\left(x, u\right) & b'\left(u\right) \frac{1}{1+c_0 x} x \\ 0 & \lambda_2\left(u\right) \end{pmatrix}$$

is the Jacobian of (5)–(6). Here

$$\lambda_1\left(x, u\right) := b\left(u\right) \frac{1}{\left(1 + c_0 x\right)^2}, \qquad \lambda_2\left(x, u\right) := 1 + \sigma^2 \frac{b\left(u\right) b''\left(u\right) - \left(b'\left(u\right)\right)^2}{b^2\left(u\right)}.$$

Therefore

$$\prod_{i=0}^{p-1} J\left(\xi_t, \upsilon_t\right) = \begin{pmatrix} \pi_1 & * \\ 0 & \pi_2 \end{pmatrix}, \quad \pi_1 := \prod_{i=0}^{p-1} \lambda_1\left(\xi_t, \upsilon_t\right), \qquad \pi_2 := \prod_{i=0}^{p-1} \lambda_2\left(\upsilon_t\right),$$

where the asterisk does not concern us, since the eigenvalues of this matrix lie along the diagonal. The assumption that υ_t is a hyperbolic, locally asymptotically stable periodic solution implies that $|\pi_2| < 1$ and hence that the stability of the periodic solution (ξ_t, υ_t) is determined by the π_1.

Note that

$$\prod_{i=0}^{p-1} \xi_{i+1} = \prod_{i=0}^{p-1} b(\upsilon_i) \frac{1}{1+c_0\xi_i}\xi_i = \left(\prod_{i=0}^{p-1} b(\upsilon_i) \frac{1}{1+c_0\xi_i}\right) \prod_{i=0}^{p-1} \xi_i.$$

Since ξ_t is p-periodic, it follows that $\prod_{i=0}^{p-1} \xi_{i+1} = \prod_{i=0}^{p-1} \xi_i$ and hence

$$1 = \prod_{i=0}^{p-1} b(\upsilon_i) \frac{1}{1+c_0\xi_i} = \prod_{i=0}^{p-1} b(\upsilon_i) \prod_{i=0}^{p-1} \frac{1}{1+c_0\xi_i}.$$

Then

$$0 < \pi_1 = \prod_{i=0}^{p-1} b(\upsilon_i) \frac{1}{(1+c_0\xi_i)^2} = \frac{1}{\prod_{i=0}^{p-1} b(\upsilon_i)} < 1$$

which establishes local asymptotic stability.

3 Examples

We give two examples of the use of Theorem 1 to analyze the evolutionary model (5)–(6) with specified dependences of the coefficient $b = b(v)$ on the phenotypic trait v. In the first example, the adaptive landscape defined by b (or by fitness $\ln b$) is unimodal with a global maximum. In the second example, the adaptive landscape is bimodal. In that example, oscillations are possible and Theorem 2 is applicable.

Example 1 A common assumption in evolutionary modeling is that vital parameters are normally distributive as functions of a phenotypic trait. If we take

$$b(v) = b_0 \exp\left(-\frac{v^2}{2w^2}\right), \quad b_0 > 0$$

then $v^e = 0$ is the only critical trait. Since

$$b''(0) = \frac{-b_0}{w^2} < 0$$

we find from Theorem 1 that if $\sigma^2 < 2w^2$ then

$(\hat{0}, 0)$ is GAS on $R^+ \times R^+$ if $b_0 < 1$ and unstable if $b_0 > 1$

$\left(\frac{b_0-1}{c_0}, 0\right)$ is GAS on $R^+ \times R^+$ if $b_0 > 1$.

Here the interval $U = R^{+}$ because $u^{e} = 0$ is globally attracting as an equilibrium of the (in this case simple linear) trait equation (6) $u_{t+1} = \left(1 - \sigma^{2}/w^{2}\right) u_{t}$. Note that the solutions of this equation are unbounded if $\sigma^{2} > 2w^{2}$ and hence so are the orbits of the evolutionary model (5)–(6).

In Example 1, the adaptive landscape, i.e., the graph of fitness

$$\ln b\,(v) = \ln b_0 - \frac{v^2}{2w^2}$$

as a function the mean phenotypic trait v, is unimodal with a maximum at the critical trait $v = 0$. When orbits approach a survival equilibrium, i.e. when $b_0 > 0$ and $\sigma^{2} < w^{2}$, the evolution of fitness $\ln b\,(u_t)$ along orbits of the model (5)–(6) tends to its maximum value $\ln b_0$. In this case, the trait $u^{e} = 0$ is said to be an evolutionarily stable strait (ESS) since it is located at the global maximum of fitness [11].

In the next example, we illustrate the application of Theorems 1 and 2 in a case when the adaptive landscape has multiple peaks and the evolutionary model can have multiple attractors.

Example 2 An example of a two peaked adaptive landscape is provided by the fitness function $\ln b\,(v)$ with

$$b\,(v) = b_0 \exp\left(-v^2\left(3v^2 - 2v - 3\right)\right), \quad b_0 > 0. \tag{19}$$

In this case,

$$\ln b\,(u) = \ln b_0 - u^2\left(3u^2 - 2u - 3\right)$$

has three critical traits

$$u^{e} = -\frac{1}{2}, \quad 0, \quad 1.$$

$b\,(u)$ has a local maximum at $u^{e} = -1/2$, a local minimum at $u^{e} = 0$, and a global maximum at $u^{e} = 1$. See Fig. 1. Calculations show

$$\begin{aligned} &b\,(-1/2) = b_0 e^{5/16} \text{ and } b''\,(-1/2) = -9b_0 e^{5/16} < 0 \\ &b\,(0) = b_0 \text{ and } b''\,(0) = 6b_0 > 0 \\ &b\,(1) = b_0 e^{2} \text{ and } b''\,(1) = -18 b_0 e^{2} < 0. \end{aligned}$$

Theorem 1 implies the stability results in Table 1 for the extinction and survival equilibria of the evolutionary Beverton-Holt equation (5)–(6) when b is given by (19). In each case the set U is the interval of attraction of u^{e} as an equilibrium of the trait equation (6), which is in this example, the scalar difference equation

$$u' = u + 6\sigma^{2} u\,(2u + 1)\,(1 - u)\,. \tag{20}$$

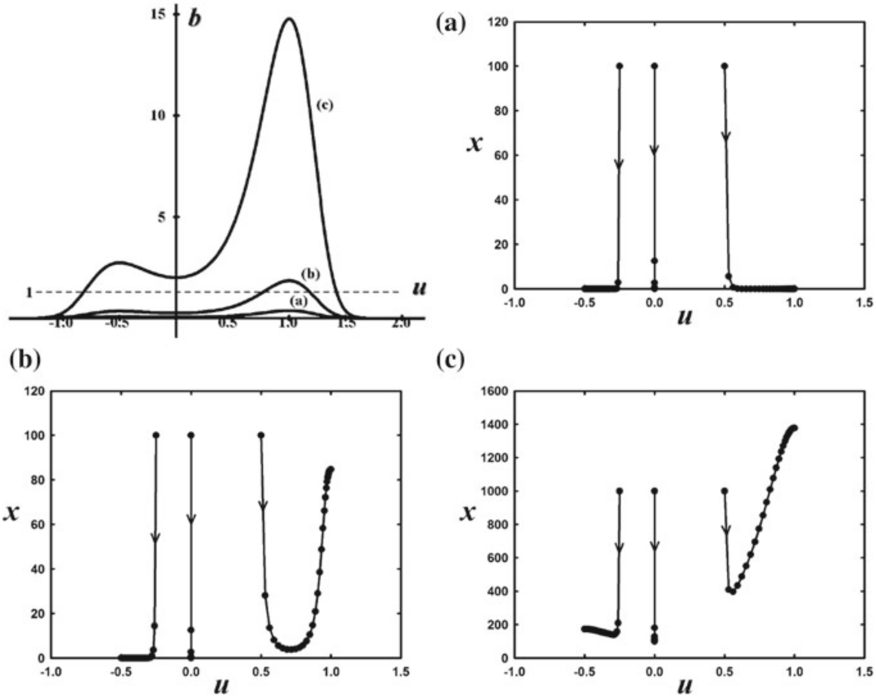

Fig. 1 The graph of $b(u)$ in (19) is shown for three values of b_0 which give rise to three different phase plane scenarios in Table 1. Phase plane plots for each case are shown, with three sample orbits, in plots (**a**), (**b**) and (**c**). In all cases $\sigma^2 = 0.01$ and $c_0 = 0.01$. **a** $b_0 = 1/20$. In this case, $b(-1/2) = e^{5/16}/20 < 1$ and $b(1) = e^2/20 > 1$ and there exists no survival equilibrium. All orbits approach an extinction equilibrium. **b** $b_0 = 1/4$. In this case, $b(-1/2) = e^{5/16}/4 < 1$ and $b(1) = e^2/4 > 1$ and there exists one survival equilibrium (7) with trait $u^e = 1$ which attracts orbits with $u_0 > 0$. Orbits with $u_0 \leq 0$ tend to an extinction equilibrium. **c** $b_0 = 2$. In this case, $b(-1/2) = 2e^{5/16} < 1$ and $b(1) = 2e^2 < 1$ and there exist three survival equilibria. Orbits with $u_0 > 0$ tend to the survival equilibrium (7) with trait $u^e = 1$. Orbits with $u_0 < 0$ tend to the survival equilibrium (7) with trait $u^e = -1/2$. Orbits with $u_0 = 0$ lie on the stable manifold of the unstable (saddle) survival equilibrium (7) with trait $u^e = 0$

When the survival equilibrium at $u^e = 1$ is stable, the trait $u^e = 1$ is an ESS since it is located at a global maximum of the fitness function. On the other hand, when the survival equilibrium at $u^e = -1/2$ is stable, the trait $u^e = -1/2$ is said to be evolutionarily convergent, but not an ESS since it does not yield a global maximum of the fitness function. It is possible, of course, for both survival equilibria at $u^e = 1$ and $u^e = -1/2$ to be stable, which occurs when $b_0 > e^{-5/16}$ and $\sigma^2 < 1/9$.

A cobwebbing analysis and a bifurcation diagram of trait equation (using the speed of evolution σ^2 as a bifurcation parameter) indicates what occurs when the slow evolution inequalities in Table 1 are violated. As σ^2 increases through the critical values 1/9 and 2/9, period doubling cascades to chaos occur as the corresponding survival equilibrium destabilizes. See Fig. 2. For any periodic cycle which results

Table 1 In the right column are the extinction and survival equilibria of the evolutionary Beverton-Holt equation (5)–(6) when b is given by (19). The middle and left columns show the criteria for the global stability and instability of each equilibrium. The set U is the interval of attraction of ue as an equilibrium of the trait equation (20)

Extinction equilibria	GAS on $R^+ \times U$	Unstable
$(0, -1/2)$	$b_0 < e^{-5/16}$ and $\sigma^2 < 2/9$	$b_0 > e^{-5/16}$ or $\sigma^2 > 2/9$
$(0, 0)$	never	always
$(0, 1)$	$b_0 < e^{-2}$ and $\sigma^2 < 1/9$	$b_0 > e^{-2}$ or $\sigma^2 > 1/9$
Survival equilibria (7)		
$\left(\frac{b_0 e^{5/16}-1}{c_0}, -1/2\right), b_0 > e^{-5/16}$	$\sigma^2 < 2/9$	$b_0 > e^{-5/16}$ and $\sigma^2 < 2/9$
$\left(\frac{b_0-1}{c_0}, 0\right), b_0 > 1$	never	always
$\left(\frac{b_0 e^2-1}{c_0}, 1\right), b_0 > e^{-2}$	$\sigma^2 < 1/9$	$\sigma^2 > 1/9$

from these bifurcations, Theorem 2 implies that there exists a periodic cycle of the evolutionary system (5)–(6) which is globally asymptotically stable on $R^+ \times U$ for some open neighborhood of the critical trait u^e.

4 Concluding Remarks

We considered the evolutionary Beverton-Holt model (2)–(3) under the assumption (4), which uncouples the trait equation (3) from the planar system (2)–(3). We proved the global stability criteria given in Theorems 1 and 2 for equilibria and for periodic cycles of the resulting system (5)–(6). The proofs of these theorems make use of the uncoupling of the equations, which produces a nonautonomous version of the Beverton-Holt equation (5) in which the coefficient $b = b\left(u_t\right)$ is driven by a solution of the scalar trait equation (6).

The dynamics of the evolutionary Beverton-Holt model (2)–(3) when the trait equation does not uncouple remains an interesting open question. For example, a common mathematical expression for the intraspecific competition coefficient $c = c\left(v - u\right)$ is [11]

$$c = c_0 \exp\left(-\frac{(v-u)^2}{2w_c^2}\right),$$

which assumes that the maximum competitive effect c_0 occurs when an individual's trait v equals the population mean trait u. If, more generally, the maximum competitive effect c_0 is dependent on the individual's trait v, then

$$c = c_0\left(v\right) \exp\left(-\frac{(v-u)^2}{2w_c^2}\right)$$

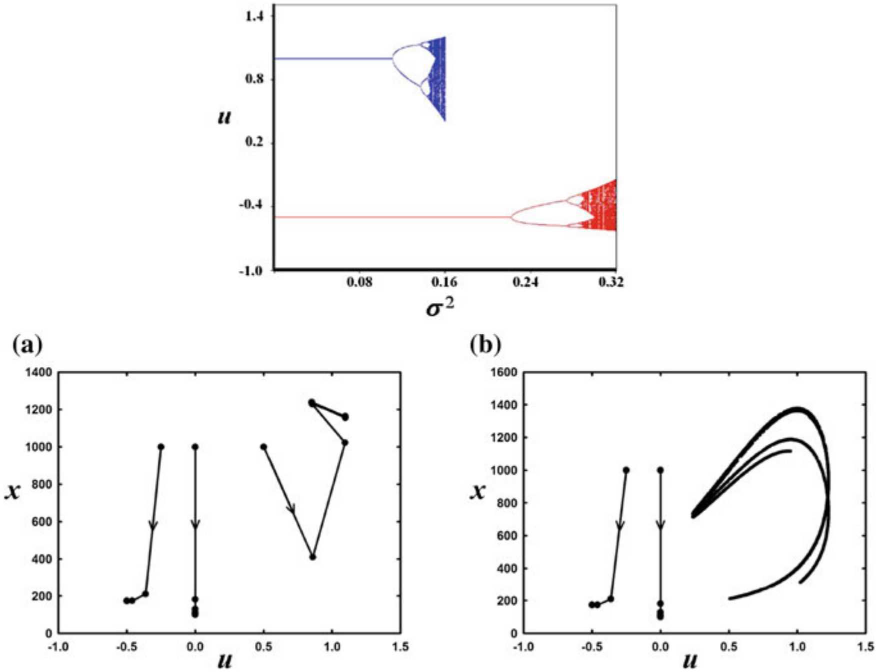

Fig. 2 The bifurcation diagram of the trait equation (20) shows a periodic doubling cascade originating at each of the survival equilibria (7) with $u^e = -1/2$ and 1 at their respective critical values of σ^2, namely, $1/9$ and $2/9$. **a** When the speed of evolution in the case of Fig. 1(**c**) is increased the $\sigma^2 = 0.12 > 1/9$, the survival equilibrium with $u_e = 1$ destabilizes, resulting in a stable period 2 cycle. **b** When the speed of evolution is further increased to $\sigma^2 = 0.17$, a chaotic attractor is reached through a period doubling cascade initiating at the survival equilibrium with $u^e = 1$

and the trait equation will no longer uncouple in the evolutionary Beverton-Holt model (2)–(3).

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Appendix

Lemma 1 *Consider the nonautonomous linear difference equation*

$$y_{t+1} = \alpha_t y_t + \beta_t \tag{21}$$

for $t = 0, 1, 2, \ldots$. *Assume* $\alpha_t, \beta_t \geq 0$ *and*

$$\lim_{t\to+\infty}\alpha_t=\alpha^e,\quad \lim_{t\to+\infty}\beta_t=\beta^e.$$

If $\alpha^e<1$ *then for all* $y_0>0$

$$\lim_{t\to+\infty}y_t=y^e:=\frac{\beta^e}{1-\alpha^e}.$$

Proof If we define $w_t:=y_t-y_e$, then

$$w_{t+1}=\alpha_t w_t+q_t$$

where

$$q_t:=\left(\alpha_t-\alpha^e\right)y^e+\beta_t-\beta^e$$

and hence

$$\lim_{t\to+\infty}q_t=0.$$

By induction

$$w_{t+1}=\left(\prod_{i=0}^{t}\alpha_i\right)w_0+\sum_{j=1}^{t}\left(\prod_{i=j}^{t}\alpha_i\right)q_{j-1}+q_t.$$

Let $\bar{\alpha}$ and $\bar{q}>0$ be upper bounds for the bounded sequences α_t and $|q_t|$ respectively. Choose a positive $\rho<1$. Since $\alpha^e<1$ and $\lim_{t\to+\infty}b_t=b^e$, for arbitrary $\varepsilon>0$, we can find a $T>0$ such that $t\geq T$ implies

$$0\leq\alpha_t\leq\rho,\quad |q_t|\leq\varepsilon\left(1-\rho\right).$$

For $t\geq T$ we have

$$\begin{aligned}|w_{t+1}|&\leq\left(\prod_{i=0}^{T}\alpha_i\right)\left(\prod_{i=T+1}^{t}\alpha_i\right)|w_0|+\sum_{j=1}^{T}\left(\prod_{i=j}^{t}\alpha_i\right)\left|q_{j-1}\right|\\&\quad+\sum_{j=T+1}^{t}\left(\prod_{i=j}^{t}\alpha_i\right)\left|q_{j-1}\right|+|q_t|\\&\leq\bar{\alpha}^{T+1}\rho^{t-T}\,|w_0|+\sum_{j=1}^{T}\left(\prod_{i=j}^{T}\alpha_i\right)\left(\prod_{i=T+1}^{t}\alpha_i\right)\left|q_{j-1}\right|\\&\quad+\sum_{j=T+1}^{t}\rho^{t-j+1}\varepsilon\left(1-\rho\right)+\varepsilon\left(1-\rho\right)\end{aligned}$$

$$|w_{t+1}| \leq \bar{\alpha}^{T+1}\rho^{t-T}\,|w_0| + \rho^{t-T}\bar{q}\sum_{j=1}^{T}\bar{\alpha}^{T-j+a} + \frac{1}{1-\rho}\varepsilon\,(1-\rho)\,.$$

Letting $t \to +\infty$ we obtain

$$\lim_{t\to+\infty}\sup|w_{t+1}| \leq \varepsilon.$$

Because $\varepsilon > 0$ is arbitrary, we conclude $\lim_{t\to+\infty}|w_{t+1}| = 0$.

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