Globally Attracting Attenuant Versus Resonant Cycles In Periodic Compensatory Leslie Models

John E. Franke
Department of Mathematics
North Carolina State University
Raleigh, NC 27695-8205
e-mail: franke@math.ncsu.edu
and

Abdul-Aziz Yakubu
Department of Mathematics
Howard University
Washington, DC 20059
e-mail: ayakubu@howard.edu

April 10, 2006

Abstract

We use a periodically forced density-dependent compensatory Leslie model to study the combined effects of environmental fluctuations and age-structure on pioneer populations. In constant environments, the models have globally attracting positive fixed points. However, with the advent of periodic forcing, the models have globally attracting cycles. We derive conditions under which the cycle is attenuant, resonant, and neither attenuant nor resonant. These results show that the response of age-structured populations to environmental fluctuations is a complex function of the compensatory mechanisms at different life-history stages, the fertile age classes and the period of the environment.

1 Introduction

Environmental fluctuations are common in nature, and they play an important role in regulating populations. Cyclic fluctuations, like the cycles of the seasons, and the light and dark periods within a day, are caused by annual or daily fluctuations in the physical environment [1, 5, 26, 43, 46]. Many studies have focused on whether or not a population is adversely affected by a periodic environment relative to a constant environment [3, 4, 6, 8, 11-14, 18-20, 30-32]. Under what biological conditions is the average of the resulting oscillations in the periodic environment less (greater) than the average of the carrying capacity in a corresponding constant environment? For example, the scalar continuous-time logistic differential equation and the discrete-time Beverton-Holt population model without age-structure have been used to show a decrease in the average population size with the advent of periodic forcing (attenuance). These results are known to be model-dependent [8, 24, 25]. The experiments of Jillson with a periodic food supply resulted in oscillations in population size of the flour beetle (*Tribolium*). In the alternating habitat, the total population numbers observed were more than twice those in the constant habitat even though the average flour volume was the same in both environments [29] (resonance). Henson and Cushing [27], Costantino *et al.* [5] and Henson *et al.* [26] have since explained Jillson's observations. In [5, 26, 27, 29], mathematical analysis and laboratory experiments were used to demonstrate that it is possible for a periodic environment to be advantageous for a population.

In this paper, we use a periodically forced nonlinear density-dependent Leslie model to study the combined effects of environmental fluctuations and age-structure on population sizes. Since the introduction of the Leslie matrix discrete-time models in the classic work of Leslie [34, 35] and Lewis [37], nonlinear Leslie models have been extensively used in a variety of studies. Some examples include Caswell [2], Cushing [7], Desharnais and Cohen [9], Franke and Yakubu [20], Fisher and Goh [16], Guckenheimer *et al.* [21], Hassell and Comins [22], Henson [25], Horwood and Shepherd [28], Levin and Goodyear [36], Kulenovic and Yakubu [33], North [44], Pennycuick [45], Travis *et al.* [49], and Wikan [50].

The response of any population to cyclic fluctuations depends on the nature and type of compensatory mechanisms at different life-history stages, the fertile age classes, and the period of the environment. Using population models without age-structure, Cushing showed that populations under compensatory dynamics are adversely affected by cyclic fluctuations of period 2 [8]. In this paper, we focus on the implications of compensatory dynamics on average population biomass in periodically forced Leslie-type age-structured models. We use a mathematical theorem to show that a population governed by an n-age class compensatory Leslie model has a globally attracting positive cycle. The population is neither diminished nor enhanced by a $p-$periodic environment when the least common multiple of the fertile age classes is a multiple of p and the oldest age class is pioneer. When the least common multiple of the fertile age classes is not a multiple of p, and the population is governed by the periodic

Beverton-Holt model with fluctuating carrying capacity and non-fluctuating intrinsic growth rate, then the population is adversely affected by the periodic environment. This result is a generalization of that of Cushing and Henson [8], Elaydi and Sacker [11-14], Kocic [30] and Kon [31, 32] to include population models with age-structure. However, the population can be enhanced via resonance cycles when the periodic Beverton-Holt model has both fluctuating carrying capacity and fluctuating intrinsic growth rate.

Section 2 reviews periodically forced single species closed population models without age-structure. The periodic Beverton-Holt is an example of the general model [8, 11-14, 20, 30, 31, 32]. Precise mathematical definitions of attenuant and resonant cycles for population models without age-structure are introduced in Section 2. In Section 3, we introduce the main model, a periodically forced, density-dependent, n-age class Leslie model. The corresponding autonomous n-age class Leslie model in constant environment is also introduced in the section. Mathematical definitions of pioneer function as well as attenuant and resonant cycles for population models with age-structure are stated in Section 3.

In constant environments, single species compensatory models without age-structure have a globally attracting fixed point [8, 10, 15, 22]. However, in cyclic environments, the models have a globally attracting periodic orbit [8, 11-14, 17, 30, 31, 32]. In Section 4, we use the monotone systems theorem of Smith [48] to show that the autonomous Leslie model has a globally attracting, positive equilibrium population vector (carrying capacity) when the contribution to the next generation from each fertile age class is a nonlinear function with compensatory dynamics, and the oldest age class is pioneer. We show, in Section 5, that the periodically forced n-age class Leslie models with compensatory dynamics have a globally attracting periodic orbit. That is, in both constant and periodically varying environments, age-structure has no impact on population models under compensatory dynamics. Conditions under which the periodic orbit is neither attenuant nor resonant are derived in Section 6. Sections 7 and 8 highlight attenuant and resonant cycles in periodically forced Leslie models, respectively. The implications of our results are discussed in Section 9.

2 Periodic Population Models Without Age-Structure

Periodically forced, single species, ecological models with no age-structure of the general form

$$x(t+1) = x(t)g(t, x(t)) \tag{1}$$

have been used to study the long-term dynamics of discretely reproducing populations in periodically varying environments, where $x(t)$ is the population size at generation t [8, 17, 18-20, 38]. The C^2 map

$$g : \mathbb{Z}_+ \times [0, \infty) \to (0, \infty)$$

is the per capita growth rate, where there exists a *smallest positive integer* p satisfying $g(t+p, x) = g(t, x)$ for each $t \in \{0, 1, 2, ...\}$. That is, g is periodic with period p, which we assume is larger than 1.

The $p-$periodic (nonautonomous) Beverton-Holt model,

$$x(t+1) = \frac{\mu K_t x(t)}{K_t + (\mu - 1)x(t)}, \tag{2}$$

is an example of Model (1), where $K_{t+p} = K_t$ and $\mu > 1$. The coefficient μ is the intrinsic growth rate of the species, and the positive periodic carrying capacity K_t is a characteristic of the fluctuating habitat or environment.

In the classical autonomous Beverton-Holt, K_t is a constant (that is, $K_t \equiv K$). The equilibrium population sizes of the model are 0 and K. In the Beverton-Holt model, every positive initial population size converges monotonically to the unique positive equilibrium point $x_\infty = K$ [8].

To understand the long-term dynamics of Model (1), we introduce the following sequence of autonomous models:

$$\begin{array}{ccc} G_0(x) & = & xg(0,x), \\ G_1(x) & = & xg(1,x), \\ \vdots & = & \ddots, \\ G_{p-1}(x) & = & xg(p-1,x). \end{array}$$

Notice that

$$G_0(x(0)) = x(1), G_1(x(1)) = x(2), ..., G_{p-1}(x(p-1)) = x(p),$$

whenever the sequence of population densities $\{x(0), x(1), ...\}$ are generated by Model (1). Each G_i is an autonomous model that describes the population dynamics of a single species in a constant environment. The set of iterates of the $p-periodic$ dynamical system,

$$\{G_0, G_1, ..., G_{p-1}\},$$

is equivalent to the set of density sequences generated by Model (1). In many ecological models, the G_i have globally attracting fixed points called the *carrying capacities*.

In recent papers, Cushing and Henson [5], Elaydi and Sacker [11-14], Franke and Yakubu [18-20], Kocic [30] and Kon [31, 32] studied the relationship between the long-term dynamics of the $p-periodic$ dynamical system, Model (1), and the average of the carrying capacities of the G_i.

Definition 1 *A periodic orbit of Model (1) is attenuant (resonant) if its average value is less (greater) than the average of the carrying capacities of the* G_i.

Using monotone $2-periodic$ nonlinear difference equations models without age-structure, Cushing and Henson derived conditions for the existence of a globally attracting attenuant cycle [8]. In particular, Cushing and Henson showed that in periodic environments population sizes are diminished via attenuance whenever the single species is governed by the Beverton-Holt model. In this paper, we show that in age-structured models, periodic environments are *not* always deleterious. That is, age-structure combined with periodicity can have a dramatic impact on the ultimate outcome of population models.

3 Periodically Forced Leslie Model with Density Dependent Fecundity Functions

To study the combined effects of age-structure and periodic environments on population sizes, we introduce a general age-structured, single species, nonautonomous ecological model with s age classes. The model is of the form

$$\left.\begin{array}{rcl} x_1(t+1) & = & \sum_{i=1}^{s} x_i(t) g_i(t, x_i(t)) \\ x_2(t+1) & = & \lambda_1 x_1(t) \\ \vdots & = & \vdots \\ x_s(t+1) & = & \lambda_{s-1} x_{s-1}(t) \end{array}\right\}, \tag{3}$$

where for each $i \in \{1, 2, ..., s\}$, $x_i(t)$ is the population size of the i^{th} age class at time t and $\lambda_i \in (0, 1)$ is the i^{th} age class constant survival "probability" per generation. The C^2 map $g_i : \mathbb{Z}_+ \times [0, \infty) \to [0, \infty)$ is the fecundity of the i^{th} age class and there exists a smallest positive integer p satisfying $g_i(t + p, x_i) = g_i(t, x_i)$ for each i and each $t \in \{0, 1, 2, ...\}$. Model (3) is a periodic, density-dependent, Leslie model [2, 34, 35, 37]. In this model, all age classes may reproduce. An age class i is *fertile* if $g_i(t, x_i) > 0$ at some point $(t, x_i) \in \mathbb{Z}_+ \times [0, \infty)$.

If System (3) has no fertile age classes, then the species goes extinct in s generations. Consequently, we assume that there is always at least one fertile age class. As in the periodic Beverton-Holt model, we assume that a fertile age class remains fertile at all points, that is $g_i : \mathbb{Z}_+ \times [0, \infty) \to (0, \infty)$. In a recent paper [20], Franke and Yakubu studied the combined effects of age-structure and periodic environments on population models with *only* one fertile age class; the oldest age class.

A rescaling of the age classes can be performed to effectively replace the λ_i with 1 giving the model

$$\left.\begin{array}{rcl} x_1(t+1) & = & \sum_{i=1}^{s} x_i(t) g_i(t, x_i(t)) \\ x_2(t+1) & = & x_1(t) \\ \vdots & = & \vdots \\ x_s(t+1) & = & x_{s-1}(t) \end{array}\right\}, \tag{4}$$

which we call the *$p-$periodic Leslie model.* To prevent population explosion, we assume that $\lim_{x\to\infty} x g_i(t, x)$ exists. In Model (4), the contribution to the first age class of generation $(t + 1)$ by the i^{th} age class is the function $f_i(t, x_i(t)) = x_i(t) g_i(t, x_i(t))$. Note that $f_i(t + p, \cdot) = f_i(t, \cdot)$.

Definition 2 *Whenever $g_s(t, 0) > 1$ for all t, we say that the contribution to the next generation from the oldest age class is a pioneer function [20].*

Definition 3 *The contribution of the i^{th} age class to the next generation, f_i, is under compensatory dynamics whenever $\frac{\partial f_i}{\partial x_i}(t, x_i) > 0$, $\frac{\partial^2 f_i}{\partial x_i^2}(t, x_i) < 0$ for all $(t, x_i) \in \mathbb{Z}_+ \times [0, \infty)$, and $\lim_{x_i\to\infty} f_i(t, x_i)$ exists for all $t \in \mathbb{Z}_+$ [33, 42].*

For example, when

$$f_i(t, x_i(t)) = \frac{\mu K_t x_i(t)}{K_t + (\mu - 1)x_i(t)} \ (p-\textit{periodic} \text{ Beverton-Holt}),$$

the contribution of the i^{th} age class to the next generation is under compensatory dynamics and the function f_i is a bounded pioneer function.

When the environment is constant, the $p-$periodic Leslie model becomes

$$\left.\begin{array}{ccc} x_1(t+1) & = & \sum_{i=1}^{s} x_i(t) g_i(x_i(t)) \\ x_2(t+1) & = & x_1(t) \\ \vdots & = & \vdots \\ x_s(t+1) & = & x_{s-1}(t) \end{array}\right\}, \tag{5}$$

where the time dependent fecundity elements $g_i(t, x_i)$ reduce to the C^2 maps $g_i : [0, \infty) \to (0, \infty)$ or $g_i \equiv 0$, fertile or non-fertile.

In Model (5), the contribution to the first age class of generation $(t+1)$ by the i^{th} age class is $f_i(x_i(t)) = x_i(t) g_i(x_i(t))$. Using Definition (2), when g_i is time independent and $g_s(0) > 1$, the contribution to the next generation from the oldest age class is a *pioneer* function [47]. Also, using Definition (3), when g_i is time independent the contribution of the i^{th} age class to the next generation, f_i, is under *compensatory* dynamics whenever $f_i'(x_i) > 0$ and $f_i''(x_i) < 0$ for all $x_i \in [0, \infty)$; where $\lim_{x_i \to \infty} f_i(x_i)$ exists.

When the dynamics is compensatory, population models in constant environments without age-structure have a globally attracting fixed point and no population size "overshoots" the fixed point under iteration (monotone dynamics) [51, 52, 53]. For example, when

$$f_i(x_i) = \frac{\mu K x_i}{K + (\mu - 1)x_i} \ (\text{Beverton-Holt}),$$

the contribution of the i^{th} age class to the next generation is under compensatory dynamics (see [23, 39-41] for more examples of single species models in constant environments).

An equilibrium of Model (5) has all age class population sizes equal. This common value of a globally attracting equilibrium vector of the age-structured non-periodic model is called the *carrying capacity.* Model (5) is a discrete-time autonomous dynamical system from $\mathbb{R}_+^s$ to $\mathbb{R}_+^s$, which we denote by F.

For each $J \in \{0, 1, ..., p-1\}$, define $FJ : \mathbb{R}_+^s \to \mathbb{R}_+^s$ by

$$FJ(x_1, x_2, ... x_s) = \left(\sum_{i=1}^{s} x_i g_i(J, x_i), x_1, x_2, ..., x_{s-1} \right).$$

The nonautonomous $p-$periodic Leslie model with density-dependent fecundity elements, Model (4), can be viewed as the compositions of these p autonomous dynamical systems. An interesting problem is to find a relationship between the carrying capacities, globally attracting fixed points, of the FJ and the long-term dynamics of the $p-$periodic Leslie model. A cycle for the $p-$periodic Leslie model produces cycles in each age class. The values that each age class goes through are the same but shifted in time. Thus, for each age class the averages of the age class populations over a cycle are the same.

Definition 4 *A $k-cycle$ of Model (4) is attenuant (resonant) when each average of the age class populations over the $k-cycle$ is less (greater) than the average of the carrying capacities of the FJ.*

This generalizes the Cushing and Henson definitions of attenuant and resonant cycles to include population models with age-structure [8, 24, 27].

4 Carrying Capacity In Constant Environments: Globally Attracting Fixed Point

The classic Beverton-Holt model without age-structure describes a pioneer population under compensatory dynamics and supports a globally attracting positive equilibrium (carrying capacity). In this section, we show that the autonomous Leslie model, Model (5), has a globally attracting, positive equilibrium population vector (carrying capacity) when the contribution to the next generation from each fertile age class, f_i, is under compensatory dynamics, and the contribution to the next generation from the oldest age class, f_s, is a pioneer function. This generalizes the results of Kulenovic and Yakubu on density-dependent Leslie models with 2 age classes [33]. Others have studied global attractors in higher dimension monotone systems [48, 54, 55].

To prove our results, we need the following monotone systems theorem of Smith [48] and auxiliary results.

Theorem 5 *(Smith [48]) Let $T : \mathbb{R}^n_+ \to \mathbb{R}^n_+$ be C^1. In addition, assume*

1. *$DT(x)$, Jacobian matrix at x, has all positive entries when x has all positive entries.*
2. *Each of the components of $DT(x)$ is a decreasing function of each component of x.*
3. *$T(0) = 0$ and $T^n(x) \nrightarrow \infty$ as $n \to \infty$ for every $x \in \mathbb{R}^n_+$.*
4. *The spectral radius (modulus of largest eigenvalue) of $DT(0) > 1$.*

Then there exists a unique non-zero fixed point q of T such that for every $x \neq 0, T^n(x) \to q$ as $n \to \infty$.

The proof of the following lemma is straightforward and is omitted.

Lemma 6 *Let f , $h : [0, \infty) \to [0, \infty)$.*

1. *If f and h are compensatory functions, then $f + h$ and $f \circ h$ are compensatory functions.*
2. *If f and h are pioneer, then $f + h$ and $f \circ h$ are pioneer.*
3. *If $f(0) = h(0) = 0$, then $(f + h)(0) = (f \circ h)(0) = 0$.*

Lemma 7 *For each $J \in \{0, 1, ..., p-1\}$, let*

$$AJ = \begin{pmatrix} a_1^J & a_2^J & a_3^J & \cdots & a_s^J \\ 1 & 0 & 0 & \cdots & 0 \\ 0 & 1 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \cdots & 1 & 0 \end{pmatrix},$$

where each $a_s^J > 1$. Then the spectral radius of any finite product of the AJ matrices is larger than 1.

Proof. The determinant of each AJ is $\pm a_s^J$ and is the product of the eigenvalues. Since $a_s^J > 1$, at least one of the eigenvalues of each AJ must have modulus larger than 1. The determinant of a finite product of the AJ matrices is the product of the determinants. Thus, any finite product of the AJ matrices has modulus larger than 1 and hence at least one eigenvalue has modulus larger than 1. Therefore, the spectral radius of any finite product of the AJ matrices is larger than 1. ■

Lemma 8 *If the contribution of oldest age class is a pioneer function, then the spectral radius of the autonomous Leslie model at the origin, $DF(0)$, is larger than 1.*

Proof. The derivative of the autonomous Leslie model at the origin is

$$DF(0) = \begin{pmatrix} g_1(0) & g_2(0) & \cdots & g_{s-1}(0) & g_s(0) \\ 1 & 0 & \cdots & 0 & 0 \\ 0 & 1 & \cdots & 0 & 0 \\ \vdots & \vdots & \cdots & \vdots & \vdots \\ 0 & 0 & \cdots & 1 & 0 \end{pmatrix}.$$

Use Lemma (7) to establish this result. ■

Lemma 9 *When the contribution of each fertile age class to the next generation is under compensatory dynamics, then there is no population explosion in the autonomous Leslie Model (5).*

Proof. Recall that for each fertile class $\lim_{x_i \to \infty} f_i(x_i)$ exists. Thus, after s generations, the population of each age class is bounded below by the sum of the lower bounds on the f_i and bounded above by the sum of the upper bounds on the f_i. ■

Lemma 10 *If the greatest common divisor of the set of fertile age classes is 1 and the oldest age class is fertile, then there is a positive integer M such that for each generation greater than or equal to M each age class is a function of all the age classes.*

Proof. If j is a fertile age class and the first age class is a function of x_i during the L^{th} generation (F_1^L), then it is also a function of x_i during the $(L+j)^{th}$ generation (F_1^{L+j}). So for every generation Q larger than L, the first age class is a function of x_i when $Q \bmod j = L \bmod j$. Suppose the fertile age classes are $\{j_1, j_2, ..., j_r\}$. Then, the first age class of the generation obtained by adding any positive integer combination of the $j_i's$ to L is also a function of x_i.

Since this set of positive integers has 1 as their greatest common divisor, there exist integers $\{a_1, a_2, ..., a_r\}$ such that $\sum_{i=1}^{r} a_i j_i = 1$. Let $\{a_{i_1}, a_{i_2}, ..., a_{i_n}\} \subset \{a_1, a_2, ..., a_r\}$ be the set of negative $a_i's$. The first age class of the $(L - \sum_{k=1}^{n} a_{i_k} j_{i_k})^{th}$ generation is also a function of x_i. Since $-\sum_{k=1}^{n} a_{i_k} j_{i_k} + \sum_{i=1}^{r} a_i j_i$ is a positive integer combination of the $j_i's$, the first age class of the $(L - \sum_{k=1}^{n} a_{i_k} j_{i_k} + \sum_{i=1}^{r} a_i j_i)^{th}$ generation is also a function of x_i. In fact, it is also true for all generations of the form $L + N_1 \left(-\sum_{k=1}^{n} a_{i_k} j_{i_k} + \sum_{i=1}^{r} a_i j_i\right) + N_2 \left(-\sum_{k=1}^{n} a_{i_k} j_{i_k}\right)$, where N_1 and N_2 are nonnegative integers. Note that $N_1 \left(-\sum_{k=1}^{n} a_{i_k} j_{i_k} + \sum_{i=1}^{r} a_i j_i\right) \bmod \left(-\sum_{k=1}^{n} a_{i_k} j_{i_k}\right) = N_1 \bmod \left(-\sum_{k=1}^{n} a_{i_k} j_{i_k}\right)$. Every integer larger than $\left(-\sum_{k=1}^{n} a_{i_k} j_{i_k}\right)^2$ can be can be written as $A\left(-\sum_{k=1}^{n} a_{i_k} j_{i_k}\right) + B$, where $A \geq \left(-\sum_{k=1}^{n} a_{i_k} j_{i_k}\right)$ and $0 \leq B < \left(-\sum_{k=1}^{n} a_{i_k} j_{i_k}\right)$. Therefore, every integer larger than $\left(-\sum_{k=1}^{n} a_{i_k} j_{i_k}\right)^2$ can be can be written as $N_1 \left(-\sum_{k=1}^{n} a_{i_k} j_{i_k} + \sum_{i=1}^{r} a_i j_i\right) + N_2 \left(-\sum_{k=1}^{n} a_{i_k} j_{i_k}\right)$, where $N_1 = B$ and $N_2 = A - B > 0$. Thus, the first age class is a function of x_i during every generation larger than $L + \left(-\sum_{k=1}^{n} a_{i_k} j_{i_k}\right)^2$. As time goes by the younger age class populations are shifted to the older age classes. Thus, all age classes are functions of x_i during every generation larger than $L + \left(-\sum_{k=1}^{n} a_{i_k} j_{i_k}\right)^2 + s$. Since the oldest age class is fertile, the first age class is a function of each x_i at least once in the first s generations. Hence, all age classes are functions of all x_i during every generation larger than or equal to $M = 2s + \left(-\sum_{k=1}^{n} a_{i_k} j_{i_k}\right)^2$. ∎

Lemma 11 *If the greatest common divisor of the set of fertile age classes is* 1*, the oldest age class is fertile, and the contribution to the next generation from each fertile age class,* f_i*, is under compensatory dynamics, then there is a positive integer* M *such that when* $m \geq M$*,* $DF^m(x)$ *has all positive entries, when* x *has all positive entries. Furthermore, each component of* $DF^m(x)$ *decreases with each* x_i*.*

Proof. Let $M = 2s + \left(-\sum_{k=1}^{n} a_{i_k} j_{i_k}\right)^2$ be the number found in Lemma (10). When $m \geq M$ each component of $F^m(x)$ is a function of each x_i. The components consist of finite sums of f_i acting on finite sums of f_j acting on finite sums of $f_k \cdots$. The partial derivative of each component with respect to each x_i consists of a finite sum of products of the f_j'. Since each $f_j'(z) > 0$ and $f_j(z) \geq 0$ when $z \geq 0$, the finite sum is positive when each component of x is nonnegative.

The second partial derivative of each component of $F^m(x)$ with respect to each x_i consists of a finite sum of products of the f_j' and one f_k''. Since each $f_j'(z) > 0, f_k''(z) < 0$ and $f_j(z) \geq 0$ when $z \geq 0$, the finite sum is negative when each component of x is nonnegative. Thus, each component of $DF^m(x)$ decreases with each x_i. ∎

Theorem 12 *If the greatest common divisor of the set of fertile age classes is* 1, *the contribution to the next generation from each fertile age class, f_i, is under compensatory dynamics, and the contribution to the next generation from the oldest age class, f_s, is also a pioneer function, then F has a unique non-zero fixed point, x_∞, and for every $x \neq 0, F^n(x) \to x_\infty$ as $n \to \infty$.*

Proof. To prove this result, we start by showing that there is a positive integer M such that for each $m \geq M, F^m$ satisfies all the hypotheses of Theorem (5). Choose $M = 2s + \left(-\sum_{k=1}^{n} a_{i_k} j_{i_k}\right)^2$, as developed in Lemma (10). Since F is C^1 and $F(0) = 0$, F^m is C^1 and $F^m(0) = 0$ for all m. By Lemma (7), $DF(0)$ has spectral radius larger than 1. Thus, $DF^m(0)$ has spectral radius larger than 1 for all m. Lemma (11) shows that if $m \geq M$, then conditions 1 and 2 of Theorem (5) are satisfied using F^m. Lemma (9) gives boundedness of orbits (condition 3). Hence, all of the hypotheses of Theorem (5) are satisfied for F^m, whenever $m \geq M$. Therefore, there exists a unique non-zero fixed point x_∞^m for each F^m such that for every $x \neq 0, F^{nm}(x) \to x_\infty^m$ as $n \to \infty$. In particular, $F^{nm}(x_\infty^{m+1}) \to x_\infty^m$ as $n \to \infty$. But $F^{n(m+1)m}(x_\infty^{m+1}) = x_\infty^{m+1}$ for all n. This implies that $x_\infty^m = x_\infty^{m+1}$. So each F^m has the same unique non-zero fixed point, x_∞. Which implies that $F(x_\infty) = x_\infty$ and for every $x \neq 0$, $F^n(x) \to x_\infty$ as $n \to \infty$. ∎

When the greatest common divisor of the fertile age classes, Q, is larger than 1, the Leslie model also has a globally attracting fixed point, whenever the contribution to the next generation from each fertile age class, f_i, is under compensatory dynamics and the contribution to the next generation from the oldest age class, f_s, is also a pioneer function. The proof of this result uses Theorem (5) on a subspace of dimension s/Q.

Lemma 13 *Let Q be the greatest common divisor of the fertile age classes and the oldest age class be fertile. Then the Q^{th} power of the Leslie model (5) decouples into Q identical subsystems of dimension s/Q which are Leslie models with greatest common divisor of the fertile age classes equal to* 1.

Proof. Let Q be the greatest common divisor of the fertile age classes. Then Q is less than or equal to the youngest fertile age class. The i^{th} component of F is a function of a subset of $\{x_j | j \bmod Q = (i-1) \bmod Q\}$. The i^{th} component of F^2 is a function of a subset of $\{x_j | j \bmod Q = (i-2) \bmod Q\}$, and the i^{th} component of F^Q is a function of a subset of $\{x_j | j \bmod Q = (i - Q) \bmod Q = i \bmod Q\}$. Thus, after Q generations the Leslie model has decoupled into Q subsystems of dimension s/Q via the equivalence classes $\bmod Q$. Notice that these subsystems are Leslie models with greatest common divisor of the fertile age classes equal to 1. The function F^Q is given by the following set of equations

$$\begin{cases} x_1(t+1) & = & \sum_{i=1}^{s/Q} f_{iQ}(x_{(i-1)Q+1}(t)) \\ x_2(t+1) & = & \sum_{i=1}^{s/Q} f_{iQ}(x_{(i-1)Q+2}(t)) \\ \vdots & \vdots & \vdots \\ x_Q(t+1) & = & \sum_{i=1}^{s/Q} f_{iQ}(x_{(i-1)Q+Q}(t)) \\ x_{Q+1}(t+1) & = & x_1(t) \\ x_{Q+2}(t+1) & = & x_2(t) \\ \vdots & \vdots & \vdots \\ x_s(t+1) & = & x_{s-Q}(t) \end{cases}$$

From this we see that the Q subsystems are identical. ■

Theorem 14 *If the contribution to the next generation from each fertile age class, f_i, is under compensatory dynamics, and the contribution to the next generation from the oldest age class, f_s, is also a pioneer function, then F has a unique non-zero fixed point, x_∞, and for every $x \neq 0, F^n(x) \to x_\infty$ as $n \to \infty$.*

Proof. Theorem (12) establishes this result when the greatest common divisor of the fertile age classes is 1. When the greatest common divisor of the fertile age classes is $Q \neq 1$, F^Q decouples into Q subsystems which are Leslie models with greatest common divisor of the fertile age classes equal to 1, (Lemma (13)). Applying Theorem (12) to each of the Q subsystems of F^Q, we obtain that each subsystem has a unique non-zero fixed point that attracts all non-zero points in the subspace. Since the subsystems are identical, the fixed points are identical. Recall that a fixed point of a Leslie model has all components equal. Thus, the point with this common value for each of its s components is a fixed point for F^Q. Since the system decouples and each of the fixed points are globally attracting, the $s-$dimensional fixed point for F^Q is also globally attracting. To see that F_1 of the $s-$dimensional fixed point is the common coordinate value of the fixed point, note that in $(Q-1)$ more iterations this value will be the Q^{th} coordinate where it must be the common coordinate value. Thus, the $s-$dimensional fixed point for F^Q is also a fixed point of F. By continuity, for every $x \neq 0, F^n(x) \to x_\infty$ as $n \to \infty$. ■

Leslie models with density-dependent non-periodic fecundity functions have a globally attracting fixed point with all coordinates equal (Theorem (14), whenever the contribution to the next generation from each fertile age class, f_i, is under compensatory dynamics, and the contribution to the next generation from the oldest age class, f_s, is also a pioneer function. This common coordinate is the carrying capacity of each age class.

Population models without age-structure have the same long-term dynamics as those with age-structure when the governing dynamics is compensatory. That is, in constant environments, adding age structure preserves compensatory dynamics.

5 Globally Attracting Cycles In Periodic Environments

Nonoscillatory dynamics are rare in fluctuating environments [18-20]. In this section, we show that in periodically varying environments, the compensatory Leslie model has a globally attracting periodic orbit. To prove this result, we use Theorem (5) of Smith and proceed as in the proof of Theorem (14). We will use the following auxiliary results to outline the proof.

Lemma 15 *If for each t the contribution to the $(t+1)$ generation from the oldest age class, $f_s(t,\cdot)$, is a pioneer function, then the spectral radius of*

$$D(F(p-1)(F(p-2)(\cdots(F1(F0(x)))\cdots)))$$

at $x=0$ is larger than 1.

Proof. Since $FJ(0)=0$ for all J,

$$D(F(p-1)(F(p-2)(\cdots(F1(F0(x)))\cdots))) \text{ at } 0 \text{ is } \Pi_{J=0}^{p-1}D(FJ)(0),$$

where each $D(FJ)(0)$ is a Leslie matrix with determinant $g_s(J,0)>1$. The result follows immediately by Lemma (7). ∎

Lemma 16 *When the contribution of each fertile age class to the next generation is under compensatory dynamics, then there is no population explosion in the p-periodic Leslie Model (4).*

The proof is similar to the proof of Lemma (9) and is omitted.

In our $p-$periodic Leslie model, the set of fertile age classes is the same from generation to generation. Thus, the greatest common divisor of the set of fertile age classes is well defined.

Lemma 17 *In the p-periodic Leslie Model (4), if the greatest common divisor of the set of fertile age classes is* 1*, then there is a positive integer M such that for each generation greater than or equal to M each age class is a function of all the age classes.*

Proof. Proceed exactly as in the proof of Lemma (10) while replacing F_1^L with $F\left((L-1) \bmod p\right)_1 \circ F((L-2) \bmod p)_1 \circ \cdots \circ F1_1 \circ F0_1$. ∎

Lemma 18 *In the p-periodic Leslie Model (4), if the greatest common divisor of the set of fertile age classes is* 1*, and for each t the contribution to the $(t+1)$ generation from each fertile age class, $f_i(t,\cdot)$, is under compensatory dynamics, then there is a positive integer M such that when $m \geq M$,*

$$D(F((m-1) \bmod p)(F((m-2) \bmod p)(\cdots(F1(F0(x)))\cdots)))$$

has all positive entries, when x has all positive entries. Furthermore, each component of

$$D(F((m-1) \bmod p)(F((m-2) \bmod p)(\cdots(F1(F0(x)))\cdots)))$$

decreases with each x_i.

Proof. Let $M = 2s + \left(-\sum_{k=1}^{n} a_{i_k} j_{i_k}\right)^2$ be the number found in Lemma (17). When $m \geq M$, each component of $F((m-1) \bmod p)(F((m-2) \bmod p)(\cdots(F1(F0(x)))\cdots))$ is a function of each x_i. The components consist of finite sums of $f_i(t, \cdot)$ acting on finite sums of $f_j(t-1, \cdot)$ acting on finite sums of $f_k(t-2, \cdot)$ $\cdots$. The partial derivative of each component with respect to each x_i consists of a finite sum of products of the $\frac{\partial f_j}{\partial x_i}$. Since each $\frac{\partial f_j}{\partial x_i} > 0$ and $f_j(t, z) \geq 0$ when $z \geq 0$, the finite sum is positive when each component of x is nonnegative.

The second partial derivative of each component of $F((m-1) \bmod p)(F((m-2) \bmod p)(\cdots(F1(F0(x)))\cdots))$ with respect to each x_i consists of a finite sum of products of the $\frac{\partial f_j}{\partial x_i}$ and one $\frac{\partial^2 f_k}{\partial x_i^2}$. Since each $\frac{\partial f_j}{\partial x_i} > 0$, $\frac{\partial^2 f_k}{\partial x_i^2} < 0$ and $f_j(t, z) \geq 0$ when $z \geq 0$, the finite sum is negative when each component of x is nonnegative. Thus, each component of $D(F((m-1) \bmod p)(F((m-2) \bmod p)(\cdots(F1(F0(x)))\cdots)))$ decreases with each x_i. ■

Theorem 19 *Let the greatest common divisor of the set of fertile age classes be 1. If for each t, the contribution to the $(t+1)$ generation from each fertile age class, $f_i(t, \cdot)$, is under compensatory dynamics, and for each t the contribution to the $(t+1)$ generation from the oldest age class, $f_s(t, \cdot)$, is also a pioneer function, then the $p-$periodic Leslie Model (4) has a unique non-zero periodic cycle which attracts all non-zero initial population sizes.*

Proof. Let $\widetilde{F}^m(x) = F((m-1) \bmod p)(F((m-2) \bmod p)(\cdots(F1(F0(x)))\cdots))$. To prove this result, we start by showing that there is a positive integer M such that for each $m \geq M, \widetilde{F}^m(x)$ satisfies all the hypotheses of Theorem (5). Choose $M = 2s + \left(-\sum_{k=1}^{n} a_{i_k} j_{i_k}\right)^2$, as developed in Lemma (17). Since each FJ is C^1 and $FJ(0) = 0$, $\widetilde{F}^m(x)$ is C^1 and $\widetilde{F}^m(0) = 0$ for all m. By Lemma (15), $D(\widetilde{F}^m(x))$ has spectral radius larger than 1 for all m. Lemma (18) shows that if $m \geq M$, then conditions 1 and 2 of Theorem (5) are satisfied using $\widetilde{F}^m(x)$. Lemma (16) gives boundedness of orbits (condition 3). Hence, all of the hypotheses of Theorem (5) are satisfied for $\widetilde{F}^m(x)$ whenever $m \geq M$. Therefore, if $m \geq M$ there exists a unique non-zero fixed point x_∞^m for $\widetilde{F}^m(x)$ such that for every $x \neq 0$, $\left(\widetilde{F}^m\right)^n(x) \to x_\infty^m$ as $n \to \infty$.

For the remainder of the proof assume $m = kp$, where k is a positive integer. Our system is p-periodic, thus $\left(\widetilde{F}^m\right)^n(x) = \left(\widetilde{F}^{kp}\right)^n(x) = \left(\widetilde{F}^p\right)^{kn}(x)$. In particular, $\left(\widetilde{F}^p\right)^{kn}(x_\infty^{m+p}) \to x_\infty^m$ as $n \to \infty$. Now, $\left(\widetilde{F}^p\right)^{(k+1)kn}(x_\infty^{m+p}) = \left(\widetilde{F}^{p(k+1)}\right)^{kn}(x_\infty^{m+p}) = \left(\widetilde{F}^{m+p}\right)^{kn}(x_\infty^{m+p}) = x_\infty^{m+p}$ for all n. This implies that $x_\infty^m = x_\infty^{m+p}$. So each $\widetilde{F}^{kp}$ has the same unique non-zero fixed point, x_∞, which implies that $\widetilde{F}^p(x_\infty) = x_\infty$ and for every $x \neq 0$, $\left(\widetilde{F}^p\right)^n(x) \to x_\infty$ as $n \to \infty$. Thus, the periodic cycle $\{x_\infty, F0(x_\infty), F1(F0(x_\infty)), ..., F(p-2)(\cdots(F1(F0(x_\infty)))), \widetilde{F}^p(x_\infty) = x_\infty\}$ is a globally attracting cycle. ■

When the greatest common divisor of the fertile age classes, Q, is larger than 1, the p-periodic Leslie model has a globally attracting cycle, whenever for each

t the contribution to the $(t+1)$ generation from each fertile age class, $f_i(t,\cdot)$, is under compensatory dynamics, and for each t the contribution to the $(t+1)$ generation from the oldest age class, $f_s(t,\cdot)$, is also a pioneer function. The proof of this result uses Theorem (5) on a subspace of dimension s/Q.

Lemma 20 *Let Q be the greatest common divisor of the fertile age classes, then the p-periodic Leslie model (4) decouples into Q p-periodic subsystems of dimension s/Q with the same fertile age classes. The subsystems are p-periodic Leslie models with greatest common divisor of the fertile age classes equal to* 1.

Proof. Let Q be the greatest common divisor of the fertile age classes. Then Q is less than or equal to the youngest fertile age class. The i^{th} component of $F0$ is a function of a subset of $\{x_j | j \bmod Q = (i-1) \bmod Q\}$. The i^{th} component of $F1 \circ F0$ is a function of a subset of $\{x_j | j \bmod Q = (i-2) \bmod Q\}$, and the i^{th} component of $F(Q-1) \circ \cdots \circ F1 \circ F0$ is a function of a subset of $\{x_j | j \bmod Q = (i-Q) \bmod Q = i \bmod Q\}$. Thus, after Q generations the system has decoupled. Since the system is p-periodic, it returns to the same decoupled systems after every pQ generations. Thus, the $p-$periodic Leslie Model (4) has decoupled into Q $p-$periodic subsystems of dimension s/Q via the equivalence classes $\bmod\, Q$. Notice that these subsystems are p-periodic Leslie models with greatest common divisor of the fertile age classes equal to 1. The function $F\left((t+Q-2) \bmod p\right) \circ \cdots \circ F((t) \bmod p) \circ F((t-1) \bmod p)$ is given by the following set of equations

$$\left.\begin{array}{lll}
x_1(t+Q) & = & \sum_{i=1}^{s/Q} f_{iQ}(t+Q-1, x_{((i-1)Q+1)}(t)) \\
x_2(t+Q) & = & \sum_{i=1}^{s/Q} f_{iQ}(t+Q-2, x_{((i-1)Q+2)}(t)) \\
\vdots & \vdots & \vdots \\
x_Q(t+Q) & = & \sum_{i=1}^{s/Q} f_{iQ}(t, x_{((i-1)Q+Q)}(t)) \\
x_{Q+1}(t+Q) & = & x_1(t) \\
x_{Q+2}(t+Q) & = & x_2(t) \\
\vdots & \vdots & \vdots \\
x_s(t+Q) & = & x_{s-Q}(t)
\end{array}\right\} . \qquad (6)$$

From this, we see that the Q subsystems have the same fertile age classes. ■

Theorem 21 *If for each t the contribution to the $(t+1)$ generation from each fertile age class, $f_i(t,\cdot)$, is under compensatory dynamics, and for each t the contribution to the $(t+1)$ generation from the oldest age class, $f_s(t,\cdot)$, is also a pioneer function, then the $p-periodic$ Leslie Model (4) has a unique non-zero periodic cycle which attracts all non-zero initial population sizes.*

Proof. Theorem (19) establishes this result when the greatest common divisor of the fertile age classes is 1. When the greatest common divisor of the fertile age classes is $Q \neq 1$, the p-periodic Leslie Model (4) decouples into Q p-periodic subsystems of dimension s/Q with the same fertile age classes, (Lemma (20)). The subsystems can be viewed as p-periodic Leslie models with greatest common divisor of the fertile age classes equal to 1, where the generational gap (step size) is Q. Applying Theorem (19) to each of the Q $p-$periodic subsystems, we obtain that each subsystem has a unique non-zero cycle, with period a divisor of p, that attracts all non-zero points in the subspace. Let $(y^K_{\infty,1}, y^K_{\infty,2}, ..., y^K_{\infty,s/Q})$ be the initial point on the cycle for the K^{th} subsystem ($K \in \{1, 2, ..., Q\}$). Then,

$$y_\infty = \left(y^0_{\infty,1}, y^1_{\infty,1}, ..., y^{Q-1}_{\infty,1}, y^0_{\infty,2}, y^1_{\infty,2}, ..., y^{Q-1}_{\infty,2}, ...y^0_{\infty,s/Q}, y^1_{\infty,s/Q}, ..., y^{Q-1}_{\infty,s/Q}\right) \tag{7}$$

is the initial point for a cycle for the p-periodic Leslie Model (4). Note that, the period of the cycle that starts at y_∞ is a divisor of pQ. Since each of the non-zero cycles attract all non-zero points under iterations of the subsystems, which corresponds to Q iteration of the full model, all non-zero points are attracted to the cycle that starts at y_∞ under Q iterations. By continuity of our $p-$periodic system, all orbits must limit on the cycle that starts at y_∞. A theorem of Elaydi and Sacker [11-14] establishes that the period of the cycle starting at y_∞ must divide p. ■

6 Nonattenuant and Nonresonant Cycles In Periodic Leslie Models

The Beverton-Holt model, the logistic differential equation and the logistic difference equation (without age-structure) have been used to show that periodic environment is always deleterious. That is, the average of the population oscillations in the periodic environment is less than the average of the carrying capacity in the corresponding constant environments (attenuance) [8, 31, 32, 30, 11-14]. In this section, we show that many periodically forced compensatory Leslie models have cycles which are neither attenuant nor resonant.

Theorem 22 *If for each t the contribution to the $(t+1)$ generation from each fertile age class, $f_i(t,\cdot)$, is under compensatory dynamics, and for each t the contribution to the $(t+1)$ generation from the oldest age class, $f_s(t,\cdot)$, is also a pioneer function of the $p-$periodic Model (4) and the least common multiple of the fertile age classes, Q, is a multiple of p, then the global attracting cycle of Model (4) is neither attenuant nor resonant.*

Proof. From Theorem (14), each FJ has a globally attracting positive fixed point and all the components of the fixed point are the same. Let y^J_∞ be this common value. We will show that $y = (y^{p-1}_\infty, y^{p-2}_\infty, ..., y^0_\infty, y^{p-1}_\infty, y^{p-2}_\infty, ..., y^0_\infty) \in \mathbb{R}^s_+$ is the initial point on the unique positive periodic cycle given by Theorem (21). Since s is a multiple of Q and Q is a multiple of p, each y^J_∞ is repeated s/p times in y and each of the fertile age classes have population y^0_∞ at the point y. Thus, $F0(y) = (y^0_\infty, y^{p-1}_\infty, ..., y^1_\infty, y^0_\infty, y^{p-1}_\infty, ..., y^1_\infty)$. Each of the fertile age classes have population y^1_∞ at the point $F0(y)$. Hence, $(F1 \circ F0)(y) = (y^1_\infty, y^0_\infty, y^{p-1}_\infty, ..., y^2_\infty, y^1_\infty, y^0_\infty, y^{p-1}_\infty, ..., y^2_\infty)$. Repeating this composition argument gives $(F(p-1) \circ F(p-2) \circ \cdots \circ F0)(y) = y$, so y is the initial point of the unique periodic cycle. Thus, the total population remains constant over the unique periodic cycle and the average age class population is $\frac{1}{p}\sum_{J=0}^{p-1} y_\infty^J$, which is also the average of the carrying capacities. Hence, this globally attracting cycle fails to be either attenuant or resonant. ■

When $Q = s$, the oldest age class is the only fertile class. Such reduced Leslie models are also known to support nonattenuant and nonresonant cycles when the environment is not constant [20].

7 Attenuant Cycles In Periodic Leslie Models

In periodic environments, age-structured population models are capable of supporting globally attracting attenuant cycles. To illustrate this diminishing effect on population sizes, we consider the p-periodic Leslie Model (4), where the contribution of each i^{th} age class to the next generation is the periodic Beverton-Holt model. Since the classical Beverton-Holt model is a pioneer map under compensatory dynamics, Theorem (21) provides a globally attracting cycle for the following Beverton-Holt age-structured model with periodic environmental carrying capacity:

$$\left.\begin{array}{rcl} x_1(t+1) & = & \sum_{i=1}^{s} \frac{\mu K(t) x_i(t)}{K(t)+(\mu-1)x_i(t)} \\ x_2(t+1) & = & x_1(t) \\ \vdots & = & \vdots \\ x_s(t+1) & = & x_{s-1}(t) \end{array}\right\}. \tag{8}$$

In contrast to Theorem (22), we show that the globally attracting cycle of Model (8) is attenuant. That is, in Model (8), fluctuating environments are deleterious to the species. We summarize this in the following result.

Theorem 23 *The globally attracting cycle in Model (8) is attenuant.*

Proof. From Theorem (14), each FJ has a globally attracting positive fixed point and all the components of the fixed point are the same. Let y_∞^J be this common value, carrying capacity. Now since y_∞^J is the first component of this positive fixed point, $y_\infty^J = \sum_{i=1}^{s} \frac{\mu K(J) y_\infty^J}{K(J)+(\mu-1)y_\infty^J} = \frac{s\mu K(J) y_\infty^J}{K(J)+(\mu-1)y_\infty^J}$ and $1 = \frac{s\mu K(J)}{K(J)+(\mu-1)y_\infty^J}$. Hence, $y_\infty^J = \frac{(s\mu-1)K(J)}{\mu-1}$ and the total population, sy_∞^J, equals $\frac{s(s\mu-1)K(J)}{\mu-1}$. The average of the total populations satisfies the equations

$$\frac{1}{p}\sum_{J=0}^{p-1} sy_\infty^J = \frac{1}{p}\sum_{J=0}^{p-1} \frac{s(s\mu-1)K(J)}{\mu-1} = \frac{s(s\mu-1)}{p(\mu-1)}\sum_{J=0}^{p-1} K(J)$$

and the average of the carrying capacities is

$$\frac{1}{p}\sum_{J=0}^{p-1} y_\infty^J = \frac{(s\mu-1)}{p(\mu-1)}\sum_{J=0}^{p-1} K(J).$$

Denote the initial point of the globally attracting $p-cycle$ by $z = (z_1, z_2, ..., z_s)$. Therefore, $F0(z) = (z_p, z_1, ..., z_{s-1})$, where $z_p = \sum_{i=1}^{s} \frac{\mu K(0) z_i}{K(0)+(\mu-1)z_i}$; $(F1 \circ F0)(z) = (z_{p-1}, z_p, ..., z_{s-2})$, where $z_{p-1} = \sum_{i=1}^{s} \frac{\mu K(1) z_{i-1}}{K(1)+(\mu-1)z_{i-1}}$ and $z_0 \equiv z_p$. After p iterations, we have $z_i = z_{p+i}$ for $i \in \{-p+1, -p+2, ..., 0\}$ and

$$z_{p-J} = \sum_{i=1}^{s} \frac{\mu K(J) z_{i-J}}{K(J) + (\mu - 1) z_{i-J}}$$

for $J \in \{0, 1, 2, ..., p-1\}$. During the cycle each age class takes on the same values, but with a shift in time. Defining $z_i = z_{i \bmod p}$ for all integers i is consistent with the $z's$ already defined. Hence, the average of the age class population is $\frac{1}{p} \sum_{j=1}^{p} z_j$.

We will show that $\sum_{j=1}^{p} z_j < \frac{(s\mu-1)}{(\mu-1)} \sum_{J=0}^{p-1} K(J)$, which implies attenuance.

Now $\sum_{j=1}^{p} z_j = \sum_{j=0}^{p-1} z_{p-J} = \sum_{J=0}^{p-1} \sum_{i=1}^{s} \frac{\mu K(J) z_{i-J}}{K(J)+(\mu-1)z_{i-J}} = \sum_{J=0}^{p-1} \sum_{i=1}^{s} \frac{\frac{\mu K(J)}{(\mu-1)} \frac{(\mu-1)z_{i-J}}{K(J)}}{1+\frac{(\mu-1)z_{i-J}}{K(J)}}$.

Clearly $h(x) = \frac{x}{1+x}$ is concave down and thus satisfies Jensen's inequality

$$h\left(\frac{\sum_{J=0}^{p-1}\sum_{i=1}^{s} w_{iJ} u_{iJ}}{\sum_{J=0}^{p-1}\sum_{i=1}^{s} w_{iJ}}\right) > \frac{\sum_{J=0}^{p-1}\sum_{i=1}^{s} w_{iJ} h(u_{iJ})}{\sum_{J=0}^{p-1}\sum_{i=1}^{s} w_{iJ}}.$$

Letting $w_{iJ} = \frac{\mu K(J)}{(\mu-1)}, u_{iJ} = \frac{(\mu-1)z_{i-J}}{K(J)}$ and applying Jensen's inequality yields

$$\begin{aligned}
\sum_{j=1}^{p} z_j &< \left(\sum_{J=0}^{p-1}\sum_{i=1}^{s} \frac{\mu K(J)}{(\mu-1)}\right) \cdot h\left(\frac{\sum_{J=0}^{p-1}\sum_{i=1}^{s} \frac{\mu K(J)}{(\mu-1)} \frac{(\mu-1)z_{i-J}}{K(J)}}{\sum_{J=0}^{p-1}\sum_{i=1}^{s} \frac{\mu K(J)}{(\mu-1)}}\right) \\
&= \left(\frac{s\mu}{\mu-1}\sum_{J=0}^{p-1} K(J)\right) \cdot h\left(\frac{s\mu \sum_{J=0}^{p-1} z_J}{\frac{s\mu}{\mu-1}\sum_{J=0}^{p-1} K(J)}\right) \\
&= \left(\frac{s\mu}{\mu-1}\sum_{J=0}^{p-1} K(J)\right) \cdot \frac{\frac{s\mu \sum_{J=0}^{p-1} z_J}{\frac{s\mu}{\mu-1}\sum_{J=0}^{p-1} K(J)}}{1 + \frac{s\mu \sum_{J=0}^{p-1} z_J}{\frac{s\mu}{\mu-1}\sum_{J=0}^{p-1} K(J)}} \\
&= \left(\frac{s\mu}{\mu-1}\sum_{J=0}^{p-1} K(J)\right) \frac{s\mu \sum_{J=0}^{p-1} z_J}{\frac{s\mu}{\mu-1}\sum_{J=0}^{p-1} K(J) + s\mu \sum_{J=0}^{p-1} z_J}.
\end{aligned}$$

Therefore, since all $K(J)$, z_J and $\mu - 1$ are positive,

$$\left(\frac{s\mu}{\mu-1}\sum_{J=0}^{p-1} K(J) + s\mu \sum_{J=0}^{p-1} z_J\right) \sum_{j=1}^{p} z_j < \left(\frac{s\mu}{\mu-1}\sum_{J=0}^{p-1} K(J)\right) s\mu \sum_{J=0}^{p-1} z_J.$$

That is,

$$\left(\frac{1}{\mu-1}\sum_{J=0}^{p-1} K(J) + \sum_{J=0}^{p-1} z_J\right) < \frac{s\mu}{\mu-1}\sum_{J=0}^{p-1} K(J).$$

Hence,

$$\sum_{J=0}^{p-1} z_J < \frac{s\mu - 1}{\mu - 1} \sum_{J=0}^{p-1} K(J)$$

and the globally attracting periodic cycle is attenuant. ■

8 Resonant Cycles In Periodic Leslie Models

There is theoretical and experimental evidence of negative and positive impact on populations by fluctuating environments [5, 26, 27, 29]. In the previous section, we discussed the diminishing effects of periodic environments in compensatory Leslie models. In this section, we use a specific example to illustrate enhancing effects of periodic environments in compensatory Leslie models. To show this, we consider a 2-age class Beverton-Holt Leslie model with 2-periodic carrying capacity and 2-periodic demographic characteristic of the species. The model is of the form

$$\left.\begin{array}{rcl} x_1(t+1) & = & \sum_{i=1}^{2} \frac{\mu(t)K(t)x_i(t)}{K(t)+(\mu(t)-1)x_i(t)} \\ x_2(t+1) & = & x_1(t) \end{array}\right\}, \tag{9}$$

where $K(t+2) = K(t)$ and $\mu(t+2) = \mu(t)$.

Example 24 *In Model (9), set the following values:*

$$\left.\begin{array}{rcl} K(0) & = & 2.2 \\ K(1) & = & 1.8 \\ \mu(0) & = & 5.5 \\ \mu(1) & = & 4.5 \end{array}\right\}.$$

As predicted by Theorem (19), Example (24) has a globally attracting 2 - cycle that oscillates between

$$(14.756, 15.473) \text{ and } (15.473, 14.756).$$

The average value of this period 2 orbit is 15.1145.

For each $J \in \{0,1\}$, define $FJ : \mathbb{R}_+^2 \to \mathbb{R}_+^2$ by

$$FJ(x_1, x_2) = \left(\sum_{i=1}^{2} x_i g_i(J, x_i), x_1 \right),$$

where

$$\left.\begin{array}{rcl} g_1(J, x_1) & = & \frac{\mu(J)K(J)}{K(J)+(\mu(J)-1)x_1(t)} \\ g_2(J, x_2) & = & \frac{\mu(J)K(J)}{K(J)+(\mu(J)-1)x_2(t)} \end{array}\right\}.$$

The positive fixed points of $F0$ and $F1$ are $(15.583, 15.583)$ and $(14.625, 14.625)$, respectively. The average of the carrying capacities is 15.104 which is less than 15.1145. That is, Example (24) has a resonant 2 - cycle.

Unlike Model (8), in Example (24), both the carrying capacity and the demographic characteristic of the species are periodically forced. The 2-parameter periodic forcing generates resonant cycles in Example (24).

9 Conclusion

We use the monotone systems theory of Smith [48] to derive conditions under which a nonlinear, density-dependent, $p-$periodically forced compensatory Leslie model has a globally attracting cycle. The average of the resulting periodic attractor may be smaller (attenuance) or larger (resonance) than the average of the carrying capacities of the associated autonomous model. When the least common multiple of the fertile age classes is a multiple of p and the oldest age class is pioneer, we use precise mathematical definitions of pioneer species and compensatory dynamics to show that the average of the periodic attractor is equal to the average of the carrying capacities. That is, environmental fluctuations do not always always enhance or diminish populations.

In a recent paper, Cushing showed that a periodic environment is always deleterious for populations modeled by a class of monotone difference equations without age-structure [8]. We use a 2-parameter Leslie model to illustrate the occurrence of resonance cycles in age class models under compensatory dynamics.

Our results support the *Tribolium* experimental evidence of Jillson and Constantino *et al.* on the diminishing and enhancing effects of periodic environments. Furthermore, our results generalize the theoretical results of Cushing and Henson, Elaydi and Sacker, Franke and Yakubu, Kocic and Kon to include compensatory Leslie models.

In both constant and periodic environments, age-structure has no impact on the ultimate outcomes of population models under compensatory dynamics. That is, the long-term attractors in constant and periodic environments are fixed points and periodic orbits (non-chaotic), respectively. However, periodically forced population models with or without age-structure are capable of generating chaotic attractors with complicated structures when the governing dynamics are overcompensatory. Response of age-structured populations to periodic environments is a complex function of the period of the environments, the type and nature of the fluctuations, and the underlying compensatory mechanisms. Our analysis have highlighted some of these relationships in compensatory Leslie models. Studies on the combined effects of periodic forcing and age-structure on overcompensatory Leslie models would be welcome [33, 53].

10 References

1. M. Begon, J. L. Harper and C. R. Townsend, Ecology: individuals, populations and communities, *Blackwell Science Ltd* (1996).

2. H. Caswell, Matrix Population Models, *Sinauer Associates, Inc. Publishers* (2001).

3. B. D. Coleman, On the growth of populations with narrow spread in reproductive age. I. General theory and examples, *J. Math. Biol.,* 6, 1-19 (1978).

4. C. S. Coleman and J. C. Frauenthal, Satiable egg eating predators, *Math. Biosc.,* 63, 99-119 (1983).

5. R. F. Costantino, J. M. Cushing, B. Dennis and R. A. Desharnais, Resonant population cycles in temporarily fluctuating habitats, *Bull. Math. Biol.* 60, 247-273 (1998).

6. J. M. Cushing, Periodic time-dependent predator-prey systems, *SIAM J. Appl. Math.* 32, 82-95 (1977).

7. J. M. Cushing, A strong ergodic theorem for some nonlinear matrix models for the dynamics of structured populations, *Nat. Res. Mod.* 3, 3, 331-357 (1989).

8. J. M. Cushing and S. M. Henson, Global dynamics of some periodically forced, monotone difference equations, *J. Diff. Equations Appl. 7, 859-872 (2001).*

9. R. A. Desharnais and J. E. Cohen, Life not lived due to disequilibrium in heterogeneous age-structured populations, *Theo. Pop. Biol.* 29, 385-406 (1986).

10. S. N. Elaydi, Discrete Chaos. *Chapman & Hall/CRC,* Boca Raton, FL, 2000.

11. S. N. Elaydi and R. J. Sacker, Global Stability of Periodic Orbits of Nonautonomous Difference Equations In Population Biology and Cushing-Henson Conjectures, *Proceedings of ICDEA8, Brno (2003) (In Press).*

12. S. N. Elaydi and R. J. Sacker, Nonautonomous Beverton-Holt Equations and the Cushing-Henson Conjectures, *J. Diff. Equations Appl (In Press).*

13. S. N. Elaydi and R. J. Sacker, Periodic Difference Equations, Populations Biology and the Cushing-Henson Conjectures, (Preprint).

14. S. N. Elaydi and R. J. Sacker, Global Stability of Periodic Orbits of Nonautonomous Difference Equations and Population Biology, *J. Diff. Eq.* 208 (1), 258-273 (2005).

15. S. N. Elaydi and A.-A. Yakubu, Global Stability of Cycles: Lotka-Volterra Competition Model With Stocking, *J. Diff. Equations Appl. 8(6), 537-549 (2002).*

16. M. E. Fisher and B. S. Goh, Stability results for delayed recruitment models in population dynamics, *J. Math. Biol.* 19, 147-156 (1984).

17. J. E. Franke and J. F. Selgrade, Attractor for Periodic Dynamical Systems, *J. Math. Anal. Appl.* 286, 64-79(2003).

18. J. E. Franke and A.-A. Yakubu, Periodic Dynamical Systems in Unidirectional Metapopulation models, *J. Diff. Equations Appl. (In Press).*

19. J. E. Franke and A.-A. Yakubu, Multiple Attractors Via Cusp Bifurcation In Periodically Varying Environments, *J. Diff. Equations Appl. (In Press).*

20. J. E. Franke and A.-A. Yakubu, Attenuant cycles In periodically forced discrete-time age-structured population models, *J. Math. Anal. Appl. (In Press).*

21. J. Guckenheimer, G. F. Oster and A. Ipaktchi, The dynamics of density dependent population models, *J. Math. Biol.* 4, 101-147 (1976).

22. M. P. Hassell, The dynamics of competition and predation, *Studies in Biol.* 72, The Camelot Press Ltd. (1976).

23. M. P. Hassell, J. H. Lawton and R. M. May, Patterns of dynamical behavior in single species populations, *J. Anim. Ecol.* 45, 471-486 (1976).

24. S. M. Henson, Multiple attractors and resonance in periodically forced population models, *Physics D* 140, 33-49 (2000).

25. S. M. Henson, The effect of periodicity in maps, *J. Diff. Equations Appl. 5, 31-56 (1999).*

26. S. M. Henson, R. F. Costantino, J. M. Cushing, B. Dennis and R. A. Desharnais, Multiple attractors, saddles, and population dynamics in periodic habitats, *Bull. Math. Biol.* 61, 1121-1149 (1999).

27. S. M. Henson and J. M. Cushing, The effect of periodic habitat fluctuations on a nonlinear insect population model, *J. Math. Biol.* 36, 201-226 (1997).

28. J. W. Horwood and J. G. Shepherd, The sensitivity of age structured populations to environmental variability, *Math. Biosci.* 57, 59-82 (1981).

29. D. Jillson, Insect populations respond to fluctuating environments, *Nature,* 288, 699-700 (1980).

30. V. L. Kocic, A note on nonautonomous Beverton-Holt model, *J. Diff. Equations Appl.* (In press).

31. R. Kon, A note on attenuant cycles of population models with periodic carrying capacity, *J. Diff. Equations Appl.* (In press).

32. R. Kon, Attenuant cycles of population models with periodic carrying capacity, *J. Diff. Equations Appl.* (In press).

33. M. R. S. Kulenovic and A.-A. Yakubu, Compensatory versus overcompensatory dynamics in density-dependent Leslie models, *J. Diff. Equations Appl., 10(13-15), 1251-1265 (2004)*.

34. P. H. Leslie, On the use of matrices in certain population mathematics, *Biometrika* 33, 183-212 (1945).

35. P. H. Leslie, Some further notes on the use of matrices in population mathematics, *Biometrika* 35, 213-245 (1948).

36. S. A. Levin and C. P. Goodyear, Analysis of an Age-structured fishery model, *J. Math. Biol,* 9, 245-274 (1980).

37. E. G. Lewis, On the generation and growth of a population, *Sankhya* 6, 93-96 (1942).

38. J. Li, Periodic solutions of population models in a periodically fluctuating environment, *Math. Biosc.* 110, 17-25 (1992).

39. R. M. May and G. F. Oster, Bifurcations and dynamic complexity in simple ecological models, *Amer. Naturalist* 110, 573-579 (1976).

40. R. M. May, Simple mathematical models with very complicated dynamics, *Nature* 261, 459-469 (1977).

41. R. M. May, Stability and complexity in model ecosystems, *Princeton University Press* (1974).

42. A. J. Nicholson, Compensatory reactions of populations to stresses, and their evolutionary significance, *Aust. J. Zool.* **2**, 1-65 (1954).

43. R. M. Nisbet and W. S. C. Gurney, *Modelling Fluctuating Populations*, Wiley & Son, New York, 1982.

44. P. M. North, A computer modelling study of the population dynamics of the screech owl (Otus asio), *Ecol. Modelling,* 30, 105-114 (1985).

45. L. Pennycuick, A computer model of the Oxford great tit population, *J. Theor. Biol.* 22, 381-400 (1969).

46. S. Rosenblat, Population models in a periodically fluctuating environment, *J. Math. Biol.*, 9, 23-36 (1980).

47. J. F. Selgrade and H. D. Roberds, On the structure of attractors for discrete, periodically forced systems with applications to population models, *Physica D* 158, 69-82 (2001).

48. H. L. Smith, Cooperative systems of differential equations with concave nonlinearities, *Nonlin. Anal. TMA*, 10, 10, 1037-1052 (1986).

49. C. C. Travis, W. M. Post, D. L. DeAngelis and J. Perkowski, Analysis of compensatory Leslie matrix models for competing species, *Theo. Pop. Biol.* 18, 16-30 (1980).

50. A. Wikan, Dynamical consequences of harvest in discrete age-structured population models, *J. Math. Biol.* 49, 35-55 (2004)

51. A.-A. Yakubu, Multiple attractors in juvenile-adult single species models, *J. Diff. Equations Appl.* 9 (12), 1083-1093 (2003).

52. A.-A. Yakubu, Periodically forced nonlinear difference equations with delay, *J. Diff. Equations Appl., (In press)*.

53. P. Yodzis, Introduction to Theoretical Ecology, *Harper & Row Publishers*, New York (1989).

54. X.-Q. Zhao, Asymptotic behavior for asymptotically periodic semiflows with applications, *Commun. Appl. Nonlinear Anal.* 3, 43-66 (1996).

55. X.-Q. Zhao, Dynamical systems in population biology, *Canadian Mathematical Society, Springer*, New York (2003).