

# Population models with periodic recruitment functions and survival rates

JOHN E. FRANKE<sup>†</sup> and ABDUL-AZIZ YAKUBU<sup>‡\*</sup>

<sup>†</sup>Department of Mathematics, North Carolina State University, Raleigh, NC 27695-8205, USA

<sup>‡</sup>Department of Mathematics, Howard University, Washington, DC 20059, USA

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We study the combined effects of periodically varying carrying capacity and survival rate on populations. We show that our populations with constant recruitment functions do not experience either resonance or attenuation when either only the carrying capacity or the survival rate is fluctuating. However, when both carrying capacity and survival rate are fluctuating the populations experience either attenuation or resonance, depending on parameter regimes. In addition, we show that our populations with Beverton–Holt recruitment functions experience attenuation when only the carrying capacity is fluctuating.

*Keywords:* Attenuance; Periodic carrying capacity; Periodic survival rate; Resonance

## 1. Introduction

In periodic environments, population sizes are often either enhanced via resonance or diminished via attenuation [1,6,7,21–25,39]. The logistic differential and difference equations have been used to show that a periodic environment is always deleterious. That is, the average of the resulting population oscillations in the periodic environment is less than the average of the carrying capacity in the corresponding constant environment (attenuance) [4,5,7,36]. In recent papers, Cushing and Henson [7], Kon [28,29], Kocic [26,27], Elaydi and Sacker [11–14] obtained a similar result for populations governed by the classic Beverton–Holt model. In this paper, we use simple population models with either constant or Beverton–Holt recruitment functions to show that periodic environments are not always deleterious [34]. In the absence of survivors per generation, our model with Beverton–Holt recruitment function reduces to the classic Beverton–Holt model. Simple models, by their own nature, cannot incorporate many of the complex biological factors. However, they often provide useful insights to help our understanding of complex processes [31–33].

In section 2, we introduce the main models for this study, periodically forced population models with survivors. Population models with constant and monotone recruitment functions are discussed in sections 3 and 4, respectively. We show in section 3 that our populations with constant recruitment functions do not experience either resonance or attenuation when either only the carrying capacity or only the survival rate is fluctuating. However, when both carrying capacity and survival rate are fluctuating the populations experience either attenuation or resonance, depending on parameter regimes. In constant environments, autonomous population models do not have globally attracting cycles [15]. In section 4,

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\*Corresponding author. Email: ayakubu@howard.edu

we prove that our models (non-autonomous) support globally attracting cycles when the recruitment functions are monotone. The Beverton–Holt recruitment functions are studied in section 5. We show that our populations with Beverton–Holt recruitment functions experience attenuation when only the carrying capacity is fluctuating. This is in stark contrast to the case when the recruitment function is constant. However, when both the carrying capacity and the survival rate are fluctuating, the populations experience either attenuation or resonance, depending on parameter regimes. The implications of our results are discussed in section 6, and technical formulas are collected in the appendices (Appendix A and B).

## 2. Periodically forced demographic equations

In constant environments, theoretical discrete-time epidemic models are usually constructed under the assumption that the dynamics of the total population size in generation  $t$ , denoted by  $x_t$ , are given by equations of the form

$$x_{t+1} = f(x_t) + \gamma x_t, \quad (1)$$

where  $\gamma \in (0, 1)$  is the constant “probability” of surviving per generation, and  $f : \mathbb{R}_+ \rightarrow \mathbb{R}_+$  models the birth or recruitment process [2,3].

In periodic environments, either the recruitment function or the survival rate is  $p$ -periodically forced. This is modeled with the  $p$ -periodic demographic equation:

$$x_{t+1} = f(t, x_t) + \gamma_t x_t, \quad (2)$$

where  $\exists p \in \mathbb{N}$  such that

$$f(t, x_t) = f(t + p, x_t) \quad \text{and} \quad \gamma_t = \gamma_{t+p} \quad \forall t \in \mathbb{Z}_+.$$

We assume throughout that  $f(t, x_t) \in C^2(\mathbb{Z}_+ \times \mathbb{R}_+, \mathbb{R}_+)$  and  $\gamma_t \in (0, 1)$ .

For example, when new recruits arrive at the constant rate  $\Lambda$  per generation then equation (1) reduces to the simple affine difference equation

$$x_{t+1} = \Lambda + \gamma x_t, \quad (3)$$

and

$$x_t = \left( x_0 - \frac{\Lambda}{1 - \gamma} \right) \gamma^t + \frac{\Lambda}{1 - \gamma}.$$

Hence, the population governed by equation (3) is asymptotically bounded. That is, the equation has a globally attracting fixed point at the carrying capacity  $k = \Lambda/(1 - \gamma)$ . To introduce  $k$  explicitly in the model we replace  $\Lambda$  with  $k(1 - \gamma)$  and obtain

$$x_{t+1} = k(1 - \gamma) + \gamma x_t.$$

When this model is subjected to  $p$ -periodic forcing in either the carrying capacity or survival rate, it becomes

$$x_{t+1} = k_t(1 - \gamma_t) + \gamma_t x_t, \quad (4)$$

where  $\gamma_t = \gamma_{t+p}$ ,  $k_t = k_{t+p}$   $\forall t \in \mathbb{Z}_+$  and  $p > 1$ .

In the next example, new recruits are now governed by the Beverton–Holt model. Consequently, equation (1) reduces to the monotone difference equation

$$x(t + 1) = \frac{\mu Kx(t)}{K + (\mu - 1)x(t)} + \gamma x(t), \tag{5}$$

where  $\mu > 1$ ,  $K > 0$  and  $\gamma \in (0, 1)$ . It is known that equation (5) has a *globally attracting* fixed point at the positive carrying capacity  $k = (\mu - 1 + \gamma)K/((\mu - 1)(1 - \gamma))$  [9,10,19,20,35]. Throughout this paper, globally attracting means “attracting” with respect to all positive initial conditions. To introduce  $k$  explicitly into the model, we replace  $K$  with  $k((\mu - 1)(1 - \gamma))/(\mu - 1 + \gamma)$  and obtain

$$x(t + 1) = \frac{(1 - \gamma)\mu kx(t)}{(1 - \gamma)k + (\mu - 1 + \gamma)x(t)} + \gamma x(t), \tag{6}$$

When this model is subjected to  $p$ -periodic forcing in either the carrying capacity or survival rate, it becomes

$$x(t + 1) = \frac{(1 - \gamma_t)\mu k_t x(t)}{(1 - \gamma_t)k_t + (\mu - 1 + \gamma_t)x(t)} + \gamma_t x(t), \tag{7}$$

where  $\gamma_t = \gamma_{t+p}$ ,  $k_t = k_{t+p} \forall t \in \mathbb{Z}_+$  and  $p > 1$ .

To study the effects of periodic environments on populations described by models (4) and (7), we introduce the following additional notation.

For each  $J \in \{0, 1, 2, \dots, p - 1\}$  define

$$FJ : \mathbb{R}_+ \rightarrow \mathbb{R}_+$$

by

$$FJ(x) = f(J, x) + \gamma_J x.$$

The set of iterates of the  $p$ -periodic dynamical system  $\{F0, F1, \dots, F(p - 1)\}$  is equivalent to the set of density sequences generated by model (2). In models (4) and (7),

$$FJ(x) = k_J(1 - \gamma_J) + \gamma_J x$$

and

$$FJ(x) = \frac{(1 - \gamma_J)\mu k_J x}{(1 - \gamma_J)k_J + (\mu - 1 + \gamma_J)x} + \gamma_J x,$$

respectively. When the recruitment function is either constant or the Beverton–Holt Model,  $FJ$  has a globally attracting positive fixed point, the carrying capacity.

Periodic dynamical systems such as models (4) and (7), usually generate cycles [17,18]. To study the effect of periodic fluctuations on populations governed by models (4) and (7), we use the following definition to compare the average of the cycles with the average of the carrying capacities.

**DEFINITION 1** *A periodic orbit is attenuant (resonant) if its average value is less (greater) than the average of the carrying capacities of the  $FJ$  [7].*

### 3. Constant recruitment function

When the recruitment rate is constant and the environment is not fluctuating, the population governed by model (3) is asymptotically constant [2,3]. However, in a periodic environment, the corresponding population fluctuates [16,30,37]. In this section, we show that it is possible for environmental periodicity to either enhance (resonance) or diminish (attenuance) populations under constant recruitment processes. First, we prove that in periodic environments, populations under constant recruitment functions have a globally attracting cycle,  $\{\bar{x}_0, \bar{x}_1, \dots, \bar{x}_{p-1}\}$ .

**THEOREM 2** *Model (4) has a globally attracting s-periodic cycle that starts at*

$$\bar{x}_0 = \frac{k_{p-1}(1 - \gamma_{p-1}) + \gamma_{p-1}k_{p-2}(1 - \gamma_{p-2}) + \dots + k_0(1 - \gamma_0)\prod_{J=1}^{p-1} \gamma_J}{1 - \prod_{J=0}^{p-1} \gamma_J},$$

where  $s$  divides  $p$

*Proof.*  $F0(x_0) = k_0(1 - \gamma_0) + \gamma_0x_0,$

$$F1 \circ F0(x_0) = k_1(1 - \gamma_1) + \gamma_1(k_0(1 - \gamma_0) + \gamma_0x_0)$$

$$= k_1(1 - \gamma_1) + \gamma_1k_0(1 - \gamma_0) + \gamma_1\gamma_0x_0,$$

and by induction for  $p > 1$

$$F(p - 1) \circ \dots \circ F1 \circ F0(x_0) = k_{p-1}(1 - \gamma_{p-1}) + \gamma_{p-1}k_{p-2}(1 - \gamma_{p-2}) + \dots + k_0(1 - \gamma_0)\prod_{J=1}^{p-1} \gamma_J + x_0\prod_{J=0}^{p-1} \gamma_J.$$

The fixed point of  $F(p - 1) \circ \dots \circ F1 \circ F0$ , which is also the initial point of a periodic cycle of model (4) is

$$\bar{x}_0 = \frac{k_{p-1}(1 - \gamma_{p-1}) + \gamma_{p-1}k_{p-2}(1 - \gamma_{p-2}) + \dots + k_0(1 - \gamma_0)\prod_{J=1}^{p-1} \gamma_J}{1 - \prod_{J=0}^{p-1} \gamma_J}.$$

Since  $F(p - 1) \circ \dots \circ F1 \circ F0$  is affine with slope  $0 < \prod_{J=0}^{p-1} \gamma_J < 1$ , its fixed point is globally attracting. Hence, the cycle is globally attracting and by a result of Elaydi and Sacker [11–14], the period must be a divisor of  $p$ . □

The length of the globally attracting cycle predicted by Theorem (2) can be any divisor of  $p$ . In the following example, we illustrate a globally attracting 2-cycle in a 4-periodic environment.

*Example 3* In model (4), set the following parameter values:

$$k_0 = 1, \quad k_1 = 2, \quad k_2 = 359/364, \quad k_3 = 2$$

$$\gamma_0 = 1/10, \quad \gamma_1 = 9/10, \quad \gamma_2 = 2/10, \quad \gamma_3 = 9/10.$$

The 4-periodic example has a globally attracting 2-cycle at  $\{101/91, 92/91\}$

We use the following bounds on the average of the periodic orbit to study the impact of periodic environments on populations governed by model (4).

**THEOREM 4** *In model (4),*

$$\frac{1 - \max\{\gamma_J\}}{1 - \min\{\gamma_J\}} \sum_{J=0}^{p-1} k_J \leq \sum_{J=0}^{p-1} \bar{x}_J \leq \frac{1 - \min\{\gamma_J\}}{1 - \max\{\gamma_J\}} \sum_{J=0}^{p-1} k_J.$$

*Proof.* Let  $k_J = k_{J \bmod p}$  and  $\gamma_J = \gamma_{J \bmod p}$ . Then  $\bar{x}_{J+1} = k_J(1 - \gamma_J) + \gamma_J \bar{x}_J$  for all  $J$ . Since  $\bar{x}_J$  is  $p$ -periodic,  $\sum_{J=0}^{p-1} \bar{x}_J = \sum_{J=0}^{p-1} (k_J(1 - \gamma_J) + \gamma_J \bar{x}_J) = \sum_{J=0}^{p-1} k_J(1 - \gamma_J) + \sum_{J=0}^{p-1} \gamma_J \bar{x}_J$ . Hence,

$$(1 - \max\{\gamma_J\}) \sum_{J=0}^{p-1} k_J + \min\{\gamma_J\} \sum_{J=0}^{p-1} \bar{x}_J \leq \sum_{J=0}^{p-1} \bar{x}_J \leq (1 - \min\{\gamma_J\}) \sum_{J=0}^{p-1} k_J + \max\{\gamma_J\} \sum_{J=0}^{p-1} \bar{x}_J.$$

Hence,

$$\frac{1 - \max\{\gamma_J\}}{1 - \min\{\gamma_J\}} \sum_{J=0}^{p-1} k_J \leq \sum_{J=0}^{p-1} \bar{x}_J \leq \frac{1 - \min\{\gamma_J\}}{1 - \max\{\gamma_J\}} \sum_{J=0}^{p-1} k_J.$$

□

**COROLLARY 5** *In model (4), if  $\min\{\gamma_J\} = \max\{\gamma_J\}$ , then  $\sum_{J=0}^{p-1} \bar{x}_J = \sum_{J=0}^{p-1} k_J$  and the periodic cycle is neither attenuant nor resonant.*

In Corollary (5), the survival rate is non-fluctuating while the carrying capacity is fluctuating. In this situation, the average total biomass remains the same as the average carrying capacity. Also, when the survival rate is fluctuating while the carrying capacity is constant  $k$  (non-fluctuating) in Theorem 2, by starting with initial population size  $x_0 = k$  it is easy to see that the globally attracting cycle is the constant carrying capacity. Consequently, the total biomass remains constant.

To illustrate the combined impact of periodic environments and fluctuating survival rates on the average biomass, we restrict ourselves to oscillations of period 2. Let

$$R_d = \frac{k_0 \gamma_1 + k_1 \gamma_0}{k_0 \gamma_0 + k_1 \gamma_1}.$$

For each  $J \in \{0, 1\}$ , when the population is at the carrying capacity  $k_J$ ,  $k_J \gamma_J$  is the population that survives a generation in the constant environment described by  $FJ$ . Similarly,  $k_J \gamma_{J+1}$  is the population that survives a generation in the varying environment described by  $F(J + 1)$ . The threshold parameter,  $R_d$  gives the effective ratio of the average survivors in the varying vs constant environments.

$R_d < 1$  is equivalent to  $(k_0 - k_1)(-\gamma_0 + \gamma_1) < 0$ . Consequently,  $R_d < 1$  when the carrying capacity and survival rate are oscillating in synchrony and  $R_d > 1$  when they are asynchronous. The next theorem shows that, if  $R_d < 1$  then the globally attracting cycle is attenuant and the periodic environment is detrimental to the population. However, if

$R_d > 1$  then the cycle is resonant and the periodic environment is beneficial to the population.

**THEOREM 6** *Model (4) with  $p = 2$  has a globally attracting attenuant cycle if*

$$(k_0 - k_1)(-\gamma_0 + \gamma_1) < 0,$$

*and a globally attracting resonant cycle if*

$$(k_0 - k_1)(-\gamma_0 + \gamma_1) > 0.$$

*That is, Model (4) with  $p = 2$  has a globally attracting attenuant cycle when the carrying capacity and survival rate are oscillating in synchrony, and a globally attracting resonant cycle if they are asynchronous.*

*Proof.*

$$\begin{aligned} \bar{x}_0 + \bar{x}_1 &= \frac{k_1(1 - \gamma_1) + k_0(1 - \gamma_0)\gamma_1}{1 - \gamma_0\gamma_1} + \frac{k_0(1 - \gamma_0) + k_1(1 - \gamma_1)\gamma_0}{1 - \gamma_0\gamma_1} \\ &= \frac{k_0(1 - \gamma_0)(1 + \gamma_1) + k_1(1 - \gamma_1)(1 + \gamma_0)}{1 - \gamma_0\gamma_1}. \end{aligned}$$

To check for attenuance and resonance,

$$\begin{aligned} \bar{x}_0 + \bar{x}_1 - (k_0 + k_1) &= \frac{k_0(1 - \gamma_0)(1 + \gamma_1) + k_1(1 - \gamma_1)(1 + \gamma_0)}{1 - \gamma_0\gamma_1} - (k_0 + k_1) \\ &= \frac{k_0(1 - \gamma_0)(1 + \gamma_1) + k_1(1 - \gamma_1)(1 + \gamma_0) - (k_0 + k_1)(1 - \gamma_0\gamma_1)}{1 - \gamma_0\gamma_1} \\ &= \frac{k_0(-\gamma_0 + \gamma_1) + k_1(-\gamma_1 + \gamma_0)}{1 - \gamma_0\gamma_1}. \end{aligned}$$

Since  $1 - \gamma_0\gamma_1 > 0$ , resonance is equivalent to

$$\begin{aligned} k_0(-\gamma_0 + \gamma_1) + k_1(-\gamma_1 + \gamma_0) &> 0 \\ \Leftrightarrow k_0\gamma_1 + k_1\gamma_0 &> k_0\gamma_0 + k_1\gamma_1 \\ \Leftrightarrow R_d = \frac{k_0\gamma_1 + k_1\gamma_0}{k_0\gamma_0 + k_1\gamma_1} &> 1. \end{aligned}$$

A similar argument establishes attenuance is equivalent to

$$R_d < 1.$$

□

#### 4. Monotone recruitment function

The Beverton–Holt Model is a pioneer, monotone function. To capture this in the general model, model (2), we introduce the following definition. We say that the recruitment function,  $f(t,x)$  is a *pioneer function* when  $f(t,0) = 0$  and  $\partial f(t,0)/\partial x > 1$  for all  $t$  [17,18]. In this section, we show that when all the recruitment functions are increasing, concave down,

bounded, pioneer functions, then the  $p$ -periodic demographic system has a global attracting positive cycle. This shows that the Beverton–Holt Model with survivors per generation supports a globally attracting cycle. Cushing and Henson [7], Kon [28,29], Kocic [26], Elaydi and Sacker [11–14] have obtained this result for the classic Beverton–Holt Model without survivors ( $\gamma_t = 0$ ).

LEMMA 7 *If  $G, H \in C^1(\mathbb{R}_+, \mathbb{R}_+)$  with  $\lim_{x \rightarrow \infty} G'(x)/\alpha = \lim_{x \rightarrow \infty} H'(x)/\beta = 1$ , then  $\lim_{x \rightarrow \infty} (H \circ G)(x)/\alpha\beta x = 1$ , where  $\alpha$  and  $\beta$  are non-zero constants.*

*Proof.* If  $\alpha$  were negative,  $G(x)$  would become negative for large  $x$ . But since we are assuming that  $G(x)$  is never negative,  $\alpha$  and similarly  $\beta$  must be positive. Note,  $\lim_{x \rightarrow \infty} G(x) = \lim_{x \rightarrow \infty} H(x) = \lim_{x \rightarrow \infty} (H \circ G)(x) = +\infty$ . Applying L’hopital’s Rule gives

$$\lim_{x \rightarrow \infty} \frac{(H \circ G)(x)}{\alpha\beta x} = \lim_{x \rightarrow \infty} \frac{H'(G(x))G'(x)}{\alpha\beta} = 1.$$

□

THEOREM 8 *If the recruitment functions of  $x$  for each  $t$ ,  $f(t, x)$  are increasing, concave down, bounded, pioneer functions, then the  $p$  periodic demographic system, model (2), has a globally attracting positive  $s$ -cycle, where  $s$  divides  $p$ .*

*Proof.* Since each  $\gamma_J \in (0, 1)$ , each  $FJ$  is an increasing, concave down, pioneer function and  $\lim_{x \rightarrow \infty} FJ(x)/\gamma_J x = \lim_{x \rightarrow \infty} (f(J, x) + \gamma_J x)/\gamma_J x = 1$ . Hence, the graph of  $FJ$  crosses the diagonal at exactly one positive point. This positive point is a globally attracting fixed point for  $FJ$  on  $(0, \infty)$ .

Using the Chain Rule on the composition map  $F(p - 1) \circ \dots \circ F1 \circ F0$  shows that it is an increasing, concave down, pioneer function. Applying induction to Lemma (7) gives  $\lim_{x \rightarrow \infty} ((F(p - 1) \circ \dots \circ F1 \circ F0)(x))/x \prod_{j=0}^{p-1} \gamma_j = 1$ . So as in the previous paragraph,  $F(p - 1) \circ \dots \circ F1 \circ F0$  has a unique attracting positive fixed point,  $\bar{x}_0$ . Now,  $\bar{x}_0$  is the initial point on the unique globally attracting  $s$ -cycle for the  $p$ -periodic demographic system, model (2). Elaydi and Sacker [11–14] showed that the period of the cycle,  $s$ , must divide  $p$ . □

Theorem (8) is a corollary of the general result of Elaydi and Sacker in [4]. Since the recruitment function in model (7) is an increasing, concave down, bounded, pioneer function. Theorem (8) implies the following corollary.

COROLLARY 9 *Model (7) has a globally attracting  $s$ -cycle, where  $s$  divides  $p$ .*

### 5. Attenuant cycles with Beverton–Holt recruitment

Cushing and Henson showed that a 2-periodic environment is always deleterious for populations governed by the classic Beverton–Holt model [7]. Kon [28,29], Kocic [26], Elaydi and Sacker [13,14] have since extended this result to include  $p$ —periodic Beverton–Holt models without survivors ( $\gamma = 0$ ). With survivors ( $\gamma \neq 0$ ), periodic environments

are not always deleterious for populations governed by the Beverton–Holt Model. However, when the carrying capacity is fluctuating and the survival rate is not fluctuating we show via the presence of a globally attracting attenuant cycle that periodic environments are always disadvantageous for our population.

**THEOREM 10** *If the survival rate is non-oscillatory, then the global attracting cycle of model (7) is attenuant.*

*Proof.* By Corollary (9), model (7) has a globally attracting cycle. Since all the  $\gamma_J$  are the same let  $\gamma$  be the common value. Let  $\{\bar{x}_0, \bar{x}_1, \dots, \bar{x}_{p-1}\}$  be the globally attracting cycle for model (7). Note that

$$\bar{x}_{J+1} = \frac{(1 - \gamma_J)\mu k_J \bar{x}_J}{(1 - \gamma_J)k_J + (\mu - 1 + \gamma_J)\bar{x}_J} + \gamma_J \bar{x}_J.$$

The sum of the  $\bar{x}_J$  is

$$\begin{aligned} \sum_{J=0}^{p-1} \bar{x}_J &= \sum_{J=0}^{p-1} \bar{x}_{J+1} = \sum_{J=0}^{p-1} \frac{(1 - \gamma)\mu k_J \bar{x}_J}{(1 - \gamma)k_J + (\mu - 1 + \gamma)\bar{x}_J} + \gamma \bar{x}_J \\ &= \sum_{J=0}^{p-1} \frac{\frac{(1-\gamma)\mu k_J}{(\mu-1+\gamma)} \frac{(\mu-1+\gamma)}{(1-\gamma)k_J} \bar{x}_J}{1 + \frac{(\mu-1+\gamma)}{(1-\gamma)k_J} \bar{x}_J} + \sum_{J=0}^{p-1} \gamma \bar{x}_J \\ &= \sum_{J=0}^{p-1} \frac{(1 - \gamma)\mu k_J}{(\mu - 1 + \gamma)} h\left(\frac{(\mu - 1 + \gamma)}{(1 - \gamma)k_J} \bar{x}_J\right) + \sum_{J=0}^{p-1} \gamma \bar{x}_J, \end{aligned}$$

where  $h(x) = x/(1 + x)$ . The function  $h$  is concave down and satisfies Jensen’s inequality:

$$h\left(\frac{\sum_{J=0}^{p-1} w_J u_J}{\sum_{J=0}^{p-1} w_J}\right) > \frac{\sum_{J=0}^{p-1} w_J h(u_J)}{\sum_{J=0}^{p-1} w_J}.$$

Letting

$$w_J = \frac{(1 - \gamma)\mu k_J}{(\mu - 1 + \gamma)},$$

$$u_J = \frac{(\mu - 1 + \gamma)}{(1 - \gamma)k_J} \bar{x}_J$$

and applying Jensen’s inequality we obtain

$$\begin{aligned} \sum_{J=0}^{p-1} \bar{x}_J &< \sum_{J=0}^{p-1} \frac{(1-\gamma)\mu k_J}{(\mu-1+\gamma)} h\left(\frac{\sum_{J=0}^{p-1} \frac{(1-\gamma)\mu k_J (\mu-1+\gamma)}{(\mu-1+\gamma)} \bar{x}_J}{\sum_{J=0}^{p-1} \frac{(1-\gamma)\mu k_J}{(\mu-1+\gamma)}}\right) + \sum_{J=0}^{p-1} \gamma \bar{x}_J \\ &= \sum_{J=0}^{p-1} \frac{(1-\gamma)\mu k_J}{(\mu-1+\gamma)} \frac{\frac{\sum_{J=0}^{p-1} \mu \bar{x}_J}{\sum_{J=0}^{p-1} \frac{(1-\gamma)\mu k_J}{(\mu-1+\gamma)}}}{1 + \frac{\sum_{J=0}^{p-1} \mu \bar{x}_J}{\sum_{J=0}^{p-1} \frac{(1-\gamma)\mu k_J}{(\mu-1+\gamma)}}} + \sum_{J=0}^{p-1} \gamma \bar{x}_J \\ &= \sum_{J=0}^{p-1} \frac{(1-\gamma)\mu k_J}{(\mu-1+\gamma)} \frac{\sum_{J=0}^{p-1} \mu \bar{x}_J}{\sum_{J=0}^{p-1} \frac{(1-\gamma)\mu k_J}{(\mu-1+\gamma)} + \sum_{J=0}^{p-1} \mu \bar{x}_J} + \sum_{J=0}^{p-1} \gamma \bar{x}_J \end{aligned}$$

Then

$$(1-\gamma) \sum_{J=0}^{p-1} \bar{x}_J < \sum_{J=0}^{p-1} \frac{(1-\gamma)\mu k_J}{(\mu-1+\gamma)} \frac{\mu \sum_{J=0}^{p-1} \bar{x}_J}{\sum_{J=0}^{p-1} \frac{(1-\gamma)\mu k_J}{(\mu-1+\gamma)} + \mu \sum_{J=0}^{p-1} \bar{x}_J}$$

So,

$$\begin{aligned} (1-\gamma) &< \sum_{J=0}^{p-1} \frac{(1-\gamma)\mu k_J}{(\mu-1+\gamma)} \frac{1}{\sum_{J=0}^{p-1} \frac{(1-\gamma)k_J}{(\mu-1+\gamma)} + \sum_{J=0}^{p-1} \bar{x}_J} \\ &\Leftrightarrow \left(\sum_{J=0}^{p-1} \frac{(1-\gamma)k_J}{(\mu-1+\gamma)} + \sum_{J=0}^{p-1} \bar{x}_J\right) < \sum_{J=0}^{p-1} \frac{\mu k_J}{(\mu-1+\gamma)} \\ &\Leftrightarrow \sum_{J=0}^{p-1} \bar{x}_J < \sum_{J=0}^{p-1} \frac{\mu k_J}{(\mu-1+\gamma)} - \sum_{J=0}^{p-1} \frac{(1-\gamma)k_J}{(\mu-1+\gamma)} = \sum_{J=0}^{p-1} k_J. \end{aligned}$$

Thus, the globally attracting cycle is attenuant. □

The above proof actually shows a bit more than

$$\frac{1}{p} \sum_{J=0}^{p-1} \bar{x}_J < \frac{1}{p} \sum_{J=0}^{p-1} \bar{k}_J$$

(i.e. attenuation). Since the period of the cycle is  $s$ , where  $p = rs$ , and since the average of an  $s$ -cycle should be taken only over  $s$  terms, not  $p$  terms, the proof shows that

$$\frac{1}{s} \sum_{J=0}^{s-1} \bar{x}_J = \frac{1}{p} \sum_{J=0}^{p-1} \bar{x}_J < \frac{1}{p} \sum_{J=0}^{p-1} k_J.$$

### 6. Resonant cycles with Beverton–Holt recruitment

Models under the periodic Beverton–Holt recruitment are capable of experiencing the resonance effect when both the survival rate and the carrying capacity are fluctuating. In this section, we use two examples to demonstrate resonance in these models. In the following example, Example 11, the survival rate and the carrying capacity are fluctuating out of phase.

*Example 11* In model (7), set the following restrictions on the parameter values:

$$\mu > 2, \quad p = 2, \quad \text{and} \quad \gamma_0 - \gamma_1 = \frac{-4}{(\mu - 2)} \frac{k_0 - k_1}{k_0 + k_1}.$$

Example 11 supports a globally attracting resonant cycle when  $|k_0 - k_1|$  is small (Proposition 12). The proof of this result is in the spirit of the methods in [21]. However, the general perturbation results in [21] cannot be applied because they allow only one parameter to vary periodically.

**PROPOSITION 12** *Example 11 has a globally attracting resonant cycle if  $|k_0 - k_1|$  is small enough.*

*Proof.* Let  $\alpha = (k_0 - k_1)/2$ ,  $k = (k_0 + k_1)/2$ , and  $\gamma = (\gamma_0 + \gamma_1)/2$ . Then  $k_0 = k + \alpha$ ,  $k_1 = k - \alpha$ ,  $\gamma_0 = \gamma - (2\alpha)/((\mu - 2)k)$ , and  $\gamma_1 = \gamma + (2\alpha)/((\mu - 2)k)$ .

$$F0 = \frac{\left(1 - \gamma + \frac{2\alpha}{(\mu - 2)k}\right)\mu(k + \alpha)x}{\left(1 - \gamma + \frac{2\alpha}{(\mu - 2)k}\right)(k + \alpha) + \left(\mu - 1 + \gamma - \frac{2\alpha}{(\mu - 2)k}\right)x} + \left(\gamma - \frac{2\alpha}{(\mu - 2)k}\right)x,$$

and

$$F1 = \frac{\left(1 - \gamma - \frac{2\alpha}{(\mu - 2)k}\right)\mu(k - \alpha)x}{\left(1 - \gamma - \frac{2\alpha}{(\mu - 2)k}\right)(k - \alpha) + \left(\mu - 1 + \gamma + \frac{2\alpha}{(\mu - 2)k}\right)x} + \left(\gamma + \frac{2\alpha}{(\mu - 2)k}\right)x.$$

When  $x = k$  and  $\alpha = 0$ ,

$$\frac{\partial F0}{\partial x} = \frac{\partial F1}{\partial x} = \frac{1 - 2\gamma + \gamma\mu + \gamma^2}{\mu} \neq 1.$$

Recall that  $k$  is a fixed point for both  $F0$  and  $F1$ . By the Implicit Function Theorem, the equation  $F1(F0(x)) = x$  can be solved for  $x$  in terms of  $\alpha$  in a neighborhood of  $(x, \alpha) = (k, 0)$ . Note that the solution,  $\bar{x}_0$ , is the initial point of the unique globally attracting 2-cycle predicted by Corollary (9). Since  $F1(F0(x)) - x$  is locally analytic in  $x$  and  $\alpha$ ,  $\bar{x}_0(\alpha)$  has a convergent power series in  $\alpha$ . Let

$$\bar{x}_0(\alpha) = k + x_1(0)\alpha + x_2(0)\alpha^2 + 0(\alpha^3)$$

be this power series. The second point on the globally attracting 2-cycle is

$$\bar{x}_1(\alpha) = F0(\bar{x}_0(\alpha)).$$

Let the convergent power series for

$$\bar{x}_1(\alpha) = k + x_1(1)\alpha + x_2(1)\alpha^2 + 0(\alpha^3).$$

Hence,

$$\bar{x}_0(\alpha) + \bar{x}_1(\alpha) = 2k + (x_1(0) + x_1(1))\alpha + (x_2(0) + x_2(1))\alpha^2 + 0(\alpha^3).$$

To show this 2-cycle is resonant when  $\alpha$  is small, we will show that

$$x_1(0) + x_1(1) = 0, \quad \text{and} \quad x_2(0) + x_2(1) > 0.$$

Since

$$k + x_1(1)\alpha + x_2(1)\alpha^2 + 0(\alpha^3) = F0(\bar{x}_0(\alpha))$$

and

$$k + x_1(0)\alpha + x_2(0)\alpha^2 + 0(\alpha^3) = F1(\bar{x}_1(\alpha)),$$

$$x_1(1) = \left. \frac{\partial}{\partial \alpha} F0(\bar{x}_0(\alpha)) \right|_{\alpha=0} = \frac{\mu - \gamma\mu - \gamma^2 + 2\gamma - 1 + (1 - 2\gamma + \gamma\mu + \gamma^2)x_1(0)}{\mu}$$

and

$$x_1(0) = \left. \frac{\partial}{\partial \alpha} F1(\bar{x}_1(\alpha)) \right|_{\alpha=0} = \frac{-\mu + \gamma\mu + \gamma^2 - 2\gamma + 1 + (1 - 2\gamma + \gamma\mu + \gamma^2)x_1(1)}{\mu}.$$

Hence,

$$x_1(1) + x_1(0) = \frac{1 - 2\gamma + \gamma\mu + \gamma^2}{\mu} (x_1(1) + x_1(0)).$$

As mentioned earlier,  $(1 - 2\gamma + \gamma\mu + \gamma^2)/\mu \neq 1$ . Thus,

$$x_1(1) + x_1(0) = 0 \quad \text{or} \quad x_1(1) = -x_1(0).$$

Furthermore,

$$x_2(1) = \left. \frac{1}{2} \frac{\partial^2}{\partial \alpha^2} F0(\bar{x}_0(\alpha)) \right|_{\alpha=0}$$

and

$$x_2(0) = \left. \frac{1}{2} \frac{\partial^2}{\partial \alpha^2} F1(\bar{x}_1(\alpha)) \right|_{\alpha=0}.$$

Explicit expressions for  $x_2(1)$  and  $x_2(0)$ , found in Appendix A, contain  $x_1(1)$  and  $x_1(0)$ . The Implicit Function Theorem on  $F1(F0(x)) - x$  gives

$$\frac{d\bar{x}_0(\alpha)}{d\alpha} = - \frac{\frac{\partial(F1(F0(x))-x)}{\partial \alpha}}{\frac{\partial(F1(F0(x))-x)}{\partial x}}.$$

Evaluating at  $(x, \alpha) = (k, 0)$  gives

$$x_1(0) = \frac{(\gamma - 1)(\mu - 1 + \gamma)}{\gamma\mu + \mu - 2\gamma + 1 + \gamma^2}.$$

Using  $x_1(1) = -x_1(0)$  and the formulas in Appendix A, we obtain

$$x_2(0) + x_2(1) =$$

$$\frac{8\mu\{(\gamma - 3)\gamma\mu^2 + (\gamma^3 - 8\gamma^2 + 9\gamma - 2)\mu + 4(1 - \gamma^3)\}}{(\gamma\mu + \mu - 2\gamma + 1 + \gamma^2)^2 k(\mu - 2)(\gamma - 1)(\mu - 1 + \gamma)}.$$

Since  $\mu > 2$  and  $0 < \gamma < 1$  the denominator is negative. To determine the sign of the numerator, note that

$$\Omega(\mu, \gamma) = (\gamma - 3)\gamma\mu^2 + (\gamma^3 - 8\gamma^2 + 9\gamma - 2)\mu + 4(1 - \gamma^3)$$

is a quadratic in  $\mu$  and cubic in  $\gamma$ .  $\Omega(0, \gamma) = 4(1 - \gamma^3) > 0$  and  $\Omega(2, \gamma) = 4(\gamma - 3)\gamma + 2(\gamma^3 - 8\gamma^2 + 9\gamma - 2) + 4(1 - \gamma^3)$  is decreasing on  $[0, 1]$  and  $\Omega(2, 0) = 0$ . Hence,  $\Omega(\mu, \gamma) < 0$  when  $\mu > 2$  and  $0 < \gamma < 1$ . Thus,

$$x_2(0) + x_2(1) > 0$$

and the globally attracting 2-cycle is resonant when  $\alpha$  is small enough. □

In the next example, Example 13, the survival and carrying capacity oscillations are in phase.

*Example 13* In model (7), set the following restrictions on the parameter values:

$$\mu = 1.1, \quad p = 2, \quad \gamma_0 + \gamma_1 = 0.4 \quad \text{and} \quad \frac{\gamma_0 - \gamma_1}{\gamma_0 + \gamma_1} = 40 \frac{k_0 - k_1}{k_0 + k_1}.$$

**PROPOSITION 14** *Example 13 has a globally attracting resonant cycle if  $|k_0 - k_1|$  is small enough.*

The proof of Proposition 14 is similar to that of Proposition 12 and is omitted.

For the classic Beverton–Holt Model (with survival term absent), it was shown in Corollary 6.5 of [13] that the minimal period of the globally asymptotically stable periodic solution is equal to the minimal period of the equation. In Examples 11 and 13, this result is true with the survival term present.

## 7. Conclusion

In the advent of either a periodic carrying capacity or survival rate, our population models support globally attracting cycles. We focus on the combined effects of periodically varying carrying capacity and survival probability on the average of the globally attracting cycles. Results of Coleman [4], Coleman and Frauenthal [5], Nisbet and Gurney [35] and Rosenblat [36] on the continuous-time logistic equation implied that a periodic carrying capacity is deleterious. Cushing [7] and Rosenblat [36] have since shown that this assertion is model dependent. Cushing and Henson showed that a period-2 environment is always deleterious (attenuant cycles) for populations modeled by a class of monotone difference equations such as the classic Beverton–Holt Model [7]. In [8], they conjectured the deleterious attenuation effect for any periodic environment. This conjecture touched off a flurry of papers [11–14,26,28,29].

Our results support the prediction of attenuant cycles when the recruitment function is described by the periodic Beverton–Holt Model and the survival rate is non-fluctuating. In periodic environments, when each recruitment rate is a constant and the survival rate is non-fluctuating, then the system’s globally attracting cycle is neither attenuant nor resonant.

However, when both the carrying capacity and survival rate are fluctuating, then the oscillatory final outcome is attenuant when the fluctuations are in synchrony and resonant when they are asynchronous.

Population models with more than one periodically varying parameters are capable of supporting attenuant and resonant cycles. Henson used a “contour method” in 2-periodic systems to derive conditions for attenuation and resonance of oscillatory solutions in models with a single periodically varying parameter [22]. Studies on conditions that predict when attracting cycles are either resonant or attenuant in general population models with multiple periodically varying parameters would be welcome [38].

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**Appendix A**

In this appendix, we provide the two technical formulas that were used in the proof of Proposition 12. In Proposition 12,

$$F0 = \frac{\left(1 - \gamma + \frac{2\alpha}{(\mu-2)k}\right)\mu(k + \alpha)x}{\left(1 - \gamma + \frac{2\alpha}{(\mu-2)k}\right)(k + \alpha) + \left(\mu - 1 + \gamma - \frac{2\alpha}{(\mu-2)k}\right)x} + \left(\gamma - \frac{2\alpha}{(\mu - 2)k}\right)x,$$

and

$$F1 = \frac{\left(1 - \gamma - \frac{2\alpha}{(\mu-2)k}\right)\mu(k - \alpha)x}{\left(1 - \gamma - \frac{2\alpha}{(\mu-2)k}\right)(k - \alpha) + \left(\mu - 1 + \gamma + \frac{2\alpha}{(\mu-2)k}\right)x} + \left(\gamma + \frac{2\alpha}{(\mu - 2)k}\right)x.$$

Hence,

$$\begin{aligned} x_2(1) &= \frac{1}{2} \frac{\partial^2}{\partial \alpha^2} F0(\bar{x}_0(\alpha)) \Big|_{\alpha=0} = \\ &-((2k\mu - k\mu^2 - 4k\gamma\mu - k\mu^3\gamma + 4k\mu^2\gamma + 2k\gamma^2\mu - k\gamma^2\mu^2)x_2(0) - 5\gamma^2\mu - 2\gamma\mu^2 \\ &+ 3\gamma\mu - 12x_1(0)\gamma^2 + \gamma^2\mu^2 - 6x_1(0)^2\gamma + 6x_1(0)^2\gamma^2 + 4x_1(0)\gamma^3 - 2x_1(0)^2\gamma^3 + \gamma^3\mu \\ &+ 4x_1(0)\mu^2\gamma + 10x_1(0)\gamma^2\mu - 2x_1(0)\gamma^2\mu^2 - 2x_1(0)^2\mu^2\gamma + 7x_1(0)^2\mu\gamma + x_1(0)^2\mu^2\gamma^2 \\ &- 10\mu x_1(0)\gamma + 2 + 12x_1(0)\gamma + -\mu^2 + x_1(0)^2\mu^2 - 3x_1(0)^2\mu + 2x_1(0)^2 + 2x_1(0)\mu \\ &- 2\gamma^3 - 4x_1(0) - 2x_1(0)\gamma^3\mu + \mu - 6\gamma + 6\gamma^2 - 5x_1(0)^2\mu\gamma^2 \\ &+ x_1(0)^2\gamma^3\mu)/(\mu - 2)k\mu^2 \end{aligned}$$

and

$$\begin{aligned}
 x_2(0) = \frac{1}{2} \frac{\partial^2}{\partial \alpha^2} F1(\bar{x}_1(\alpha)) \Big|_{\alpha=0} = & \\
 -((2k\mu - k\mu^2 - 4k\gamma\mu - k\mu^3\gamma + 4k\mu^2\gamma + 2k\gamma^2\mu - k\gamma^2\mu^2)x_2(1) - 5\gamma^2\mu - 2\gamma\mu^2 & \\
 + 3\gamma\mu - 12x_1(1)\gamma^2 + \gamma^2\mu^2 - 6x_1(1)^2\gamma + 6x_1(1)^2\gamma^2 + 4x_1(1)\gamma^3 - 2x_1(1)^2\gamma^3 + \gamma^3\mu & \\
 + 4x_1(1)\mu^2\gamma + 10x_1(1)\gamma^2\mu - 2x_1(1)\gamma^2\mu^2 - 2x_1(1)^2\mu^2\gamma + 7x_1(1)^2\mu\gamma + x_1(1)^2\mu^2\gamma^2 & \\
 - 10\mu x_1(1)\gamma + 2 + 12x_1(1)\gamma + -\mu^2 + x_1(1)^2\mu^2 - 3x_1(1)^2\mu + 2x_1(1)^2 + 2x_1(1)\mu & \\
 - 2\gamma^3 - 4x_1(1) - 2x_1(1)\gamma^3\mu + \mu - 6\gamma + 6\gamma^2 - 5x_1(1)^2\mu\gamma^2 & \\
 + x_1(1)^2\gamma^3\mu)/(\mu - 2)k\mu^2. &
 \end{aligned}$$

Since the coefficients of the  $x_2(0)$  and  $x_2(1)$  on the right hand side are the same, we can add the two equations and solve for  $x_2(0) + x_2(1)$ .

**Appendix B**

In this appendix, we provide the technical formulas that were used in the proof of Proposition 14. In Proposition 14,

$$F0 = \frac{1.1(0.8 + 8\frac{\alpha}{k})(k + \alpha)x}{(0.8 - 8\frac{\alpha}{k})(k + \alpha) + (0.3 + 8\frac{\alpha}{k})x} + \left(0.2 + 8\frac{\alpha}{k}\right)x,$$

and

$$F1 = \frac{1.1(0.8 + 8\frac{\alpha}{k})(k - \alpha)x}{(0.8 + 8\frac{\alpha}{k})(k - \alpha) + (0.3 + 8\frac{\alpha}{k})x} + \left(0.2 - 8\frac{\alpha}{k}\right)x.$$

$$x_1(1) = \frac{\partial}{\partial \alpha} F0(\bar{x}_0(\alpha)) \Big|_{\alpha=0} = 0.7818181818x_1(0) + 0.2181818182$$

and

$$x_1(0) = \frac{\partial}{\partial \alpha} F1(\bar{x}_1(\alpha)) \Big|_{\alpha=0} = 0.7818181818x_1(1) - 0.2181818182.$$

Hence,

$$x_1(1) + x_1(0) = 0.7818181818(x_1(1) + x_1(0))$$

and

$$x_1(1) = -x_1(0).$$

$$\begin{aligned}
 x_2(1) = \frac{1}{2} \frac{\partial^2}{\partial \alpha^2} F0(\bar{x}_0(\alpha)) \Big|_{\alpha=0} & \\
 = 0.7818181818x_2(0) - \frac{3.319008264x_1(0)}{k} + \frac{3.477685950}{k} - \frac{0.1586776860(x_1(0))^2}{k} &
 \end{aligned}$$

and

$$\begin{aligned} x_2(0) &= \frac{1}{2} \frac{\partial^2}{\partial \alpha^2} F1(\bar{x}_1(\alpha)) \Big|_{\alpha=0} \\ &= 0.7818181818x_2(1) - \frac{3.319008264x_1(1)}{k} + \frac{3.477685950}{k} - \frac{0.1586776860(x_1(1))^2}{k}. \end{aligned}$$

Since the coefficients of the  $x_2(0)$  and  $x_2(1)$  on the right hand side are the same, we can add the two equations and solve for  $x_2(0) + x_2(1)$ .

Since

$$x_1(0) = \frac{d\bar{x}_0(\alpha)}{d\alpha} \Big|_{(k, 0)} = - \frac{\frac{\partial(F1(F0(x))-x)}{\partial \alpha}}{\frac{\partial(F1(F0(x))-x)}{\partial x}} \Big|_{(k, 0)},$$

$$x_1(0) = -0.12245.$$

This gives

$$x_2(0) + x_2(1) = \frac{35.5824}{k} > 0.$$