

## RESEARCH ARTICLE

Population Models with Allee Effect:  
A New ModelSaber N. Elaydi\*<sup>‡</sup> and Robert J. Sacker<sup>¶</sup><sup>†</sup><sup>‡</sup>Department of Mathematics, Trinity University, San Antonio, TX 78212 USA<sup>¶</sup>Department of Mathematics, University of Southern California, Los Angeles, CA  
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In this paper we develop several population models with Allee effects. We start by defining the Allee effect as a phenomenon in which individual fitness increases with increasing density. Based on this biological assumption, we develop several fitness functions that produce corresponding models with Allee effects. In particular, a rational fitness function yields a new mathematical model that is our focus of study. Then we study the dynamics of 2-periodic systems with Allee effects and show the existence of an asymptotically stable 2-periodic carrying capacity.

**Keywords:** Allee effect, fitness function, carrying capacity, threshold point, stability.

**AMS Subject Classification:** 39A11, 92D25

## 1. Introduction

In the last decade, there has been a renewed interest in a biological phenomenon called the Allee effect. A biology book [5] just appeared that is solely dedicated to study this phenomenon and hundreds of papers dealing with the Allee effect were cited in this book. Surprisingly, the literature on mathematical modeling of the Allee effect is lagging behind. For the convenience of the reader we cite some of the recent mathematical papers on modeling the Allee effect: [3, 6, 14, 15, 18, 19, 22, 25, 28, 29].

But what is the Allee effect? The Allee effect is a phenomenon in population dynamics attributed to the biologist Warder Clyde Allee [1, 2]. Allee proposed that the per capita birth rate declines at low population densities. Under such scenario, a population at low densities may slide into extinction. Allee found that the highest per capita growth rates of the population of the flour beetles, *Tribolium cofusum*, were at intermediate densities. Moreover, when fewer mates were available, the females produced fewer eggs, a rather unexpected outcome. Allee did not provide a definite and precise definition of this new notion. Stephens, Sutherland, and Freckleton [26] defined the Allee effect as “a positive relationship between any component of individual fitness and either numbers or density of conspecifics.” In classical dynamics, we have a negative density dependence, that is, fitness decreases

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with increasing density. The Allee effect, however, produces a positive density dependence, that is, fitness increases with increasing density.

The instability of the lower equilibrium (Allee threshold)[5] means that natural populations subject to a demographic Allee effect are unlikely to persist in the range of population sizes where the effect is manifest. Another issue that may cause some confusion in the use of the term Allee effect whether the phenomenon is caused by low population sizes or by low population densities. Though for field ecologists, a drop in number will be inseparable from a corresponding reduction in density. Allee himself considered both types of Allee effect and observed the Allee effect caused by reduction in the number of mice, and the Allee effect caused by the reduction in density of flour beetles, *Tribolium confusum* [1]. In [27], Stephens and Sutherland described several scenarios that cause the Allee effect in both animals and plants. For example, cod and many freshwater fish species have high juvenile mortality when there are fewer adults. While fewer red sea urchin give rise to worsening feeding conditions of their young and less protection from predation. In some mast flowering trees, such as *Spartina alterniflora*, with a low density have a lower probability of pollen grain finding stigma in wind-pollinated plants [27].

The main aim of this paper is to derive various single-species models with Allee effects based on sound biological assumptions. Starting with the assumption that individual fitness increases for small population densities, we develop a variety of fitness functions which produce corresponding models with Allee effects.

In the sequel, we will consider the difference equation

$$x_{t+1} = f(x_t) \quad f : \mathbb{R}^+ \rightarrow \mathbb{R}^+ = [0, \infty), \quad t = 0, 1, 2, \dots$$

whose dynamics exhibit the Allee effect and in certain cases obtain some new results. Some of the models are modifications of old well studied models [3, 14], while others are new models introduced to give the modeler the ability to take into account effects not available from older models. We must leave it to others to glean whatever benefit can be had from looking at these new models. Any function  $f$  whose graph passes through the origin and remains below the diagonal near zero and later crosses the diagonal twice will give rise to the Allee effect. For simplicity in discussion we will refer to the first crossing as the *Allee threshold*,  $A$  and the later crossing as the *carrying capacity*,  $K$ .

In investigating certain phenomena such as *resonance* or *attenuation* it is advantageous to have the carrying capacity  $K$  as a parameter in the model. For example the Cushing-Henson conjecture [7, 8] for the Beverton-Holt equation

$$x_{t+1} = \frac{\mu K x_t}{K + (\mu - 1)x_t} \tag{1.1}$$

stated that a periodically varying environment  $\{K_0, K_1, \dots, K_{p-1}, K_p = K_0\}$ , (1) gives rise to a periodic state  $\{\bar{x}_0, \bar{x}_1, \dots, \bar{x}_{p-1}\}$  that globally attracts all positive solutions and (2), the average

$$Av(\bar{x}_t) \doteq \frac{1}{p} \sum_{i=0}^{p-1} \bar{x}_i$$

satisfies  $Av(\bar{x}_t) < Av(K_t)$ , i.e. there is *attenuation*. Cushing and Henson established these fact for  $p = 2$  and later, [10, 13, 21] solved the general case by a variety of different methods. In [16] it was established in the case of randomly varying  $K$ . In [12] it was also shown by the authors (for  $p = 2$ ) that if the growth parameter  $\mu$

is allowed to vary as well then the opposite inequality in the averages can occur, namely *resonance*, if the parameters are sufficiently *in phase*.

The existence of the periodic solution follows directly from the *concavity* of the functions

$$x_{t+1} = \frac{\mu K_t x_t}{K_t + (\mu - 1)x_t}$$

and the fact their graphs cross the diagonal [10] since the class of such functions form a *semigroup* under composition. Further, if the fixed points  $x_f$  and  $x_g$  of  $f$  and  $g$  satisfy  $x_f < x_g$  then the fixed points of the compositions,  $x_{f \circ g}$  and  $x_{g \circ f}$  lie strictly between

$$x_f < x_{f \circ g} < x_g, \quad x_f < x_{g \circ f} < x_g, \quad (1.2)$$

the *containment property*. From this it follows that the periodic state lies inside the *envelope* of the fixed points of the component maps.

What is interesting is that the same containment property holds if the functions are increasing and *convex* and can thus be applied to most of the models displaying the Allee effect since their functions are convex in some neighborhood of the origin. Thus let us define

$$\mathcal{F}_0 \doteq \{f : \mathbb{R}^+ \rightarrow \mathbb{R}^+ \mid f(0) = 0, f \uparrow \text{ continuous and } f \text{ convex on some interval } [0, b_f]\},$$

$$\mathcal{F}_A \doteq \{f \in \mathcal{F}_0 \mid \exists x_1, x_2 \in [0, b_f], \quad (1.3)$$

$$f(x_1) < x_1, f(x_2) > x_2\},$$

$$\mathcal{F}_K \doteq \{f \in \mathcal{F}_A \mid \exists \text{ unique } K_f > b_f \ni f(K_f) = K_f\}. \quad (1.4)$$

Then  $f \in \mathcal{F}_A$  implies that  $f$  has a unique Allee fixed point  $A_f$  in  $[0, b_f]$ . The following theorem can then be proved

**Theorem 1.1:** *Let  $\mathcal{U} \subset \mathcal{F}_K$  be a subset such that*

$$\sup_{f \in \mathcal{U}} A_f < \inf_{f \in \mathcal{U}} K_f, \quad \text{then } f, g \in \mathcal{U} \implies$$

$$A_f < A_{f \circ g} < A_g \quad \text{and} \quad A_f < A_{g \circ f} < A_g .$$

*and  $\mathcal{U}$  is a semigroup under composition.*

**Proof:** Since  $f$  and  $g$  are convex and increasing on  $[0, b_f]$ , it follows that  $g \circ f$  is also convex on  $[0, b_f]$ . Hence  $A_f < A_g \implies g(A_f) < A_f$  and  $A_g < f(A_g)$ . Therefore,  $g \circ f(A_f) = g(A_f) < A_f$ . Choose  $z$  such that  $f(z) = A_g$  and  $A_f < z < A_g$ . Then  $g(f(z)) = A_g > z$ . By the intermediate value theorem, there exists a fixed point  $A_{g \circ f}$  between  $A_f$  and  $A_g$ . Similarly,  $f \circ g(A_f) < f(A_f) = A_f$ , and  $f \circ g(A_g) = f(A_g) > A_g$ .  $\square$

From the above we see that it is important that the carrying capacity, growth rate, or Allee threshold appear in the model as parameters if we want to consider their respective variations with time (periodic, stochastic, almost periodic, etc.).

As an aid in the construction of models we define the *fitness function*

$$u(x_t) = \frac{x_{t+1}}{x_t} \quad (1.5)$$

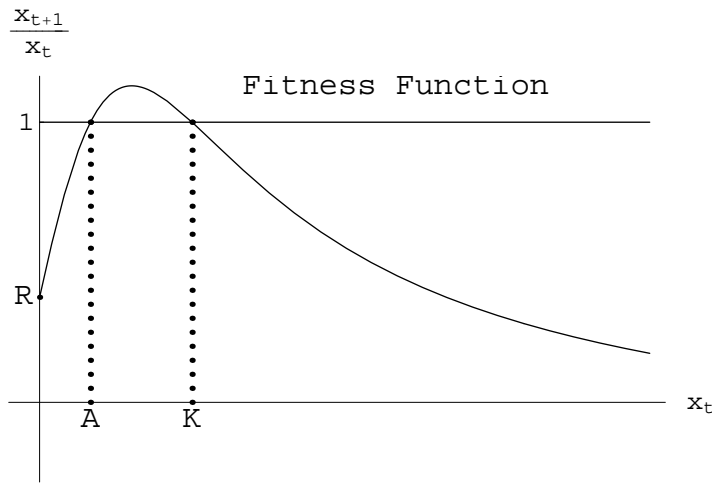


Figure 1. Fitness Function

as a function that passes through the points  $(0, R)$ ,  $(A, 1)$ ,  $(K, 1)$ , where  $R$  is the repulsion ( $R > 1$ ) or attraction ( $R < 1$ ) rate when  $x_t = 0$ .

When the population is sufficiently small (close to zero), the competition is negligible and the net reproductive rate can be approximated by  $R$ . Thus  $\frac{x_{t+1}}{x_t} = R$  when  $x_t$  is close to zero. This gives us the point  $(0, R)$  in the graph  $\frac{x_{t+1}}{x_t}$  versus  $x_t$ . When the population grows larger, intra-specific competition becomes significant and at some population sizes  $x_t = A$ , and  $x_t = K$ , the birth and death rates are equal and thus  $\frac{x_{t+1}}{x_t} = 1$ . This gives us the points  $(A, 1)$  and the point  $(K, 1)$ . Then we join these three points by a suitable curve (Figure 1). The fixed point  $A$  will be called the Allee threshold and the fixed point  $K$  will be called the carrying capacity.

## 2. The $\lambda$ -Ricker Map

In this section we obtain some properties of a modification of the Ricker map that possesses the Allee effect. The development here follows closely the argument given in [23]. In [23] the periodic Ricker System  $R_j(x) = xe^{p_j - x}$ ,  $p_j \in (0, 2)$ ,  $j = 0, 1, \dots, k-1$  was carried out and it was shown that the periodic Ricker map always has a periodic solution  $\{\bar{x}_0, \bar{x}_1, \dots, \bar{x}_{k-1}\}$  that globally attracts all positive solutions and there is neither attenuation nor resonance, i.e. one has  $\text{Av}(\bar{x}_j) = \text{Av}(p_j)$ .

To obtain the modified Ricker map, we define the fitness function

$$u(x_t) = \frac{x_{t+1}}{x_t} = x_t^{\lambda-1} e^{p-x_t}, \lambda > 1 \quad (2.1)$$

Now  $u(0) = R = 0$ ,  $u(A) = 1 = A^{\lambda-1} e^{p-A}$ , and  $u(K) = 1 = K^{\lambda-1} e^{p-K}$ . Thus  $p = A - (\lambda - 1) \ln A = K - (\lambda - 1) \ln K$ . Hence the modified Ricker map is now defined as

$$R_p(x) = x^\lambda e^{p-x}, x, p \in \mathbb{R}^+, \lambda > 1 \quad (2.2)$$

Furthermore,

$$R'_p(x) = (\lambda - x)x^{\lambda-1} e^{p-x} \quad (2.3)$$

Now we make the following observations.

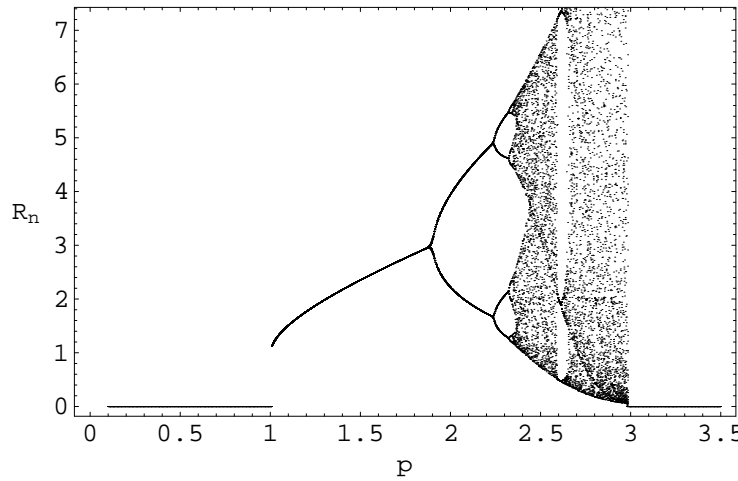


Figure 2. The bifurcation diagram for the map  $R_p(x) = x^2 e^{p-x}$ .

- (1) Notice that the fixed point 0 is always asymptotically stable since  $R'_p(0) = 0$ ,
- (2) The Allee threshold  $A$  is always unstable if it exists ( $p > 1$ ). This may be proved by a simple argument [9].
- (3) The carrying capacity  $K$  is asymptotically stable if

$$(\lambda - 1) - (\lambda - 1) \ln(\lambda - 1) < p < (\lambda + 1) - (\lambda - 1) \ln(\lambda + 1).$$

This can be shown by noticing that  $|R'_p(K)| < 1$  if  $\lambda - 1 < K < \lambda + 1$ . However,  $K^{\lambda-1} e^{p-K} = 1$ . Hence  $(\lambda - 1) \ln K + p - K = 0$ , which implies that  $p = K - (\lambda - 1) \ln K$ . Now consider the function  $h(x) = x - (\lambda - 1) \ln x$ ,  $\forall x \in (\lambda - 1, \lambda + 1)$ . Then  $h(x)$  attains its minimum  $(\lambda - 1) - (\lambda - 1) \ln(\lambda - 1)$  when  $x = \lambda - 1$  and its maximum  $(\lambda + 1) - (\lambda - 1) \ln(\lambda + 1)$  at  $x = \lambda + 1$ . Hence the carrying capacity  $K$  is asymptotically stable if

$$(\lambda - 1) - (\lambda - 1) \ln(\lambda - 1) < p < (\lambda + 1) - (\lambda - 1) \ln(\lambda + 1).$$

In particular, if  $\lambda = 2$ , then the carrying capacity  $K$  is asymptotically stable if  $1 < p < 3 - \ln 3$ . Moreover, if  $p = 3 - \ln 3$ ,  $K = 3$ , then the Schwarzian derivative  $SR_p(3) < 0$ . Thus  $K = 3$  is also asymptotically stable [9]. As  $p$  passes the value  $3 - \ln 3$ , a period doubling bifurcation begins as  $R'_p(3) = -1$ . Numerical computation shows that the new born 2-periodic orbit is asymptotically stable for  $3 - \ln 3 < p < \approx 2.235$ . The period-doubling scenario continues until  $p \approx 2.35$  after which we enter the chaotic region. Now for  $p > \approx 2.977$  the chaotic region disappears and the fixed point 0 becomes locally asymptotically stable, where its basin of attraction is  $\mathbb{R}^+ \setminus \{EFix\}$ , where  $EFix$  is the eventually fixed points of the Allee threshold and the carrying capacity. Figure 2 depicts the bifurcation diagram for the map  $R_p(x) = x^2 e^{p-x}$ . For instance, when  $p = 3$ , the Allee threshold is  $A \approx 0.0524$ . Note that for the critical point  $c = 2$   $R_p^2(2) = R_p \circ R_p(2) < 0.0524$  and hence the critical point converges to 0.

Now consider the  $k$ -periodic sequence  $\{p_0, p_1, \dots, p_{k-1}\}$  with  $p_{i+k} = p_i$ , and the  $k$ -periodic difference equation

$$x_{n+1} = R_{p_n}(x_n) = x_n^\lambda e^{p_n - x_n}, \quad n = 0, 1, \dots \quad (2.4)$$

Now consider the composition

$$\Phi_k = R_{p_{k-1}} \circ R_{p_{k-2}} \circ \cdots \circ R_{p_1} \circ R_{p_0}, \quad (2.5)$$

For any  $m$ -periodic orbit

$$\{\bar{x}_0, \bar{x}_1, \dots, \bar{x}_{m-1}\},$$

we have from (2.2) and (2.3),

$$R'_{p_n}(\bar{x}_n) = \bar{x}_n^{\lambda-1}(\lambda - \bar{x}_n)e^{p_n - \bar{x}_n} = \frac{\lambda - \bar{x}_n}{\bar{x}_n} \bar{x}_n^\lambda e^{p_n - \bar{x}_n} = (\lambda - \bar{x}_n) \frac{\bar{x}_n^{\lambda+1}}{\bar{x}_n}$$

Taking the derivative of (2.5),

$$\begin{aligned} |\Phi'_k(\bar{x}_0)| &= |R'_{p_{k-1}}(\bar{x}_{k-1})R'_{p_{k-2}}(\bar{x}_{k-2}) \times \cdots \times R'_{p_0}(\bar{x}_0)| \\ &= \left| \frac{\bar{x}_k}{\bar{x}_0} \prod_{i=0}^{k-1} |\lambda - \bar{x}_i| \right| = \prod_{i=0}^{k-1} |\lambda - \bar{x}_i|. \end{aligned} \quad (2.6)$$

The next step is to find a forward invariant interval  $\mathcal{I}$  on the  $x$ -axis on which  $|\Phi'_k(x)| < 1$ . Consider only the case  $\lambda = 2$  and define  $\bar{p} = 3 - \ln 3$ . Let  $\mathcal{I} = [a, b]$ . Then the right endpoint of  $\mathcal{I}$  must be less than or equal to  $R_{\bar{p}}(2) = 4e^{1-\ln 3} = \frac{4}{3}e \approx 3.6244$  since each function  $R_p$  attains its maximum value at  $x = 2$ .

In defining the left endpoint, there is a subtle distinction between the period  $k > 2$  and  $k = 2$  and in order to appreciate this let us recall that for  $k = 1$ , as  $p$  increases through 1 the fixed points constituting the Allee threshold  $A$  and the carrying capacity  $K$  are created through a saddle-node bifurcation so that at  $p = 1, A = 1 = K$ , and for  $p > 1$  we have  $A < 1 < K$ . As  $p$  increases further,  $A$  and  $K$  move monotonically away from 1. Consequently,  $1 \leq a < b < R_{\bar{p}}(2)$

### 2.1. Invariant Interval ( $\lambda = 2$ , Period $k > 2$ case)

What we will show is that for  $p \in (1, 3 - \ln 3)$ , the interval  $\mathcal{I} = [1, b]$ ,  $b \approx 3.17179$  (later we give an appropriate explanation for these chosen values) is invariant but under certain restrictions on the *variation of the adjacent  $p$  values*, i.e. the  $p$  values of adjacent maps  $R_j \circ R_{j-1}$  in (2.5). To see why this is needed we consider points very close to the endpoints of the  $p$ -interval,  $p_0 = \bar{p} - 0.001$  and  $p_1 = 1.001$  in (2.5). A calculation shows

$$x_2 = R_{p_1} \circ R_{p_0}(2) \approx 0.95467 \quad (2.7)$$

Now let  $A_p$  denote the Allee threshold of  $R_p$  and choose  $p_2, p_3, \dots, p_{k-1}$  so close to 1 that  $x_2 \in (0, A_p)$  for all  $p \in \{p_2, p_3, \dots, p_{k-1}\}$ . Then let  $k$  be so large that  $x_k = R_{p_{k-1}}(x_{k-1}) \in (0, A_{p_0})$ , the smallest of the ‘‘Allee intervals’’. Then the orbit  $\{x_n\}$  starting at  $x_0 = 2$  will go extinct,  $\lim_{n \rightarrow \infty} x_n = 0$ .

However, if we restrict the variation

$$\max |p_j - p_{j-1}| < 0.8523$$

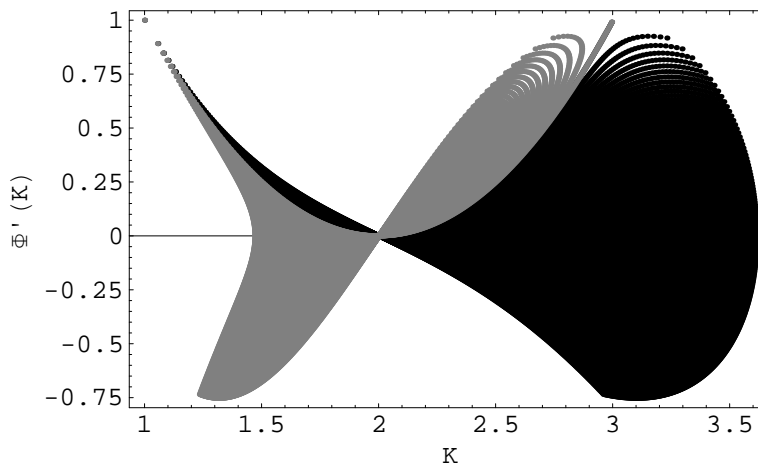


Figure 3. The black region shows the values of the derivatives of  $\Phi_2$  at the carrying capacity of  $f \circ g$ , while the grey region depicts the values of the derivatives of  $\tilde{\Phi}_2$  at the carrying capacity of  $g \circ f$ .

it can be verified numerically that  $R_{p_j} \circ R_{p_{j-1}} > 1 > A_p$  for all  $p \in [1, 3 - \log 3]$ .

**Note:** The length of the allowable  $p$  interval  $[1, 3 - \ln 3]$  is  $\approx .90138$  so the above restriction on the allowable variation between the  $p$  values of successive maps doesn't seem too restrictive.

To see that  $|\Phi'_k(x)| < 1$  for  $x \in \mathcal{I}$  we argue as in [23] and assume one of the factors  $|2 - x_j| \geq 1$  in (2.6). Now consider the product

$$|(2 - x_{j-1})(2 - x_j)| = |(2 - x)(2 - x^2 e^{p-x})|, \quad x = x_{j-1},$$

and define

$$g(x) = (2 - x)(2 - x^2 e^{p-x}), \quad 1 \leq p \leq 3 - \ln 3, x \in \mathcal{I}. \quad (2.8)$$

When  $p = 1$ ,  $g$  is a decreasing function on  $\mathcal{I}$ , and attains its maximum value 1 when  $x = 1$  and attains its minimum value  $-1$  at  $x = 3.17179$ . As  $x$  passes the value 3.17179, the absolute value of  $g$  becomes greater than 1. Furthermore, the maximum of  $g$  is less than 1 whenever  $p > 1$  and  $x \in \mathcal{I}$ . When  $p = 3 - \ln 3$ ,  $g$  attains its maximum value 1 at  $x = 3$ . Moreover, the maximum value of  $g$  is  $< 1$  whenever  $p < 3 - \ln 3$  and  $x \in \mathcal{I}$ . Another critical point of  $g$  is computed numerically and is approximated by  $x = 1.315166$ , when  $p = 3 - \ln 3$ . Notice that  $g(1.315166) = -0.759154$ ,  $g(1) = -0.463019$ , and  $g(3.17179) = 0.965673$ . This is demonstrated clearly in figures 3 and 4.

Thus, we have shown that the interval  $\mathcal{I}$  is invariant under the mapping  $\Phi_k$  for  $1 < p < 3 - \ln 3$ . This implies that  $\Phi_k$  has at least one fixed point in the interval  $\mathcal{I}$ .

## 2.2. Invariant Interval ( $\lambda = 2$ , Period $k = 2$ case)

Here the restriction on the  $p$ -variation is not needed since although  $x_2 < 1$ , the next function to act is  $R_{p_0}$  and  $R_{p_0}(x_2) \approx 2.3465$ . Thus, using the endpoints of the  $p$ -interval we define the invariant interval

$$\mathcal{I} = [a, b], \quad \text{where } b \approx 3.17179, \quad \text{and } a = R_1(b) \approx 1.1466.$$

Again, the argument given above for the function  $g$  defined in (2.8), gives

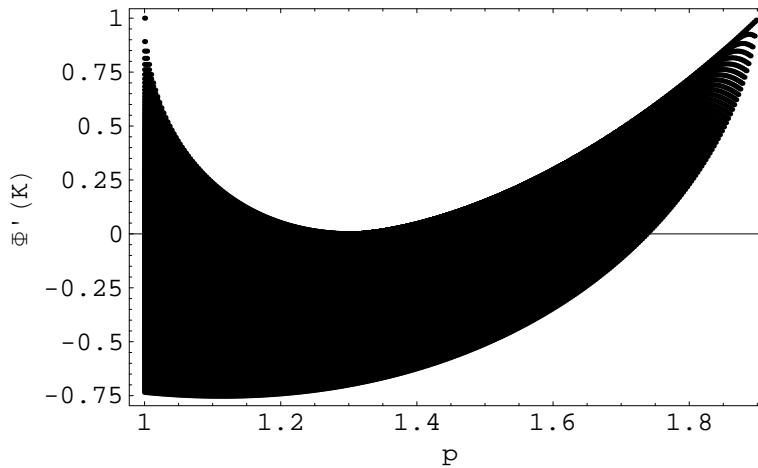


Figure 4. The black region represents the values of the derivatives of  $\Phi_2$  and  $\tilde{\Phi}_2$  at the carrying capacity of  $f \circ g$  and  $g \circ f$  when the parameter  $p_0$  and  $p_1$  vary between 1 and  $3 - \ln 3$ .

$$|(2 - x_{j-1})(2 - x_j)| < 1.$$

### 2.3. Asymptotic Stability of Fixed Point

From (2.6) it follows that any fixed point in the invariant interval  $\mathcal{I}$  is asymptotically stable. From this it follows that the fixed point is unique and attracts all orbits in  $\mathcal{I}$ , see [9, p.52, Th. 1.30]. Hence we have a globally asymptotically stable  $k$ -periodic orbit. Moreover, the period  $k$  is minimal since the family of maps  $R_p$  is one to one with respect with the parameter  $p$ , [13]

## 3. A Canonical Form

In this section we study the following fractional quadratic map

$$f(x) = \frac{x}{\alpha + x} \frac{x}{p + qx}.$$

By proper choice of  $p$  and  $q$  one obtains

$$f(x) = \frac{x}{\alpha + x} \frac{(\alpha + A)(\alpha + K)x}{AK + \alpha x}. \quad (3.1)$$

In this form it follows that

$$f(0) = 0, \quad f(A) = A \quad \text{and} \quad f(K) = K.$$

Also,

$$f'(x) = \frac{(\alpha + A)(\alpha + K)(2\alpha AK + \alpha^2 x + AKx)x}{(\alpha + x)^2(AK + \alpha x)^2} \quad (3.2)$$

and since  $A$  and  $K$  occur symmetrically in (3.1) we assume without loss of generality that  $A < K$ . Direct computation shows that  $f'(0) = 0$  and

$$f'(A) = \frac{2\alpha K + \alpha^2 + AK}{(\alpha + A)(\alpha + K)} > 1 > f'(K) = \frac{2\alpha A + \alpha^2 + AK}{(\alpha + A)(\alpha + K)}.$$



Thus for the difference equation

$$x_{n+1} = f(x_n) ,$$

the origin is the attracting *extinction* state,  $A$  is the repelling, or *Allee* threshold and  $K$  is the attracting fixed point or *carrying capacity*.

Note also that the mean

$$\frac{f'(A) + f'(K)}{2} = 1.$$

#### 4. A New Model

In this section we develop a general model of populations with the Allee effects. By a suitable choice of the parameters, one may be able to generate maps with the same qualitative dynamics as the previously discussed maps. Moreover, this new model may produce a Beverton-Holt type map with an Allee effect. The authors believe this new model is the right model for populations that are under the influence of the Allee effects. The model also allows one to study the dynamics of the map after a large surge (overstocking) in the population. For maps of the Ricker type, if the surge is large enough the population will *always* go extinct, whereas for maps of the Beverton-Holt type (concave) the population *always* returns toward the carrying capacity. We note that, the competition of the Ricker type and Beverton-Holt type are often called the scramble and contest competition, respectively. In the following map there is an additional parameter “ $b$ ” which we call the *shock recovery* parameter which controls this effect.

Consider the fitness function of the form

$$u(x) = \frac{dx + e}{x^2 + bx + c}. \quad (4.1)$$

Forcing the graph of  $u$  to pass through the three points in Figure 1 we obtain

$$u(x) = \frac{(A + K + b)x + R \frac{AK}{1-R}}{x^2 + bx + \frac{AK}{1-R}}$$

and the corresponding difference equation  $x_{t+1} = f(x_t; R) = x_t u(x_t)$ , or

$$f(x_t; R) = x_t \frac{(A + K + b)x_t + R \frac{AK}{1-R}}{x_t^2 + bx_t + \frac{AK}{1-R}}$$

where  $b$  is still a free parameter. The parameter  $R$  is the *attraction rate* at the extinction point 0. Introducing the *growth rate*  $\mu$  at the Allee threshold,  $\mu = f'(A; R)$  and using this to eliminate  $R$  one obtains the difference equation  $x_{t+1} = G(x_t; \mu)$  where

$$G(x; \mu) \doteq x \frac{(A + K + b)x + \frac{A}{(\mu-1)}[2K + b - \mu(A + K + b)]}{x^2 + bx + \frac{A}{(\mu-1)}[K - \mu A - (\mu - 1)b]}. \quad (4.2)$$

Then we have

$$\begin{aligned} f(0; R) = G(0; \mu) = 0, \quad f(A, R) = G(A, \mu) = A, \\ f(K; R) = G(K, \mu) = K, \quad f'(0; R) = R, \quad G'(A, \mu) = \mu \\ \lim_{x \rightarrow \infty} f(x; R) = \lim_{x \rightarrow \infty} G(x; \mu) = A + K + b. \end{aligned}$$

Parameter  $b$  regulates the asymptotic value at  $\infty$ .

For  $b = 0$

$$G(x; \mu) = \frac{(A + K)x^2 + \frac{A}{(\mu-1)}[2K - \mu(A + K)]x}{x^2 + \frac{A}{(\mu-1)}[K - \mu A]}. \quad (4.3)$$

Since

$$f(x_t, R) = f(x) = xu(x), \quad (4.4)$$

it follows that

$$f'(x) = u(x) + xu'(x). \quad (4.5)$$

Moreover,

$$u'(x) = (R - 1) \frac{(R - 1)(A + K + b)x^2 + 2RAKx + (bR - A - K - b)}{[(1 - R)x^2 + b(1 - R)x + AK]^2}.$$

Since  $A + K + b \geq 0$ ,  $u'(x) = 0$  has at most one positive real root  $C_u$  as shown in figure 1.

Notice that  $u(x) > 0$ . By a simple computation one concludes that  $u''(x) < 0$  on  $(0, \infty)$ . Thus  $u(x)$  is concave on  $(0, \infty)$ . Moreover,  $f'(x) = u(x) + xu'(x) \geq 0$  on  $(0, C_u)$ . Notice also that  $f(x)$  is decreasing on  $(C_u, \infty)$ .

To insure that  $f'(x) \geq 0$  on  $[0, K]$ , we require that  $f'(K) = u(K) + Ku'(K) \geq 0$ . This implies that

$$b \geq -A \left( \frac{2 - R}{1 - R} \right) \quad (4.6)$$

**Standing assumption:** In the sequel, (4.6) is always assumed.

Under this assumption  $f(x)$  is increasing on  $[0, K]$ . In this case, it is easy to prove the following result

**Theorem 4.1:** Under assumption (4.6) we have the following

- (1)  $x^* = 0$  is locally asymptotically stable,
- (2)  $x^* = A$  is unstable,
- (3)  $x^* = K$  is locally asymptotically stable.

**Proof:** See [9]. □

If in addition,  $A + K + b \geq A$  or  $b \geq -K$ , then  $\mathcal{B}(0) = [0, A)$  and  $\mathcal{B}(K) = (A, \infty)$ , where  $\mathcal{B}$  denotes the basin of attraction.

## 5. New class of maps

Let us define a subset of  $\mathcal{F}_K$ , see (1.4).

$$\mathcal{F} = \{h \in \mathcal{F}_K \mid h \uparrow \text{ and concave on } [b_h, K_h] \text{ and } h \text{ has at most one critical point in } [K_h, \infty)\}$$

**Lemma 5.1:** *Let  $\mathcal{W}$  be a subset of  $\mathcal{F}$  such that*

$$\sup_{h \in \mathcal{W}} A_h < \inf_{h \in \mathcal{W}} K_h. \quad (5.1)$$

*Let  $f, g \in \mathcal{W}$ , with  $K_f < K_g$ . Then*

- (1)  $K_f < K_{f \circ g} < K_g$
- (2)  $K_f < K_{g \circ f} < K_g$ .

**Proof:**  $g(f(K_f)) = g(K_f) > K_f$  and  $g(f(K_g)) < g(K_g) = K_g$ . Hence there exists a fixed point  $K_{g \circ f}$  of  $g \circ f$  with  $K_f < K_{g \circ f} < K_g$ . Now  $f(g(K_g)) = f(K_g) < K_g$ . Moreover, since  $g(K_f) > K_f$ , it follows that  $f(g(K_f)) > K_f$ . Hence there exists a fixed point  $K_{f \circ g}$  of  $f \circ g$  with  $K_f < K_{f \circ g} < K_g$   $\square$

**Corollary 5.2:** *Under assumption (5.1), the system  $\{f, g\}$  has a 2-periodic cycle for  $f, g \in \mathcal{W}$ .*

**Theorem 5.3:** [24](Theorem 2.1, p. 47) [12](Corollary 2.4) *Let  $x^*$  be a fixed point of a continuous map on the compact interval  $I = [a, b]$ . Then  $x^*$  is globally asymptotically stable relative on  $(a, b)$  if and only if  $f^2(x) > x$  for  $x < x^*$  and  $f^2(x) < x$  for  $x > x^*$ , for all  $x \in (a, b)$ .*

**Theorem 5.4:** *Let  $f, g \in \mathcal{F}$  with  $K_f < K_g$  and let  $h = g \circ f$ . We also assume that  $g(x) > f(x)$  on  $[K_f, \infty)$ . Then the following statements hold true:*

- (1) *if  $C_f > K_g$ , where  $C_f$  is the critical point of  $f$ , then  $K_{g \circ f}$  is asymptotically stable under  $h$ ,*
- (2) *if  $C_f < K_g$  and  $h^2(C_f) > C_f$ , then  $K_{g \circ f}$  is asymptotically stable under  $h$ .*

**Proof:**

- (1) Since  $h'(x) = g'(f(x))f'(x)$ , it follows that the critical point of  $h$  are  $C_f$  and all the points in the set  $\{f^{-1}(C_g)\}$ . Since  $g(x) > f(x)$  on  $[K_f, \infty)$ ,  $\{f^{-1}(C_g)\} = \emptyset$ . Thus  $C_f = C_h > K_g$ . By Lemma 5.1,  $C_h > K_{g \circ f}$ . Hence  $h \in \mathcal{F}$  and the conclusion follows.
- (2) Now assume that  $C_f < K_g$  and  $h^2(C_f) > C_f$ . If  $C_f \geq K_{g \circ f}$  we are done as in (1). So let us assume that  $C_h = C_f < K_{g \circ f}$ . Hence  $h(C_h) > K_{g \circ f}$  and  $h^2(C_h) < K_{g \circ f}$ . From the assumption  $C_h < h^2(C_h) < K_{g \circ f}$ . Thus in the invariant set  $[C_h, h(C_h)]$ , we have  $h^2(x) > x$  if  $x < K_{g \circ f}$  and  $h^2(x) < x$  if  $x > K_{g \circ f}$ . Hence by Theorem 5.3, we conclude that the fixed point  $K_{g \circ f}$  is asymptotically stable.  $\square$

**Lemma 5.5:** *Suppose that assumption (4.6) holds. Then for any  $K$ ,  $f(x)$  in (4.4) belongs to  $\mathcal{F}$ .*

**Proof:** The proof follows from the discussion in Section 6.  $\square$

**Theorem 5.6:** *Let  $\{f, g\} = \mathcal{W}$  be a 2-periodic system, where  $f, g$  as defined in (4.4) with carrying capacities  $K_f, K_g$ , respectively. Then under the assump-*

tion of theorem 5.4, System  $\mathcal{W}$  has an asymptotically stable 2-periodic cycle,  $\{K_{g \circ f}, f(K_{g \circ f})\}$ .

**Proof:** The proof follows from 5.4. □

## 6. Conclusions

Several discrete models have been discussed using the Fitness Function approach. These models exhibit the Allee effect and have the further attribute similar to the Beverton-Holt equation, that the parameters in the equations have biological meaning, e.g. Allee threshold, carrying capacity, growth parameter. Certain classes of maps (right hand sides of difference equations) are shown to form semigroups with respect to composition thus allowing one to treat equations with periodic parameters with great ease. In addition the Allee thresholds satisfy the *containment property*, namely the Allee threshold of a composition lies strictly between the thresholds of the component maps, another property shared by the carrying capacities in the Beverton-Holt map.

A new model belonging to a sub-class of the above maps is introduced whose carrying capacities also exhibit the containment property. For a pair of maps, conditions are given guaranteeing a modified global asymptotic stability of the carrying capacity, i.e. with initial states avoiding the Allee capture interval. The new model also contains an additional parameter called the *shock recovery parameter* that allows the modeler to take into account the effect of a gross overstocking of the population.

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## References

- [1] W.C. Allee, *The Social Life of Animals*, William Heinemann, London, 1938.
- [2] W.C. Allee, A.E. Emerson, O. Park, T. Park & K.P. Schmidt, *Principles of animal ecology*, Saunders, Philadelphia, 1949.
- [3] M. Anazawa, *Bottom-up of derivation of discrete discrete-time population models with the Allee effect*, Theoretical Population Biology, Vol. 75, 1 (2009), pp. 56-67
- [4] P. Bezandry, T. Diagana and S. Elaydi, *On the stochastic Beverton-Holt equation with survival rates*, J. Diff. Eq. & Appl., **14** (2008), 175-190.
- [5] F. Courchamp, L. Berec and J. Gascoigne, *Allee Effects*, Oxford University Press, Oxford, 2008.
- [6] J.M. Cushing, *The Allee effect in age-structured population dynamics* in T. Hallam, L. Gross, and S. Levin (Eds.), *Mathematical Ecology*, Springer-Verlag (1988), 479-505.
- [7] J.M. Cushing, and S.M. Henson, *Global dynamics of some periodically forced, monotone difference equations*, J. Difference Equ. & Appl., **7** (2001), 859-872.
- [8] J.M. Cushing, and S.M. Henson, *A periodically forced Beverton-Holt equation*, J. Difference Equ. & Appl., **8** (2002), 1119-1120.
- [9] Elaydi, S., *Discrete Chaos: With Applications in Science and Engineering, Second Edition*, Chapman & Hall/CRC, Boca Raton, 2008.
- [10] S. Elaydi, and R. Sacker, *Global stability of periodic orbits of nonautonomous difference equations and population biology*, J. Differential Equations **208** (2005), 258-273.
- [11] S. Elaydi, and R. Sacker, *Global stability of periodic orbits of nonautonomous difference equations in population biology and the Cushing-Henson conjectures*, Proceedings of the eighth International Conference on Difference Equations and Applications, Brno, 2003. 113-126, Chapman & Hall/CRC, Boca Raton, FL, 2005.
- [12] S. Elaydi, and R. Sacker, *Basin of attraction of periodic orbits of maps in the real line*, J. Difference Equ. & Appl., Vol. **10** (2004), 881-888.
- [13] S. Elaydi, and R. Sacker, *Nonautonomous Beverton-Holt equations and the Cushing-Henson conjectures*, J. Difference Equ. & Appl., **11** (2005), pp. 337-347.
- [14] H. Eskola, K. Parvinen, *On the mechanistic underpinning of discrete-time populations models with Allee effect*, Theoretical Population Biol., **72** No. 1 (2007), pp. 41-51.
- [15] M.S. Fowler and G.D. Ruxton, *Population dynamic consequences of Allee effects*, J. Theor. Biol., **215**(2002), pp. 39-46.
- [16] C. Haskell, R.J. Sacker, *The Stochastic Beverton-Holt Equation and the M. Neubert Conjecture*, J. Dynamics and Differential Equations, **17** (No. 4) (2005), pp. 825-842.

## REFERENCES

- [17] S.M. Henson, *Multiple attractors and resonance in periodically forced population models*, Physica D, **40**(2000), pp. 33-49.
- [18] S.R.-J. Jang, *Allee effects in a discrete-time host-parasitoid model*. J. Difference Equ. & Appl., **12** (2006), 165-181.
- [19] R. Luís, S.Elaydi, and H.Oliveira, *Nonautonomous periodic systems with Allee effects*, Journal of Difference Equations and Applications, to appear
- [20] V.L. Kocic, *A note on the nonautonomous Beverton-Holt model*, J. Difference Eq. & Appl., **11**, Numbers 4-5,(2005), 337-347.
- [21] R. Kon, *A note on attenuant cycles of population models with periodic carrying capacity*, J. Difference Equ. & Appl., **10**(8) (2004), 791-793.
- [22] Jia Li, Baojun Song, and Xiaohong Wang, *An extended discrete Ricker population model with allee effects*. J. Difference Equ. & Appl., **13** (2007), 309-321.
- [23] Robert J. Sacker, *A note on periodic Ricker maps*, J. Difference Eq. & Appl., 13(1):89–92, January 2007.
- [24] A. N. Sharkovsky, Yu. L. Maistrenko and E. Yu. Romanenko, *Difference equations and their applications*, Kluwer Academic Publishers, London, 1993.
- [25] S. J. Schreiber, *Allee effects, extinctions, and chaotic transients in simple population models*, Theoretical Population Biology **64** (2003), 201-209.
- [26] P.A. Stephens, W.J. Sutherland & R.P. Freckleton, 'What is the Allee Effect?', Oikos **87** (1999), 185-90.
- [27] P.A. Stephens, &W.J. Sutherland, Vertebrate mating systems, Allee effects and conservation. In M. Apollonio, M. Festa-Bianchet and D. Mainardi, eds. *Vertebrate mating systems*, pp. 186-213, World Scientific Publishing, Singapore, 2000.
- [28] Abdul-Aziz Yakubu, *Allee effects in discrete-time SIUS epidemic models with infected newborns*. J. Difference Equ. & Appl., **13** (2007), 341-356.
- [29] S. Zhou, Y. Liu, and G.Wang, *The stability of predator-prey systems subject to the Allee effects*. Theoretical Population Biology, Vol. **67** (2005), 23-31.