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Stability Analysis of a Population Dynamics Model with Allee Effect

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Abstract— **In this study, we focus on the stability analysis of equilibrium points of population dynamics with delay when the Allee effect occurs at low population density is considered. Mainly, mathematical results and numerical simulations illustrate the stabilizing effect of the Allee effects on population dynamics with delay.**

Keywords: Delay difference equations, Allee effect, population dynamics, stability analysis, bifurcation

1 Introduction

Dynamic population models are generally described by the differential and difference equations with or without delay. These models have been considered by many authors, for these related results we refer to [1], [4], [6]-[10].

In 1931, Allee [1] demonstrated that a negative density dependence, the so called Allee effect, occurs when population growth rate is reduced at low population size. The Allee effect refers to a population that has a maximal per capita growth rate at low density. This occurs when the per capita growth rate increases as density increases, and decreases after the density passes a certain value which is often called threshold. This effect can be caused by difficulties in, for example, mate finding, social dysfunction at small population sizes, inbreeding depression, food exploitation, and predator avoidance of defence. The Allee effects have been observed on different organisms, such as vertebrates, invertebrates and plants. (see, for instance, [2], [3]).

The purpose of this paper is to study the following general non-linear delay difference equation with or without the Allee effect

$$N_{t+1} = F(\lambda, N_t, N_{t-T}), \tag{1}$$

where λ is per capita growth rate which is always positive, N_t represents the population density at time t, T is the time sexual maturity. Here, F has the following form

$$F(\lambda; N_t, N_{t-T}) := \lambda N_t f(N_{t-T})$$

where $f(N_{t-T})$ is the function describing interactions (competitions) among the mature individuals. It is generally assumed that f continuously decreases as density increases. Mainly, we work on the stability analysis of this model and compare the stability of this model with or without Allee effects.

Eq. (1) is an appropriate model for single species without an Allee effect. Therefore, a natural question arising here is that "How the stability of equilibrium points are effected when an Allee effect is incorporated in Eq. (1)" . In this work, we answer this question, especially, for the case when $T = 1$.

2 Stability analysis of Eq. (1) for $T = 1$

Before we give the main results of this paper, we shall remind the following well-known linearized stability theorem (see, for instance, [5] and [9]) for the following non-linear delay difference equation

$$N_{t+1} = F(N_t, N_{t-1}). \tag{2}$$

Theorem A (Linearized Stability). *Let N^* be an equilibrium point of Eq.* (2)*. Then N^* is locally stable if and only if*

$$|p| < 1 - q < 2,$$

where

$$p := \frac{\partial F}{\partial N_t}(N^*, N^*) \;\; \textit{and} \;\; q := \frac{\partial F}{\partial N_{t-1}}(N^*, N^*).$$

We now consider the following non-linear difference equation with delay

$$N_{t+1} = \lambda N_t f(N_{t-1}) =: F(\lambda; N_t, N_{t-1}), \quad \lambda > 0, \tag{3}$$

where λ is per capita growth rate, N_t is the density at time t, and $f(N_{t-1})$ is the function describing interactions (competitions) among individuals. Firstly, we assume that f satisfies the following conditions:

1° $f'(N) < 0$ for $N \in [0, \infty)$; that is, f continuously decreases as density increases.

2° $f(0)$ is a positive finite number.

Then we have the following result.

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Theorem 1 Let N^* be a (positive) equilibrium point of Eq. (3) with respect to λ. Then N^* is locally stable if and only if

$$N^* \frac{f'(N^*)}{f(N^*)} > -1. \tag{4}$$

Proof. By hypothesis, we have

$$1 = \lambda f(N^*). \tag{5}$$

Let $p := F_{N_t}(\lambda; N^*, N^*)$. Then, the equality (5) implies that $p = 1$. Also, observe that

$$q := F_{N_{t-1}}(\lambda; N^*, N^*) = N^* \frac{f'(N^*)}{f(N^*)}. \tag{6}$$

Theorem A says that N^* is locally stable if and only $|p| < 1 - q < 2$. Since $p = 1$, we conclude that N^* is locally stable if and only if $-1 < q < 0$. However, since f is a decreasing function for all N, we get from (6) that the inequality $q < 0$ is always valid. So the proof is completed.

Now we find a sufficient condition that increasing λ in Eq. (5) decreases the stability of the corresponding equilibrium points.

Theorem 2 Let λ_1 and λ_2 be positive numbers such that $\lambda_1 < \lambda_2$, and let $N^{(1)}$ and $N^{(2)}$ be corresponding positive equilibrium points of Eq. (3) with respect to λ_1 and λ_2, respectively. Then the local stability of $N^{(2)}$ is weaker than $N^{(1)}$ provided that

$$\int_{N^{(1)}}^{N^{(2)}} [N(\log f(N))']' \, dN < 0 \tag{7}$$

holds; that is, increasing λ decreases the local stability of the equilibrium point in Eq. (3) if (7) holds.

Proof. By the definitions of $N^{(1)}$ and $N^{(2)}$, it is easy to see that

$$1 = \lambda_1 f(N^{(1)}) \text{ and } 1 = \lambda_2 f(N^{(2)}). \tag{8}$$

Since $\lambda_1 < \lambda_2$, it follows from (8) that $f(N^{(1)}) > f(N^{(2)})$. Also, since f is decreasing function, we have $N^{(1)} < N^{(2)}$. Now, for each $i = 1, 2$, $q_i := F_{N_{t-1}}(\lambda_i; N^{(i)}, N^{(i)})$. Then, we can easily get that

$$q_i = N^{(i)} \frac{f'(N^{(i)})}{f(N^{(i)})} \text{ for } i = 1, 2$$

holds. So, by Theorem 2.1, each $N^{(i)}$ is locally stable if and only if

$$N^{(i)} \frac{f'(N^{(i)})}{f(N^{(i)})} > -1 \text{ for } i = 1, 2. \tag{9}$$

If the condition (7) holds, then we have

$$N^{(1)} \frac{f'(N^{(1)})}{f(N^{(1)})} > N^{(2)} \frac{f'(N^{(2)})}{f(N^{(2)})}. \tag{10}$$

Now by considering (9) and (10) we can say that the local stability in $N^{(2)}$ is weaker than $N^{(1)}$, which completes the proof.

The following condition is weaker than (7), but it enables us to control easily for increasing λ being a destabilizing parameter.

Corollary 3 Let λ_1, λ_2, $N^{(1)}$ and $N^{(2)}$ be the same as in Theorem 2.2. Then the local stability of $N^{(2)}$ is weaker than that of $N^{(1)}$ provided that

$$\left[N\left(\log f(N)\right)'\right]' < 0 \text{ for all } N \in [N^{(1)}, N^{(2)}]. \tag{11}$$

Remark If there is no time delay in model (3), i.e.,

$$N_{t+1} = \lambda N_t f(N_t) =: F(\lambda; N_t), \quad \lambda > 0, \tag{12}$$

then *we have the same result as in theorem 2 where the stability condititon reduces to*

$$N^{(i)} \frac{f'(N^{(i)})}{f(N^{(i)})} > -2 \text{ for } i = 1, 2. \tag{13}$$

See Example 2 below.

Example 1 Consider the difference equation

$$N_{t+1} = \lambda N_t \left(1 - \frac{N_{t-1}}{K}\right), \lambda > 0 \text{ and } K > 0, \tag{14}$$

with the initial values N_{-1} and N_0. An obvious drawback of this specific model is that if $N_{t-1} > K$ and $N_{t+1} < 0$. However, if we assume $0 < N_{-1} < K$ and $0 < N_0 < K$, then, by choosing appropriate $\lambda > 0$, we can guarantee that $N_t > 0$ for any time t. According to this example $f(N) = 1 - N/K$. In this case, we have, for all $0 < N < K$,

$$\left[N\left(\log f(N)\right)'\right]' = -\frac{K}{(K-N)^2} < 0.$$

So, by Corollary 2, we easily see that if the λ increases, then the local stability in the corresponding equilibrium point of Eq. (14) decreases.

Example 2 Consider the difference equation with no delay term

$$N_{t+1} = \lambda N_t \exp[r(1 - N_t/K)] \tag{15}$$

$\lambda > 0, r > 0$ and $K > 0$,with the initial value N_0. According to this model

$$f(N) = \exp[r(1 - N_t/K)].$$

In this case, we have, for all $N > 0$,

$$\left[N\left(\log f(N)\right)'\right]' = -N\frac{r}{K} < 0.$$

So, Corollary 2 immediately implies that if λ increases, then the local stability of the corresponding equilibrium point of Eq. (15) decreases.

3 Allee effects on the discrete delay model (3)

3.1 Allee effect at time $t-1$

To incorporate an Allee effect into the discrete delay model (3) we first consider the following non-linear difference equation with delay

$$N_{t+1} = \lambda^* N_t a(N_{t-1}) f(N_{t-1}) =: F^{(a^-)}(\lambda; N_t, N_{t-1}), \tag{16}$$

where $\lambda^* > 0$ and the function f satisfies the conditions $1°$ and $2°$. As stated in the first chapter, the biological facts lead us to the following assumptions on a :

3° if $N = 0$, then $a(N) = 0$; that is, there is no reproduction without partners,

4° $a'(N) > 0$ for $N \in (0, \infty)$; that is, Allee effect decreases as density increases,

5° $\lim_{N\to\infty} a(N) = 1$; that is, Allee effect vanishes at high densities.

By the conditions $1° - 5°$, Eq. (16) has at most two positive equilibrium points which satisfy the equation of

$$1 = \lambda^* a(N) f(N) := h(N).$$

Assume now that two equilibrium points N_1^* and N_2^* ($N_1^* < N_2^*$) exist so that we have $h(N_1^*) = h(N_2^*) = 1$. In this case, by the mean value theorem, there exists a critical point N_c such that $h'(N_c) = 0$ and $N_1^* < N_c < N_2^*$.

Then we have the following theorem.

Theorem 4 The equilibrium point N_1^* of Eq. (16) is unstable. On the other hand, N_2^* is locally stable if and only if the inequality

$$N_2^* \left(\frac{a'(N_2^*)}{a(N_2^*)} + \frac{f'(N_2^*)}{f(N_2^*)} \right) > -1 \tag{17}$$

holds.

Proof. Notice that since for each $i = 1, 2$, N_i^* is positive equilibrium point of Eq. (16), we have

$$p_i^* := F_{N_t}^{(a^-)}(\lambda^*, N_i^*, N_i^*) = \lambda^* a(N_i^*) f(N_i^*) = 1$$

and

$$q_i^* := F_{N_{t-1}}^{(a^-)}(\lambda^*, N_i^*, N_i^*) = N_i^* \left(\frac{a'(N_i^*)}{a(N_i^*)} + \frac{f'(N_i^*)}{f(N_i^*)} \right). \tag{18}$$

Then, by Theorem A, we get

$$\begin{aligned} N_i^* \text{ is stable} \quad &\Leftrightarrow \quad |p_i^*| < 1 - q_i^* < 2 \\ &\Leftrightarrow \quad -1 < q_i^* < 0 \text{ for } i = 1, 2. \end{aligned}$$

Since $N_1^* \in (0, N_c)$, it is easy to see that $q_1^* > 0$, which implies that N_1^* must be unstable. On the other hand, for $N_2^* \in (N_c, +\infty)$ the inequality $q_2^* < 0$ always holds so that N_2^* is locally stable if and only if (17) holds.

Now, choose $\lambda = \lambda^* a(N_2^*)$ and consider the following

$$N_{t+1} = \lambda N_t f(N_{t-1}) =: F(\lambda; N_t, N_{t-1}) \tag{19}$$

Then observe that N_2^* is also positive equilibrium point of Eq. (19). Furthermore, since $a(N_2^*) < 1$ and $\lambda = \lambda^* a(N_2^*)$, we get $\lambda < \lambda^*$.

We have the following result.

Theorem 5 The Allee effect increases the stability of the equilibrium point, that is, the local stability of the equilibrium point in Eq. (16) is stronger than that of in Eq. (19).

Proof. By the definition of a, for each $i = 1, 2$, we get

$$N_2^* \left(\frac{a'(N_2^*)}{a(N_2^*)} \right) > 0,$$

which yields

$$N_2^* \frac{f'(N_2^*)}{f(N_2^*)} < N_2^* \left(\frac{a'(N_2^*)}{a(N_2^*)} + \frac{f'(N_2^*)}{f(N_2^*)} \right). \tag{20}$$

Now considering (20), Theorem 2 and Theorem 3.1 we can say that the stability in Eq. (16) is stronger than the stability in Eq. (19).

Observe that Theorem 5 implies the following result.

Corollary 6 There is a locally stable equilibrium point for Eq. (16) such that it is unstable for Eq. (3)

3.2 Allee effect at time t

In this part we incorporate an Allee effect into the discrete delay model (3) as follows:

$$N_{t+1} = \lambda N_t a(N_t) f(N_{t-1}) =: F^{(a^+)}(\lambda; N_t, N_{t-1}). \tag{21}$$

Assume now that N_1^* and N_2^* ($N_1^* < N_2^*$) are positive equilibrium points of Eq. (21).

Then we have the following theorem.

Theorem 7 We get that N_1^* is an unstable equilibrium point of Eq. (21). On the other hand, N_2^* is locally stable if and only if the inequality

$$N_2^* \frac{f'(N_2^*)}{f(N_2^*)} > -1. \tag{22}$$

holds.

Proof. Since, for each $i = 1, 2$, N_i^* is positive equilibrium point of Eq. (16), we have

$$p_i^* := F_{N_t}^{(a^+)}(\lambda^*, N_i^*, N_i^*) = 1 + N_i^* \, \frac{a'(N_i^*)}{a(N_i^*)}$$

and

$$q_i^* := F_{N_{t-1}}^{(a^-)}(\lambda^*, N_i^*, N_i^*) = N_i^* \frac{f'(N_i^*)}{f(N_i^*)}.$$

Then, by Theorem A, we get for each $i = 1, 2$

$$\begin{aligned} N_i^* \text{ is stable} \quad &\Leftrightarrow \quad |p_i^*| < 1 - q_i^* < 2 \\ &\Leftrightarrow \quad 1 + N_i^* \frac{a'(N_i^*)}{a(N_i^*)} < 1 - N_i^* \frac{f'(N_i^*)}{f(N_i^*)} < 2. \\ &\Leftrightarrow \quad N_i^* \frac{a'(N_i^*)}{a(N_i^*)} < -N_i^* \frac{f'(N_i^*)}{f(N_i^*)} < 1 \end{aligned}$$

i.e.,

$$N_i^* \left(\frac{a'(N_i^*)}{a(N_i^*)} + \frac{f'(N_i^*)}{f(N_i^*)} \right) < 0 < 1 + N_i^* \frac{f'(N_i^*)}{f(N_i^*)}.$$

Since $N_1^* \in (0, N_c)$, it is easy to see that

$$N_1^* \left(\frac{a'(N_1^*)}{a(N_1^*)} + \frac{f'(N_1^*)}{f(N_1^*)} \right) > 0,$$

which implies that N_1^* is an unstable equilibrium point. Furthermore, since $N_2^* \in (N_c, +\infty)$, the inequality

$$N_2^* \left(\frac{a'(N_2^*)}{a(N_2^*)} + \frac{f'(N_2^*)}{f(N_2^*)} \right) < 0$$

always holds. So N_2^* is locally stable if and only if (22) holds.

Let N^* be a positive equilibrium point of Eq. (3). So, by the choice of $\lambda = \lambda^* a(N^*)$, N^* is also an equilibrium point of Eq. (21). In this case, combining Theorem 1 with Theorem 7, we get the following result at once.

Corollary 8 Equilibrium point N^* is locally stable for Eq. (21) if and only if it is locally stable for Eq. (3).

4 Numerical simulations

In this section, we numerically verify our analytical results (or theorems) obtained in previous sections by using MATLAB programming. In Matlab programs, by taking the initial conditions of the population density as N_{-1} and N_0 in the difference equations we compute N_i's for the model that we discussed in previous sections. After computing N_i's, mainly we illustrate the graph of the trajectory of models in 2D graph in which we can see the stability of equilibrium points. Note that in each graph, we connect the discrete points of population by straight lines.

As we prove analytically in Theorem 2, if we graph the population density function N_t with respect to t (time) in the model (14) of Example 1, we can easily see in Figure 1- (a)-(b)-(c) that as the parameter λ increases, the local stability of the equilibrium points decreases.

In Figure 2 we graph the 2D trajectory of the population dynamics model (14) respectively with and without Allee

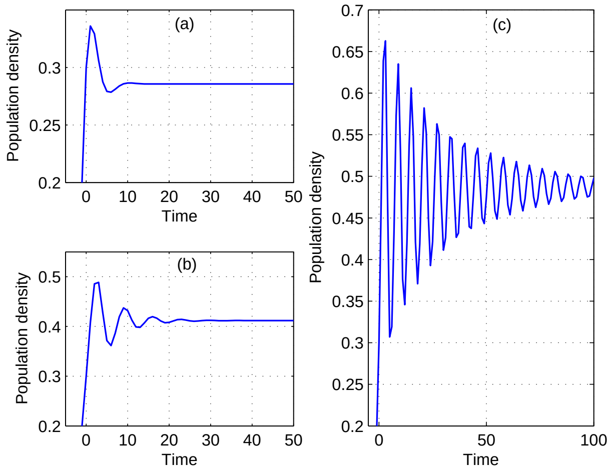

Figure 1: Density-time graphs of the model (14) with $K = 1$ and the initial conditions $N_{-1} = 0.2$ and $N_0 = 0.3$. (a) $\lambda = 1.4$. (b) $\lambda = 1.7$. (c) $\lambda = 1.95$.

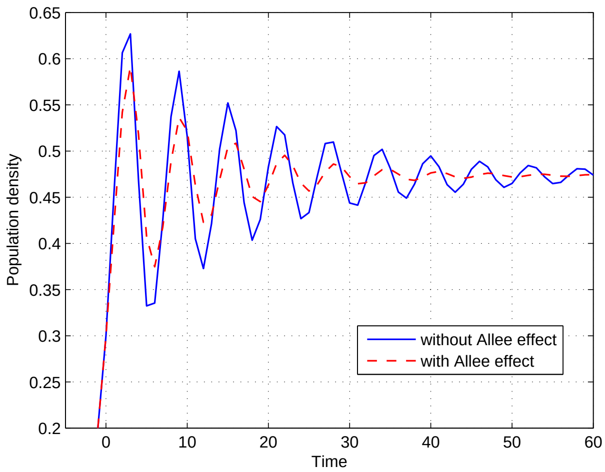

Figure 2: Density-time graphs of the models $N_{t+1} = \lambda N_t(1 - N_{t-1}/K)$ and $N_{t+1} = \lambda^* N_t a(N_{t-1})(1 - N_{t-1}/K)$ with $K = 1$, $\lambda = 1.9$, $a(N_{t-1}) = N_{t-1}/(\alpha + N_{t-1})$, $\alpha = 0.03$, $\lambda = \lambda^* a(N^*)$ and the initial conditions $N_{-1} = 0.2$ and $N_0 = 0.3$.

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effect at time $t-1$, which verifies our Theorem 4. In these figures we take the Allee effect function as $a(N_{t-1}) = N_{t-1}/(\alpha + N_{t-1})$, where α is a positive constant. As we can see from the graph that population density function obviously verify that when we impose the Allee effect at time $t-1$ into our model in Example 1, the local stability of the equilibrium point increases and trajectory of the solution approximates to the corresponding equilibrium point much faster.

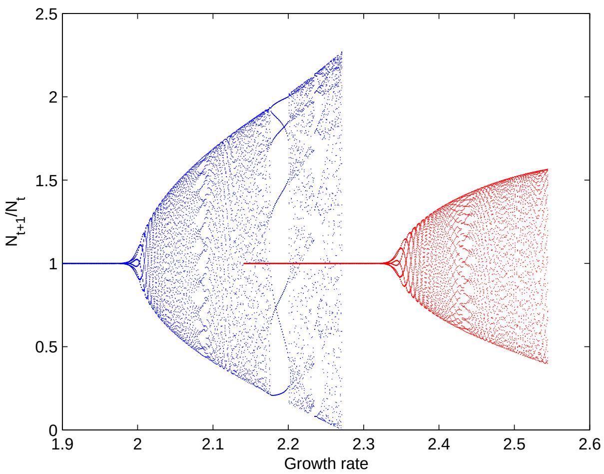

Figure 3: Bifurcation diagram of the models in Figure 2 with $K = 1$, $\alpha = 0.06$, $\lambda = 1.9 : 0.001 : 2.3$, $\lambda = \lambda^* a(N^*)$ and the initial conditions $N_{-1} = 0.2$ and $N_0 = 0.3$.

Finally, Figure-3 shows bifurcation diagram of the model in Example 1 as a function of intrinsic growth rate λ without the Allee effect (on the left) and with the Allee effect (on the right). In this numeric simulations, $N_{-1} = 0.2$ and $N_0 = 0.3$ are taken as the initial conditions as in the previous calculations. Here we again take the Allee function as $a(N_{t-1}) = N_{t-1}/(\alpha + N_{t-1})$, where α is a positive constant. It is obvious from the graph that the comparison of bifurcation diagrams still verifies the stabilizing effect of Allee effect. Besides this result, we also observed that the Allee effect diminishes the fluctuations in the chaotic dynamic which is different from the results obtained in the former studies.

5 Conclusions and remarks

Previous studies demonstrate that Allee effects play an important role on the stability analysis of equilibrium points of a population dynamics model (see, for example, [10] and [6]). Generally, an Allee effect has a stabilizing effect on population dynamics. In this paper, we consider a second order discrete models (i.e. with delay), where increasing per capita growth rate decreases the stability of the fixed point. First, we characterized the stability of equilibrium point(s) of this model. Imposing an Allee effect into the system, the stability of equilibrium points were also studied. Keeping the normalized growth rate the same, we compared the stability of the same equilibrium point corresponding to the model with and without Allee effect.

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